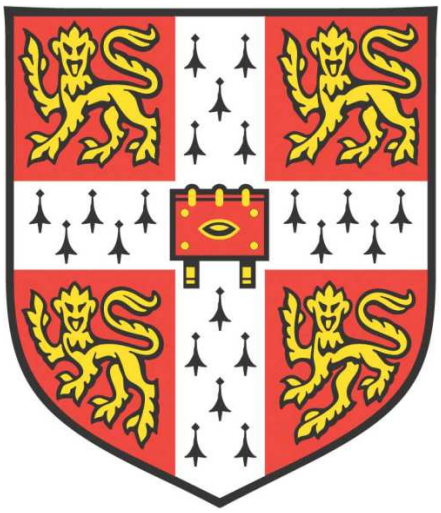
Quantifying genotypic and environmental factors affecting potato canopy growth



Sarah Louise Roberts

Newnham College

NIAB - CUF

Department of Plant Sciences

University of Cambridge

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QUANTIFYING GENOTYPIC AND ENVIRONMENTAL FACTORS AFFECTING POTATO CANOPY GROWTH

SARAH LOUISE ROBERTS

SUMMARY

There is a high degree of variation in potato yield which may contribute to the current UK yield plateau. There is a strong correlation between light intercepted, total biomass produced and biomass partitioned to the tubers as yield. Variation in potato canopy growth can be analysed using non-destructive measurements and the size of the canopy determines radiation interception. Proportion of soil covered by green leaves (percentage of ground covered, GC) is a simple proxy for light intercepted.

Two empirical models were compared for ability to summarize GC throughout the growing season. Both models showed a similar ability to describe GC, but differed in output and ease of interpretation, so the simpler, more descriptive model was selected for use in further canopy quantification.

The effects of planting date, nitrogen rate, cultivar and stem density were examined in two multi-year experiments. Planting date had a strong effect on early growth, though subsequent growth was less sensitive to temperature. Leaf production and canopy duration varied with cultivar determinacy. Cultivar and nitrogen fertilizer rate determined the potential for branch and branch leaf production (and therefore canopy longevity), altering distribution of leaf area index (LAI) within the canopy, but duration of growth was determined by planting date, which when delayed, shortened the season. The effects of stem density were most noticeable early in the season when higher stem density resulted in faster canopy expansion and earlier canopy closure. Branch production was reduced at high stem densities, but total LAI varied little. Canopy quantification was also used to analyse historical data and across 20 cultivars, decreasing duration of early canopy expansion was the only universal response to increasing stem density.

By quantifying the growth and maintenance of experimental and commercial crop canopies, causes of variation in light interception and subsequent yield can be identified. 'Best agronomic practice' can then be identified, enabling targeted changes to reduce the variability in yields and improve resource use efficiency. Additionally, this greater understanding of canopy development will refine existing potato yield models, enabling more specific and more accurate predictions. Future yield models should include stem density to better predict early season canopy growth and cultivar determinacy to predict interactions between canopy production and season length.

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LIST OF APPENDICES

ACKNOWLEDGEMENTS

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ABBREVIATIONS

Abbreviation	Definition	Units
aveBLeaves	Mean number of leaves per axillary branch	leaves
B	Dimensionless unit linked to rate of canopy expansion, in CQ model	% GC/day
CanReq	Canopy required to produced 1 tonne dry weight tuber yield	% days
C_{max}	Maximum canopy extent, in CQ model	% GC
CQ	Canopy quantification, can precede either 'model' or 'curve'	n/a
cv.	Cultivar, also referred to—particularly by growers—as varieties	n/a
D	Dimensionless unit linked to rate of canopy senescence, in CQ model	% GC/day
d	Willmott's index of agreement	unitless
D.F.	Degrees of freedom	n/a
DAE	Days after emergence	days
dLength2575	Mean daylength during mid-canopy expansion	hours (h)
dLength90	Mean daylength during near-complete canopy cover	hours (h)
dLengthEM	Daylength at emergence	hours (h)
dLengthSen	Daylength at the onset of senescence	hours (h)
DM	Dry matter, haulm, tuber or total biomass	kg
DWyield	Dry weight tuber yield	t/ha
EmDAP	Duration between planting and emergence	days
Expt	Experiment	n/a
GC	Ground cover	%, or % GC
GCDur90	Duration of time for which the canopy cover is 90 % or greater	days
GCRate2575	Rate of canopy expansion between 25 and 75 % ground cover	%/day
GCRate9050	Rate of canopy senescence between 90 and 50 % ground cover	%/day
GDD	Growing degree days, measure of thermal time	°C day
GrowDur	Duration of canopy growth between emergence and senescence onset	days
HI	Harvest index	unitless
IGC	Integrated ground cover, area under the ground cover curve	% days
IQR	Interquartile range	n/a
LAI	Leaf area index	unitless
M	Date at which canopy reaches 50 % of C_{max}, in CQ model	day
maL	Number of leaves on the main axis (mainstem and sympodial branches)	leaves
msL	Number of leaves on the mainstem	leaves
msLA	Rate of main stem leaf appearance	leaves/day
N	Duration of canopy cover at or over 50 % of C_{max}, in CQ model	day
NoB	Number of axillary branches	branches
PAR	Photosynthetically active radiation, 400-700 nm	MJ/m^2
pLA	Rate of whole plant leaf appearance	leaves/plant/day
RMSE	Root mean square error	*
RUE	Radiation use efficiency	g/MJ
S.E.	Standard error	n/a
SBInsert	Insertion point of sympodial branch, height up mainstem	mm
sbLA	rate of leaf appearance on the sympodial branch	leaves/day
SBLeaves	Number of sympodial branch leaves per stem present at harvest	leaves
SLA	Specific leaf area	cm^2/g
SMD	Soil moisture deficit	mm
TiE25	Time interval between emergence and reaching 25 % ground cover	days
TotLength	Total stem length, from height of soil to leaf tip, when stretched flat	mm
TT	Thermal time	°C day

* uses the same units as the quantity being analysed

1 INTRODUCTION

The yield of the potato (*Solanum tuberosum* L.) is variable at field, farm and national level as well as between growing seasons, with large differences found between and within cultivars. Whilst some of the variation can be related to meteorological differences between seasons, much of it is unaccounted for. In order to reduce this variability, it must first be quantified, and its sources identified. In the UK, this high variability likely contributes to the plateau in national potato yields discussed by Allen *et al.* (2005) and which remains around 45 t/ha (Maslowski *et al.* 2019). As the most visible structure of the crop, the canopy of the potato offers insight into potato growth and variation. The canopy is a major interface between plant and environment; the leaves which make up the canopy are not only the site of light interception and photosynthesis, enabling carbon fixation and further growth, but are also an indicator of plant development and health. Observing and analysing canopy growth throughout the growing season can offer insight into the underlying causes of the variability seen in commercial potato yields. In addition, canopy quantification can equip researchers with another tool to better understand the mechanisms by which yield differences occur between experimental treatments. This work aims to develop a method to quantify potato canopy growth, in order to better understand the differences in potato growth and subsequent yield within research and agriculture.

In this introduction a brief overview of variability in the potato crop highlights known sources of variation in growth and yield as well as gaps in understanding (1.1). Then, the fundamental relationship between light interception and yield is presented, setting the foundation for use of the canopy as an indicator of yield (1.2). Thirdly, the main methods for quantifying canopy light interception are discussed (1.3) and, finally, the aims (1.4) and structure of the thesis (1.5) are set out.

1.1 Variability

Potato is high yielding and the most important non-grain crop worldwide (FAO 2017), yet yields can vary greatly at the national, regional, farm, field and within-field level as well as between years (Bradshaw 2009; Allison *et al.* 2016) and this variation can result in uncertainty at harvest, fluctuating prices and insecurity within the supply chain. Sources of variation include cultivar, water availability, disease, soil type and quality,

nitrogen and mineral nutrition and duration of the growing season, yet the extent of influence of these factors and their interactions on tuber yield is not clear. So, before the variability in potato yields can be addressed it must be quantified.

Some of the differences in yield are the result of variation in yield potential between cultivars (e.g. Oliveira *et al.* 2016) and to some extent this can be grouped by end-market. Since cultivars are bred and grown for specific end-markets, particular cultivar traits, such as number of tubers and tuber size have been selected for, and in combination with different agronomic treatments, these traits result in variation in yield. For example, salad crops are defoliated early and produce lower yields than crops destined for crisp production, home consumption or processing due to a shorter growing season and smaller mean tuber size (Smart 2020).

Expectations of differences in yield and canopy growth between cultivars are also reflected in cultivar maturity or determinacy groupings. Both classifications suggest the expected lifespan of the canopy; determinacy groups indicate cultivar ability to continue leaf production after the first flower (assigned from nitrogen response experiments and canopy longevity data (Naylor 2017)). Whilst maturity is defined by the European Community Plant Variety Office as the point when '80 % of the leaves are dead' (CPVO 2017) and cultivars are ranked accordingly from very early to very late on a 9-point scale. Yet these groupings represent a limited proportion of the variation in canopy growth and yield, partially due to challenges in assigning either classification. Relatively few cultivars have been assigned determinacy groups due to the time consuming and expensive nature of the experiments required, whilst comparisons between cultivar maturity rankings are often confounded by the effects of different nitrogen supplies in rank-assignment experiments. For example, the cultivar Ditta has been described as early, early to intermediate and intermediate maturity types by three different research organisations contributing to the European Cultivated Potato database (SASA) and this inconsistency reduces the utility of the grouping system. Whilst both maturity and determinacy describe aspects of canopy longevity, determinacy will be used henceforth since it is defined by the extent of leaf production, more closely describing canopy growth, as opposed to maturity, which is defined by senescence and is typically more variable.

Genetic differences may however be responsible for a relatively small proportion of the variation in potato yields (Kooman *et al.* 1996a; Haverkort & Kooman 1997) and a high degree of variability occurs within cultivars due to between-farm differences

(Appendix 1). This is illustrated by a £ 10 000/ha and £ 2000/ha difference in crop revenue between the highest and lowest yielding Belana and Nectar crops, respectively, grown for ASDA in East Anglia, in 2017 (Tompkins *et al.* 2019). An analysis of variation in wheat yields also suggests that a low proportion of yield variability (an average of 2 %) was due to differences between cultivars, whilst between 11 and 24 % of the variation was attributable to between-farm differences, excluding differences in soil type, rotations, manure and nitrogen fertilizer use, which were accounted for separately (Sylvester-Bradley *et al.* 2019). Similarly, in a study of variability in potato tuber production, most of the variation in mean tuber size occurred within cultivars, indicating that a high degree of variation in tuber size (and likely also yield) is influenced by 'agronomic practices or environmental conditions' (Smart 2020). For example, one source of within-cultivar variation can be field topography, which has been shown to explain between 22 and 36 % (by slope and elevation, respectively) of the variation in tuber yield in an experiment in eastern Canada (Zare *et al.* 2019).

The above examples highlight the relative importance of agronomic over genetic differences on gross potato yield. Whilst the effects of agronomic practice on yield, in particular; nitrogen application, planting density and water availability, are widely reported in the literature, the mechanisms resulting in yield variation are often omitted. As noted by Khan (2012), the effect of variation in above ground plant development, particularly canopy cover, on yield is an understudied area which can give insight into the physiological mechanism of yield generation. Whilst a small number of papers have evaluated differences in yield in relation light interception and canopy cover, considering variation in response to nitrogen application (Ospina *et al.* 2014) and drought (Aliche *et al.* 2018), this approach is under-utilized and should be applied to examine further instances of variation in potato growth and yield. Hence the following two sections will summarize the relationship between light interception and yield (1.2), then evaluate methods to measure or estimate light interception (1.3) to develop a theoretical framework from which to quantify physiological differences in the potato crop between agronomic treatments to better understand differences in yield.

1.2 Light interception and yield

There is a strong correlation between total biomass produced by a crop and the light intercepted (Monteith 1977), since greater light interception allows greater light absorption, photosynthesis and carbon fixation in unstressed plants. Consequently, maximum potential yield is linked to canopy size and duration by the 'seasonal distribution of leaf area' as this determines the light intercepted throughout the growing season (Monteith 1977).

Subsequently, Allen and Scott (1980) identified 'good evidence' of a positive linear relationship between total plant biomass and tuber yield in potato, and this was reported across a range of cultivars, planting dates and planting densities. Allen and Scott (1980) also demonstrated a linear relationship between tuber dry weight and total radiation intercepted, though the conversion efficiency of intercepted light into tuber dry matter differed between experiments. Furthermore, Khurana and McLaren (1982) found that photosynthetically active radiation (PAR, 400-700 nm) intercepted throughout the season explained 87 % of the variation in tuber dry weight produced. Hence, intercepted radiation explains most of the variation in yield and the remaining variation can be explained by differences in radiation use efficiency (RUE) and biomass partitioning between cultivars and crops.

The importance of light interception in relation to yield is further illustrated by the central role it has in two major potato growth and yield models; LINTUL-POTATO (Kooman & Haverkort 1995) and the APSIM potato model (Brown *et al.* 2011). In LINTUL-POTATO total dry matter production is calculated from light intercepted and light use efficiency, using daylength and temperature early in the season to calculate canopy lifespan and therefore total light interception throughout the season (Kooman & Haverkort 1995). The APSIM potato model also estimates dry matter production from intercepted radiation (derived from solar radiation and leaf area index (LAI)) and RUE, with final yield moderated by stress factors, including water availability, temperature and CO_2 concentration (Brown *et al.* 2011). Hence, in both models, foliage coverage and longevity determine total light interception and final yield.

In summary, the size and extent of the canopy throughout the season set a maximum potential limit for light interception and therefore maximum potential yield, which is then moderated by environmental conditions and the genetic background of each cultivar (Figure 1). Intercepted light has been shown to explain the majority of the

variation in tuber dry weight yield in a number of studies (van der Zaag & Doornbos 1987; Kooman *et al.* 1996a), yet the majority of research focuses solely on differences in yield, despite the strong relationship between light interception and tuber yield illustrated above. Hence, developing a reliable methodology for quantifying light interception by the canopy will offer useful insights into variation in the development of the potato crop and subsequent yield.

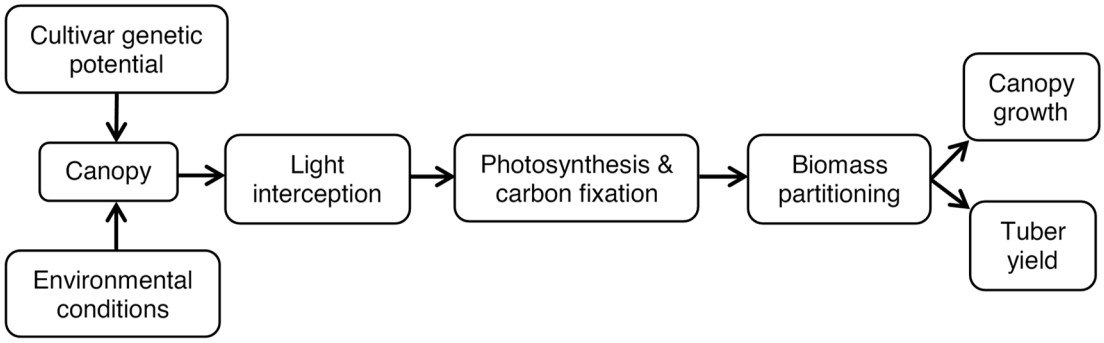

Figure 1. Illustration of the link between canopy and yield.

1.3 Measuring complexity

As discussed above (1.2), cumulative light intercepted by the canopy is one of the key variables determining final tuber yield. Hence quantifying the canopy and the light it intercepts is an important research priority, yet the complex three-dimensional structure of the canopy and indeterminate growth exhibited are challenging to describe. This has resulted in a range of different approaches devised to quantify it, which vary depending on the specific research aims. Light intercepted by the canopy has been quantified throughout the literature in three main ways; direct measurements of intercepted light, LAI and percentage ground cover (GC), which are briefly considered below.

Firstly, light intercepted can be measured directly, with either tube solarimeters or ceptometers installed beneath the crop, recording the proportion of light (total or PAR, respectively) intercepted in relation to a reference measurement taken above the canopy. Yet there are practical limitations to this data collection methodology as noted by Burstall and Harris (1983); both solarimeters and ceptometers are expensive and are therefore best suited to small-scale experiments; each device only samples a small area within a plot; and shade cast by photosynthetically active leaves and dead plant material cannot be discriminated between, reducing the accuracy of measurements later in the season. Early light interception is also underestimated as the crop must first exceed the height of the solarimeter before light interception is detected.

Secondly, LAI, the total one-sided area of leaf tissue per unit ground area (Watson 1947), is a measure of crop surface area and hence indicates the ability of the crop to intercept light (Monteith 1977). Initially there is a good relationship between LAI and light intercepted, although above LAI of 4 there is little increase in light interception (Khurana & McLaren 1982; Burstall & Harris 1983; Firman & Allen 1989a; Haverkort *et al.* 1991; Jin *et al.* 2013). Leaf area index can be measured directly with destructive harvests, measuring leaf area with a scanner or gravimetrically; calculating LAI from the mass of the canopy sample and the mass of leaf discs of known area (Bréda 2003). Whilst both direct methods are accurate (Haverkort *et al.* 1991), they are time consuming and require large experimental plots if measurements are to be repeated throughout the season. Leaf area index can also be measured indirectly and many indirect methods have been developed including hemispherical photography, LiDAR and multispectral satellite data (Zheng & Moskal 2009), all using image analysis software, and an understanding of light transmission through the canopy and the typical distribution of leaves within the canopy to calculate the surface area of leaves within the canopy. However, these methods have typically focused on estimating LAI of large-scale ecosystems and forests (which cannot be measured directly) and there are few instances of potato-specific parameters defined to calculate LAI, reducing the reliability of estimated LAI values. For example, Rinaldi *et al.* (2010) found that across five vegetation indices (VI), VI were better able to describe differences in LAI in durum wheat and sugar beet (mean $R^2 = 0.85$), than in other crops including potato (mean $R^2 = 0.60$). Remotely measuring LAI is further complicated by the saturation of VIs when LAI exceeds 3.5, around canopy closure, only providing accurate estimates of LAI during the initial phases of growth (Rinaldi *et al.* 2010).

In addition to describing whole canopy leaf area, LAI can also be used to describe the distribution of leaf material within the canopy, granting greater insight into the structural components which contribute to differences in whole canopy light interception. Once a destructively harvested canopy has been divided into components such as mainstems and branches, LAI can be calculated with respect to canopy component, although descriptors of canopy structure vary within the literature. Mainstems are produced from individual apical buds on the seed tuber and secondary stems are branches formed from the mainstem below the surface of the soil, although both types of stem are commonly grouped together as above-ground stems (5.1.1). Meanwhile, descriptions of branching patterns vary throughout the literature; herein

branches are described as either axillary (formed on the mainstem below the first flower) or sympodial (produced one or two nodes below the first flower, continuing main axis growth, 3.2.4, Figure 6). In contrast, others distinguish between basal and apical branches on the mainstem (Oliveira 2000; Fleisher *et al.* 2006b) or describe the degree of branching, with second and third order branches being produced on the axillary branches and on axillary branch branches, respectively (Vos & van der Putten 2001). This variety of different canopy classifications reflects the variability of canopy growth but also the variation in research objectives within the literature.

Thirdly, the 'size' of the canopy can be represented by the area of the ground covered by green leaves, or percent ground cover (GC), indicating the proportion of incident radiation that can be intercepted by the crop. Ground cover can be measured at different scales ranging from within-field to remotely from space. In the field, GC can be measured by handheld grid (Burstall & Harris 1983) or using a smart-phone app such as Canopeo (Patrignani & Ochsner 2015). When measurements are collected consistently by experienced operators the results of both grid and app are typically in close agreement, although app-collected data tends to over-estimate grid measurements (Allison *et al.* 2013). Drone-mounted cameras (Allison & Firman 2015) and satellites (Allison *et al.* 2015; Piccard *et al.* 2017) can also collect GC data. These methods increase the area over which data is collected, with reasonable agreement with data collected on the ground (Allison & Firman 2015; Piccard *et al.* 2017), though limitations in expense (particularly with drone flights) and also image processing reduce the relatability and feasibility of these emerging technologies at present.

Despite the relatively strong relationships between both GC and LAI, and intercepted radiation, neither is a perfect proxy. Whilst GC is a simple, non-destructive measure which reflects the ability of the canopy to absorb incident radiation, it does not account for canopy structure and light intercepted at 100 % GC can vary between 80-95 % (Firman & Allen 1989a). LAI provides a better indication of light interception after canopy closure and can also be used to describe leaf distribution within the canopy. However, LAI is challenging to measure, either directly, with the cost of destructive measurements, or indirectly, requiring careful calibration. Moreover, the main focus on total leaf surface area, similar to LAI, in early analysis of potato growth was limited in ability to identify the causes of yield variation (Allen & Scott 1980), with a greater proportion of the yield variation explained when intercepted light was quantified (van der Zaag & Doornbos 1987; Kooman *et al.* 1996a). In addition to better representing

light intercepted and better predicting yield produced, modelling approaches have been developed (2.3) to fit descriptive curves to GC data from the whole season (e.g. (Khan 2012), used by (Khan *et al.* 2013; Ospina *et al.* 2014; Aliche *et al.* 2018)), providing a rigorous method to compare differences between crops or experimental treatments across the whole season. Within research it can be valuable to record both GC and LAI, whilst GC determines intercepted light on a given day, LAI can indicate how long maximum GC will be maintained throughout the season, since, as noted by Bremner and Radley (1966), maximum LAI must exceed LAI of 3 in order for complete GC to be maintained in the face of high leaf turnover within the potato canopy.

In summary, the non-destructive nature of GC data collection enables regular approximation of canopy light interception and calculation of cumulative light intercepted throughout the season. Focusing on GC has the potential to provide both researchers and growers with insight into variation in canopy growth, light interception and yield at low equipment and effort costs for data collection, making the methodology more accessible and creating the possibility for more widespread usage, both to better understand variation caused by experimental treatments and variation in farm yields. Additionally, regular canopy measurements allow identification of time-specific effects on yield during crop growth, for example characterising periods of potato development when the crop is most sensitive to water shortage, enabling growers to prioritise irrigation at specific points in the growing season.

1.4 Thesis aims

The relationships between ground cover and intercepted radiation, intercepted radiation and total biomass production, total biomass production and tuber yield are well established. Therefore, the primary focus of this work was on the canopy and quantifying differences in canopy growth, hypothesising that understanding the differences in canopy growth will improve understanding of yield variability. Firstly, it aims to provide a simple method of canopy quantification suitable for use in both research and on farm. Then, through greater knowledge of variation in canopy growth under differing agronomic conditions, this work aims to better understand the physiological processes underlying variation in potato yields, extending the canopy quantification work of Khan (2012). This thesis focuses on three agronomic factors over which growers have a degree of control; planting date (which dictates light and temperature regimes experienced during growth), applied nitrogen and plant density.

The overarching aims are as follows:

1. To identify and develop a simple method to quantify canopy growth throughout the season, capable of analysing canopies grown under a wide range of agronomic conditions.
2. To quantify canopy development and maintenance under a range of experimental agronomic conditions, with reference to yield.
3. To investigate the variation in canopy architecture in relation to differences in whole canopy growth and maintenance.
4. To identify how canopy growth varies within and between cultivars in response to agronomic variables including panting date, nitrogen rate, seed size and seed spacing, providing data for future canopy and yield modelling, in addition to crop management insights for growers.

1.5 Thesis structure

This thesis comprises of six chapters, including this introduction. As the main experiments addressed discrete aspects of potato agronomy, chapters four and five are self-contained, with introduction, additional methods, results, and discussion. Previous research detailing the influence of agronomy, nitrogen, cultivar and determinacy group on potato yields is evaluated in targeted literature reviews within each chapter introduction, setting the experiments in immediate context. After the general introduction (1), chapter two discusses the function of crop modelling within research and agriculture, then presents two methods for canopy quantification and evaluates their utility (2). Biologically relevant features of canopy growth are identified and quantified, then used throughout this thesis to describe canopy growth, addressing the first and second thesis aims. Chapter three describes general methods common across experiments (3). Chapter four considers the agronomic importance of planting date, and conditions which co-vary with it; and applied nitrogen, through the results of two field experiments, quantifying both whole canopy growth and variation in canopy components, addressing aims two to four (4). Chapter five focuses on planting density and the effects of changing stem density upon canopy expansion, maintenance, and senescence in three field experiments and archival data, again addressing aims two to four (5). Finally, the present utility and future potential of the canopy description method are discussed and reviewed in chapter six, including suggestions to improve the accuracy of future yield modelling (6).

2 MODELLING

2.1 Introduction

There are multiple approaches to representing and quantifying the growth, maintenance and decline of a crop's canopy, ranging from the simple; plotting the percentage area covered by green leaves (ground cover, GC) against time, to more complicated curve fitting procedures and predictive models. Plotting GC (Engels *et al.* 1993), canopy reflectance (Zhou *et al.* 2018) or leaf area index (LAI (Ifenkwe & Allen 1978a; Jones & Allen 1982)) throughout the season allows qualitative comparisons of the canopy between treatments, but growth must be described mathematically before differences between treatments or crops can be quantitatively compared. Across the literature, a wide range of approaches have been used for quantifying potato growth and the different methods for canopy quantification developed therein will be considered below. Firstly, methods of canopy description developed within general crop physiology models, then canopy description model-components used to predict yield and, lastly, models primarily focused on canopy description will all be discussed. The modelling approaches are explored below to identify a simple method of canopy quantification to enable analysis of canopy growth under varying agronomic conditions, addressing the first aim of this thesis. The original purpose of each model and the data inputs required will be considered in addition to the model's ability to accurately represent canopy growth, since together these factors can determine the practical utility of a model within research and agriculture.

2.1.1 An overview of existing potato models

Mathematical equations can be used to describe crop development throughout the season and the crop models produced offer a method of quantifying growth in relation to environmental conditions. Modelling approaches have been used extensively in relation to crop performance, both improving understanding of the underlying biological mechanisms and simulating potato crop responses to environmental changes; ranging from different irrigation schedules (Fabeiro *et al.* 2001) to climate change (Holden *et al.* 2003; Daccache *et al.* 2011) and yield forecasting for procurement within the potato industry (Machakaire 2015). Additionally, modelling has direct applications within agriculture and is used to inform and guide grower practice (Potato Yield Model (Firman *et al.* 2018)), breeding strategies (Spitters & Schapendonk

1990; Ramirez-Villegas *et al.* 2015) and government policy (McPharlin 2013). Yet, model utility varies depending on the extent to which the original purpose for which it was developed, the data required to run it, and the output produced align with intended usage.

Though on a spectrum, crop models can broadly be divided into two categories: mechanistic, capturing underlying biological processes, and empirical, based on statistical correlations without using an explicit canopy growth relationship (Lewis 2001). Over 30 potato models have been reported in the literature, each quantifying different aspects of potato growth and differing in structure, function and level of validation (Raymundo *et al.* 2014), resulting in differing suitability for canopy quantification and on-farm yield forecasting. The range of different models within the literature, and the purposes for which they were developed, were briefly summarized below, then the suitability for canopy quantification of firstly mechanistic (2.1.2) and then empirical (2.1.3) models was assessed.

The purposes of crop growth models have changed over time. Many early models focused on describing canopy photosynthesis, for example ELCROS (developed by de Witt *et al.* in 1970 and summarized by Bouman *et al.* (1996)) was used to estimate the production capacity of crops under specific conditions. Later POTATO, the 'first comprehensive potato crop growth model', was developed by Ng and Loomis (1984) to better understand the physiological processes of the potato crop at organ, plant and community level in different genotypes and under different climatic and management conditions. Carbohydrate reserves were calculated after simulation of photosynthesis and plant-water status, modified by climate and respiration, then above- and below-ground growth was simulated including initiation of new plant organs (Ng & Loomis 1984). Since then, many models have utilised the strong link between intercepted radiation and yield produced shown by Monteith (1977) (1.2), though these vary in complexity. Models ranged from the SCRI- (Scottish Crop Research Institute) model—a simple model which calculates yield from light intercepted and biomass partitioned between canopy and tubers (MacKerron & Waister 1985) and formed the basis of the, now obsolete, Management Advisory Package for Potatoes (Marshall 2001)—to the more complicated LINTUL-POTATO, whose calculated yield is moderated by temperature and daylength to account for differences in yield production between locations (Kooman & Haverkort 1995). Other models have a greater focus on tuber development: the SUBSTOR-potato model simulates the transition between five stages

of growth, calculating biomass and yield accumulation daily, moderated by soil water, leaf nitrogen, temperature, photoperiod and light interception (Griffin *et al.* 1993). A fourth type of models focus on growth in response to the availability of a specific resource, such as the crop water-use model developed by Ejieji and Gowing (2000). There are further examples of models developed to describe the growth of cultivars and aid cultivar selection in breeding programmes, such as Khan's model (Khan 2012). Finally, there are models with a greater agricultural focus such the APSIM potato module, which quantifies dry matter partitioning in the context of crop rotations in the context of farm management (Brown *et al.* 2011) and LINTUL-POTATO-DSS, an adaptation of LINTUL-POTATO for potato industry yield forecasting (Haverkort *et al.* 2015).

2.1.2 Mechanistic models

Whilst mechanistic crop models have the potential to be useful—simulating potential yield, yield limited by resource shortages or yield in response to changing climate—there are challenges to their use. The majority of potato crop models simulate potato canopy growth, either capturing changes in LAI or (less commonly) modelling differences in leaf production, position and canopy structure (Raymundo *et al.* 2014), allowing intercepted light and yield to be calculated. Yet these estimations do not explicitly quantify canopy size or light intercepted throughout the growing season, and the model output describing the canopy often provides more detail than necessary to quantify canopy light interception, making it difficult to interpret. For example, LINTUL-POTATO describes the weight of canopy green leaf, dead leaf, shoot and dry stem material in addition to leaf longevity, LAI, intercepted PAR and rate of leaf senescence (Kooman & Haverkort 1995).

Additionally, mechanistic models can only describe the differences that they are encoded to represent (by the relationships described in their underlying equations), so are limited in ability to identify new links between agronomic or environmental variables and their effect on the canopy. This is illustrated by the overestimation of end of season growth by SUBSTOR-potato, which does not simulate differences in cultivar determinacy and consequent cultivar ability to continue growth later in the season, nor does it simulate the senescence-triggering effects of high temperatures at the end of season, curtailing growth (Raymundo *et al.* 2017).

Mechanistic models are inherently complex, mathematically representing the different processes contributing to canopy growth. For example, LINTUL-POTATO represents emergence, leaf area, light interception, total growth, biomass partitioning, tuber initiation, tuber growth leaf senescence and whole crop biomass using 21 equations (Kooman & Haverkort 1995). Whilst these highly detailed models have the potential to describe the growth of a given crop more precisely, large quantities of data are required to parameterize the models accurately. Poor parameterization results in inaccurate predictions of canopy growth, as illustrated by the large overestimation of yield in South Africa (Franke *et al.* 2011) in which LINTUL-POTATO predicted yields of 52-96 t/ha and growers reported yields of 36-58 t/ha. Whilst data describing the soil characteristics and weather of the study area was used to run the model, growth responses in relation to low water availability were parameterized using data collected in the Netherlands (Franke *et al.* 2011), not reflecting patterns of water-limited potato growth in South Africa.

In addition to having insufficient data to predict growth responses in a specific location, highly detailed mechanistic models are often insufficiently parameterized to accurately predict changes in growth in response to meteorological conditions. For example, when modelling potato yield in response to drought, Spitters and Schapendonk (1990) noted the need for better model parameterization due to the absence of data on the response of assimilate partitioning, specific leaf area, and leaf senescence, to water stress. Similarly, SUBSTOR has been shown to underestimate the effect on yield of elevated atmospheric CO_2 and high temperatures, as the model was not parameterized for growth under these conditions, reducing reliability when predicting potato yield responses to climate change (Raymundo *et al.* 2017).

Mechanistic models are also typically unsuitable for agricultural use, as the majority were developed by the scientific community to further understanding of potato growth processes (Antle *et al.* 2017). This often results in models which require large numbers of essential parameters (including in SUBSTOR-potato and LINTUL-POTATO) for which it is hard to collect calibration data, especially at the agricultural scale. This mismatch between developer aims and user needs is highlighted by Rose *et al.* (2016) who include in their 15 criteria for good decision support tools (DST) 'the need to match a tool to existing habits of farmers'—namely, not requiring substantial investment of time or resources in data collection to parameterize or run a DST or model. Rose *et al.* (2016) also found that the level of detail provided by models is

sometimes superfluous, reducing the relevance to the user and the likelihood of use of the DST.

In summary, mechanistic models offer the potential to tailor predictions of crop development to a given location, cultivar and set of environmental conditions, based on mathematically described biological processes. However, it is often not possible to parameterize a model to the specific conditions of interest due to lack of relevant experimental data and this inability to account for the differences in conditions results in inaccurate predictions. Consequently, canopy development, as measured by the simple yet informative metric of percentage ground cover, may be better described by empirical than mechanistic models, avoiding unnecessary complexity in either inputs or outputs.

2.1.3 Empirical models

Model complexity can be reduced by using an empirical approach, based on statistical associations rather than representing all the relevant biological processes within crop growth. An example of this is the adaptation of LINTUL-POTATO to create LINTUL-POTATO-DSS. The number of equations and parameters in LINTUL-POTATO were reduced, decreasing both the potential for error and the quantity of input data required (Haverkort *et al.* 2015). Although the model does not account for disease or nitrogen availability and assumes that 100 % GC will be reached by 650 degree days (with a base temperature of 2.2 °C) after emergence and that 100 % GC is maintained until the end of the season (neither of which assumptions are met by poor performing crops), Machakaire *et al.* (2016) found a reasonable correlation ($R^2 = 0.635$) between forecasted actual yield and observed yield. Models such as LINTUL-POTATO-DSS tend to be more suited for use within agriculture and industry due to their lower complexity and the smaller quantity of input data required, though they are not necessarily more suitable for canopy description than mechanistic models, since their outputs may be solely yield focused, as is the case with LINTUL-POTATO-DSS.

There are several empirical models with a greater focus on canopy development, using the strong link between cumulative light intercepted throughout a season and biomass production to predict yield without the complexity of the mechanistic models. An early example is the SCRI-model, which splits crop growth into three stages, with overall growth dependent upon light intercepted throughout the season and progression between developmental stages determined by environmental factors

(MacKerron & Waister 1985). The SCRI-model uses 'simple inputs' and produces outputs describing crop development from which yield is calculated, allowing identification of stages of growth where poor canopy performance reduced final yield potential. Whilst the SCRI-model predicts the ordinal date of canopy closure and uses the linear relationship between accumulated solar radiation and total dry matter production to calculate potential yield, it does not explicitly describe canopy growth, and so will not be considered further.

Empirical plant growth models based on statistical associations are commonly composed of two functional parts: light interception and yield generation. The light interception components have the potential to be used as stand-alone tools for canopy description. In sugar beet, empirical models have been used to explicitly describe the expansion and senescence of the canopy including Gompertz-, Richards- and Chanter-like functions (Werker & Jaggard 1997). Whilst the Gompertz-like function best described the rising and falling canopy cover of sugar beet (Werker & Jaggard 1997), visual inspection (Appendix 2) found that the function was unable to satisfactorily describe potato canopy growth. The Gompertz-like function was unable to describe the mid-season ground cover plateau common in potato crops, likely reflecting differences in canopy structure between the rosette-formation of sugar beet leaves and the more expansive compound leaves of the potato.

Similarly, to the SCRI-model, two other empirical models also divide the canopy into different phases of growth, although both place a greater emphasis on describing potato canopy development than the SCRI-model. Allison (personal communication, 2015; model developed in 2012) describes the rising and falling growth of the potato canopy using one equation to quantify the differences in canopy growth between commercial crops. Using the emergence date and weekly GC readings, canopy growth from emergence to complete senescence is visually represented by a smooth curve whose parameters are fitted iteratively to the GC data using a least squares method. Canopy growth can then be summarized by calculating the area under the curve, indicating the potential for light interception during the growing season. Curve parameters are iteratively fitted to the GC data to fit the descriptive curve, from which further values, relative to ordinal date, can be calculated, quantifying the shape of the curve. This model has the potential to be used for canopy description in both research and agriculture, due to the limited quantity of input data required and to a simple

output which can describe the different phases of canopy growth; though it has not been published in a peer-reviewed journal.

The model developed by Khan (2012) also focuses on empirical canopy description, using three equations to describe canopy expansion, maintenance, then senescence. This model also requires limited input data, using GC and temperature data to describe canopy development in relation to thermal time (base, optimum and ceiling temperatures; 5.5, 23.4 and 34.6 °C, respectively), allowing the comparison of crops grown in different locations without the confounding effect of different temperature regimes (Khan 2012). From the fitted curve, descriptive variates can also be calculated allowing quantitative comparisons to be made; these values have been used to phenotype an F1 population and are also proposed as a tool to streamline cultivar breeding (Khan 2012). Khan's descriptive variates have also been used to reduce ambiguity when classifying maturity types (Khan *et al.* 2013), describe cultivar responses to nitrogen (Tiemens-Hulscher *et al.* 2014; Ospina *et al.* 2014) and quantify cultivar drought responses (Aliche *et al.* 2018).

In summary, empirical models are typically more suitable for quantifying canopy size and light interception throughout the season since fewer equations and parameters are required to describe canopy development. Yet the original purpose for which each was developed shapes model ability to describe the pattern of canopy growth and not all are suitable, such as the SCRI-model. However, Khan's and Allison's models appear suitable and offer the greatest potential for future development of a simple canopy quantification method to be used in both research and agriculture, and these will be compared subsequently.

2.2 Chapter focus

The potential for using mathematical modelling to quantify the growth of the potato canopy in this project was explored in the literature (2.1), establishing that empirical models are more suitable for canopy quantification due to lower data requirements for parameterisation and simpler outputs than mechanistic models. Two candidate models (by Khan (2012) and Allison (personal communication, 2015)) which capture changes in canopy cover throughout the season were identified. These models were described (2.3) and then compared using a set of experimental test data (2.4). Their ability to fit a curve to the data and to produce useful canopy development metrics was compared and Allison's model was deemed more suitable and was consequently

selected to describe future experimental results (2.5). Amendments made to the canopy quantification model and output are detailed (2.6). The chapter aims are as follows:

1. To compare the ability of candidate models to describe canopy development under different agronomic conditions.
2. To select the simplest, yet most informative, model for further canopy quantification.
3. To develop a programme using the selected model to enable rapid canopy quantification and analysis.

2.3 Candidate models

Two similar empirical models, developed by Khan (2012), for analysing genotype-by-environment interactions, and Allison (personal communication, 2015), as an in-house model to compare canopy growth between crops, were identified as candidates for canopy quantification (2.1.3). Khan's and Allison's models were described, then compared using Willmott's index of agreement (*d*, (Legates & McCabe Jr. 2005; Greaves & Wang 2016)) and root mean square error (RMSE, (Greaves & Wang 2016)) to determine goodness of fit of the curves to the raw data. The curve parameters were calculated using programmes written in Genstat 17.1 (VSN International 2014) allowing rapid curve fitting to a test dataset (2.4). In addition to goodness of fit, the utility of each model's output was also considered and a model for future canopy quantification was selected.

2.3.1 Khan's model

Khan splits canopy development into three phases, describing canopy expansion, maintenance of maximal ground cover, and senescence, with each phase of growth described by a separate equation in relation to thermal time (Khan 2012). Initial growth and early production of the canopy is described using an asymmetrical sigmoidal curve (Equation 1) based on a curve for capturing the determinate growth of plant organs (Yin *et al.* 2003) and represents growth with a variable rate, slowing as maximum GC (v_{max}) is approached. Equation 2 represents the period of maximum canopy cover and is the duration between the end of canopy expansion (t_1) and the beginning of canopy senescence (t_2), with no changes in gradient. Equation 3 is an adaptation of a reversed sigmoidal curve with an initially shallow gradient (at the beginning of senescence) which increases over time, ending when 0 % GC is reached,

whether naturally or due to crop defoliation. There is no inflection point within Equation 3 to reduce the likelihood of overfitting (Khan 2012). Khan fitted these three equations to raw GC data for individual plots or crops in the SAS software, with parameters iteratively estimated by the Gauss method implemented using the 'PROC NLIN' procedure (Khan 2012).

Equation 1. Canopy expansion phase.

$$v = v_{\max}\left(1 + \frac{t_1 - t}{t_1 - t_{\mathrm{m1}}}\right)\left(\frac{t}{t_1}\right)^{\frac{t_1}{t_1 - t_{\mathrm{m1}}}} \quad when\ 0 \le t \le t_1$$

Equation 2. Period of maximum ground cover.

$$v = v_{\max} \quad when\ t_1 \le t \le t_2$$

Equation 3. Canopy senescence phase.

$$v = v_{\max}\left(\frac{t_{\mathrm{e}} - t}{t_{\mathrm{e}} - t_2}\right)\left(\frac{t + t_1 - t_2}{t_1}\right)^{\frac{t_1}{t_{\mathrm{e}} - t_2}} \quad when\ t_2 \le t \le t_{\mathrm{e}}$$

The descriptive curve is plotted against thermal time (Figure 2) and the non-linear relationship between temperature and growth rate, as developed by Yin *et al.* (1995), accounts for the differences in growth rate in response to changing temperatures during each day and throughout the season. Base, optimum and celling temperatures (5.5, 23.4, and 34.6 °C, respectively (Khan 2012)) for growth are used, accounting for the inhibitory effect of extremes in temperature on plant growth (Yin *et al.* 1995).

Descriptive variates, which describe specific phases of canopy growth, can be calculated from the curve parameters t_{m1}, t_1, t_2, t_{e} and $v_{\max}$ (Table 1). This allows quantitative comparison of early canopy growth (duration of canopy expansion (D_{P1}), mean canopy expansion rate (C_1) and the maximum rate of canopy expansion (C_{m1})), maximum canopy cover (duration of maximum canopy cover (D_{P2})) and canopy senescence (duration of senescence (D_{P3}) and average rate of senescence C_3)). The area under the canopy curve, A_{sum}, can also be calculated, reflecting crop potential to intercept solar radiation throughout the season.

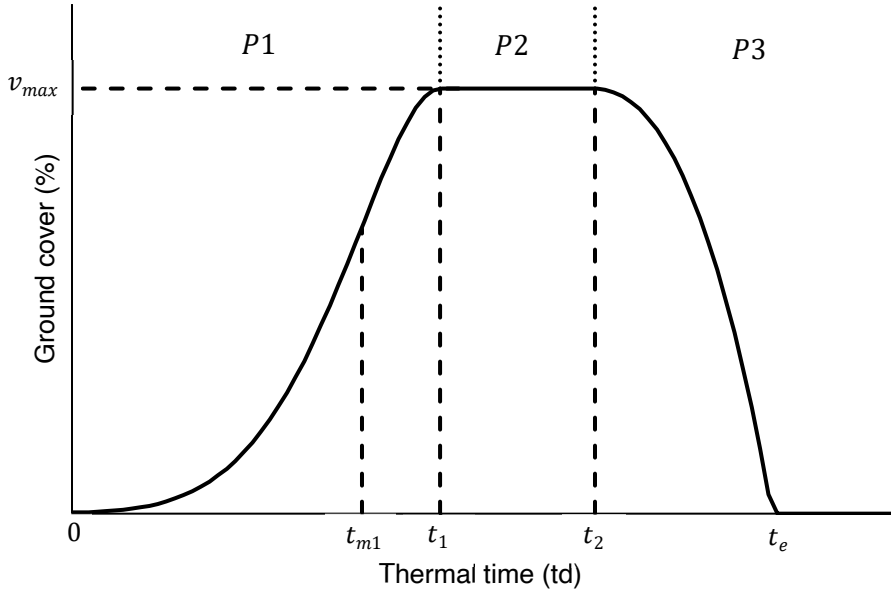

Figure 2. Potato canopy development over time, modelled in three stages. *P*1; growth and expansion (Equation 1), *P*2; maintenance of maximum canopy cover (v_{max}, Equation 2) and *P*3; senescence (Equation 3). t_{m1} is the inflection point of Equation 1, when 50% of v_{max} is achieved and the canopy is expanding most rapidly. At t_1, maximum canopy cover, v_{max} is reached. At t_2 senescence begins and at t_e the canopy has completed senescence. Adapted from Khan (2012).

Table 1. Descriptive canopy variates calculated from Khan's canopy quantification curve, adapted from Khan (2012).

Variate	Description	Units	Comments
D_{P1}	Duration of canopy expansion	Thermal days (td)	Time from plant emergence to maximum canopy cover, equal to the value of t_1.
D_{P2}	Duration of maximum canopy cover	Thermal days (td)	Time during which the canopy covers maximum ground (this percentage value can vary between crops as different maxima are achieved), calculation; t_2 - t_1.
D_{P3}	Duration of canopy senescence	Thermal days (td)	Time from maximum canopy ground cover to complete senescence, calculation t_2 - t_e.
C_1	Average growth rate for canopy expansion phase	% / Thermal days (% td^{-1})	Rate of canopy growth across whole growth period, calculation; v_{max}/t_1.
C_{m1}	Maximum growth rate during canopy expansion	% / Thermal days (% td^{-1})	Fastest growth achieved at t_{m1} (inflection point) and estimated using Equation 4 from (Yin *et al.* 2003).
C_3	Average rate of senescence	% / Thermal days (% td^{-1})	Average canopy senescence rate across whole senescence period, v_{max}/D_{P3}.
A_1, A_2, A_3	Areas under individual curve segments	Thermal days % (td %)	Area under the canopy curve for D_{P1}, D_{P2} and D_{P3} respectively.
A_{sum}	Integrated ground cover	Thermal days % (td %)	Area under whole green canopy curve, sum of A_1, A_2 and A_3.

Equation 4. Maximum growth rate estimation.

$$c_{\mathrm{m1}} = \frac{2t_1 - t_{\mathrm{m1}}}{t_1(t_1 - t_{\mathrm{m1}})}\left(\frac{t_{\mathrm{m1}}}{t_1}\right)^{\frac{t_{\mathrm{m1}}}{t_1 - t_{\mathrm{m1}}}} v_{\mathrm{max}}$$

2.3.2 Allison's model

Allison also represents canopy development in terms of canopy expansion, maintenance and senescence, yet in contrast to Khan's model, the pattern of canopy growth is described with a single equation in relation to time (Equation 5). The equation consists of linked positive and negative logistic functions which describe canopy expansion and senescence, respectively, and duration of ground cover at 50 % of the maximum ground cover is represented by the *N* term within the negative function (Equation 5). The logistic curve captures rate of change within fixed boundaries, between 0 % and a potential maximum of 100 % GC, with an inflection point 'midway between the asymptotes' (Windsor 1932), reflecting the assumption that growth is fastest during the middle of canopy expansion. Furthermore, during both canopy expansion and senescence the gradient of the curve is initially shallow, steepest in the middle and becomes shallow again at the end of that phase of growth, reflecting the rate of change in percentage GC during canopy growth and senescence. The terms common to both halves of the equation, C_{max} and *M*, mathematically link senescence to expansion, since processes which affect canopy expansion can alter the pattern of canopy senescence (Werker & Jaggard 1997). Similar to Khan's model, this equation is iteratively fitted to the raw GC data of individual plots using the Gauss-Newton method within the 'RCYCLE' directive in Genstat. The curve is plotted against time (Figure 3), measured either as days after emergence (DAE) or ordinal date (*O*, days numbered from 1 to 366, typically starting on 1 January). Changes in canopy growth are quantified in relation to 'real' time, increasing ease of interpretation, and allowing the effects of temperature to be explicitly investigated since temperature is not incorporated into the timescale.

Equation 5. Canopy development thoughout the growing season.

$$C = \frac{C_{\max}}{1 + e^{(-B(O-M))}} - \frac{C_{\max}}{1 + e^{(-D(O-M-N))}}$$

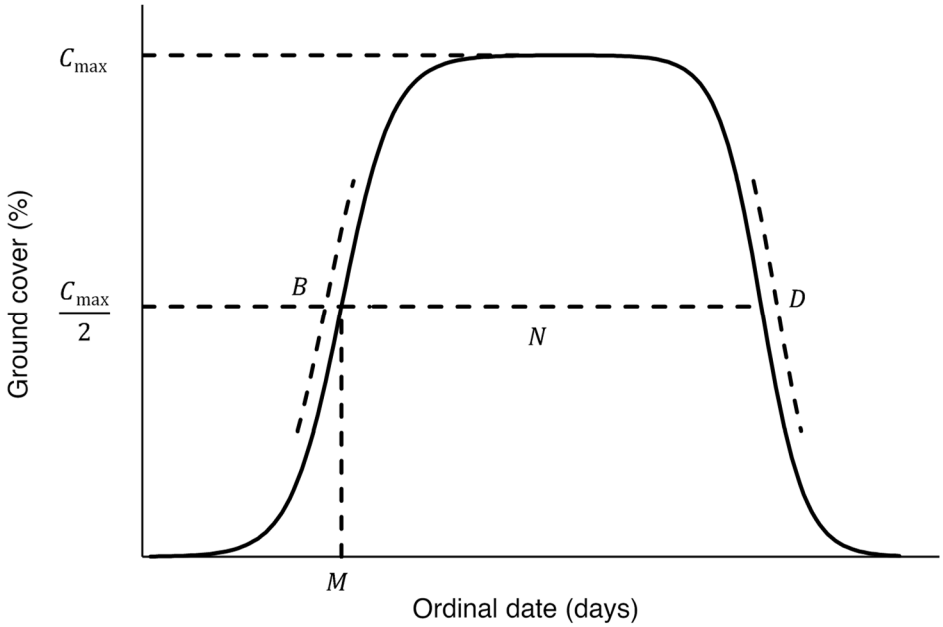

Figure 3. Potato canopy development over time, modelled by a single equation. Equation 5 allows the calculation of *C* (canopy ground cover) on any given day in the growing season. C_{max}; maximum percentage ground covered (the upper asymptote), *B*; dimensionless unit linked to rate of canopy expansion, *D*; dimensionless unit linked to rate of canopy senescence, *M*; ordinal date at which growing canopy reaches 50 % of maximum ground cover, *N*; number of days after *M*, at which senescing canopy reaches 50 % of maximum ground cover. Specific ordinal dates are represented by *O*.

Rearrangement of Equation 5 in two parts, representing the phases of canopy expansion and senescence (Equation 6 and Equation 7, respectively), enables the calculation of the ordinal date at which any given GC is reached by the canopy during expansion or senescence. This allows flexibility in the suite of descriptive variates which can subsequently be used to describe canopy growth during the growing season, consequently curve descriptors can be tailored to end-user needs. From the dates at which 25, 50, 75 and 90 % GC are achieved during canopy expansion and senescence a series of descriptive variates were calculated (Table 2) describing canopy expansion (duration of early canopy expansion (TiE25) and rate of mid-canopy expansion (GCRate2575)); canopy longevity (near-complete canopy duration (GCDur90) and duration of canopy growth, between emergence and onset of senescence (GrowDur)); and canopy senescence (GCRate9050). Integrated ground cover (IGC) was also calculated, providing a summary variate capturing the size and duration of the canopy throughout the season from planting to either complete senescence or the final ground cover measurement. Similarly, to Khan's A_{sum}, IGC indicates the light interception potential of the canopy throughout the season.

Equation 6. Date when a given ground cover *C* is achieved during canopy expansion.

$$O = \frac{\log^e \left(\frac{C_{\max}}{C} - 1\right)}{B} + M$$

Equation 7. Date when a given ground cover *C* is achieved during canopy senescence.

$$O = \frac{\log^e \left(\frac{C_{\max}}{C} - 1\right)}{D} + M + N$$

Table 2. Descriptive canopy variates calculated from Allison's canopy quantification curve.

Variate	Description	Units	Comments
TiE25	Time interval between emergence and canopy at 25 % ground cover	Days	A measure of early canopy expansion (recorded as a time interval, not rate as early growth is non-linear).
GCRate2575	Rate of canopy expansion between 25 and 75 % ground cover	Percentage GC/day (%/day)	A measure of mid-canopy expansion, typically the most rapid period of canopy growth.
GCDur90	Duration of ≥ 90 % ground cover	Days	A measure of near-complete canopy cover achieved by most well-grown crops, when the canopy is theoretically intercepting all PAR.
GCRate9050	Rate of canopy senescence between 90 and 50 % ground cover	Percentage GC/day (%/day)	The rate of canopy decline over an interval passed through by most crops (excluding those which did not reach 90% ground cover nor senesced before harvest).
GrowDur	Time interval between emergence and the onset of senescence	Days	A measure of whole season growth duration, onset of senescence defined as 90 % of C_{max}, after C_{max} has been reached.
IGC	Integrated ground cover for the whole season measured	Percent days (% days)	A summary variate capturing maximum ground cover reached and canopy duration for the whole season, calculated between planting and the final ground cover measurement, equivalent to $C_{max} * N$ (as the logistic curves are symmetrical around the inflection point).

2.4 Model comparison

The models were compared first graphically, then statistically, assessing their ability to fit curves to GC data from a range of canopies with contrasting patterns of growth. Curves were fitted to three years of experimental data collected at NIAB CUF, Cambridge (2015-2017, n = 272 (Firman 2016, 2017, 2018)), consisting of irrigated and unirrigated plots of the contrasting cultivars Cara and Estima, at a range of different nitrogen rates. The determinate and indeterminate cultivars (Estima and Cara, respectively) illustrate a wide range of canopy growth patterns as the plots respond to diverse agronomic conditions, enabling the assessment of model curve fitting ability against canopies which ranged from well-grown to poorly performing.

The curves were fitted iteratively to GC data in Genstat using the 'RCYCLE' and 'FITNONLINEAR' directives, allowing starting values for parameter estimation to be specified and estimates limited to prevent biologically impossible outputs (e.g. maximum GC > 100 %). Since there are advantages to describing growth in relation to both time and thermal time, curves of both models have been plotted against each timescale to enable more complete comparison. Visually, there were few apparent differences between the fit of each curve to the data (as illustrated in Figure 4), though each model fits more closely or loosely at different points of each curve. For example, the Khan curve reaches maximum ground cover before the Allison curve, more closely representing the raw data (Figure 4a), but at the end of the season the slowing rate of senescence is captured more accurately by the Allison curve (Figure 4a). Ability to describe GC data also varied between plots; the very slow canopy expansion shown in Figure 4c & d was best represented by Khan's curve which began the curve at 0 % GC whether plotted against time (after emergence) or thermal time, unlike either of Allison's curves. Conversely, GC was slightly overestimated by Khan's curve during senescence in Figure 4e and Allison's curve better represented the canopy at the end of the season.

2.4.1 Goodness of fit

Both models, fitted against time and thermal time, were quantitatively compared using two measures of goodness of fit. The test dataset allowed assessment of the ability of the different models to fit a curve to GC data from plants grown under a wide range of conditions, including those which did not senesce and canopies which achieved a maximum ground cover of less than 75 % GC. Goodness of fit was quantified using Willmott's index of agreement (*d*, (Legates & McCabe Jr. 2005; Greaves & Wang 2016)) and root mean square error (RMSE, (Greaves & Wang 2016)) for each plot described by both Khan's and Allison's curves, against time (measured in days after emergence, DAE) and thermal time (TT). Goodness of fit for each combination of curve and timescale (Allison's curve against time and thermal time; AllisonDAE and AllisonTT, respectively, and Khan's curve against time and thermal time; KhanDAE and KhanTT, respectively) was then compared using ANOVA in R (R Core Team 2019). R^2 was not used since it is overly sensitive to outliers (Legates & McCabe Jr. 2005) which are not uncommon in the ground cover data due to the stochastic effects of weather (e.g. windy periods during canopy measurement) and the lodging of individual stems within the canopy. There was little difference in the goodness of fit between the

models (Figure 4) and the majority of curves showed a good fit (d > 0.99, where a score of 1 is a perfect fit and RMSE < 6 % GC, where 0 is a perfect fit).

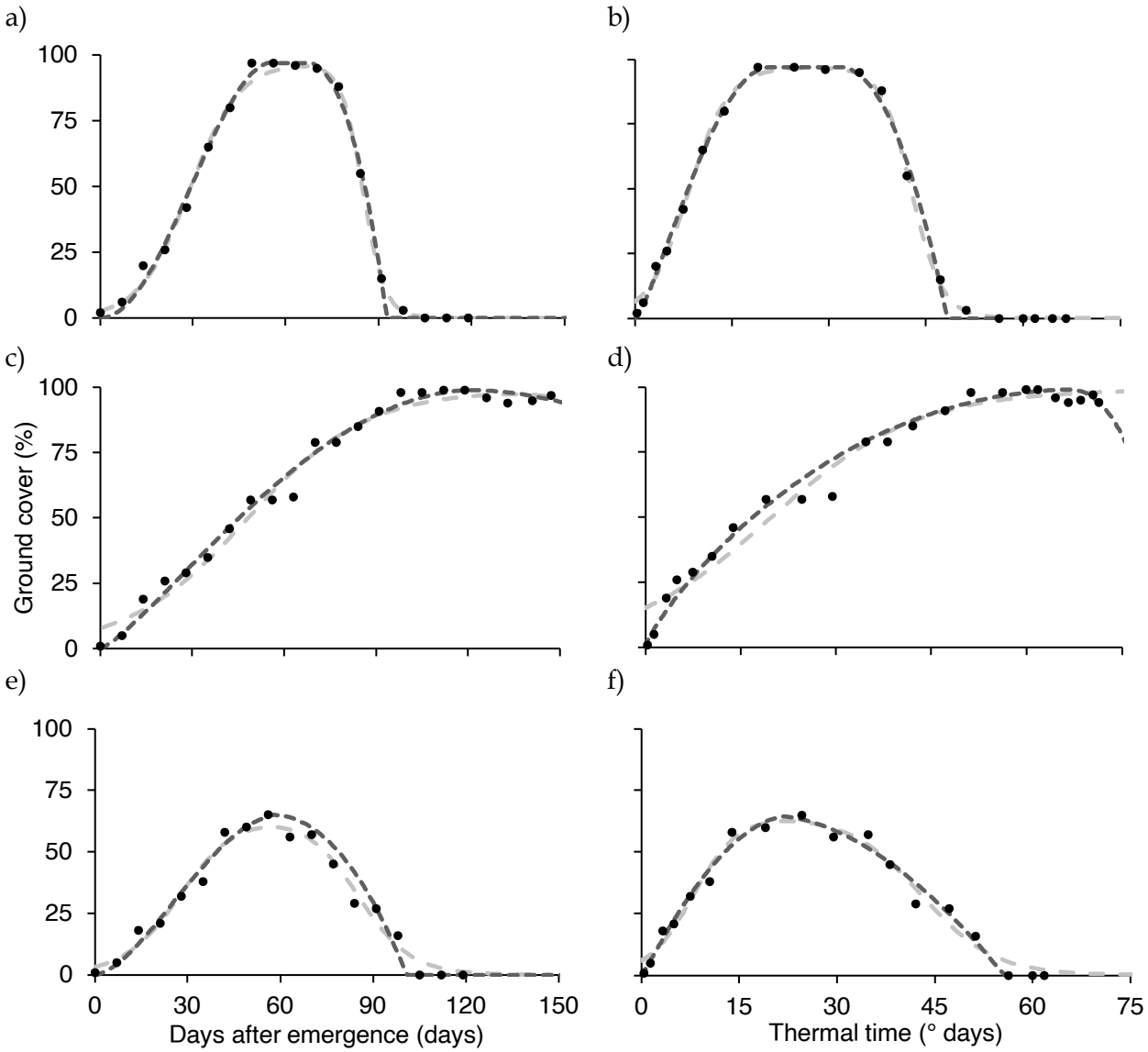

Figure 4. Curves fitted to example ground cover data. Representative plots of 'normal', 'non-senescing' and 'stunted' canopies from 2015 in the test dataset (Estima, unirrigated at 150 kg N/ha; Cara, unirrigated at 20 kg N/ha and Estima, irrigated 30 kg N/ha, respectively). Allison (– –) and Khan's (– – –) curves have been fitted to experimental plots with (a & b) normal, (c & d) non-senescing and (e & f) stunted patterns of growth. Raw data is shown (●) and curves are to fitted days after emergence (a, c & e) and thermal time (b, d & f).

Goodness of fit to the raw data, as measured by both Willmott's index of agreement (d) and RMSE, differed significantly between the fitted curves (ANOVA, P = 0.010 and 0.003, respectively), yet the absolute differences were small and of limited practical significance (Figure 5). The fit of AllisonDAE was shown to be better than the fit of KhanTT (Tukey's HSD, P = 0.013 and 0.005, d and RMSE, respectively) and the fit of KhanDAE was also significantly better than the fit of KhanTT (Tukey's HSD, P = 0.027

and 0.020, *d* and RMSE, respectively), although absolute differences were negligible ($d < 0.004$ and RMSE < 0.7 % GC, Table 3).

Plots with a significantly worse fit than the majority, as measured by *d* and RMSE, were identified as outliers (Figure 4, outliers had a *d* value over 1.5 times the interquartile range (IQR) less than the value of the first quartile (Q1) or an RMSE value 1.5 times IQR greater than the value of the third quartile (Q3)). There was a similar number of outliers per model (*d*: AllisonDAE; 16, AllisonTT; 12, KhanDAE; 17, KhanTT; 18. RMSE: AllisonDAE; 7, AllisonTT; 8, KhanDAE; 8, KhanTT; 7), yet the magnitude of the outliers was typically greater when curves were fitted against thermal time, indicating a slightly worse fit of the curve to the data (Figure 4). Curves fitted in relation to DAE could describe every plot within the test dataset, whereas Khan's model plotted against TT failed to fit a curve to one plot and Allison's curve against TT failed to fit three plots, though this may indicate that the curve fitting programme (rather than the curves themselves) had not been optimized to fit curves in relation to thermal time.

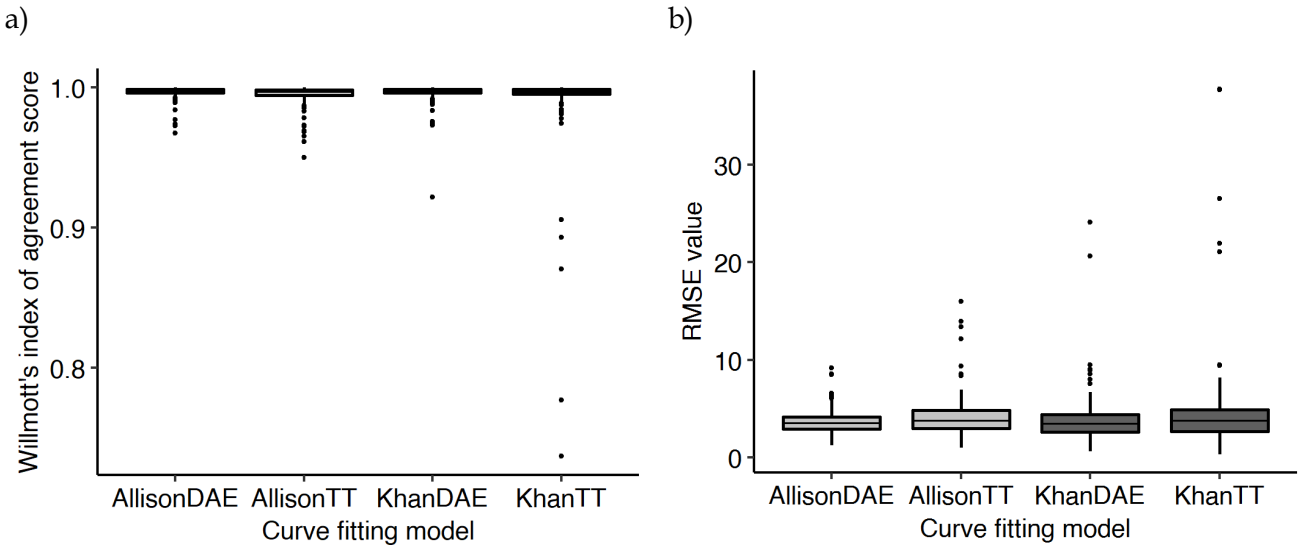

Figure 5. Two measures of model ability to fit a curve to ground cover data using a) Willmott's index of agreement and b) the root mean square error. Allison's (▒) and Khan's (■) models were fitted against both days after emergence (DAE) and thermal time (TT). Treatment medians are shown as horizontal bars, box shows interquartile range (with hinges at the 25th and 75th percentiles, Q1 and Q3 respectively), whiskers show the full range of the data and values more than 1.5 x IQR outside the IQR are plotted individually as outliers. See Table 3 for mean goodness of fit scores for each model.

Table 3. Mean goodness of fit scores for Allison and Khan's models fitted against days after emergence (DAE) and thermal time (TT). Goodness of fit measured using Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC).

		Goodness of fit score	
Model	Measure of time	*d*	RMSE
Allison	DAE	0.997	3.63
	TT	0.995	4.09
Khan	DAE	0.996	3.72
	TT	0.993	4.33

2.5 Model selection

Both models use a similar approach to describe canopy growth, dividing growth into expansion, maintenance and senescence phases and fitting the curve equation(s), both consisting of five parameters, iteratively to GC data with a similar degree of accuracy (Figure 5 and Table 3). The differences between the models arise from the timescales they are fitted against and their output.

There were advantages to quantifying time using either number of days or thermal time. Quantifying canopy growth in relation to thermal time reflects the non-linear response of crop growth to temperature as ambient temperature varies throughout the season (Yin *et al.* 1995). Incorporating temperature into the measure of time also allows comparison of patterns in canopy development without the confounding effects of different temperatures between sites and years (Tiemens-Hulscher *et al.* 2014). Yet combining temperature with the index of time increases the complexity of determining the effects of temperature on canopy growth. Consequently, a thermal time based model is less suitable for investigating the effects of planting date, since temperature is one of the predominant differences. For example, the non-linear nature of thermal time masks slow post-emergence growth (compare Figure 4a & b), reducing the ability to describe differences in early canopy growth between planting dates. Quantifying the canopy in relation to time also produces more straightforward output, which is more intuitive to interpret due to the linear timescale.

Model output is the second point of differentiation between the two models and whilst canopy expansion, maintenance and senescence are described using the output of both models, they can be described in greater detail using Allison's curve. Since Allison's curve can be rearranged to calculate the date on which a given GC value is achieved, the rate of expansion or senescence can be calculated over a specifiable period of canopy growth. In contrast, Khan's equations cannot be rearranged to calculate the thermal time at which a given GC value is reached and consequently the descriptive

variates summarize whole canopy expansion and senescence in two immutable variates; C_1 and C_3 (Table 1). Hence, Allison's curve enables a more precise understanding of canopy growth than is afforded by Khan's.

Furthermore, it is inaccurate to calculate a single rate of canopy expansion for the whole period of growth; this involves treating canopy expansion as linear, which is not an accurate reflection of canopy growth. Rather, the rate of canopy expansion is variable, starting slowly, increasing to a maximum at the inflection point (at time t_{m1} or M), then slowing down as v_{max} or C_{max} is approached. The rearrangement of Allison's curve allows flexible segmentation of canopy expansion and senescence into both time intervals, for non-linear phases of canopy development, and into rates, where appropriate. Variates from Allison's curve can be adjusted to suit specific research questions or the needs of a grower, for example, rate of canopy expansion could be finely subdivided (into intervals of 10 % GC) to identify the specific point when canopy expansion begins to slow as a result of water stress.

In summary, the potentially increased biological accuracy of canopy quantification based on thermal time did not result in better model fit compared to the ordinal time-based model. Thermal time also increased model complexity, requiring the calculation of thermal time prior to canopy quantification and reduced output clarity since it is in relation to time and temperature, rather than time alone. Additionally, the versatility of descriptive variates produced by Allison's model makes it more attractive than Khan's curve, since more specific periods of canopy growth can be compared, more clearly reflecting biologically relevant periods of growth. Allison's model also allows the explicit investigation of the effects of temperature upon canopy growth. Hence due to greater simplicity and flexibility, Allison's model was selected as the more appropriate descriptive model for quantification of potato canopy growth and is referred to as the canopy quantification (CQ) curve or model in subsequent chapters.

2.6 Model developments

Prior to the above model comparison, a basic curve fitting programme was developed for each model in Genstat from programmes provided by the authors (Allison, personal communication, 2015; Khan, personal communication, 2018) in order to process the test data and compare both models. Developments reduced user input required, increasing the speed and accuracy of data processing, and included:

- Looping commands to batch process plot data from multiple experiments or years, accounting for different numbers of measurements between experiments (both).
- Graphing the fitted curve and raw data of each plot for quick visual assessment of canopy growth throughout the season (both).
- Reading the maximum GC value from the raw data, for C_{max} and v_{max}, capping C and v to prevent estimation of GC greater than 100 % (both).
- Calculating specific starting points for iteratively estimating parameters by:
    - Identifying the first and last time points of maximum canopy extent to estimate t_1 and t_2 respectively (Khan).
    - Identifying the GC measurement closest to 50 % of maximum canopy cover, and thermal time thereof, to estimate t_{m1} (Khan).
    - Identifying thermal time of the final GC measurement to estimate t_e (Khan).
    - Using the date of plot emergence to estimate M (Allison).
    - Approximating the duration for which GC was greater than 50 % GC to estimate N (Allison).

After the selection of Allison's model for all subsequent canopy quantification, further developments were made to the programme and data workflow, increasing the utility of model output. Major innovations included the development of a programme to sort raw GC data based on C_{max} and final GC values; reducing the likelihood of programme faults and the need for user intervention; and the development of a programme to generate plot specific meteorological descriptors. Details of developments included:

- Sorting raw GC data to determine which canopies showed atypical development, which either did not senesce or C_{max} < 75 % GC, then streamlining the calculation of descriptive variates when data was absent (i.e. not attempting to calculate rate of senescence when the crop canopy did not senescence).
- Removing excess 0 % GC values after senescence from the raw data to prevent them from skewing the fit of the curve.
- Calculating the descriptive variates TiE25, GCRate2575, GCDur90, TiESc, GCRate9050 and IGC (Table 2).
- Calculating IGC between planting date and the final ground cover measurement, reflecting canopy light absorption potential for the complete

duration of plot canopy maintenance and providing a better link with end of season yield.

- Calculating mean and cumulative, temperature and radiation during early (TiE25) and mid-canopy expansion (GCRate2575), as well the whole season for individual plots.

Challenges to curve fitting remain, particularly when the progression of canopy growth is abnormal. Wider use of the programme is also limited since it was developed within Genstat, a programme not commonly used due to the availability of free alternatives such as R and Python. To increase the accessibility of the canopy quantification programme it should be translated into a more widely used language.

2.7 Modelling summary

Empirical models can be useful for describing statistical relationships between plant growth and factors affecting it, although they encode less detail on growth processes. Two measures of goodness of fit were used to compare the ability of two candidate models (Khan's and Allison's) to describe potato canopy growth, plotted against both time and thermal time. Thermal time did not improve model fit compared to models fitted against time and does not allow the effects of temperature during different periods of the growing season to be explicitly investigated; hence the final model was plotted against time. The output of Allison's model could be tailored to quantify specific periods of canopy development and so has the potential to provide greater, more relevant detail than Khan's model hence Allison's model was selected and is referred to as the canopy quantification (CQ) curve or model henceforth. Further developments have increased the suitability of the CQ model for description of experimental and commercial potato canopy data. The full annotated Genstat code for the CQ model used throughout this thesis is in Appendix 3.

3 General Methods

Fieldwork was carried out over three years, 2016–2018 on the trial grounds at the National Institute for Agricultural Botany (NIAB), Cambridge. Two experiments, relating to planting date and planting density, were carried out using shared methodology in data collection and analysis. Processes and techniques common to both experiments are described below with amendments or unique treatments described in the methods sections of the individual experiments.

3.1 Pre-season set up

3.1.1 Site and soil

Experiments 1 and 2 were grown in Field 1 in 2016, located at 52 ° 13 ′ 58 ″ N, 0 ° 05 ′ 57 ″ E at 14 m above sea level. The soil was a sandy clay loam/clay loam with 3.6 % soil organic matter. It was initially ploughed 3 October 2015 and secondary cultivations were carried out 31 March to 8 April, with roto-ridging in the following week.

Experiments 3 and 4 were grown in Field 2 in 2017, located at 52 ° 13 ′ 53 ″ N, 0 ° 05 ′ 47 ″ E at 16 m above sea level. The soil was a sandy loam/sandy clay loam with 3.9 % organic matter. Ploughing and secondary cultivations were carried out 14 March, with tined cultivations the following week and power harrowing and roto-ridging at the end of March. Wet soil conditions at cultivation resulted in a cloddy and sub-optimal seed bed.

Experiment 5 was grown in Field 3 in 2018, located at 52 ° 14 ′ 05 ″ N, 0 ° 05 ′ 53 ″ E at 14 m above sea level. The soil was a sandy loam with 2.9 % soil organic matter. Spring oats had been grown as a cover crop and were ploughed into the soil on 19 April. Tined cultivations and roto-ridging were carried out on 20 April.

Herbicide was applied prior to emergence and hand-weeding carried out where herbicide was ineffective. History of previous cultivation in each field is shown in Table 4 and potatoes have not been grown on any of the fields for at least 24 years prior to the experiments described here. Soil texture, organic matter and nitrogen content are reported in Table 5.

Table 4. History of previous cropping in experimental fields.

Years preceding experiment	Year of experiment		
	2016	2017	2018
5	Winter wheat	Winter barley	Winter oats
4	Short ley	Oil seed rape	Winter wheat
3	Short ley	Winter wheat	Winter wheat
2	Winter barley	Winter wheat	Spring linseed
1	Oil seed rape	Winter barley	Spring oats

Table 5. Detail of soil analysis for each experimental field. Soil samples taken prior to planting and analysed by NRM Laboratories.

Year and experiment	Soil texture	Soil organic matter (%)	Available nitrogen (kg N/ha)	
			0-30 cm	30-60 cm
2016 (1 & 2)	Sandy clay loam / clay loam	3.6	78.9	70.1
2017 (3 & 4)	Sandy loam / sandy clay loam	3.9	71.0	38.0
2018 (5)	Sandy loam	2.9	31.5	20.6

3.1.2 Plot layout

Plots (or subplots in Expts 1 and 3) consisted of four rows. The two outer rows functioned as 'guard' rows, reducing the impact of neighbouring treatments on the two central harvest rows from which all measurements and harvests were taken. Both experiments were blocked to account for within-field variation, and Expts 1 and 3 had a split-plot design.

3.1.3 Cultivar selection

Cultivars Maris Piper and Estima were chosen to represent different ends of the determinacy spectrum, to capture the range of growth responses to different agronomic variables. Estima is determinate and Maris Piper more indeterminate, and both are widely grown in the UK.

3.1.4 Seed

Certified seed was obtained and after delivery was stored at 2 °C until planting.

3.1.5 Planting

The experiments were planted by hand in 75 cm wide ridges. Seed was spaced according to experimental design and placed approximately 15 cm below the soil surface using a hand dibber. Ridges were raked to ensure that seed was covered by soil and to maintain the shape of the ridge.

3.2 In-season measurements and data analysis

3.2.1 Weather data

Incident solar radiation (MJ), average ambient air temperature (°C), average soil temperature (°C), wind speed (km/h) and rainfall (mm) were recorded daily by the onsite weather station situated on the headland of the experimental field. Rainfall, air temperature and wind speed were used in a modified version of the Penman-Monteith equation (Stalham & Allen 2004) to schedule irrigation and in soil moisture deficit (SMD) calculations. Mean air temperature and cumulative air temperature during the whole growth period (from emergence until harvest) of each individual plot or subplot were calculated. Mean soil temperature was calculated for the duration between planting and emergence. Mean and cumulative air temperatures were also calculated for the period of early canopy expansion (from emergence to 25 % GC) and the period of mid-canopy expansion (from 25-75 % GC). Mean daily radiation and cumulative radiation were calculated for the whole growth period, the period of early canopy expansion (from emergence to 25 % GC) and the period of mid-canopy expansion (from 25-75 % GC).

3.2.2 Emergence

Emergence was defined as the day when the first sprout was visible at the surface of the soil and counts were carried out twice weekly. Date of emergence for each plot was defined as the first day on which at least 50 % of the plants in the central two rows of the plot had emerged.

3.2.3 Ground cover

Canopy cover was recorded with a handheld grid twice weekly. The grid was divided into 100 equal rectangles, with the same width as the row and height a multiple of plant spacing (Burstall & Harris 1983). Proportion of ground cover (GC) was estimated by counting each rectangle containing over 50 % green leaf, as observed from directly above to avoid parallax, whilst the grid was held *c.* 10 cm from the canopy surface. The grid was positioned centrally over a single row, ensuring that plants within the row were not bisected by the grid edges and measuring GC for one to three whole plants (depending upon plant spacing). The grid method was deemed the most suitable for GC data collection due to greater ease of use in the field compared to photographic methods.

Canopies were quantified by iteratively fitting the canopy quantification (CQ) curve to raw GC data, as described in the modelling chapter (2.3.2), using Genstat 17.1 (VSN International, 2014). Descriptive variates were then calculated from the CQ curves to allow quantitative comparison of different aspects of canopy development (Table 6).

Table 6. Summary of descriptive variates calculated from the canopy quantification curve.

Variate	Abbreviation	Description
Early canopy expansion	TiE25	Time interval between emergence and reaching 25 % ground cover.
Mid-canopy expansion rate	GCRate2575	Rate of canopy expansion between 25 and 75 % ground cover.
Duration of near-complete canopy cover	GCDur90	Duration of time for which the canopy cover is 90 % or greater.
Senescence rate	GCRate9050	Rate of canopy senescence between 90 and 50 % ground cover.
Duration of canopy	TiESc	Time interval between emergence and the start of senescence (when canopy cover is less than 90 % of plot maximum canopy cover).
Integrated ground cover	IGC	Area under the ground cover curve; encapsulates extent and duration of canopy cover for the whole season.

3.2.4 Leaf appearance

Leaf appearance was recorded weekly, counting number of leaves and branches produced on the main axis (mainstem, then sympodial branch) of two median sized stems from separate plants per plot. Every 5th leaf was tagged with wire. A minimum leaf length (from stem to leaf tip) of 10 mm was used to indicate leaf appearance (Firman *et al.* 1995). Sympodial branches were numbered according to the leaf whose node they grew at and were initially identified by checking for branch production beneath the inflorescence. See Figure 6 for an example. Recording ended after a constant number of leaves was recorded for three consecutive weeks. In some cases, senescence and animal damage prevented further leaf production, ending the count earlier. Number of above-ground stems (on the two plants on which leaf appearance was measured) was also recorded in the first month.

The rate of mainstem leaf appearance (msLA) was calculated between the appearance of the 5th leaf and the sympodial branch. This time interval represents the predominately linear phase of leaf production by the mainstem and excludes the first four leaves, typically formed prior to emergence. If no sympodial branch was produced by a stem, msLA was calculated between the appearance of the 5th and 12th leaves to ensure that the variate was calculated during the linear phase of leaf production, comparable to the values calculated between the 5th leaf and sympodial

branch appearance (mean sympodial branch production occurred at the 12th and 17th leaves for Estima and Maris Piper, respectively (mean cultivar sympodial branch insertion points calculated from Expts 1-5)).

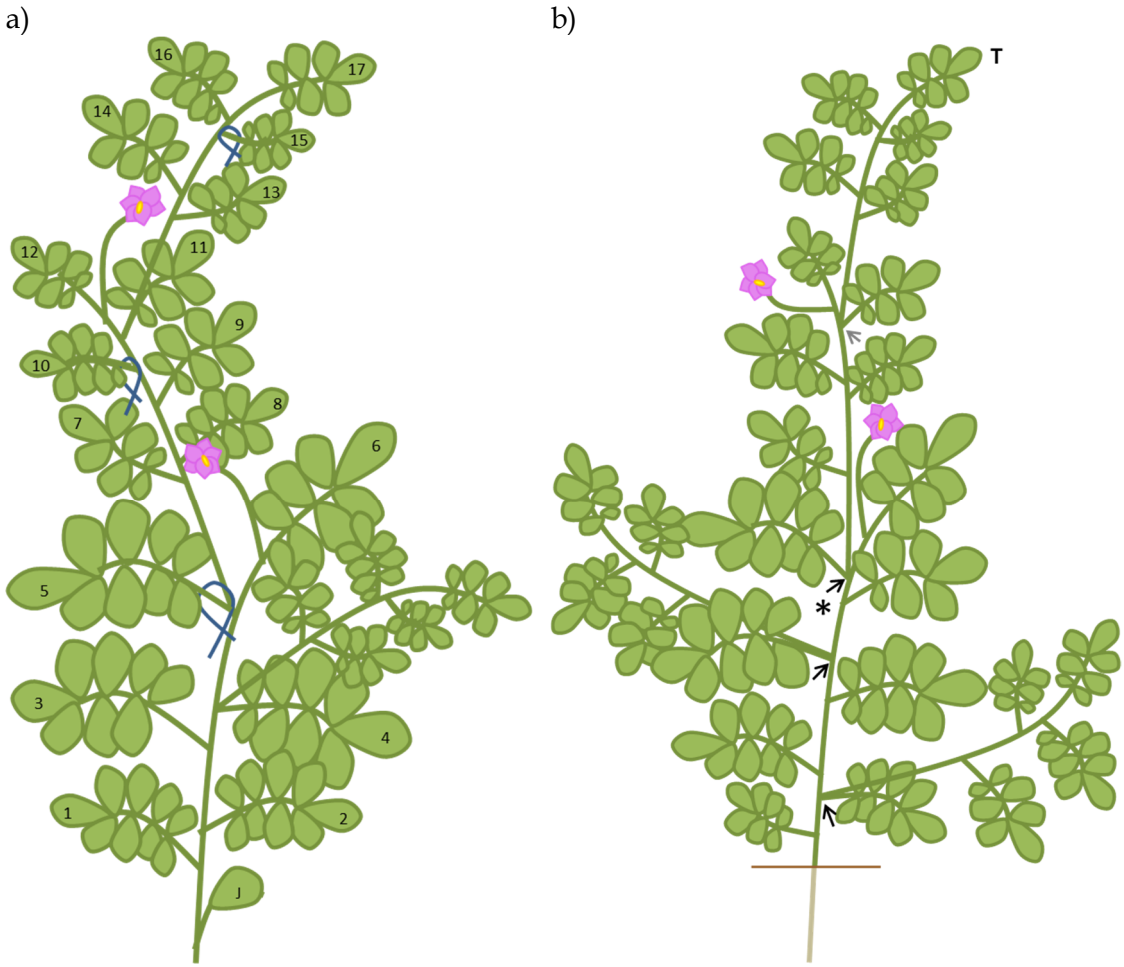

Figure 6. Diagrams illustrating leaf tagging and branch identification. (a) Example of leaf tagging procedure. The first sympodial branch is at the 5th leaf, the second at the 11th leaf. At a sympodial branch point the leaf count continues up the mainstem then begins on the sympodial branch. There is also a non-sympodial, or axillary branch at the 4th leaf, this does not contribute to the total leaf count. (b) Illustration of branch height data collection. Branch insertion points are marked with arrows and the distance from the soil (brown line) recorded for branches marked by black arrows. Whilst there is a second sympodial branch, marked by a grey arrow, all material after the first sympodial branch, marked with a starred arrow, was considered part of the first sympodial branch. Total stem length was measured from soil to stem tip, marked 'T'.

Leaf production by the sympodial branches (sbLA) was treated as a separate phase of growth and was not included in the above calculation for leaf production rate as not all stems produce sympodial branches and sympodial branch leaf appearance has been reported to be slower than that on the mainstem (Firman *et al.* 1995). The rate of whole plant leaf appearance (pLA) was calculated, multiplying rate of mainstem leaf production by number of stems per plant, accounting for variation in stem number between plants. Number of leaves on the mainstem (msL) and on the main axis (mainstem and sympodial branches, maL) were analysed separately.

Phyllochron, the thermal time between the production of successive leaves (Wilhelm & McMaster 1995), was calculated for the mainstem with a base temperature of 0 °C (Firman *et al.* 1991). Mean daily air temperature during mainstem leaf production (between appearance of the 5th leaf and sympodial branch production, or 12th leaf appearance if no sympodial branch was produced) was summed then divided by the number of leaves produced during that period.

3.2.5 Harvest

Plots were harvested by hand. Rotten or animal-damaged tubers were replaced with equivalent (in shape and size) tubers from neighbouring guard plants within the harvest rows. Diseased plants were also replaced from within the harvest row. Tubers were graded (at 10 mm intervals) and weighed, then a subsample was washed, chipped, dried (at 90 °C for a minimum of 48 h) and weighed to calculate tuber percentage dry matter. Fresh weight and dry weight yields were then calculated. Haulm material was harvested concomitantly and stored in sealed polythene bags (PolyPostalPackaging.com) at 2 °C until processing for leaf area index and branch height measurements. Number of above-ground stems was also recorded, allowing calculation of stem density at the end of the season.

3.2.6 Leaf area index

Leaf area index (LAI) is defined as the total one-sided area of photosynthetic tissue per unit ground area (Watson 1947) and is used to quantify the volume of leaves produced by a plant. The haulm from each plot was weighed, then a subsample of three stems was taken and LAI was estimated gravimetrically, using specific leaf area (SLA, cm^2/g, (Bréda 2003)). Each stem was divided into canopy components: mainstem, axillary branches (produced by the mainstem) and sympodial branch (the continuation of the main axis after production of a floral meristem) and processed separately. Leaves were stripped from the petioles and 50 leaf disc samples were taken. Leaves, leaf discs and stems were dried (at 90 °C for a minimum of 48 h) and weighed, then SLA was calculated and used to estimate the LAI (Firman & Allen 1989a) for each component of the canopy. Specific leaf area was derived by dividing the area of 50 leaf discs (2.26 cm^2 each) by their dry mass. SLA was then used to convert dry leaf mass (g) for each subsection of the canopy (mainstem, axillary branch or sympodial branch) into subsample leaf area (cm^2). The ratio of subsample fresh weight (g) to plot fresh weight (g) was used to calculate plot leaf area. Plot leaf area (cm^2) was divided by harvest area (cm^2) to obtain the unit-less value of LAI.

3.2.7 Branch production

The number of leaves, number of axillary branches (NoB) and height (from soil level) of branches on three stems per plot was recorded. Number of leaves on each axillary branch was also recorded and the average number of leaves per branch was calculated (aveBLeaves). After senescence had begun, and branches present only as stems (i.e. where leaves had senesced) were not included when calculating average number of leaves per branch.

The branch below the first inflorescence was identified as the sympodial branch and was treated as a single branch despite subsequent production of additional inflorescences and branches (Figure 6b). Sympodial branch height (from soil) was measured (SBInsert), indicating mainstem length. Each stem was stretched out against a ruler to measure complete stem length, from soil level to leaf tips (TotLength). Length of the sympodial branch was calculated from stem length and sympodial branch height data. Number of leaves on the sympodial branch was recorded (SBLeaves).

3.3 Statistical analyses

Statistical tests were carried out in both R (R Core Team 2019) using RStudio version 1.1.463 (RStudio Team 2015) and Genstat 17.1 (VSN International 2014). Two-way analysis of variance, accounting for experimental block and plot structure, was used to determine the effect of treatments and their interactions upon different aspects of canopy development using the 'ANOVA' directive in Genstat. Treatment effect significance was determined by F-test (within the 'ANOVA' directive) and reported if significant at the 95 % or 99.9 % confidence intervals, $P \leq 0.05$ and $P < 0.001$, respectively. Standard error (S.E.) was indicated by error bars on bar charts of treatment means and degrees of freedom were reported in figure captions. Adjusted R^2 values are reported throughout.

4 PLANTING DATE

4.1 Introduction

Date of planting and applied nitrogen are two key features of crop management, each influencing canopy development, crop longevity and subsequent yield. Consequently, it is important to understand how varying each will affect canopy growth and crop ability to intercept light and generate yield, as per the overall thesis hypothesis (1.4).

The meteorological conditions under which a potato crop is grown have considerable influence over the development and final yield of that crop. Whilst the weather cannot be controlled, management strategies can enable growers to optimize crop growth under their local conditions including well-scheduled irrigation or using a fleece covering to raise soil temperature and speed early development. Growers may also adjust the planting date to alter the environmental conditions that a crop is likely to experience at each stage of development.

Crop development is further shaped by nitrogen availability, another key aspect of agronomy under grower control. Nitrogen is essential for plant growth and has a large influence upon canopy development by promoting leaf expansion, increasing canopy size and ultimately increasing final tuber yield (Allen & Scott 2001). Yet the degree of influence of applied nitrogen upon canopy growth and yield varies with cultivar and growing season length (Tiemens-Hulscher *et al.* 2014), so must be considered in relation to these other aspects of agronomy.

This introduction will explore current understanding of the influence of planting date and applied nitrogen on potato growth, with particular focus on the canopy, in preparation to address thesis aims two, three and four (1.4) in the chapter body. Firstly, the separate effects on canopy development and yield of key environmental components (temperature (4.1.1), and light intensity and daylength (4.1.2)), which change with altered planting dates will be considered. Then, research which focuses on variation in potato growth with planting date will be examined (4.1.3), considering the combined effects of the environmental variables that change with date of planting. Thirdly, the effect of applied nitrogen on canopy growth, and how this varies between cultivars and length of growing season, will be described (4.1.4). Finally, experimental aims will be detailed (4.1.5), and the chapter structure set out (4.1.6).

4.1.1 Temperature effects on canopy growth

Firstly, advancing or delaying planting affects the air and soil temperatures experienced by the crop throughout the season, potentially promoting growth when the temperature is optimal, theoretically maximizing canopy growth, size and light interception. Yet, at a single location, large differences in planting date typically result in limited differences in mean temperature across the growing season. This was illustrated by a 1 °C range in mean air temperature throughout the growing season (from 16.8-17.8 °C), found between planting dates 13 weeks apart by Wang *et al.* (2015) in Gansu Province, China. Consequently, developmental differences are not associated with variation in average temperature across the whole growing season but rather with variation in mean temperature over key developmental stages.

For example, it has been widely reported that the duration between planting and emergence decreases with increasing mean temperature (Bodlaender 1963). Wang *et al.* (2015) described a linear reduction in the duration between planting and emergence with increasing mean air temperature experienced during the pre-emergence period (Wang *et al.* 2015). Bremner and Radley (1966) also observed shortening of the interval between planting and emergence in four cultivars of contrasting determinacy and, similarly, Firman *et al.* (1992) reported an increasing rate of sprout growth and emergence with increases in soil temperature up to 20 °C. Moreover, MacKerron and Waister (1985) modelled the temperature dependence of sprout growth, with 1 mm of sprout growth occurring per degree day above a base temperature of 2 °C (based on earlier work by MacKerron) and this linear relationship has also been used to predict the rate of development in the LINTUL-POTATO model (Kooman & Haverkort 1995). Thus, there is strong evidence for faster growth prior to emergence with increasing temperatures.

The influence of temperature on post-emergence growth appears to be more complex, with differing results between experiments. For example, Wang *et al.* (2015) found no direct correlation between duration of developmental period (i.e. between branch formation and inflorescence development or flowering to maturation) and either average or accumulated temperature in field grown potatoes. Yet, optimum temperatures have been identified for specific aspects of potato development (Bodlaender 1963; Struik 2007). For example, under growth chamber conditions, 24 °C was found to be the optimal air temperature for canopy growth, light interception and photosynthesis for the cultivar Atlantic, whilst tuber production was greatest at 20 °C

(Timlin *et al.* 2006). Conversely, maximum rate of photosynthesis in *cv.* Russet Burbank was found to occur between at leaf temperatures between 24-30 °C in a glasshouse (Dwelle *et al.* 1981), indicating variability in the temperature response of photosynthesis between cultivars.

Additionally, in both field and growth chamber experiments, leaf appearance rate increased linearly with increasing temperature, though the relationship was reported over a narrower range in the field; *c.* 11-19 °C (Firman *et al.* 1995), than in the growth chamber; 9-25 °C (Kirk & Marshall 1992). Similarly, Cao and Tibbitts (1995) reported a linear increase in number of leaves on the main axis (mainstem and subsequent sympodial branches) with accumulated thermal time (measured using growing degree days, with a base temperature of 6 °C) whilst Minda *et al.* (2019) reported quadratic relationship between accumulated temperature (with a base temperature of 5.5 °C) and percent canopy cover during canopy expansion. Hence, rate of leaf appearance increases at warmer temperatures, though the relationship appears to be weaker in the field than growth chamber. Increased leaf production at warmer temperatures may also be associated with increased rate of canopy expansion, though this is yet to be confirmed by measurements of both in the same experiment.

In contrast, duration of leaf expansion negatively correlated with increasing air temperature under growth chamber conditions (Kirk & Marshall 1992; Fleisher & Timlin 2006) and individual leaves were largest at cooler temperatures (Fleisher & Timlin 2006). Similarly, Kooman *et al.* (1996b) reported a reduction in the duration of leaf production at higher temperatures in the field, though the effect varied between cultivars and was not significant in four of eight cultivars in the experiment. Moreover, canopy size, as measured by leaf area and leaf mass, was found to be greatest between *c.* 17 and 22 °C in a growth chamber experiment, exhibiting a non-linear response to air temperature (Fleisher *et al.* 2006b). Despite greater axillary branch production (described as either basal or apical by Fleisher *et al.* (2006b)) at warmer air temperatures, total leaf area decreased due to more rapid mainstem leaf senescence and smaller leaf size under warmer conditions (Fleisher *et al.* 2006b). Hence, canopy leaf area is not simply greatest when temperatures are warmest and leaf appearance is most rapid.

Increased temperature has also been shown to change biomass distribution between the haulm and tubers, with more resources allocated to the haulm, lowering harvest index (HI) at warmer temperatures (Menzel 1985; Timlin *et al.* 2006; George *et al.* 2017;

Lizana *et al.* 2017). Changes in resource partitioning between haulm and tubers were seen over a wide range of temperatures in a growth chamber experiment (Fleisher *et al.* 2006b). Total biomass decreased at higher temperatures (above *c.* 17 °C, as tuber mass decreased) and a greater proportion of leaves were produced by the axillary and sympodial branches (relative to the mainstem) above 23 °C, suggesting that branch production increases in response to rising temperatures (Fleisher *et al.* 2006b).

Changes in biomass partitioning with temperature increases have also been observed in the field and indicate that timing of temperature increases, relative to tuber development and the day-night cycle, alter canopy growth (Kim & Lee 2019). Kim and Lee (2019) observed greater effects of increased air temperature on biomass production during tuber initiation than during tuber bulking and increasing night temperatures by *c.* 4 °C (to *c.* 22 °C) delayed tuber development, reducing the number of large (> 100 g) tubers, HI and total yield, whilst similar increases in day temperatures (to *c.* 31 °C) reducing photosynthesis, with proportional reductions in haulm and tuber production (Kim & Lee 2019). These findings partially confirmed the limited differences in tuber and haulm production found as a result of similar increases in mean daily air temperature during tuber bulking (between 3 and 5 °C, in line with the Intergovernmental Panel on Climate Change expectations for the study area in southern Chile (Lizana *et al.* 2017)). Differences in haulm and tuber production were only found within a few cultivars and bigger differences in HI were found between cultivars, irrespective of temperature regime (Lizana *et al.* 2017). Furthermore, Fleisher *et al.* (2006b) proposed that more efficient potato canopies develop at cooler temperatures, as less carbon was required to produce longer-lived canopies, able to maintain maximal light interception and tuber production throughout the season. Hence the relationship between temperature, canopy growth and yield is not straightforward. Whilst warmer temperatures are associated with faster leaf production this does not necessarily result in a larger canopy, with greater light interception and yield, since high temperatures not only inhibit tuber initiation, but also decrease resources partitioned to tubers.

Thus far, the majority of temperature-response experiments have been carried out under controlled conditions, in either growth chamber or glasshouse (e.g. Bodlaender 1963; Fleisher *et al.* 2006b; Timlin *et al.* 2006), yet how well these relationships represent field growth is uncertain. Pot-grown plants, under controlled conditions with constant temperatures on a fixed day-night cycle are more able to acclimate to the environment,

hence optimal temperatures for canopy growth and biomass production temperatures of field grown potatoes may differ, since temperatures fluctuate considerably, both diurnally and between days. Pot-grown potatoes may also be more sensitive to increases in air temperature as soil in pots warms faster than in the field, where the greater bulk of soil may buffer soil temperature against changes in air temperature. Furthermore, potato growth in pots may also not accurately represent that of field-grown potatoes due to limitations in rooting and differences in water and nutrient availability.

In summary, increasing temperature advances emergence in both the field and growth chamber, and optimum temperatures for maximum canopy growth, light interception and tuber production have been reported in the glasshouse. However, these optima may not be universal, therefore canopy growth responses to varying temperatures in the field must be quantified. This will enable understanding of the different growth responses, both to the modest temperature differences which result from varying with planting date, and to inconstant field temperatures which fluctuate within treatments.

4.1.1.1 Describing variation in temperature throughout the growing season

As established above, temperature plays an important role in regulating the rate of canopy and tuber development, yet multiple methods are used throughout the literature to describe the variations in temperature during the growing season and have the potential to alter the relationships derived. These approaches include averaging daily temperature over the whole season or specific stages of crop growth, calculating growing degree days (GDD) or thermal time and calculating phyllochron (to identify how the rate of leaf appearance varies with temperature), and each will be briefly evaluated below.

Calculating mean temperature is the simplest approach to describing variation in temperature and has been used by both Wang *et al.* (2015) and Firman *et al.* (1995) to compare the temperature of the whole-season and specific developmental stages between planting dates, and mean temperature during leaf appearance, respectively. Simplicity makes mean temperature an easy metric to interpret, yet extreme temperature events may be masked, and if calculated over a long period, such as the whole season, there may be little difference in the final value.

Differences in temperature can also be quantified by calculating accumulated temperature using either GDD or thermal time, both describing duration of growth

relative to temperature. GDD are calculated daily from the mean of the minimum and maximum temperatures and subtracting a crop specific base temperature, below which no growth will occur (Mix *et al.* 2012) and assume a linear relationship between temperature and growth rate. Thermal time is an alternative measure of accumulated heat, commonly measured in °C/day, and acknowledges that growth rates vary from day to day due, in part, to variation in temperature which changes the rates of enzymatic reactions. The relationship between plant growth and thermal time can be described using a non-linear beta function (Yin *et al.* 1995, 2003). The non-linear beta function captures the variable rate of potato canopy development as temperature increases from a base temperature (below which no growth occurs) to the optimum temperature (maximum growth rate) and the ceiling temperature (above which no growth occurs, (Khan 2012)). The beta function is a more sophisticated and biologically accurate approach than GDD which assume that every degree above the base temperature contributes equally to growth. However, greater biological accuracy does not necessarily result in greater descriptive power and Fleisher *et al.* (2006) found that both thermal time and GDD approaches modelled the rate of leaf appearance in pot and field experiments with similar accuracy.

Thermal time and GDD are widely used, yet are not consistently defined within the literature, with some even failing to define the 'heat units' used e.g. Khan *et al.* (2011). A wide range of base temperatures for potato development and growth have been used; from 2 °C, which has been derived experimentally (Oliveira 2015), to 0 °C (Hu *et al.* 2017), 4 °C (O'Brien *et al.* 1986), 4.4 °C (Mix *et al.* 2012) and 5 °C (Wang *et al.* 2015) which have no citations for their derivations, making it difficult to compare temperature requirements for potato between researcher groups and study sites. Firman *et al.* (1991) concluded that a base temperature of 0 °C may be most appropriate, since although limited sprout growth occurred below 4 °C, sprouts of tubers stored at 2 °C continued to grow and produce nodes. Greater variation still is found in estimations of optimum and ceiling temperatures, varying between developmental stage and cultivar (Struik 2007). Temperature thresholds for growth may have a limited effect on the precision of thermal time, since potato growth is typically above the threshold level (Bonhomme 2000), so the range of base temperatures in the literature may not detract from the usefulness of the measure. Yet it is important to note the base temperature and methodology used to calculate either thermal time or GDD when comparing results within the literature. Furthermore,

Bonhomme (2000) warns against ill-defined uses of thermal time (often where growth measured is undefined) which may result in misleading conclusions. Consequently, whilst both thermal time and GDD can summarize the temperature at which growth occurs across the whole, or part of the, growing season, care must be taken when comparing studies using thermal time between different authors. Additionally, the use of a ceiling temperature in calculating thermal time filters out extreme temperatures and negative effects of high temperatures may be unaccounted for if temperature is only described using thermal time.

Thermal time can also be used to calculate phyllochron, describing the influence of temperature on the rate of leaf appearance. Phyllochron is the interval of time or thermal time between the appearance of successive leaf tips and is the inverse of the rate of leaf appearance (Wilhelm & McMaster 1995). It is widely used to predict leaf appearance in many crops, though was originally developed for describing leaf production in wheat (Streck *et al.* 2007a). Phyllochron is based on the premise that leaf appearance is primarily driven by temperature, although variations in phyllochron have been reported with cultivar, water availability and type of branch or leaf (Firman *et al.* 1995; Davidson *et al.* 2017, 2019). It is more accurate to describe phyllochron as a measure of development, than a measure of temperature, yet it can be useful to describe variation in the rate of leaf appearance whilst accounting for variation in temperature or thermal time. As with thermal time, it can be difficult to compare phyllochrons within the literature due to the variation in base temperatures used.

A final consideration when determining the effect of temperature on crop growth is the original field data collection methodology. Air temperature is most commonly recorded, yet leaf and soil temperature provide data more pertinent to the rate of photosynthesis and tuber growth, respectively, as these measurements will all differ slightly within the same crop. These measurements, however, can be more challenging to collect than air temperature, hence why air temperature is often used as a proxy for the temperature experienced by the whole plant.

In summary, there are challenges to each method of quantifying temperature which are important to consider, both when calculating the temperature descriptors, and when comparing between the different metrics in the literature. As with all summary statistics, each has the potential to mask extreme high or low temperature events, which may have a more significant effect on growth than the small changes to summary temperature descriptors would suggest. Indeed, the selection of time period

over which temperature is summarized may be more important to calculating an informative summary of temperature experienced by the crop during growth than the temperature measure used, as it can allow better links to be made between specific temperature regimes and discrete aspects of growth events. None of the metrics are demonstrably better than the others; mean temperature is useful in simplicity, but potentially oversimplistic, and whilst all three variations of thermal time describe temperature most pertinent to growth, discounting temperatures below which growth does not occur (and above, in the case of thermal time and phyllochron), the range in published base temperatures makes interpretation difficult. Both mean temperature and phyllochron will be used to explore variation in whole canopy growth and leaf appearance in relation to temperature variation between planting dates.

4.1.2 Influence of photoperiod and light intensity on canopy photosynthesis, canopy development and yield

The linear relationship between intercepted light and potato yield, as described by Monteith (1977) and Allen and Scott (1980) provides a useful framework for understanding differences in potato yields (1.2), yet varying light intensity and photoperiods have the potential to alter this relationship. Whilst photosynthetically active radiation (PAR, 400-700 nm) directly indicates light available to a crop for photosynthesis, both total solar radiation and PAR can be measured to quantify crop light availability since the relationship between the two is constant throughout the growing season and 99.9 % of the variation in PAR can be explained by total solar radiation (Khurana & McLaren 1982). PAR accounts for *c.* 50 % of total solar radiation (Khurana & McLaren 1982).

Light intensity affects both biomass production and partitioning between haulm and tubers and, under controlled environmental conditions, a reduction from 67 to 33 % full daylight reduced whole plant biomass by 38 %, yet reduced yield by 80 % due to the relative decrease in tuber production and increase haulm production (Bodlaender 1963). Tibbitts *et al.* (1994) proposed that yield is directly proportional to photons absorbed as similar yields were achieved by plants grown under 800 μmol/m^2/s with 12 hours of light and at 400 μmol/m^2/s in continuous light and Wheeler (2006) also described an increasing rate of photosynthesis with increasing PAR. Yet again, just as in temperature-related experiments, relationships described in growth chamber experiments may not reflect field growth responses as the light intensity of direct sunlight is substantially greater than that generated in growth chamber experiments

(*c.* 2000 μmol/m^2/s compared to 800 μmol/m^2/s) and is also more variable, fluctuating with cloud cover and time of day. Tropical and sub-tropical field experiments indicate that the relationship between light intensity and canopy photosynthesis plateaus under high light intensities, saturating at 400 W/m^2 (equivalent to *c.* 1840 μmol/m^2/s (Sale 1974)), with minimal increases in the rate of canopy photosynthesis once light intensity exceeded *c.* 1000 μmol/m^2/s (half brightness of full sunlight (Midmore 1990)). Likewise, in Idaho, USA, maximum photosynthesis in two cultivars (Russet Burbank and Clone A6948-4) plateaued in both field and glasshouse at *c.* 1350 μmol/m^2/s and *c.* 900 μmol/m^2/s, respectively, with differences likely linked to differences in leaf temperature between experimental settings (Dwelle *et al.* 1981). Similarly, in the UK, a field-based shading experiment reported greater radiation use efficiency (RUE) in shaded than unshaded plots (1 TJ of radiation was converted into *c.* 2.1 t DM/ha and *c.* 1.3 t DM/ha, respectively, (Allison 2007)). Consequently, despite decreasing radiation received by the crop by *c.* 45 %, reductions in total DM and tuber fresh yield were modest under shaded conditions (Allison 2007). Yet the original relationship between total biomass and cumulative radiation described by Monteith (1977) was linear and did not plateau and this has been reported on multiple occasions since (Allen & Scott 1980; Khurana & McLaren 1982; Bangemann *et al.* 2014).

It is possible that the daily difference between maximum radiation and the light saturation point of potato photosynthesis is both masked by variation in maximum photosynthetic rates (due to varying leaf temperatures and plant water availability) and 'lost' as daily radiation values are summed to produce a value of cumulative radiation, resulting in a slightly noisy, but linear relationship between cumulative radiation absorbed and biomass produced. Whilst the relationship between intercepted radiation and biomass produced may be improved by quantifying usable radiation (in accordance with Sale (1974), Midmore (1990) and Alison (2007)), that may be excessively complicated. Indeed Monteith (1977) suggests that, due to limited variation in total insolation across the growing season (± 10 % around the long-term mean), crop ability to intercept light will be more important than radiation intensity and hence that the seasonal distribution of LAI may be more effective at identifying the causes of variation in biomass between crops than the quantified brightness of the season. Consequently, this work will focus on variation in crop ability to intercept light, as measured using percent canopy ground cover (1.3), to test the hypothesis of Monteith (1977).

Detrimental effects were also reported in association with extreme photoperiods in some cultivars; including severe stunting when the photoperiod exceeded 16 h (Tibbitts *et al.* 1994) and 'physiological intolerance' to continuous light, whether at higher (400 μmol/m^2/s PAR) or lower (200 μmol/m^2/s PAR) intensities, with chlorotic and rust-flecked leaves (Wheeler 2006). In five cultivars (Russet Burbank, Norland, Norchip, Superior and Kennebec), HI was greatest under 12/12 h day/night cycle, though Russet Burbank and Norland were also able to grow well and tuberize under continuous light conditions (Wheeler 2006). Whilst ancestral potatoes tuberize under short-day conditions, photoperiodic responses have been selected against in modern cultivars, and tuber initiation in European cultivars is considered to be insensitive to photoperiod under temperate conditions (O'Brien *et al.* 1998). However, tuberization sensitivity to photoperiod varies between cultivars and Wheeler (2006) found that cultivars bred at higher latitudes had a greater tolerance to long-day conditions. However, the responses to extreme photoperiods in the above experiments may not be indicative of changes to the smaller differences in daylength recorded at different planting dates, hence the need to quantify both variation in photoperiod length in the field and the effect on crop growth.

Most of the literature on plant responses to changing light intensities and photoperiods focuses variation in rate of photosynthesis, yet differences in light regime also affect canopy structure, in turn influencing the ability of potatoes to intercept and utilise the available light. Increased stem elongation is associated with increasing photoperiod (Tibbitts *et al.* 1994) and decreasing light intensity (Bodlaender 1963; Lorenzen & Ewing 1992), but it remains unclear how these differences in canopy architecture affect canopy ability to intercept light as canopy cover and LAI were not reported. Within-canopy shading experiments have also shown an increase in stem growth relative to leaf growth (Vos & van der Putten 2001). Vos and van der Putten (2001) also reported a limited effect of 50 % shade on total leaf area, but rapid mainstem leaf senescence at 90 % shade, suggesting that relatively dim conditions have little effect on canopy coverage, despite lower specific leaf weight, and that severe reductions in light intensity are required to alter canopy architecture. When light intensity was reduced across the whole plot total plant mass decreased, due to greater biomass partitioning to the leaves at the expense of the tubers (Menzel 1985). Shade also promoted stem elongation and leaf production, although leaf size was reduced relative to non-shaded treatments (Menzel 1985). Daylength can also influence canopy structure, with greater

axillary branch production reported under long day conditions (18 h at *c.* 460 μmol/m^2/s) and extending daylength with dim lighting (a short 10 h day at *c.* 460 μmol/m^2/s, with 8 additional hours at *c.* 5 μmol/m^2/s) resulted in taller stems, lower leaf biomass and smaller leaves, (Lorenzen & Ewing 1992). Shorter days (11 h) have been associated with reduced duration of leaf production in the field, yet this response varies between cultivars and the duration of leaf production was insensitive to daylength in three of eight cultivars (Kooman *et al.* 1996b). Finally, short-days have also been associated with more rapid senescence in leaf cuttings (where plants were exposed to 5 or 10 short-days prior to cutting removal), though sensitivity to short-days differed between cultivars (McGrady & Ewing 1990). Yet once more, it is unclear from published data to what extent canopy structures will change in response to modest differences in photoperiod and light intensity between planting dates, hence the need to quantify them in the field.

Many of the experiments above directly link changes in radiation and photoperiod to variation in yield, not considering canopy ability to intercept that light. This may indicate that canopy cover is not essential for defining predictive relationships between yield and light availability. However, these experiments were typically carried out under well-watered conditions, where differences in canopy cover may be minimal. When canopy coverage varies between plots or crops, understanding how differences in canopy cover affect differences in light intercepted may be important to identifying differences in yield. Leaf area index has been used by both Bremner and Radley (1966) and Khurana and McLaren (1982) to quantify light intercepted, concluding that an LAI of 3 is the 'minimum necessary' for maximal light interception. At an LAI of 4 canopy cover is complete and *c.* 95 % of solar radiation is intercepted (Khurana & McLaren 1982), whilst the duration of LAI > 3 explained 95 % of the variation in yield across six cultivars (Bremner & Radley 1966). Yet, as discussed above (1.3), LAI is costly to measure and it is hypothesised that duration of complete, or near-complete, canopy cover may provide an alternative, non-destructive measure of maximal light interception which could be used to explain variation in yield.

4.1.3 Variation in crop growth with planting date

The effects of growing season length on canopy development are of agricultural importance due to the linear relationship between intercepted radiation and tuber dry mass (as shown by Khurana and McLaren (1982), which sets 'a clear priority' for potato growers 'to maximize amount of radiation intercepted' (Allen & Scott 1980). Growing

season length is constrained by seasonal variation in environmental conditions, commonly delineated by extremes in temperature which restrict potato growth (He *et al.* 1998; Mori *et al.* 2015). Planting early both lengthens the growing season and enables canopy establishment during the longer days of the season, increasing radiation interception; in the UK approximately half of the radiation receipts between April and October are received in April, May and June (Allen & Scott 1980). However, there are caveats to early planting.

Firstly, the ability of a crop to respond to earlier planting depends on the minimum or base temperature at which that cultivar can grow and produce a canopy, and so the temperature must be sufficiently warm to support growth and utilize the extra days at the beginning of the season. In the UK, early planting can expose the canopy to the risk of frost damage and the advantage of an early planting may be lost through slowed growth and frost damage. For example the earliest February and March plantings in three trials reported by Jones and Allen (1982) suffered frost damage, resulting in similar leaf areas and yields to crops planted two weeks later (Jones & Allen 1982). Mid-April was identified as the critical period for growers to have planted by in the UK (Jones & Allen 1982), with earlier planting providing slight gains whilst planting after this point resulted in yield losses due to shortening of the season and reduced light interception.

The benefits of early planting can also be negated by detrimental precipitation conditions; when planting in the autumn in subtropical China, He *et al.* (1998) found that later planting was optimal as heavy rainfall in August and September significantly reduced seed survival when planted early. Consequently, it can be necessary to delay cultivations and planting to allow soil drying, since cultivating waterlogged soil is also associated with compaction, which can slow emergence, limit canopy development and yield (Stalham *et al.* 2007). Whilst under a rain-fed cropping system, Tang *et al.* (2018) recommended early planting in dry seasons to maximise season length and potential water availability, whilst advocating later planting in wetter seasons to align tuber initiation and bulking with periods of higher precipitation and solar radiation for greater yields, highlighting the necessity of manipulating of planting dates in relation to the meteorological conditions of the farmed area.

Moreover, early planting is only beneficial if cultivars can maintain canopy cover for the extended season, with greater yield responses typically seen in indeterminate cultivars which produce greater total leaf area, enabling a greater potential duration of

tuber bulking, as noted by Bremner and Radley (1966). Cultivars which tuberize early and have a shorter growth cycle (typically more determinate cultivars) are favoured when the growing season is shorter (He *et al.* 1998), whilst indeterminacy is favoured in longer growing seasons to ensure that crop growth continues for the full duration of the available season (Mori *et al.* 2015). Cultivars also vary in RUE (total plant biomass divided by cumulated intercepted radiation, measured using NDVI (Oliveira *et al.* 2016)) and biomass partitioning (Fowler 1992; Allison 2020), modifying the relationship between intercepted radiation and yield, hence, increases in length of growing season will not have the same effect on every cultivar. Indeterminate cultivars typically have a lower mid-season HI (Allison 2020) and partition a higher proportion of biomass to the canopy, hence increased radiation interception may result in greater canopy production rather than increased tuber yield in a more indeterminate cultivar. So, planting date affects both daylength and length of season, determining the amount of radiation the canopy can potentially intercept, although ability to utilize available radiation throughout the extended growing season differs between cultivars, due to differences in canopy size and partitioning, resulting in differing yield responses between cultivars to increased light availability.

Furthermore, manipulating planting date will typically result in changes to seed chronological and physiological age. Delays to planting increase seed age and older seed emerge faster, produce more stems and tuberize earlier (Demagante & van der Zaag 1988). Physiologically older seed also typically have greater sprout development at the point of planting, partially explaining faster rates of emergence (in addition to increased rate of development from warmer temperatures (4.1.1, (Bremner & Radley 1966)). Yet more heavily sprouted seed has also been linked with earlier and more rapid senescence at the end of the season (Allen & Scott 1980). Allen and Scott (1980) suggest that there is an optimum physiological age of seed and optimal planting date to achieve the greatest yield for each cultivar and environment combination. However, most studies in this area have included fewer than five varieties, typically at a single study site and so data on cultivar canopy responses across different environments are incomplete.

A final consideration is that weather can vary considerably on the same calendar date between years, so planting early in one year will not necessarily have the same effect as an early planting in the previous year (Allen 1977). For example, in field experiments, Allen (1977) found that delayed planting reduced plant canopy size and yields in 1973,

but increased plant canopy size (though not yield) in 1974. Differences in environmental conditions, between locations and years, can be accounted for using GDD and thermal time (4.1.1.1), yet as noted by Tang *et al.* (2018), current limitations in weather forecasting prevent growers from adjusting planting dates to account for weather conditions in the upcoming season.

4.1.4 Effects of nitrogen on canopy development

Rate of applied nitrogen influences most elements of canopy growth including leaf expansion rate and branch production, and these changes to individual canopy components determine the effect of nitrogen on whole canopy form and function as shown below. However, determining the effects of applied nitrogen is complicated by variation in soil nitrogen prior to fertilizer application, differences in nitrate leaching between soil types and irrigation regimes (Woli & Hoogenboom 2018), rate of mineralisation of organic matter within the season (Vos 2009) and the microbial community within the soil. Consequently plants often have access to more nitrogen than the amount applied during the experiment, complicating estimation of crop nitrogen requirement (MacKerron *et al.* 1995), though explaining some of the variation in results between nitrogen response experiments. The effects of applied nitrogen on canopy growth, from leaf expansion to total LAI, are described below.

On the individual leaf scale, faster leaf expansion at higher rates of applied nitrogen has been found in both field (Firman 1987) and glasshouse (Biemond & Vos 1992; Vos & van der Putten 1998) experiments, resulting in a greater final leaf length (Firman 1987) and area (Vos & Biemond 1992). Maximum leaf area is not solely limited by nitrogen availability since doubling applied nitrogen from 80 to 160 g N/pot made no difference in the final area of mainstem leaves or sympodial branch leaves (described by Vos and Biemond (1992) as first order apical lateral branches). Yet, leaves were slightly larger at the higher nitrogen rate on branches produced by the sympodial branches (second and third order apical branches, (Vos & Biemond 1992)), suggesting that increasing nitrogen promotes a higher degree of branching with greater differences in leaf area found where a higher degree of branching has occurred.

In contrast, rate of applied nitrogen has been found not to affect the number of leaves on the mainstem, before the first flower (Vos & Biemond 1992; Firman *et al.* 1995) or the rate of leaf appearance (number of new leaves, greater than 10 mm in length from insertion point to tip, produced per day) on the mainstem in pot-grown potatoes,

varying little from the average rate of 0.5 leaves/day (Vos & Biemond 1992; Vos & van der Putten 1998). Yet, response of leaf appearance to increased nitrogen was more variable in the field, showing no effect of N in one experiment, but slower leaf appearance at 0 N in another experiment with the same cultivars (Firman *et al.* 1995), whilst in a previous series of experiments Firman (1987) found that rate of leaf appearance tended to be faster at higher rates of nitrogen. Additionally, both duration of leaf production and number of main axis leaves was greater (by *c.* 30 days (Millard & MacKerron 1986), and *c.* 4 leaves (Firman *et al.* 1999), respectively) at high nitrogen than without additional nitrogen.

Branch production is also promoted under high nitrogen resulting in a larger total leaf area in both glasshouse (Vos & van der Putten 2001) and field grown (Oliveira 2000) potatoes. The size of individual branches is also strongly influenced by nitrogen availability, with larger branches produced at high nitrogen (Firman 1987). Increased branch leaf production is associated with faster canopy expansion, and allows the canopy to achieve maximum ground cover more rapidly (Ospina *et al.* 2014). Furthermore, the increased number of branches within the canopy appear to act as a nitrogen store and nitrogen is remobilised from lower leaves and branches as they senesce, allowing continued branch production at the top of the canopy towards the end of the season when nitrogen uptake from the soil has slowed (Millard & MacKerron 1986).

At the whole canopy level, total LAI is greater at high nitrogen (Firman 1987; Allen & Scott 2001) due to increases in axillary and sympodial branch leaf production (Biemond & Vos 1992). Lack of nitrogen can limit maximum canopy cover and stem length in Maris Piper, preventing canopy closure between the rows (MacKerron & Davies 1986), whilst Millard and MacKerron (1986) found that maximum canopy cover was limited to approximately 85 % GC when no additional nitrogen was applied. Yet, Li *et al.* (2016) found that extreme application of nitrogen was detrimental to leaf production and maintenance in a pot-based experiment and total leaf area was found to be greatest at sufficient rather than the highest rate of nitrogen application (171 kg N/ha was considered excessive).

Increased integrated ground cover (IGC) at high nitrogen partially explained by a longer duration of complete canopy cover in response to high nitrogen (MacKerron & Davies 1986; Firman 1987; Vos 2009; Ospina *et al.* 2014), increasing integrated ground cover (Ospina *et al.* 2014) and enables greater light interception (Vos 2009). This

increased duration of canopy cover extends the growing season and is the mechanism by which nitrogen has a positive effect on yield (Clutterbuck & Simpson 1978; Harris 1992), increasing net photosynthesis throughout the season and providing more resources for tuber bulking (Li *et al.* 2016). Yet, linear increases in nitrogen availability resulted in non-linear increases in canopy size, intercepted radiation (Harris 1992; Zhou *et al.* 2016) and tuber yield (Vos 1997), suggesting a reduction in the additive benefit of additional nitrogen to canopy size and light interception as rate of applied nitrogen increases.

Moreover, high nitrogen rates can delay the onset of canopy senescence (Millard & MacKerron 1986; Ospina *et al.* 2014), due to the progressive nature of senescence within large potato canopies growing at high nitrogen; whilst leaves lower within the canopy senesce, leaf production at the top of the canopy continues, maintaining complete canopy cover. Millard and MacKerron (1986) reported that, without additional nitrogen, leaf production finished 38 days after emergence (DAE) and canopy mass remained constant until 80 DAE. Whilst at 250 kg additional N/ha canopy biomass increased until 54 DAE and continuing leaf production prevented net loss of canopy mass until 68 DAE, at which point leaf production ceased and haulm dry matter decreased (Millard & MacKerron 1986). Ospina *et al.* (2014), and MacKerron and Davies (1986) reported respectively that the duration of senescence (measured between maximum and minimum ground cover) was shorter and that reductions in LAI were faster at higher rates of nitrogen than low or no additional nitrogen in the field. Loss of green leaf area per plant in the glasshouse was also most rapid at the higher nitrogen treatments (Vos & Biemond 1992). Hence, high rates of nitrogen are associated with delayed, but faster senescence.

4.1.4.1 Effects of nitrogen on photosynthesis

Leaf nitrogen content is a better predictor of the maximum rate of photosynthesis (P_{max}) in potato leaves than rate of applied nitrogen (Marshall & Vos 1991; Vos & van der Putten 2001) and similar P_{max} values were reported between 0–180 kg applied N/ha (Firman & Allen 1988). Firman and Allen (1988) also suggested that there is typically sufficient nitrogen within arable soils prior to fertilizer application to prevent applied nitrogen availability limiting photosynthesis, akin to the findings of Gregory *et al.* (Gregory *et al.* 1981) in winter wheat. Whilst high rates of applied nitrogen have been associated with higher concentrations of leaf nitrogen (Marshall & Vos 1991), the main effects of nitrogen on potato photosynthesis result from structural changes to the

canopy. More specifically, leaf area, rather than photosynthetic rate, is systematically increased by applied nitrogen (Vos & van der Putten 1998), increasing whole plant photosynthesis. Although, increased branching increases shade within the lower canopy, speeding up senesence of shaded leaves, reducing both leaf nitrogen and photosynthetic rate (Firman & Allen 1988; Vos & van der Putten 2001), there is a net increase in plant photosynthesis. Potato also responds to limited nitrogen availabilty by reducing whole plant leaf area as opposed to down-regulating the photosynthetic machinery within the leaf (Vos 2009).

4.1.4.2 Differences in nitrogen response between cultivars

Canopy and tuber growth responses to additional nitrogen availability vary between individual cultivars (Harris 1992; Firman *et al.* 1995; Bangemann *et al.* 2014; Cohan *et al.* 2018), moreover this variation has been linked to determinacy levels (Fowler 1992, 1993, 1994; Firman *et al.* 1995; Tiemens-Hulscher *et al.* 2014; Ospina *et al.* 2014). Whilst cultivars are commonly described with respect to maturity in the literature, here, equivalent determinacy levels are used (1.1). There are inherent differences in canopy growth between determinacy levels and determinate cultivars cease leaf production earlier than indeterminate cultivars and also tend to produce fewer axillary branches (Biemond & Vos 1992) with smaller canopies (Firman *et al.* 1995) at similar levels of nitrogen.

High rates of nitrogen result in greater dry matter partitioning to the haulm early in the season (Saluzzo *et al.* 1999), slowing early tuber growth (Dyson & Watson 1971; Saluzzo *et al.* 1999), but increasing the rate of canopy expansion in indeterminate cultivars (Tiemens-Hulscher *et al.* 2014; Ospina *et al.* 2014). Fowler (1993) found that relatively modest applications of nitrogen resulted in considerable increase in LAI in the indeterminate cultivar Cara, whilst large applications of nitrogen had a comparatively small effect on the LAI of determinate Estima. Despite a smaller increase in determinate cultivar LAI, the effect of nitrogen on canopy persistence were much greater in Estima than in Cara since Estima typically did not achieve complete ground cover without applied N whilst indeterminate Cara maintained complete ground cover for *c.* 50 days at 0 kg applied N/ha (Fowler 1994). Similarly, Tiemens-Hulscher *et al.* (2014) reported greater increases in maximum ground cover to additional nitrogen in determinate, than indeterminate, cultivars, due to lower maximum canopy cover of determinate cultivars without applied nitrogen. Yet little difference in nitrogen response was found between determinacy levels by Ospina *et al.*

(2014), as the indeterminate cultivars typically did not achieve 100 % GC without applied nitrogen enabling them to benefit from additional nitrogen with increased maximum ground cover, light interception and yield in a similar way to the determinate cultivars in the study.

Additionally, seasonal light interception only increased with increases in nitrogen rate up to 60 kg N/ha in indeterminate Cara, but up to 120 kg N/ha in determinate Estima (Fowler 1993), despite a greater increase in dry matter partitioning to the haulm in Cara than Estima (Fowler 1992). Despite producing a smaller canopy with fewer branches (Firman *et al.* 1995), more determinate cultivars tended to show a greater increase in intercepted radiation and yield in response to applied nitrogen (Firman *et al.* 1999). Yet this interaction between cultivar and nitrogen rate is dependent upon season length; both Ospina *et al.* (2014) and Tiemens-Hulscher *et al.* (2014) reported a greater increase in canopy duration, light interception and yield in response to additional nitrogen in indeterminate than determinate cultivars in a long growing season when canopies were able to reach the end of their 'natural lifespan' (Ospina *et al.* 2014), whilst determinate cultivars showed the greatest yield response to additional nitrogen in a short season (Tiemens-Hulscher *et al.* 2014). Similarly, when length of growing season was unlimited, Saluzzo *et al.* (1999) also found no interaction of cultivar and nitrogen rate on final yield as high nitrogen investment in the canopy enabled tuber growth of the more indeterminate cultivar to continue for 20 days longer than the more determinate cultivars. Consequently, the interaction between determinacy and nitrogen rate, in terms of both canopy production and yield, must be investigated in relation to growing season length.

4.1.5 Chapter aims

The majority of the literature considering the effects of planting date, temperature and radiation has focused on yield outcome, rather than documenting changes to the canopy which might be influencing those differences in yield. This chapter tests the overall thesis hypothesis in relation to varying planting date and nitrogen rate; that understanding variation in canopy growth in contrasting cultivars, following different planting dates and at different nitrogen rates will provide greater insight into yield variability, than considering the effects of the above treatments upon yield directly. Consequently, this chapter will quantify variation in canopy growth and maintenance in relation to differences in applied nitrogen, planting date and cultivar, along with differences in temperature and light regime associated with planting date, thus

addressing thesis aim two (1.4). Differences in canopy architecture, including branch production and LAI, will also be recorded and the extent to which they can explain variation in whole canopy growth will be considered in accordance with thesis aim three (1.4). Once it is understood how the patterns of leaf production and branching change in response to varying temperature and nitrogen application in the field, it will be possible to better model crop canopy growth and structure, and therefore to better estimate light interception, and ultimately predict yield, addressing thesis aim four (1.4). Below, specific gaps within the literature are highlighted and subsequent aims for the planting date experiments are set out.

4.1.5.1 Temperature associated aims

Significant changes to canopy morphology and development have been reported in relation to differences in temperature in growth chamber experiments (4.1.1), yet it remains unclear how less extreme differences in mean temperature, generated by varying planting date, will influence canopy growth in field grown crops. Similarly, many previous experiments have increased temperature for the full duration of crop growth and so reported changes in canopy structure may differ from those resulting from transient increases temperature due to the shift in timing of crop development associated with changing planting date. Additionally, few experiments have linked temperature-related changes to canopy structure and leaf appearance, to changes in whole canopy growth (and canopy ability to intercept light), hence both will be measured to quantify the variation in leaf appearance rate which can explain differences in canopy expansion in relation to temperature.

1. To quantify differences in mean temperature, and subsequent variation in canopy growth at each stage of canopy development, between the planting date treatments, linking to thesis aim two.
2. To quantify the extent to which differences in leaf appearance, canopy expansion and other canopy descriptors can be explained by differences in temperature and determine if within-canopy differences can explain variation in whole canopy growth, addressing thesis aim three.

4.1.5.2 Light associated aims

Across the literature a range of approaches, varying in complexity, have been used to describe biomass production and tuber yield, in relation to available or intercepted light (4.1.2), with both more and less complex methods able to explain a similarly high proportion of yield variation. The suitability of a simple approach, using percent

ground cover to quantify canopy ability to intercept light, similar to the LAI quantification methods of Bremner and Radley (1966) will be examined, testing the hypothesis of Monteith (1977) that yield is dependent upon canopy ability to intercept radiation, as opposed to the incident radiation in a given season.

Additionally, the literature considering the effect of photoperiod predominantly compares the effects of highly contrasting photoperiods, generated in a growth chamber or by comparing crops grown in different locations. It is uncertain what the effect of more modest differences in light availability, due to variation in planting date, at different stages of canopy development would have on canopy structure and growth.

3. To assess the extent to which variation in percent ground cover throughout the season accounts for variation in yield.
4. To quantify the differences in mean daylength between planting dates at emergence, during canopy expansion, complete ground cover and the onset of senescence and identify any effects on canopy development of these differences in photoperiod, linking to thesis aim two and four.

4.1.5.3 Planting date associated aims

Literature concerning the effect of planting date on potato growth predominantly focuses on variation in the final yield (4.1.3), but quantifying changes in canopy development can grant greater insight into the mechanism by which those yield differences occur. Hence, this work will quantify how differences in season length, resulting from variation in planting dates, affect canopy growth, maintenance, and senescence.

Secondly, for UK grown crops, mid-April has been suggested as the crucial time to plant by, yet optimal planting date has been shown to vary with cultivar (Bremner & Radley 1966), which may be linked to differences in determinacy. If so, this would allow differences in optimal planting date to be generalised from experimental results of individual cultivars, aiding development of future canopy models.

5. To identify variation in canopy growth unexplained by variation in temperature and light regimes (quantified following chapter aims two and four), addressing thesis aim two.

6. To quantify the canopy growth responses of cultivars of contrasting determinacy to delay in planting and reduced growing season length, addressing thesis aim four.

4.1.5.4 Nitrogen rate associated aims

Whilst changes in canopy development in response to additional nitrogen have been widely reported (4.1.4), it is less clear how these general findings apply to cultivars in different determinacy groups. Consequently, this work aims to quantify how a higher rate of nitrogen affects leaf appearance, canopy branching, distribution of LAI within the canopy and whole canopy ground cover throughout the season in two cultivars of contrasting determinacy. Moreover, since one of the effects of nitrogen is to extend canopy duration, variation in both canopy longevity and yield in response to additional nitrogen must be considered in relation to season length and planting date, also considering cultivar determinacy which further affects canopy longevity.

7. To quantify differences in leaf appearance rate and main axis leaf number between cultivars of contrasting determinacy in response to applied nitrogen, linking to thesis aims three and four.
8. To quantify variation in branch production in relation to cultivar determinacy and applied nitrogen, again linking to thesis aims three and four.
9. To quantify increases in LAI, in cultivars of contrasting determinacy, to applied nitrogen and describe the effects on LAI in relation to yield and biomass partitioning, further addressing thesis aims three and four.
10. To investigate the effect of additional nitrogen on canopy longevity and the onset of senescence with regard to season length, cultivar determinacy and yield, addressing thesis aims two and four.

4.1.6 Chapter structure

This chapter focuses on the planting date experiments (Expts 1 and 3) where planting date was staggered in order to expose the plots to different meteorological conditions at each stage of development within the same growing season. Two different nitrogen rates were applied to quantify differences in canopy growth responses in cultivars of differing determinacy to nitrogen application and to better understand the interaction between length of growing season and nitrogen application on canopy growth and maintenance. After a brief methods section (4.2) the results are presented in detail from, firstly, in season measurements relating to emergence (4.3.1), percentage ground

cover (4.3.3) and leaf appearance (4.3.4). Then secondly, data from the mid-season harvests, concerning leaf area index (4.3.5) and branch production (4.3.6), are reported. Thirdly, end of season yield data is briefly shown (4.3.7), maintaining the focus of this work on the effects of planting date on the canopy. The chapter finishes with a discussion (4.4), considering the key points highlighted throughout the results section and the links between the different aspects of canopy growth measured are considered and set in the context of the wider literature, illustrating how potential canopy growth is determined by cultivar, then promoted by additional nitrogen and moderated by planting date, which determines season length.

4.2 Methods

Full details of methodology common to both Planting Date and Planting Density experiments are detailed in general methods (3), below are details specific to the Planting Date experiments.

4.2.1 Experimental details

4.2.1.1 Experimental design

Experiment 1 (Expt 1) was sown in 2016 and treatments consisted of all combinations of three planting dates (13 April, 16 May and 16 June), two contrasting cultivars (determinate Estima and indeterminate Maris Piper) and two nitrogen rates (0 and 250 kg N/ha) within a split-plot design with planting dates as main plots. Each subplot consisted of four rows. There were four replicates. Experiment 3 (Expt 3) was sown in 2017 according to the same design as Expt 1 but planting date treatments were earlier; on 29 March, 24 April, and 24 May.

4.2.1.2 Seed

Unsprouted, 40-50 mm seed was planted.

4.2.1.3 Planting

Seed was planted at 30 cm intervals in 6.6 m long plots. Nitrogen fertilizer (ammonium nitrate, 34.5 % N) was applied by hand following planting to individual plots as per the experimental design.

4.2.1.4 Irrigation

In Expt 1 plots were irrigated by in-plot sprinklers with each planting date receiving irrigation according to the demands of canopies at different stages of development as

determined by best practice (Stalham & Allen 2004). In Expt 3 irrigation was carried out by boom with each planting date again irrigated according to requirements.

4.2.2 In-season measurements

4.2.2.1 Emergence counts

In Expt 3 the date of emergence of individual plants tagged for recording leaf appearance was also recorded.

4.2.2.2 Ground cover

Canopy ground cover (GC) was measured at two locations within each plot for within-plot replication and the canopy quantification (CQ, Figure 3) curve was fitted to the mean GC values of the two replicates. The grid was 75 x 60 cm, consisting of 100 equal-sized rectangles, measuring GC for two plants within the same ridge. The CQ programme fitted a curve to mean GC values from each plot in all but two cases (one Maris Piper, one Estima) in Expt 1, then, curves were fitted to the separate replicates, then the calculated variates were averaged to produce a single canopy descriptor for each plot. Curves were fitted to mean GC plot values in all plots in Expt 3.

4.2.2.3 Leaf appearance

There were some discrepancies in the leaf count in Expt 1. In some plots the juvenile leaves at the base of the plant were excluded from the total leaf count as they had senesced when the whole stem was recounted mid-season to confirm the accuracy of the leaf tagging at top.

4.2.2.4 Harvest

A harvest area of 0.9 x 1.5 m was dug per harvest, per plot, comprising of six plants. Three mid-season harvests were carried out in both Expts 1 and 3 with a final harvest at the end of the season. In Expt 1 the first occurred at approximately 50 % GC (H1), the second at canopy closure (first measure of 100 % GC, H2) and the third at the start of canopy decline (approximately 95 % GC during decline, H3). In Expt 3 harvests 2 and 3 were repeated and H1 was replaced with a mid-senescence harvest at approximately 50 % GC (H4); see Table 7 for calendar dates of each harvest. Due to earlier senescence, Estima plots were harvested before the Maris Piper plots at final harvest for Expt 1 and H4 in Expt 3.

4.2.2.5 Leaf area index

Leaf area index was measured at each of the destructive harvests.

4.2.2.6 Branch production

The percentages of stems with a minimum of one axillary branch, and percentage of stems with a sympodial branch were calculated at each destructive, mid-season harvest and treatment means were compared using Fisher's exact test and the Fisher multiway comparison directive in R for Post Hoc analysis.

4.2.2.7 Harvest index

Tuber dry yield was divided by total dry biomass at harvest to obtain harvest index (HI) (Mackerron & Heilbronn 1985).

4.2.2.8 Daylength calculations

Daylength data for Cambridge was downloaded for each experiment from *https://www.timeanddate.com/sun* and daylength (h) at different points of the growing season, relative to canopy development, was calculated for each plot, then analysed using the Genstat 'ANOVA' directory. The daylength variates were as follows; daylength at emergence (dLengthEM), and the onset of senescence (dLengthSen), and mean daylength during mid-canopy expansion (dLength2575) and near-complete canopy cover (dLength90).

4.2.3 Statistical analysis

Multiple linear regression (Faraway 2016) was used to quantify the variation in whole canopy growth variates (GC variates, as described in Table 2), meteorological variables and canopy components, and was carried out in R. A minimal model, lm(GC variate ~ explanatory variable + block/main plot), was fitted to determine the proportion of variation, as measured by adjusted R^2, in the GC variate explained by either the meteorological factor or canopy component (the explanatory variables) alone, whilst accounting for within-field variation with the 'block/main plot' term. The model was extended to include a 'year' term, representing variation between experiments carried out in different years, a common feature of field trials due to the wide range of uncontrolled factors which vary between experimental years including seed age, weather and soil quality (including soil structure, clay content, field operations); lm(GC variate ~ explanatory variable + year + block/main plot). Finally, effect of experimental treatments on the GC variate were assessed, determining significance using the 'Anova' command with type II sum of squares (from the 'car' package (Fox & Weisberg 2019)) and, even if not significant, the 'block/main plot' term was retained in the model, accounting for experimental structure (Faraway 2016).

Table 7. Planting and harvest details for experiments 1 (2016) and 3 (2017). (E) and (MP) indicate cultivars Estima and Maris Piper when harvested on different dates.

Expt	Planting date	Harvest number				
		1	2	3	4	5
1	13 April	15 June	27 June	8 August	n/a	28 September (E) 11 October (MP)
	16 May	29 June	13 July	24 August	n/a	3 October (E) 12 October (MP)
	16 June	1 August	12 August	14 September	n/a	14 October
3	29 March	n/a	5 July	7 August	8 September (E) 26 September (MP)	16 October
	24 April	n/a	17 July	21 August	19 September (E) 9 October (MP)	20 October
	24 May	n/a	1 August	22 August	22 September (E) 12 October (MP)	23 October

4.3 Results

4.3.1 Emergence

The interval between planting and emergence (EmDAP) decreased with delay in planting in both years (Figure 7, $P < 0.001$). Average soil temperature between planting and emergence increased with delay in planting in both experiments (Table 8) and there was a strong negative correlation between soil temperature and EmDAP (Figure 8). Low variability (of both EmDAP and soil temperature) within planting dates meant that assumptions of normality were not met, so linear regression was not carried out. Sprouting in the seed for the later planting dates was prevented by cold storage, consequently reductions in EmDAP were due to increasing soil temperature not increasing physiological seed age. There was no significant difference in EmDAP between the nitrogen treatments or cultivars. The effects of all treatments and their interactions on emergence are reported in Appendix 4.

Table 8. Dates of planting and mean emergence, with mean soil temperature (°C, S.E in table, 6 D.F.) between planting and emergence for each planting date treatment in Expts 1 and 3.

Expt	Planting date	Emergence date	Soil temperature	S.E.
1 (2016)	13 April	21 May	11.0	0.0059
	16 May	14 June	14.5	
	16 June	10 July	17.3	
3 (2017)	29 March	18 May	11.6	0.0591
	24 April	31 May	13.7	
	24 May	19 June	17.9	

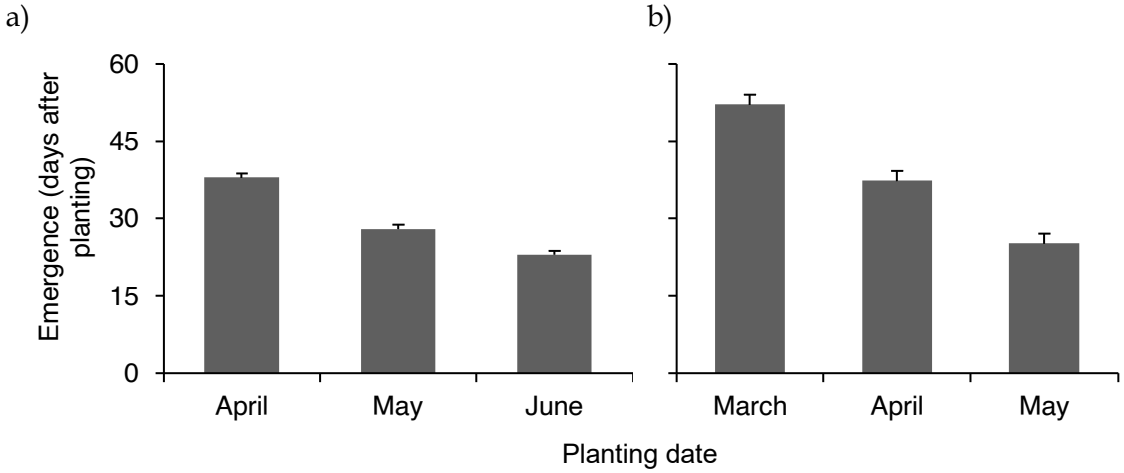

Figure 7. Effect of planting date on interval between planting and emergence in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (6 D.F.). Data presented are means of cultivars and nitrogen treatments.

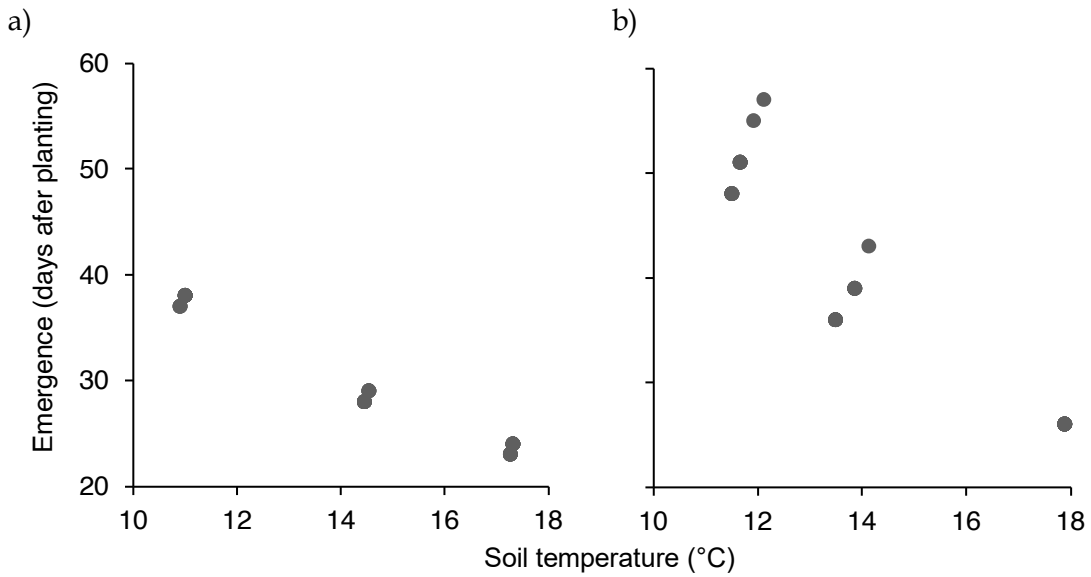

Figure 8. Relationship between interval from planting to emergence (EmDAP) and average soil temperature during that time period in (a) Expt 1 and (b) Expt 3

4.3.1.1 Key points: Emergence

- Duration between planting and emergence decreased with delay in planting.
- Decreases in duration were associated with increasing soil temperatures.

4.3.2 Number of stems

The number of stems produced by individual plants was counted within the first month after emergence and more than double the number of stems was produced in Expt 1 than Expt 3 (5.4 and 2.6 respectively, Figure 9). Maris Piper produced more than twice the number of stems of Estima (7.5 and 3.2, respectively, $P < 0.001$) in Expt 1 (Figure 9a). More stems were produced at the later planting dates (5.8 in May and June plantings, compared to 4.5 in April, $P = 0.007$, Figure 9a). There was an interaction between cultivar and planting date in Expt 3 ($P = 0.027$), not seen in Expt 1, and Estima produced the greatest number of stems in the March planting, whilst Maris Piper produced the greatest number of stems in the April and May plantings, though in each cultivar the difference was less than one stem. There were no significant differences in the number of stems produced between planting dates or cultivars in Expt 3 (Figure 9b). Nitrogen had no effect on number of stems produced per plant in either experiment. The effects of all treatments and their interactions on number of stems are reported in Appendix 4 with treatment means.

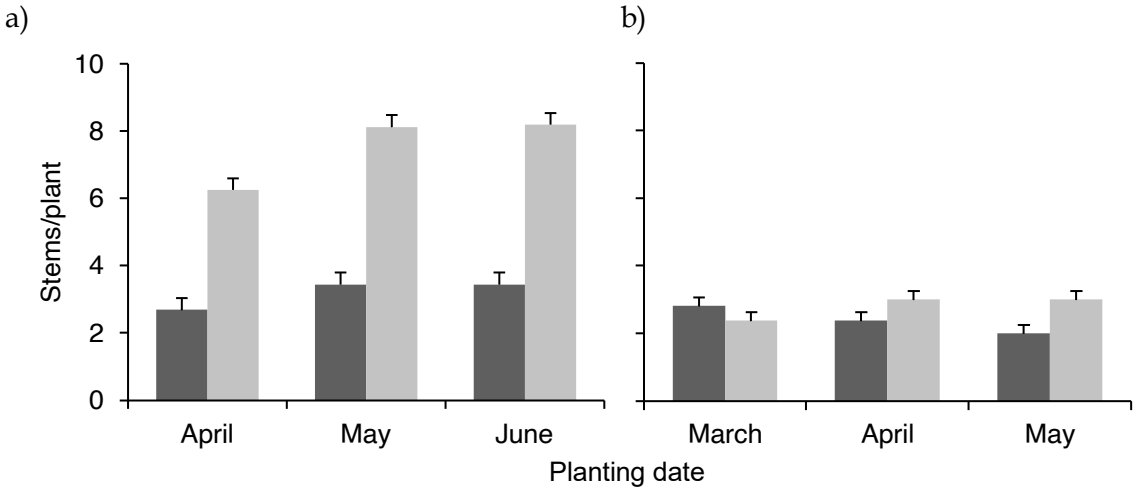

Figure 9. Effect of planting date and cultivar on average number of stems per plant in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (27.2 D.F. (a), 18.14 D.F. (b)). Data presented are a mean of nitrogen treatments.

Number of stems per plant was also recorded at the final harvest but the early stem count data were used in subsequent analyses (despite a lower number of plants sampled than in the final harvest stem count) as the count was carried out on the plants used for the leaf appearance measurements. Using data from the same individual plants together where possible should reduce noise from between-plant variation.

4.3.2.1 Key points: Number of stems

- More than double the number of stems were produced in Expt 1 than Expt 3.
- Maris Piper produced more than double the number of stems than Estima in Expt 1 but there was no difference between cultivars in Expt 3.

4.3.3 Ground cover growth patterns

Percentage ground cover (GC) was measured throughout the season and the canopy quantification (CQ) model fitted a curve to the raw data, describing canopy growth throughout the season in relation to the interval after emergence (4.3.3.1). Descriptive variates were then calculated from the curve as described above (2.3.2). The months of planting differed between Expt 1 and Expt 3 to extend the range of conditions over which data was collected, though April and May planting dates were common to both experiments. The effects of all treatments and their interactions on GC variates are reported in Appendix 5.

4.3.3.1 Season overview

Treatment means were calculated from raw GC values, the CQ curve was fitted to the treatment mean GC data (4.2.2.2) and goodness of fit was determined using both Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC). The

curves show the effect of each treatment on canopy growth across the whole season, beyond the point of final harvest. Interactions between all treatment combinations are in Appendix 6.

Ground cover curves for each planting date were plotted against days after emergence (DAE) to enable direct comparison of canopy development between the planting dates (Figure 10). In Expt 1, early canopy growth was delayed in the April planting relative to the May and June plantings which showed very similar patterns of canopy expansion (Figure 10a). Maximum ground cover was maintained for a similar duration in each planting date, though occurred later in the April than the May and June plantings (Figure 10a). The rate of senescence was fastest in the June planting, with similar rates of senescence in the April and May plantings, though senescence occurred relatively late in the season in the April planting (Figure 10a). In Expt 3, early planting in March resulted in slower canopy expansion than at all other planting dates, which expanded at a similar rate (Figure 10). Both March and April plantings reached 100 % GC in Expt 3, but the May planting did not and began to senesce *c.* 15 DAE before the other plantings (Figure 10b). The March and April plantings began to senesce the same duration of time after emergence (*c.* 95 DAE), the March planting maintaining complete GC for a shorter duration due to slower expansion, and the April planting senesced at a faster rate than the March planting (Figure 10b). Treatment means were well represented by the CQ curves as shown by Willmott's index of agreement (≥ 0.996) and RMSE (< 4.1 % GC) across both experiments and planting dates (Table 9).

Date of harvest, or mean harvest date when Estima and Maris Piper were harvested on separate occasions, was earlier relative to emergence in Expt 1 than Expt 3, and this varied between planting date treatments (Figure 10).

Canopy curves with respect to planting date were also plotted against ordinal date (Figure 13, 4.3.3.2), illustrating how the pattern of ground cover expansion and maintenance changed in relation to time and light regime.

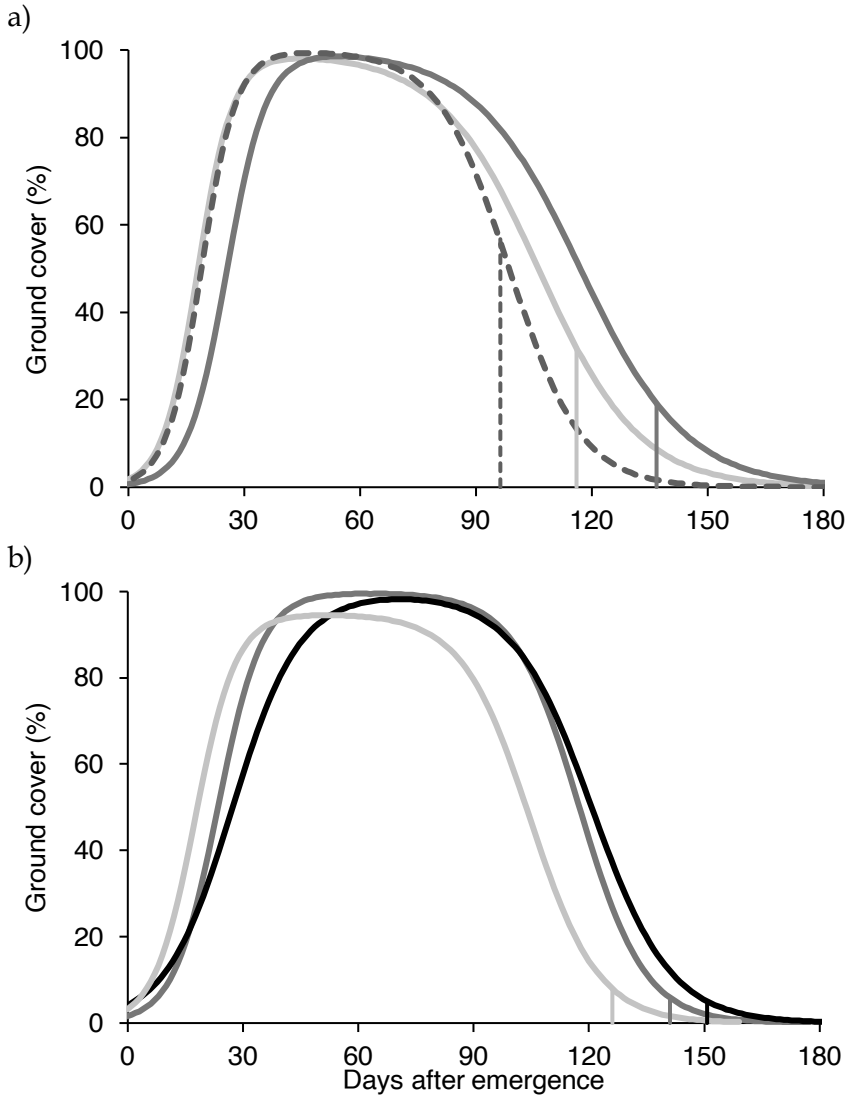

Figure 10. Average ground cover curve by planting date, plotted against days after emergence, (a) Expt 1 and (b) Expt 3. March, ——; April, ——; May, ——; June, - - - . Date of harvest indicated by vertical line in colour of planting date treatment. Data presented are means of cultivar and nitrogen rate treatments. Goodness of fit for each curve is shown in Table 9.

Table 9. Goodness of fit scores for planting date treatment means in Expts 1 and 3. Goodness of fit measured using Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC).

		Goodness of fit score	
Expt	Cultivar	*d*	RMSE
1	April	0.996	4.07
	May	0.996	3.96
	June	0.999	1.79
3	March	0.999	2.28
	April	0.999	2.56
	May	1.000	1.57

Early season canopy growth was very similar between cultivars, but there were differences in canopy maintenance in both experiments (Figure 11). The average Estima canopy did not achieve 100 % GC in either experiment, but the difference

between maximum canopy extent of Estima and Maris Piper was greater in Expt 1 than in Expt 3. Similarly, duration of maximal canopy cover was greater in Maris Piper than Estima in both experiments, but the difference was greatest in Expt 1 (Figure 11a). There was little difference between cultivars in rate of canopy senescence in either experiment (Figure 11). Again, treatment means were well represented by the CQ curves as shown by Willmott's index of agreement ≥ 0.995 and RMSE < 4.3 % GC across both experiments and cultivars (Table 10).

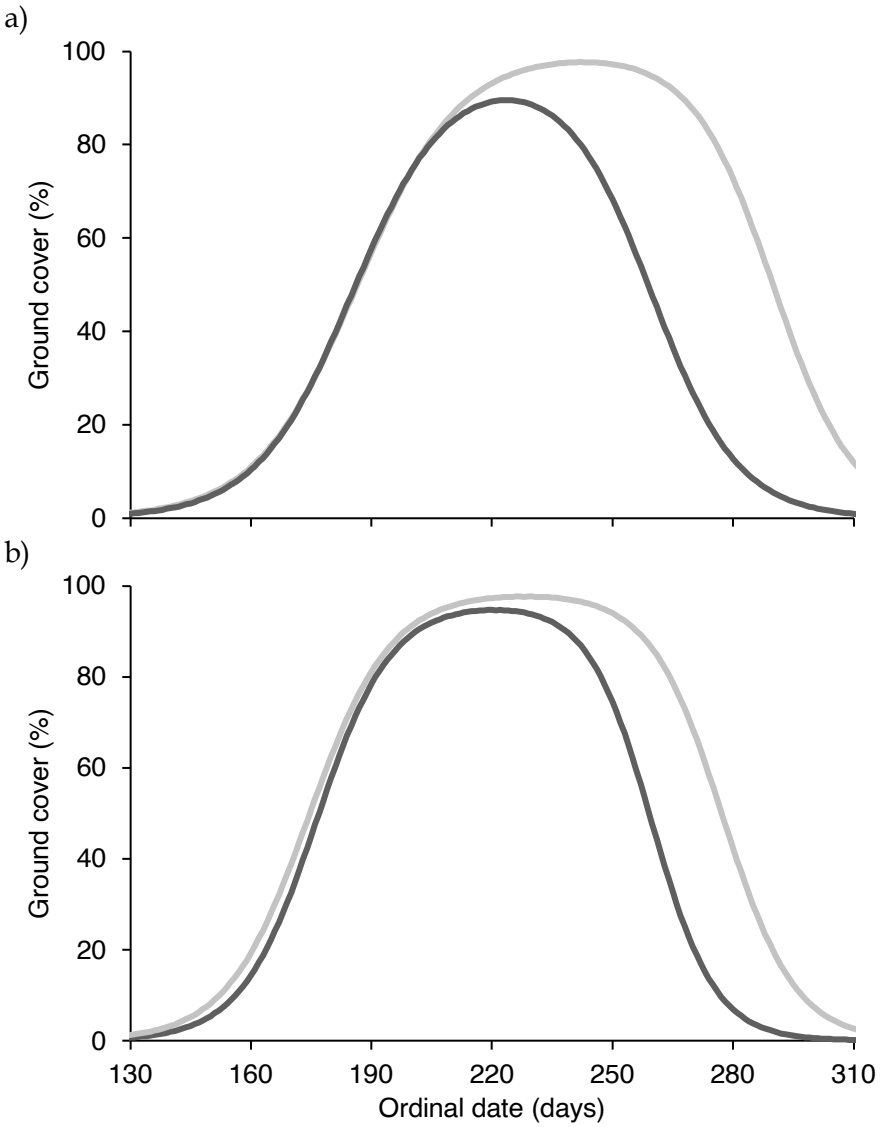

Figure 11. Average ground cover curve by cultivar, (a) Expt 1 and (b) Expt 3. Estima, ——; Maris Piper, ——. Data presented are means of planting date and nitrogen rate treatments. Goodness of fit for each curve is shown in Table 10.

Table 10. Goodness of fit scores for cultivar treatment means in Expts 1 and 3. Goodness of fit measured using Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC).

		Goodness of fit score	
Expt	Cultivar	*d*	RMSE
1	Estima	0.995	4.29
	Maris Piper	0.998	3.37
3	Estima	0.998	3.21
	Maris Piper	0.996	4.11

There was little difference in the pattern of ground cover development between the 0 and 250 kg N/ha treatment means in either experiment (Figure 12). Plots with high nitrogen availability typically produced canopies which expanded marginally faster, achieved a greater maximum GC, maintained it for longer and senesced faster than plots grown without additional nitrogen. The difference between nitrogen treatments was slightly greater in Expt 3 than Expt 1, but differences were still limited. High levels of available nitrogen in the soil may have diminished the differences in canopy growth throughout the season between 0 and 250 kg N/ha treatments. Small differences were also seen between nitrogen rates within cultivars (Appendix 7), suggesting that the small differences between nitrogen treatments are not an artefact of averaging the canopy data of contrasting cultivars, Estima and Maris Piper, together. The CQ curves represented the nitrogen treatment means well as shown by Willmott's index of agreement (≥ 0.995) and RMSE (< 4.3 % GC) across both experiments and nitrogen rates (Table 11).

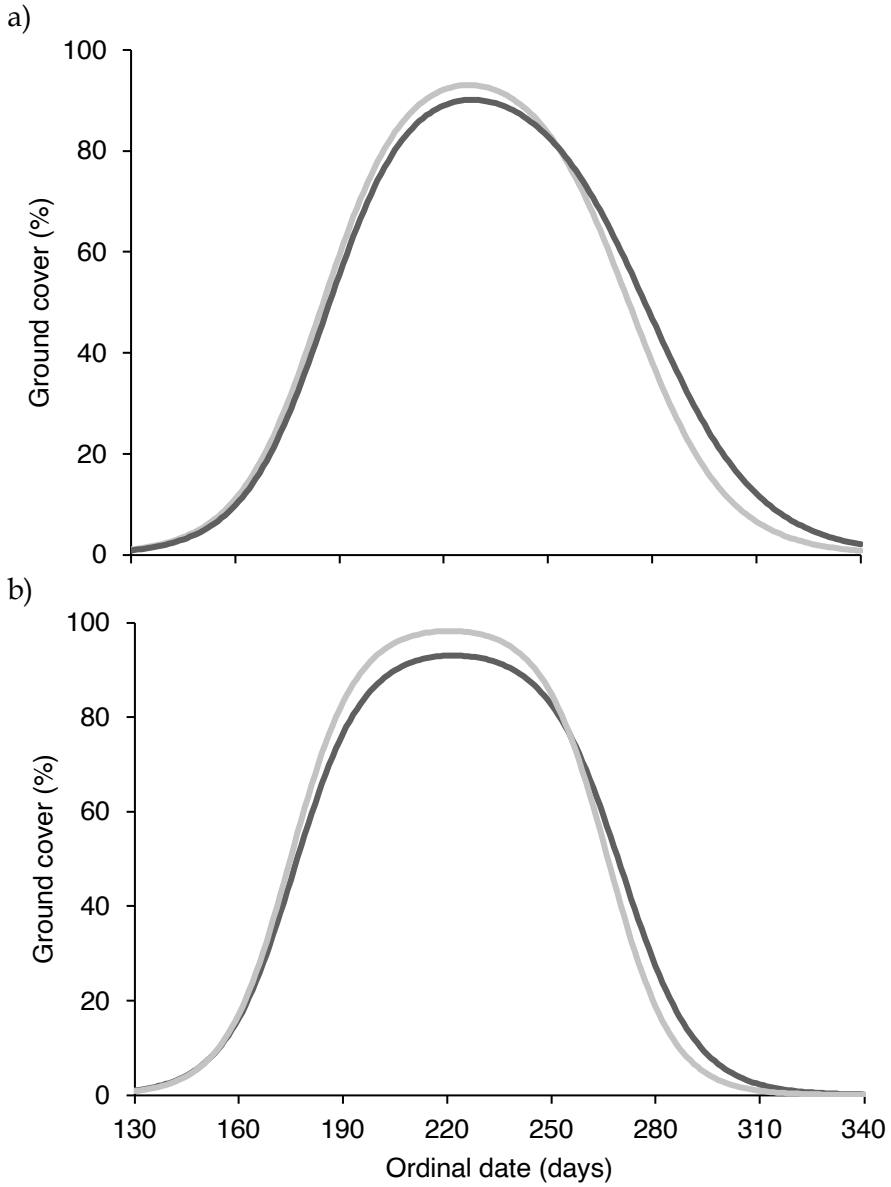

Figure 12. Average ground cover curve by rate of applied nitrogen, (a) Expt 1 and (b) Expt 3. 0 kg N/ha, ——; 250 kg N/ha, ——. Data presented are means of cultivars and planting date treatments. Goodness of fit for each curve is shown in Table 11.

Table 11. Goodness of fit scores for nitrogen treatment means in Expts 1 and 3. Goodness of fit measured using Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC).

Expt	Applied nitrogen (kg N/ha)	Goodness of fit score	
		d	RMSE
1	0	0.996	3.73
	250	0.995	4.23
3	0	0.997	3.81
	250	0.998	3.47

4.3.3.2 Variation in daylength in relation to canopy development

The greatest variation in daylength at emergence (dLengthEM) occurred between planting dates and dLengthEM was greatest in the May plantings in each experiment

($P > 0.001$), as expected, since these plots emerged closest to the summer equinox (vertical dashed line in Figure 13). The numerical difference in dLengthEM between planting dates was relatively small (43 and 53 min range in Expts 1 and 3, respectively) and other significant differences in dLengthEM are reported in Appendix 7, not the main results, due to their small effect size and likely limited effect on subsequent canopy growth.

Mean daylength during mid-canopy expansion (dLength2575) in Expt 1 was similar between the April and May plantings but was *c.* 53 min shorter in the June planting ($P < 0.001$, Figure 13a). Whilst in Expt 3 the differences in dLength2575 were smaller than those at emergence, with canopies planted in May expanding under slightly shorter daylength conditions (by *c.* 15 min, $P < 0.001$) than plots planted earlier (Figure 13b). In both experiments, applied nitrogen was associated with marginally longer dLength2575 (< 2 min, $P = 0.046$ and $P = 0.002$ in Expts 1 and 3, respectively), reflecting faster canopy expansion at the higher nitrogen rate (Figure 18), which finished *c.* 3 days earlier, under marginally longer daylength conditions. Other significant, yet marginal, results are reported in Appendix 7.

Mean daylength during near-complete ground cover (dLength90) decreased with planting date in Expts 1 and 3, yet dLength90 differed between planting dates common to both experiments. Figure 13 illustrates how the periods of near-complete canopy cover overlapped in Expt 3, with a 48 min range in dLength90 between planting dates and resulting in similar dLength90 values (15 h 19 min, 14 h 52 min and 14 h 31 min in the March, April and May plantings, respectively, $P = 0.002$). Whereas, in Expt 1, the May planting achieved near-complete canopy cover *c.* 16 days after the April planting, and the June planting *c.* 42 days after that, resulting in greater variation in daylength between the planting dates than in Expt 3, with a range of 126 min (dLength90; 15 h 30 min, 14 h 49 min and 13 h 24 min in the April, May and June plantings, respectively, $P < 0.001$). In both experiments, dLength90 was greater in Estima than Maris Piper (by 50 and 20 min, respectively, $P < 0.001$) reflecting the longer GCDur90 of Maris Piper than Estima, which reduced mean dLength90 as near-complete canopy cover was maintained until later in the season, when daylength shortened. In Expt 1, dLength90 was 22 min longer in Maris Piper at 250 than 0 kg N/ha, whilst there was no difference in dLength90 between nitrogen rates in Estima ($P = 0.002$). Whilst in Expt 3, cultivar variation in dLength90 to additional nitrogen was similar, and the overall effect of nitrogen was non-significant, yet there was a greater range in

dLength90 between planting dates at 250 than 0 kg N/ha (61 compared to 35 min, $P = 0.006$). Again, other statistically significant, yet marginal, results are reported in Appendix 7.

Mean daylength at the onset of canopy senescence (dLengthSen) decreased with delay in planting in both Expt 1 (13 h 35 min, 12 h 46 min and 11 h 25 min in the April, May and June plantings, respectively, $P < 0.001$) and Expt 3 (13 hr 35 min, 12 h 47 min and 12 h 28 min in the March, April and May plantings, respectively, $P = 0.002$), though dLengthSen was not consistent in the April and May planting dates across the experiments. The range in dLengthSen was greater in Expt 1 (130 min), than in Expt 3 (67 min) due to later senescence of the June planting date (Figure 13). In Expt 1, dLengthSen was longer at 0 than 250 kg N/ha in Estima (17 min), but longer at 250 than 0 kg N/ha in Maris Piper (32 min, $P = 0.001$), but there was no interaction between cultivar and nitrogen rate in Expt 3. In both experiments, dLengthSen was longer in Estima than in Maris Piper (111 and 53 min in Expts 1 and 3, respectively, both $P < 0.001$).

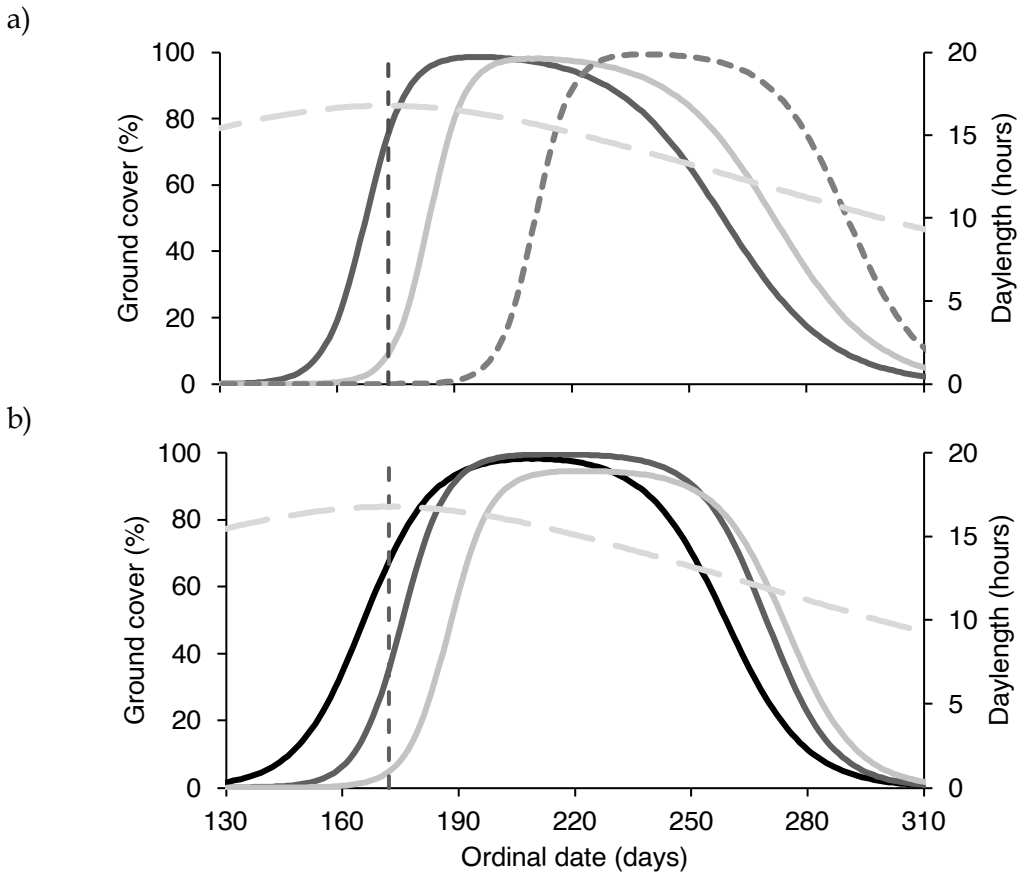

Figure 13. Average ground cover curve by planting date, plotted against days after emergence, (a) Expt 1 and (b) Expt 3. March, ——; April, ——; May, ——; June, - - -. The longest day of the year, 21st June, is marked with a vertical dashed line and daylength is indicated by the dashed pale grey line, - - -. Data presented are means of cultivar and nitrogen rate treatments.

4.3.3.3 Integrated ground cover

Integrated ground cover (IGC, % days) combines whole season canopy cover and duration and was on average greater in Expt 3 (9128 % days) than in Expt 1 (8320 % days), equivalent to 91 and 83 days at 100 % GC, respectively. Maris Piper was able to sustain a large canopy for longer at earlier than later planting dates, as shown by a difference in canopy extent between the April and June plantings equivalent to 31 days at full canopy cover (3071 % days), whereas Estima IGC varied less with planting date, with a difference equivalent to 7 days at full canopy cover (726 % days). This interaction between planting date and cultivar was significant in Expt 1 (Figure 14a, $P < 0.001$), but not observed in Expt 3 (Figure 14b), potentially as delaying planting until June reduced the length of the growing season relative to an April planting (in Expt 1) to a greater extent than the delay in planting between March and May in Expt 3. The difference in daylength at maximal GC was greatest between the early and late plantings in Expt 1 than in Expt 3 (4.3.3.2), and shorter daylength at maximal GC in the June planting (Figure 13a) potentially triggered earlier senescence (4.4.4.1).

In Expt 3, the effect of applied nitrogen on IGC varied between planting dates; with no difference between nitrogen rates in the March planting, greater IGC at 0 than 250 kg N/ha in the April planting (9644 and 9279 % days, respectively) and greater IGC at 250 than 0 kg N/ha in the May planting (8897 and 8267 % days, respectively). Moreover, IGC was also more variable at 0 kg N/ha than at 250 kg N/ha, with a range of 1377 % days compared to 439 % days (D.F. = 12.12, S.E. = 228.7, $P = 0.032$). There was no interaction between nitrogen rate and planting date in Expt 1. Nitrogen had no overall effect on IGC in either experiment.

IGC was greater at the earlier planting dates in both experiments ($P < 0.001$, $P = 0.033$, in Expts 1 and 3, respectively), though the magnitude of the difference varied between experiments. In Expt 1, IGC was greater at the April planting (9148 % days) than at May and June plantings (8562 and 7250 % days, respectively, Figure 14a) and in Expt 3 IGC was greatest in the March and April plantings (9341 and 9461 % days, respectively) and IGC of the May planting was lowest (8582 % days), equivalent to 9 fewer days at 100 % GC than the other planting dates (Figure 14b).

Maris Piper consistently produced greater IGC values than Estima ($P < 0.001$, in both experiments). In Expt 1 the extent of the difference decreased with delay in planting and was equivalent to 25 days at 100 % GC in the April planting but equivalent to 9 days at 100 % GC in the June planting (Figure 14a). Whilst in Expt 3 Maris Piper

consistently produced an IGC 2176 % days larger than Estima (equivalent to 22 days at 100 % GC) across the planting dates (Figure 14b).

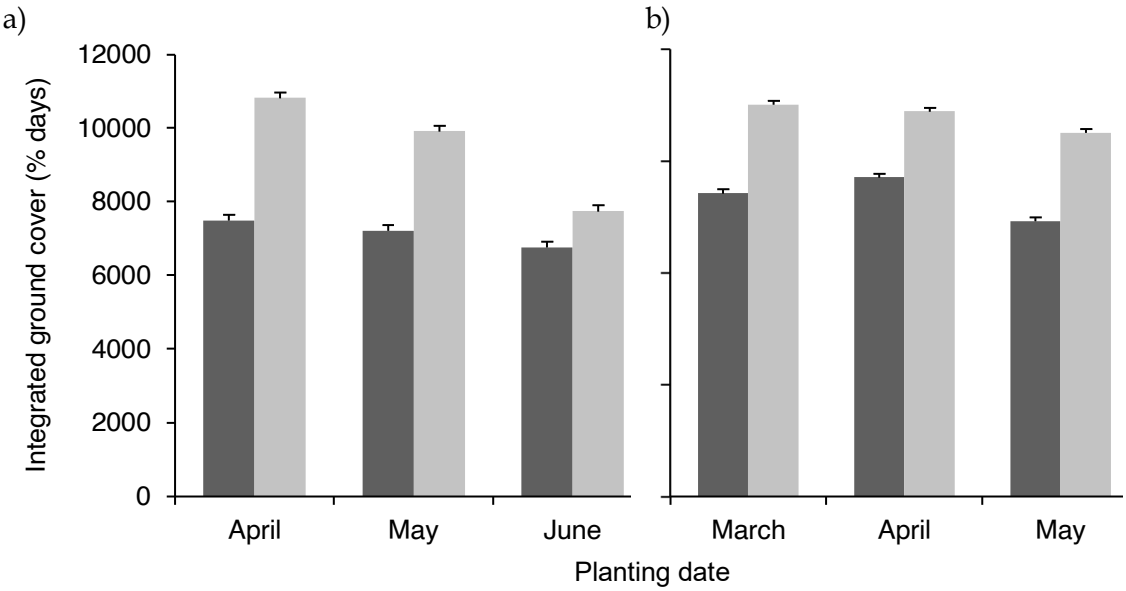

Figure 14. Effects of planting date and cultivar on integrated ground cover in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (15.55 D.F. (a) and 12.12 D.F. (b)). Data presented are a mean of nitrogen treatments.

4.3.3.4 Duration of early canopy expansion

In both experiments, the interval between emergence and 25 % GC (TiE25) was shorter at later planting dates, indicating more rapid early canopy expansion ($P < 0.001$, in both experiments, Figure 15). There was a significant decrease in TiE25 between the April and May plantings in Expt 1 (Figure 15a), and Expt 3 (Figure 15b), however neither year showed a simple negative trend of decreasing TiE25 with later planting. Neither cultivar nor nitrogen rate had a significant effect on TiE25 in either experiment.

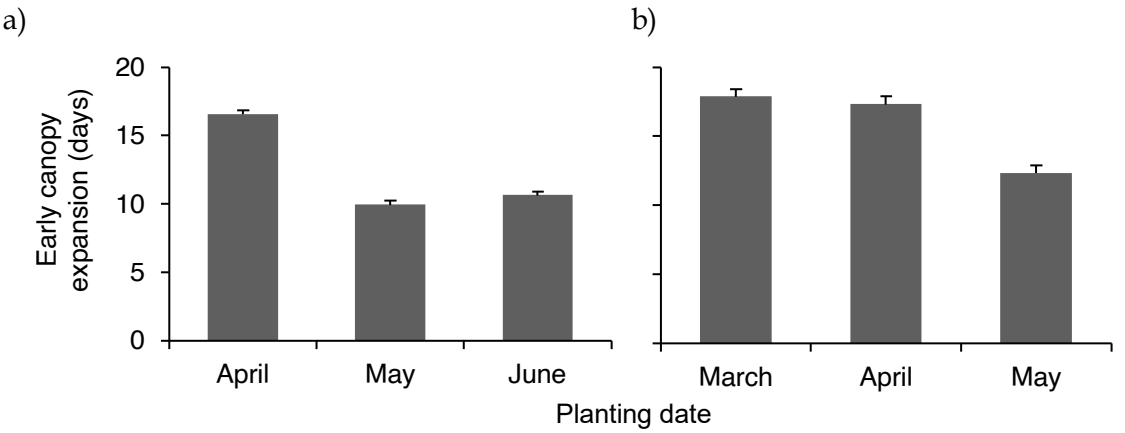

Figure 15. Effects of planting date on the interval between emergence and 25 % GC in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (6 D.F.). Data presented are a mean of cultivar and nitrogen treatments.

Mean air temperature during early canopy expansion increased with delay in planting (Table 12) and TiE25 tended to decrease with increasing mean air temperature in both

Expts 1 and 3 (Figure 16), but since mean daily air temperature was highly clustered with planting date and was non-normally distributed, linear regression could not be performed to quantify the relationship.

Table 12. Mean air temperature during early canopy expansion (°C), by planting date in Expts 1 and 3 (S.E in table, 6 D.F.).

Expt	Planting date	Air temperature	S.E.
1	April	12.8	0.0290
	May	15.8	
	June	18.8	
3	March	16.5	0.115
	April	17.4	
	May	18.0	

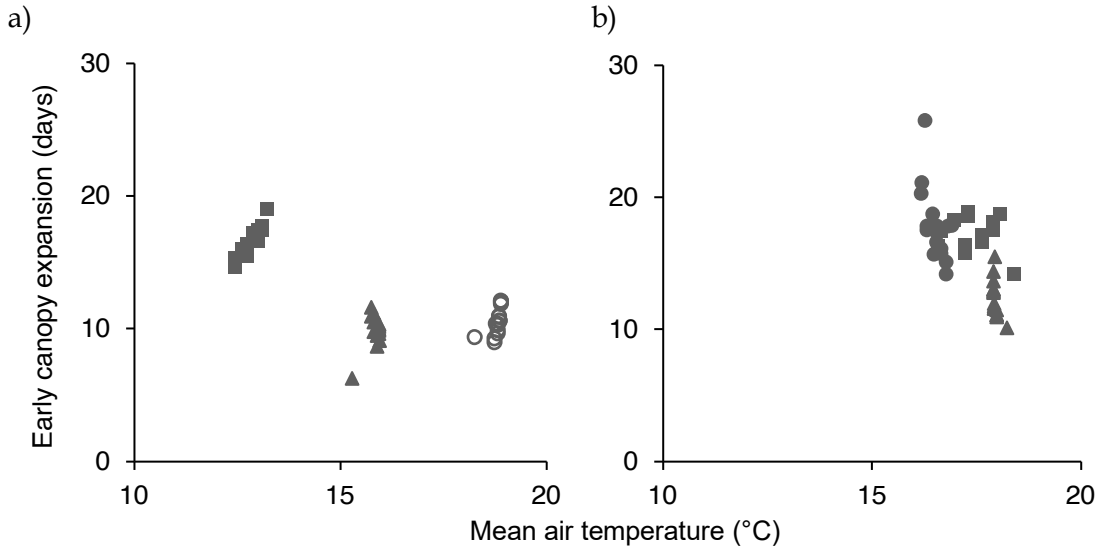

Figure 16. Relationship between early canopy expansion (TiE25) and mean air temperature (T) over the period of early canopy expansion for each plot in (a) Expt 1 and (b) Expt 3. Planting dates: March, ●; April, ■; May, ▲; June, O.

4.3.3.5 Mid-season canopy expansion rate

The rate of mid-season canopy expansion (GCRate2575) was calculated between 25-75 % GC and was on average greater in Expt 1, at 4.88 % GC/day, than in Expt 3, at 3.62 % GC/day. The greatest rates of GCRate2575 were associated with later planting dates in both Expts 1 and 3 (P = 0.002 and 0.015, respectively, Figure 17). There was no difference in GCRate2575 between cultivars in Expt 1 and the April planting expanded 0.60 % GC/day slower than both the May and June plantings (Figure 17a). In Expt 3, the Maris Piper canopy expanded 0.81 % GC/day faster than that of Estima in the May planting, but there was no significant difference between cultivars in either the March or April plantings (P < 0.001, Figure 17b). On average Maris Piper canopies expanded 0.26 % GC/day faster than Estima (P = 0.007, Figure 17b), though this was due to the difference between cultivars in the May planting. Canopy expansion was slowest in

the March planting and expanded 1.35 % GC/day slower than both the April and May plantings (Figure 17b). Average canopy expansion (in the April and May plantings) was faster in Expt 1 (4.79 % GC/day) than in Expt 3 (4.07 % GC/day), indicating the influence of factors additional to planting date, cultivar and nitrogen on GCRate2575.

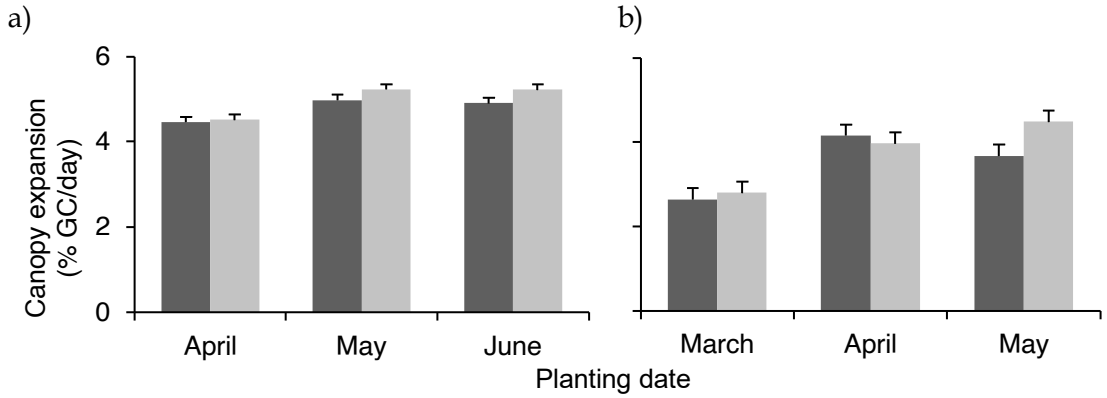

Figure 17. Effect of planting date and cultivar on rate of mid-season canopy expansion (between 25-75 % GC) in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (28.59 D.F. (a), 7.12 D.F. (b)). Data presented are a mean of nitrogen treatments.

In both experiments canopy expansion was most rapid at later planting dates with applied nitrogen (P = 0.011 and P = 0.008 in Expts 1 and 3, respectively). At 0 kg N/ha in Expt 1, there was a negligible increase in GCRate2575 with delay in planting, whilst at 250 kg N/ha the April planting expanded at a slower rate (4.49 % GC/day) than both the May and June plantings (5.10 and 5.06 % GC/day respectively, Figure 18a). The difference in GCRate2575 between nitrogen treatments was also greater at later planting dates in Expt 3, although GCRate2575 was more variable at 0 kg N/ha than in Expt 1 (2.40, 3.65 and 3.40 % GC/day at the March, April and May plantings, respectively, Figure 18b). Plots without additional nitrogen consistently expanded at a slower rate than those with applied nitrogen (P < 0.001 in both experiments, Figure 18) and there was no difference in nitrogen response between cultivars.

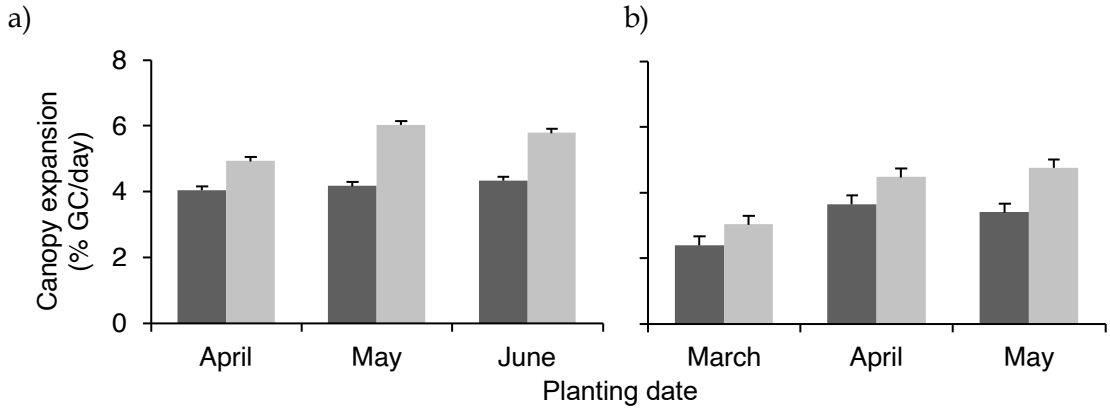

Figure 18. Effects of planting date and nitrogen rate on rate of mid-season canopy expansion (between 25-75 % GC), (a) Expt 1 and (b) Expt 3. 0 kg N/ha, ■; 250 kg N/ha, ■. Bars represent S.E. (28.59 D.F. (a), 7.12 D.F. (b)). Data presented are a mean of cultivars.

Mean air temperature during mid-canopy expansion was greater in the June than either the April or May plantings in Expt 1 (Table 13), yet there was no significant relationship between mid-season canopy expansion and mean air temperature (Figure 19a). There was also no relationship between mean air temperature and GCRate2575 in Expt 3 (Figure 19b), though mean temperature did not differ significantly between planting dates (Table 13), so the lack of relationship is less surprising.

Table 13. Mean air temperature during mid-canopy expansion (°C), by planting date in Expts 1 and 3 (S.E in table, 6 D.F.).

Expt	Planting date	Air temperature	S.E.
1	April	15.8	0.0571
	May	15.5	
	June	18.8	
3	March	18.1	0.147
	April	18.2	
	May	18.5	

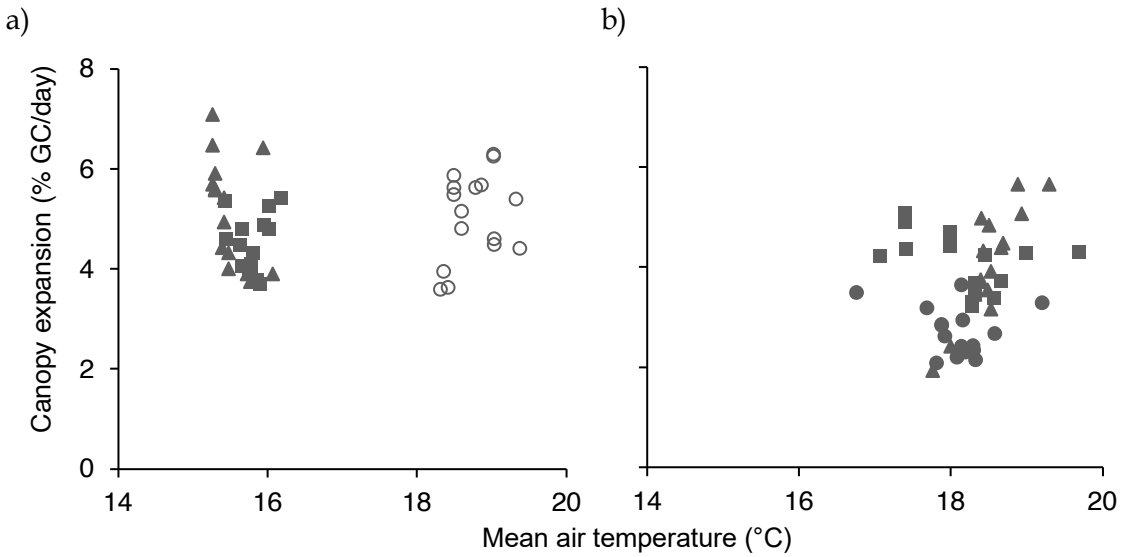

Figure 19. Rate of mid-season canopy expansion (GCRate2575) plotted against mean daily air temperature over the period of mid-season canopy expansion for each plot in (a) Expt 1 and (b) Expt 3. Planting dates: March, ●; April, ■; May, ▲; June, O.

4.3.3.6 Duration of near-complete ground cover

The duration of near-complete ground cover (GCDur90, when ground cover was ≥ 90 %), was greater in Expt 1 than Expt 3 (65 and 60 days, respectively) and was longer in Maris Piper than Estima by an average of 29.2 days in Expt 1 and 16.2 days in Expt 3 ($P < 0.001$ in both experiments, Figure 20). In Expt 3, two plots of May planted Estima at 0 kg N/ha did not reach 90 % GC (maximum GC; 78.5 and 82.5 %) and so GCDur90 was recorded as missing values for those plots. GCDur90 declined with delay in planting in Expt 1 ($P = 0.014$, Figure 20a), whilst in Expt 3, GCDur90 was greatest in the

April planting (P = 0.029, Figure 20b). There was no significant interaction between cultivar and planting date in either experiment.

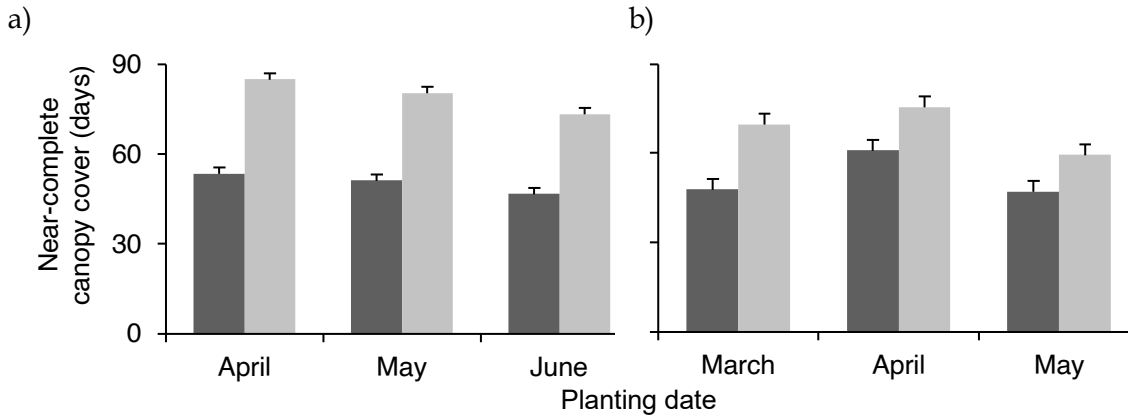

Figure 20. Effects of planting date and cultivar on duration of near-complete ground cover (GCDur90) in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (18.36 D.F. (a), 14.19 D.F. (b)). Data presented are a mean of nitrogen treatments.

In Expt 3 the high N treatment reduced the range in GCDur90 between planting dates from 27.5 days at 0 kg N/ha to 4.8 days at 250 kg N/ha (P = 0.002, Figure 21b). In Expt 3, GCDur90 was an average of 13.3 days longer at 250 kg N/ha than at 0 kg N/ha (P < 0.001, Figure 21b) and the same affect was observed in both cultivars. In Expt 1 the effect of nitrogen on canopy duration differed between cultivars and GCDur90 was greater at 250 than 0 kg N/ha in Estima (55.3 and 45.7 days, respectively), whilst in Maris Piper GCDur90 was shorter at 250 than 0 kg N/ha (77.8 and 81.5 days, respectively, P < 0.001). Hence, there was no significant overall effect of applied nitrogen on GCDur90 in Expt 1 (Figure 21a). High available soil nitrogen in Expt 1 (Table 5) may have masked the effect of additional nitrogen on canopy duration whilst in Expt 3 it is possible that additional nitrogen helped to mitigate the negative effects of a poor-quality seed bed, as crops grown on compacted soil have a higher nitrogen requirement (Hamza & Anderson 2005).

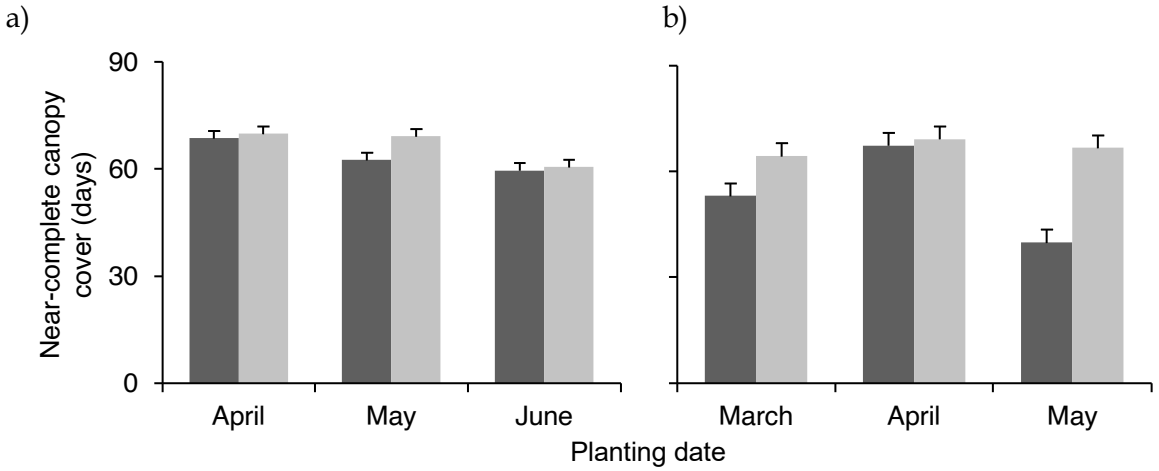

Figure 21. Effect of planting date and nitrogen on duration of near-complete canopy cover (GCDur90) in (a) Expt 1 and (b) Expt 3. 0 kg N/ha, ■; 250 kg/N/ha, ■. Bars represent S.E. (18.36 D.F. (a), 14.19 D.F. (b)). Data presented are a mean of cultivars.

There were small, < 2 °C, but significant differences in mean air temperature during near-complete canopy between cultivars, planting dates and, in Expt 1, between cultivars at the different planting dates (Appendix 8).

As expected, IGC increased with increasing GCDur90, and GCDur90 explained 48.7 % of the variation in IGC once variation between experimental block and plot layout was accounted for (multiple linear regression; IGC ~ GCDur90 + block/main plot, $P < 0.001$). Yet the relationship varied between experiments, and the increase in IGC with each additional day of GCDur90 was smaller in Expt 3 than in Expt 1 (see β1 and β2 slope coefficients, Table 14) due to lower mean ground cover in during near-complete canopy cover in Expt 3 than Expt 1. Including year in the model explained 68.5 % of the variation (multiple linear regression; IGC ~ GCDur90 * year + block/main plot, $P < 0.001$, Figure 22). Further variation, 89.0 %, was explained by including experimental treatments in the model, and differences between treatments removed the need for the interaction between GCDur90 and year of experiment (multiple linear regression; IGC ~ GCDur90 + year + planting date + nitrogen rate + cultivar + block/main plot, $P < 0.001$, Table 15).

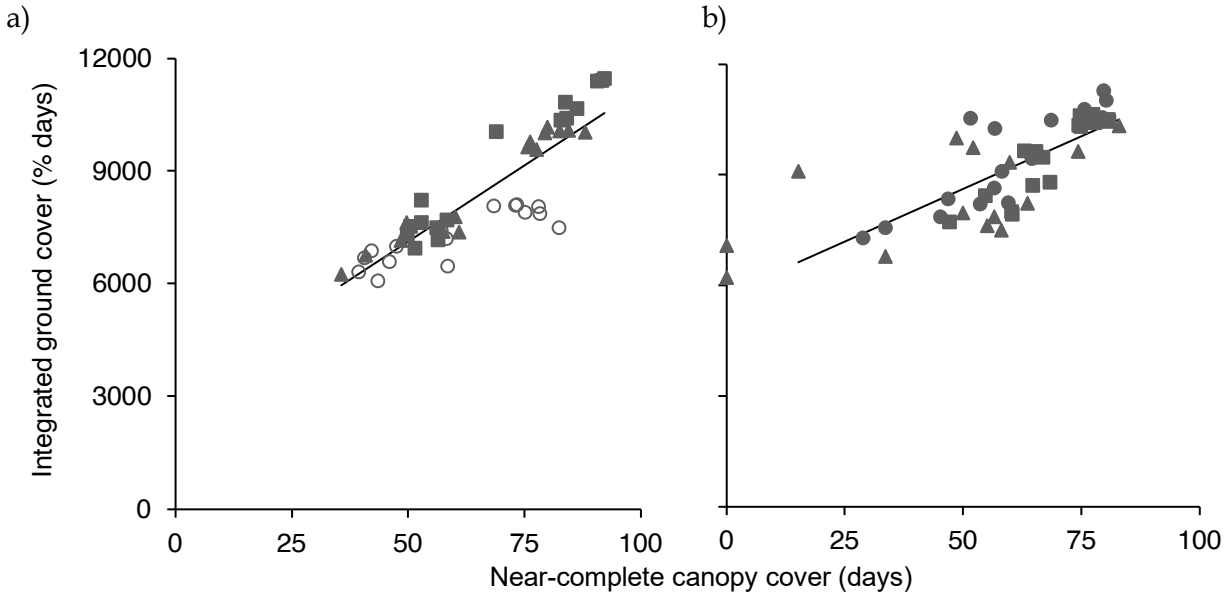

Figure 22. Relationship between integrated ground cover (IGC) and duration of near-complete ground cover (GCDur90) in (a) Expt 1 and (b) Expt 3. Planting dates: March, ●; April, ■; May, ▲; June, O. R^2 = 0.685. See Table 14 for details of multiple linear regression.

Table 14. Relationship between integrated ground cover (IGC), duration of near-complete ground cover (GCDur90) and experiment (Expts 1 or 3). IGC = β0 + β1*GCDur90 + β2*Expt 3 + β3*(GCDur90*Expt 3).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	3070	566	< 0.001
1	GCDur90	81.1	7.4	< 0.001
2	Expt 3	2700	732	< 0.001
3	GCDur90 * Expt 3	-24	11.3	0.038

Table 15. Relationship between integrated ground cover (IGC), duration of near-complete ground cover (GCDur90), cultivar (MP), planting date (March, April, May or June), nitrogen rate (250 N) and experiment (Expts 1 or 3). IGC = β0 + β1*GCDur90 + β2*Expt 3 + β3*June + β4*March + β5*May + β6*250 N + β7*MP.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	5920	381	< 0.001
1	GCDur90	37.9	5.39	< 0.001
2	Expt 3	470	129	< 0.001
3	June	-1200	282	< 0.001
4	March	470	277	0.093
5	May	-410	148	0.007
6	250 N	-320	109	0.004
7	MP	1370	157	< 0.001

4.3.3.7 Ground cover senescence

The rate of canopy senescence (GCRate9050) was calculated between 90–50 % GC and average senescence was faster in Expt 1 (Figure 23a), -3.52 % GC/day compared to -2.76 % GC/day in Expt 3 (Figure 23b). GCRate9050 could not be calculated for two plots (both May planted Estima at 0 kg N/ha) in Expt 3 and were omitted from the analysis, as they did not achieve 90 % GC. The difference in rate of senescence between

the cultivars was greater at 250 kg N/ha (2.22 and 1.80 % GC/day in Expt 1 and Expt 3, respectively) than at 0 kg N/ha (0.75 and 0.25 % GC/day in Expt 1 and Expt 3, respectively (P = 0.026 and P < 0.001 in Expts 1 and 3, respectively, Figure 23). Estima senesced at a more rapid rate than Maris Piper (-4.26 and -2.78 % GC/day respectively in Expt 1 and -3.28 and -2.25 % GC/day respectively in Expt 3, P < 0.001 in both experiments, Figure 23). In Expt 3, the difference in GCRate9050 between cultivars was greatest in the May planting; -0.64, -0.85 and -1.61 % GC/day in the March, April and May plantings, respectively (P = 0.047). Senescence was faster at 250 kg N/ha than 0 kg N/ha (-2.78 and -4.25 % GC/day respectively in Expt 1 (Figure 23a) and -2.02 and -3.51 % GC/day respectively in Expt 3 (Figure 23b), P < 0.001 in both experiments). In Expt 3, the difference in GCRate9050 between nitrogen treatments varied with planting date and was greatest in the May planting; -1.26, -0.93 and -2.29 % GC/day in the March, April and May plantings, respectively (P = 0.005). There was no overall effect of planting date on rate of senescence in either experiment.

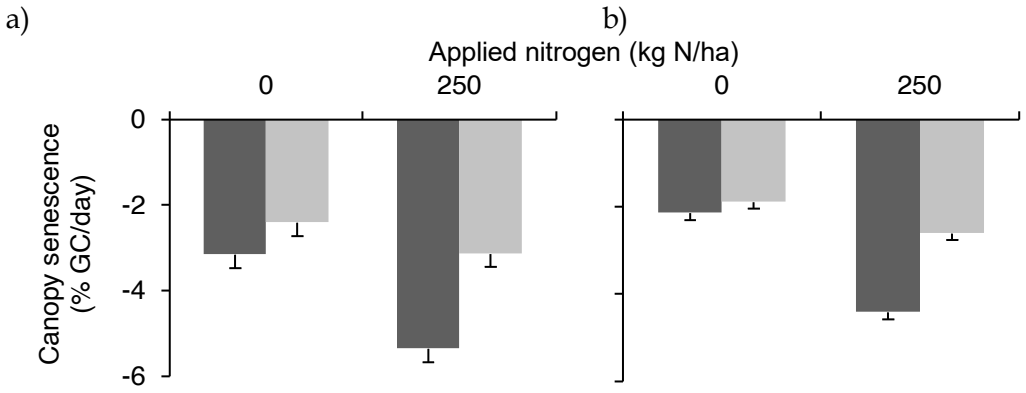

Figure 23. Effect of cultivar and nitrogen rate on the rate of canopy senescence in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (27 D.F. (a), 25 D.F. (b)). Data presented are a mean of planting dates.

Duration of growth was calculated between the date of emergence and the start of senescence (defined as the date when canopy cover declined past 90 % of maximum GC, GrowDur). Duration of growth was similar at planting dates shared between experiments, and canopy was maintained for 102.8 and 104.4 days in the April plantings of Expts 1 and 3, respectively and 91.7 and 90.9 days in the May plantings of Expts 1 and 3, respectively, Figure 24). In Expt 3, Estima GrowDur varied little between planting dates, with a range of 9.4 days between the longest and shortest GrowDur in April and May, respectively, whereas Maris Piper GrowDur differed by 20.9 days between March and May plantings (P = 0.030, Figure 24b). There was no interaction between cultivar and planting date in Expt 1 (Figure 24a). GrowDur decreased with delay in planting in both experiments (P < 0.001 and P = 0.004, in

Expts 1 and 3, respectively, Figure 24). Maris Piper maintained canopy for longer than Estima in both experiments ($P < 0.001$, Figure 24) with a mean GrowDur of 107.6 days in both experiments, whilst Estima canopy duration was shorter in Expt 1 than Expt 3 (79.7 and 92.8 days respectively). In Expt 1 GrowDur increased in Estima in response to additional nitrogen and was 4.3 days longer at 250 than 0 kg N/ha, whilst Maris Piper GrowDur was shorter by 8.5 days at 250 than 0 kg N/ha ($P < 0.001$), reflecting differences in Expt 1 GCDur90 (4.3.3.6). There was no interaction between cultivar and nitrogen rate in GCDur90 in Expt 3 and no overall effect of nitrogen on duration of canopy growth before senescence.

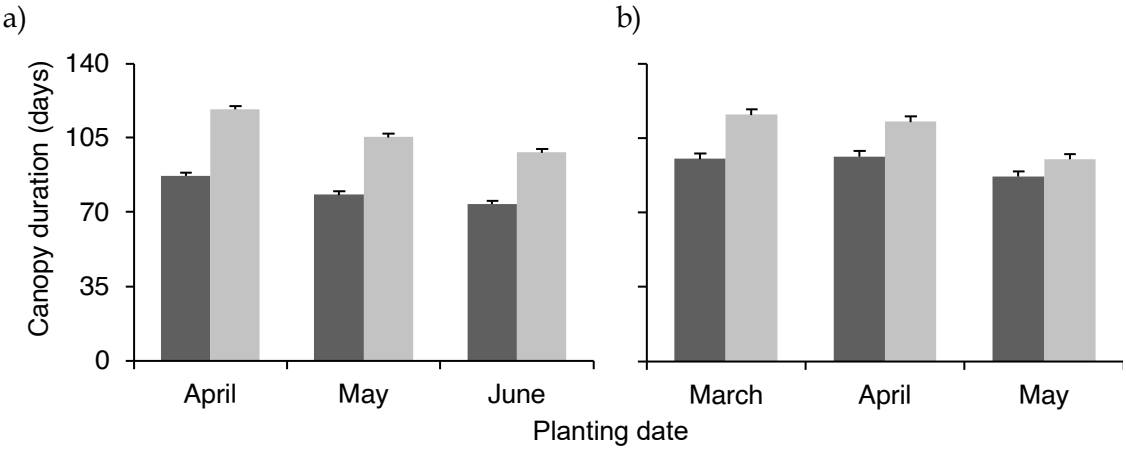

Figure 24. Effect of planting date and cultivar on duration of growth (between emergence and the beginning of senescence, at 90 % of maximum canopy cover) in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (20.11 D.F. (a), 14.54 D.F. (b)). Data presented are a mean of nitrogen rates.

4.3.3.8 Key points: Ground cover dynamics

- IGC tended to be greater at earlier planting dates, with a longer growing season.
- IGC was greater in Maris Piper than Estima, though was typically more variable between planting dates in Maris Piper.
- TiE25 was shorter with later planting and tended to be faster at warmer temperatures, although temperature alone explained a limited amount of variation.
- GCRate2575 was slower without additional nitrogen.
- There was little difference in GCRate2575 between the two cultivars.
- GCRate2575 was slowest at the earliest planting dates but there was no direct correlation with either temperature or radiation during expansion.
- GCDur90 was longer in Maris Piper than Estima, though the difference was greater in Expt 1 than Expt 3 and decreased with planting date in Expt 1.

- GCDur90 varied little between nitrogen treatments, but high nitrogen may have enabled longer canopy maintenance in Expt 3.
- IGC increased with increasing GCDur90.
- Estima senesced at a faster rate than Maris Piper.
- Both cultivars senesced faster at high nitrogen, but the difference in GCRate9050 was greater in Estima than Maris Piper.

4.3.4 Leaf appearance

The number of mature leaves on both the mainstem and sympodial branches was recorded throughout the season to better understand the influence of individual leaves on whole canopy growth. The effects of all treatments and their interactions on leaf appearance are reported in Appendix 9.

4.3.4.1 Mainstem leaves

Maris Piper produced a greater number of leaves on the mainstem (before appearance of the first flower, msL) than Estima in both Expt 1 (4.8 more, $P < 0.001$) and Expt 3 (5.2 more, $P < 0.001$, Figure 25). The number of mainstem leaves was similar in both experiments (Figure 25). Planting date and nitrogen rate had no effect upon the number of leaves produced on the mainstem in either experiment.

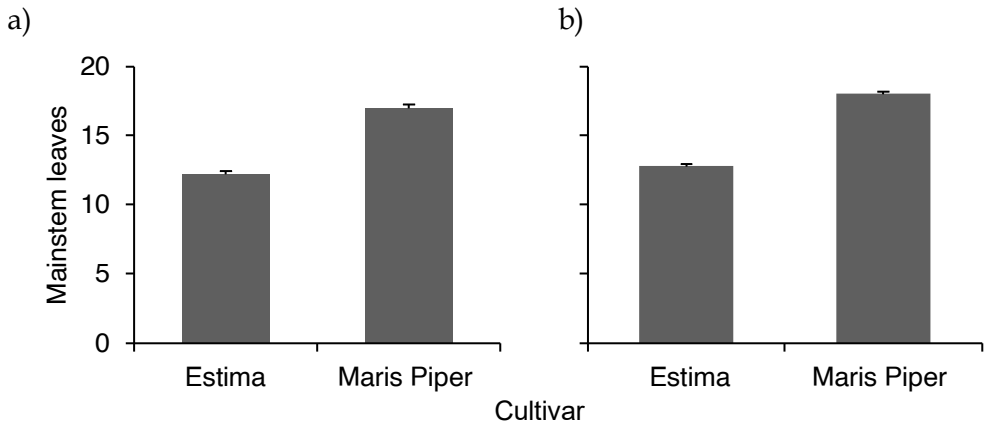

Figure 25. Effect of cultivar on number of leaves produced on the mainstem in (a) Expt 1 and (b) Expt 3, bars represent S.E. (25 D.F.). Data presented are a mean of nitrogen treatments and planting dates.

4.3.4.2 Mainstem leaf appearance

Rate of mainstem leaf appearance (msLA) was measured between the appearance of the fifth leaf and the sympodial branch (or the 12th leaf if no flower and no sympodial branch was produced (3.2.4)) and mean msLA differed little between Expt 1 and Expt 3 (0.577 and 0.585 leaves/day, respectively). In Expts 1 and 3, 9 and 1 % of stems measured, respectively, did not produce a sympodial branch, the majority of which

were Maris Piper stems at 0 kg N/ha. In Expt 3 there was little difference between msLA in Estima and Maris Piper in the March planting, but at the later plantings the rate of leaf appearance was greater in Estima than Maris Piper by *c.* 0.105 leaves/day (P = 0.001, Figure 26b). Additionally, Estima msLA was greater at later planting dates whilst Maris Piper msLA varied little with planting date and there was no overall effect of planting date on msLA (Figure 26b). There was no interaction between planting date and cultivar in Expt 1 and no significant effect of planting date on msLA, though leaf appearance was numerically fastest in the June planting, followed by the April, then the May planting (Figure 26a). In both experiments, msLA was greater in Estima than Maris Piper and Estima produced 0.205 and 0.055 leaves/day more than Maris Piper in Expts 1 and 3, respectively (P < 0.001 and P = 0.003, respectively, Figure 26).

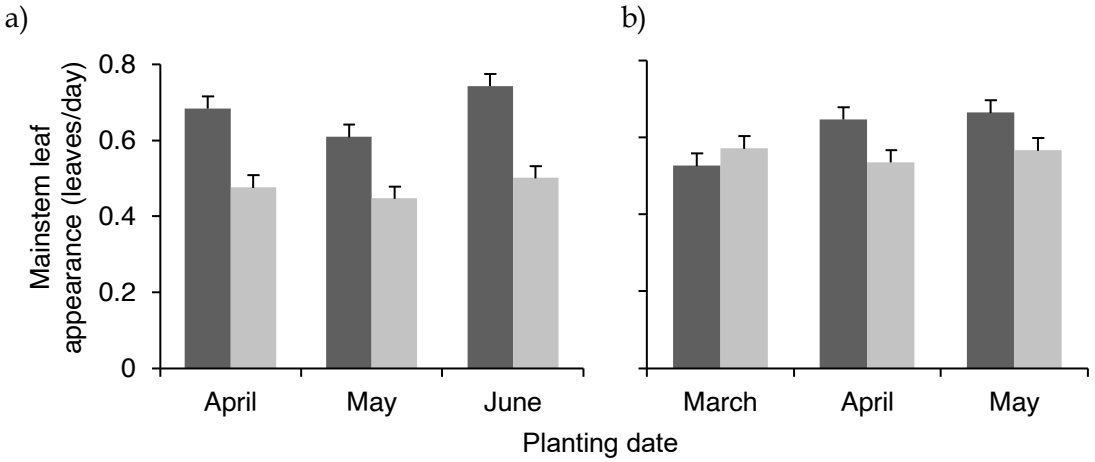

Figure 26. Effects of planting date and cultivar on rate of mainstem leaf appearance in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (23.27 D.F. (a), 9.41 D.F. (b)). Data presented are a mean of nitrogen treatments.

Without additional nitrogen, the difference in msLA between cultivars was greater than at 250 kg N/ha; in Expt 1 there was a 0.272 and 0.136 leaves/day difference between cultivars at 0 and 250 kg N/ha, respectively (P = 0.024, Figure 27a), though the interaction was not significant in Expt 3. There was no overall effect of nitrogen rate on the rate of mainstem leaf production in either experiment.

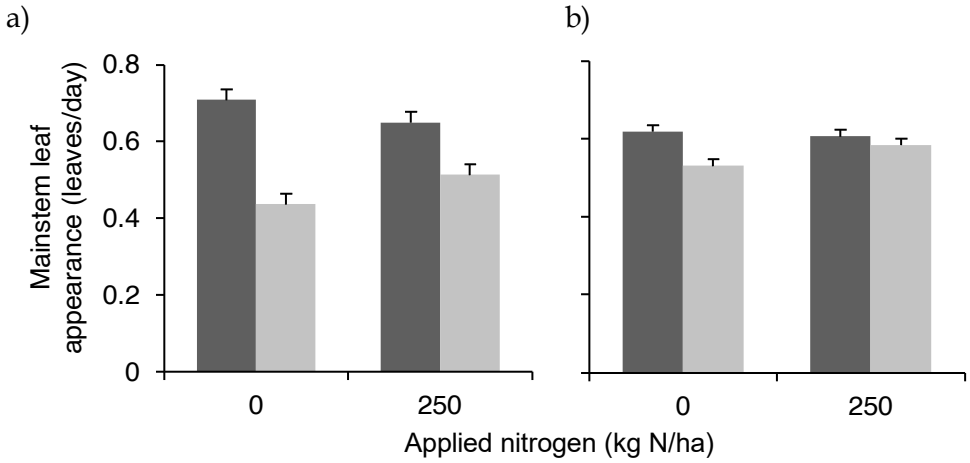

Figure 27. Effects of nitrogen rate and cultivar on rate of mainstem leaf appearance in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (27 D.F.). Data presented are a mean of planting date treatments.

Despite significant differences between mean air temperature during the period of mainstem leaf appearance in both experiments (Table 16), temperature alone did not predict any variation in msLA in either experiment (Figure 28).

Table 16. Mean air temperature during the period of mainstem leaf appearance (°C) for each planting date treatment in Expts 1 and 3.

Expt	Planting date	Air temperature	S.E.
1	April	14.1	0.15
	May	16.3	
	June	18.7	
3	March	16.7	0.15
	April	17.8	
	May	18.1	

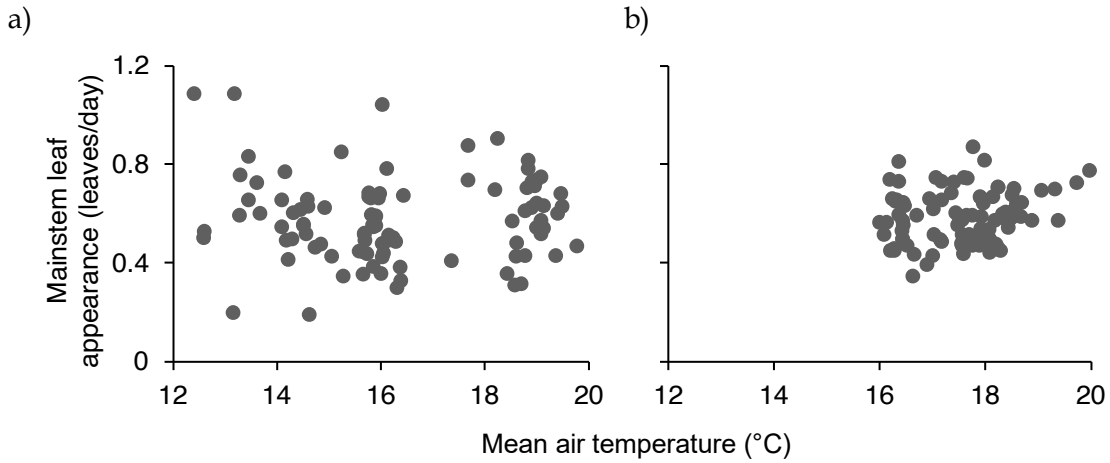

Figure 28. Mainstem leaf appearance rate plotted against mean air temperature during the period of mainstem leaf appearance in (a) Expt 1 and (b) Expt 3.

Rate of mainstem leaf appearance on an individual stem decreased as number of stems per plant increased in both experiments (Figure 29). Stems per plant (S) explained 45.5 % of the variation in msLA, once variation between year of experiment and

experimental blocks were accounted for (multiple linear regression; msLA ~ S + year + block/main plot, $P < 0.001$). Though the intercept for one main plot differed significantly from the rest there was no overall significant effect of the block and main plot structure (ANOVA, $P = 0.123$) and regression coefficients without accounting for the differences between blocks were reported below (Table 17 and Figure 29). There was no difference in rate of decrease between experiments, and msLA declined by 0.045 leaves/day with each additional stem per plant, though mean msLA was lower in Expt 3 than in Expt 1 (as shown by a lower intercept, Figure 29). Including mean air temperature during mainstem leaf appearance (msLAtemp) increased the variation in msLA explained to 53.8 % (multiple linear regression; msLA ~ S + msLAtemp + year + block/main plot, $P < 0.001$) and msLA increased by 0.026 (± 0.0067) leaves/day as msLAtemp increased by 1 °C. Yet greater variation in msLA was explained (62.5 %) by experimental treatments (multiple linear regression; msLA ~ S + cultivar * planting date * nitrogen rate + block/main plot, $P < 0.001$), indicating that the effect of variation in msLAtemp was masked by variation in the experimental treatments, particularly by planting date, with which msLAtemp covaried (Table 16).

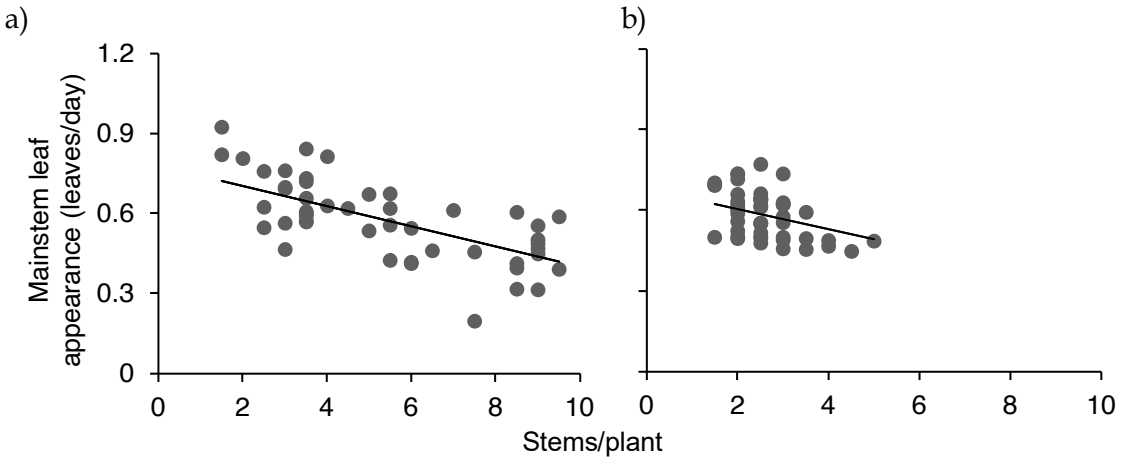

Figure 29. Relationship between number of stems per plant (S) and rate of leaf appearance on individual stems (msLA) in (a) Expt 1 and (b) Expt 3. $R^2 = 0.412$. See Table 17 for details of multiple linear regression.

Table 17. Relationship between rate of leaf appearance on individual stems (msLA), number of stems per plant (S) and experiment (Expts 1 or 3). msLA = β0 + β1*S + β2*Expt 3.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.779	0.0261	< 0.001
1	S	-0.0378	0.00429	< 0.001
2	Expt 3	-0.098	0.0211	< 0.001

4.3.4.3 Phyllochron

Phyllochron (base temperature, 0 °C) was greater in Maris Piper than Estima (39.0 and 26.7 °C days/leaf, respectively, $P < 0.001$, Figure 30a) in Expt 1, and did not vary significantly between planting dates. Whilst in Expt 3, phyllochron was greatest in Estima in the March planting, yet greatest in Maris Piper in the April and May plantings (difference of *c.* 4.5 °C days/leaf between cultivars at each planting date, $P < 0.001$, Figure 30b). Phyllochron values were highly variable and there was a wide range within each planting date in Expt 1 (56.6, 39.0 and 29.6 °C days/leaf range in the April, May and June planting dates respectively), though the range was smaller in Expt 3 (13.6, 14.2 and 14.6 °C days/leaf range in the March, April and May planting dates, respectively).

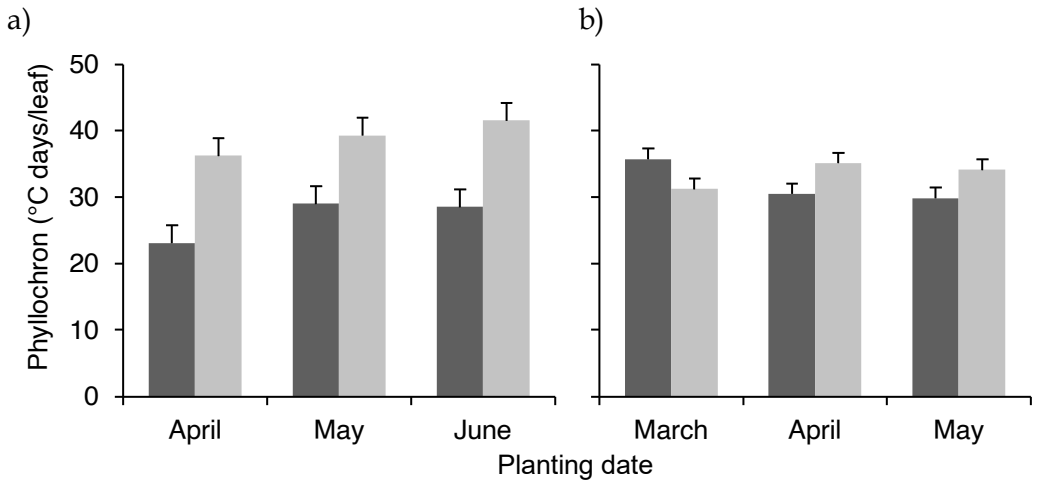

Figure 30. Effects of planting date and cultivar on mainstem phyllochron in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (25.28 D.F. (a), 9.38 D.F. (b)). Data presented are a mean of nitrogen treatments.

In Expt 3, the mean phyllochron of Estima was 32.0 °C days/leaf irrespective of nitrogen rate, yet additional nitrogen reduced the phyllochron of Maris Piper by 3.3 7 °C days/leaf ($P = 0.046$, Figure 31b). Phyllochron did not vary with nitrogen rate in Expt 1 (Figure 31a).

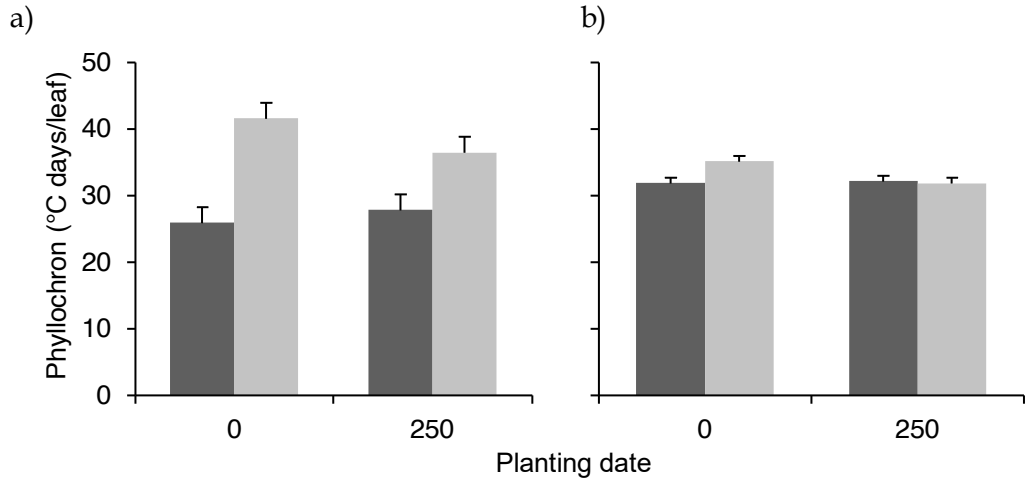

Figure 31. Effects of nitrogen rate and cultivar on mainstem phyllochron in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (27 D.F.). Data presented are a mean of planting date treatments.

4.3.4.4 Main axis leaves

Total number of main axis leaves (maL) included all mature leaves on the mainstem and sympodial branch. In both experiments, Estima maL varied little in response to planting date (range between planting dates of 1.6 and 1.1 leaves in Expts 1 and 3, respectively), whilst, in Maris Piper, maL was greatest at the early planting dates (a range of 7.3 and 3.6 leaves in Expts 1 and 3, respectively, between planting dates, $P = 0.005$ in both experiments, Figure 32). Maris Piper produced more main axis leaves than Estima in both Expt 1 (4.9 leaves more, $P < 0.001$, Figure 32a) and Expt 3 (6.0 leaves more, $P < 0.001$, Figure 32b). The number of main axis leaves produced by Estima varied little between experiments (mean of 21.8 leaves, Figure 32). In Expt 1, more main axis leaves were produced by the April planting than in the May and June plantings (26.3, 21.9 and 23.8 leaves respectively, $P < 0.001$, Figure 32a). Despite variation in maL between planting dates in Maris Piper in Expt 3, there was no overall difference in number of main axis leaves produced at the different planting dates (Figure 32b).

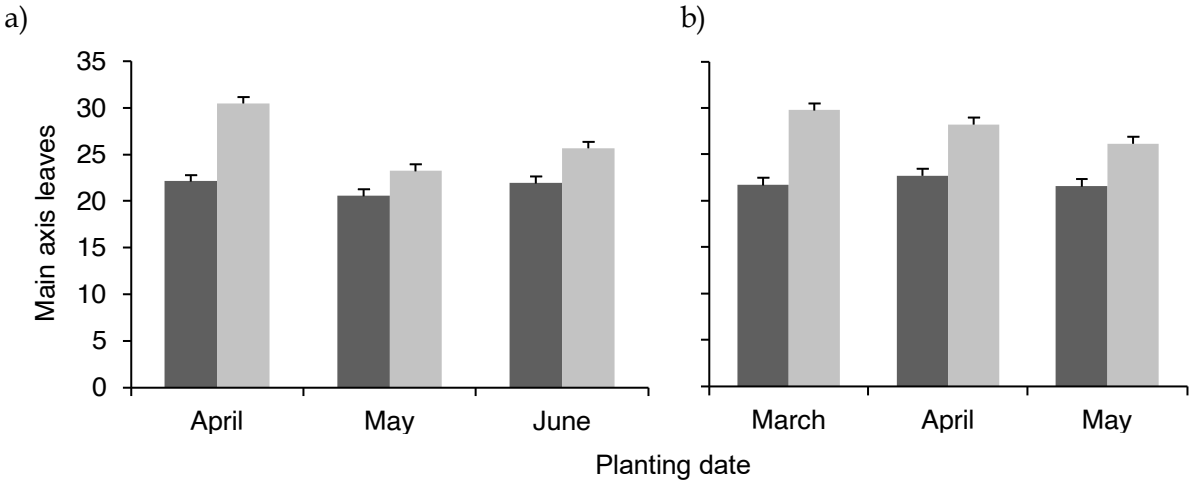

Figure 32. Effects of planting date and cultivar on total number of leaves on the main axis in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (29.81 D.F. (a), 9.49 D.F. (b)). Data presented are a mean of nitrogen treatments.

The high nitrogen treatment produced an average of four more leaves on the main axis than the low nitrogen treatment in both Expt 1 (4.2 leaves, $P < 0.001$) and Expt 3 (3.9 leaves, $P < 0.001$, Figure 33).

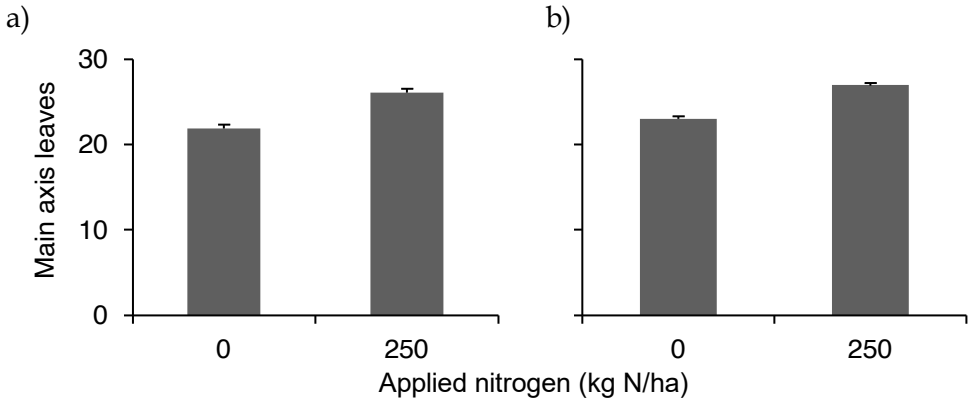

Figure 33. Effect of nitrogen on total number of leaves produced on the main axis in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (27 D.F.). Data presented are a mean of cultivars and planting dates.

Collectively, there was a relatively weak relationship between maL and GCDur90 and a higher number of leaves on the main axis was associated with longer GCDur90, explaining 33.7 % of the variation in GCDur90, once variation between experiments and blocks were accounted for (multiple linear regression; GCDur90 ~ maL + year + block/main plot, $P < 0.001$, Table 18). Yet the overall relationship appears to result from differences in mean maL and GCDur90 between Maris Piper and Estima (Figure 34), since including experiment and cultivar in the model (multiple linear regression; GCDur90 ~ maL * year + cultivar * year + block/main plot, $P < 0.001$) increased the variation explained to 63.5 %, but GCDur90 only varied with maL in Maris Piper in Expt 3 (Table 19). Hence, maL is a poor predictor of GCDur90.

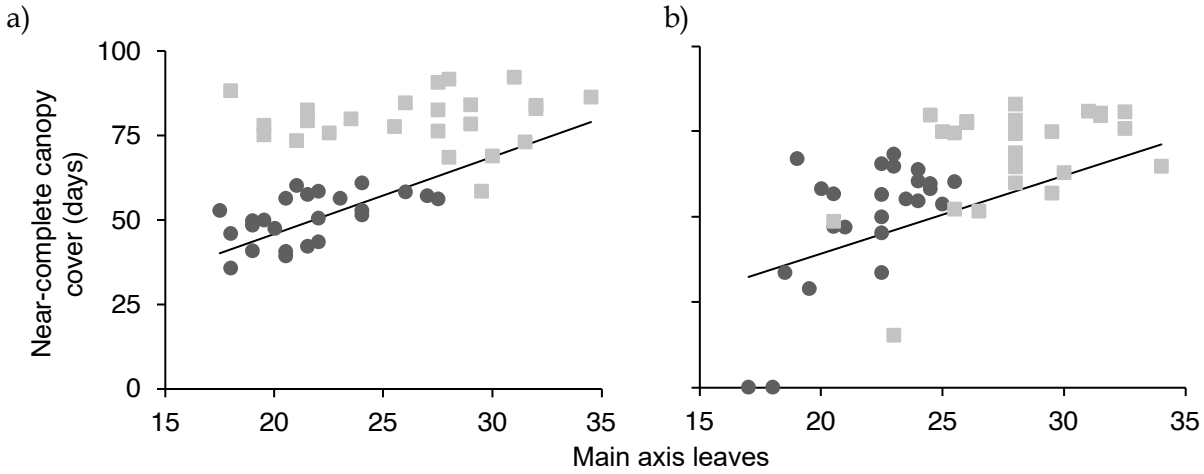

Figure 34. Relationship between number of leaves on the main axis (maL) and duration of near-complete ground cover (GCDur90) in (a) Expt 1 and (b) Expt 3. Estima, ●; Maris Piper, ■. R^2 = 0.337, see Table 18 for details of multiple linear regression.

Table 18. Relationship between duration of near complete canopy cover (GCDur90), number of leaves on the main axis (maL) and experiment (Expts 1 or 3). GCDur90 = β0 + β1*maL + β2*Expt 3.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	15.9	8.98	0.080
1	maL	2.29	0.328	< 0.001
2	Expt 3	-6.7	2.70	0.015

Table 19. Relationship between duration of near complete canopy cover (GCDur90), number of leaves on the main axis (maL), cultivar (MP) and experiment (Expts 1 or 3). GCDur90 = β0 + β1*maL + β2*Expt 3 + β3*MP + β4*(maL * Expt 3) + β5*(MP * Expt 3).

β	Coefficient	Estimate	S.E.	*P* value
0	(Intercept)	50.2	9.21	< 0.001
1	maL	0.20	0.406	0.624
2	Expt 3	-48	15.6	0.003
3	MP	28.2	3.42	< 0.001
4	maL * Expt 3	2.30	0.698	0.002
5	Expt 3 * MP	-28.1	5.50	< 0.001

Similarly, greater maL was associated with greater IGC, and maL explained 41.0 % of the variation in IGC, once variation between experiments and blocks were accounted for (multiple linear regression; IGC ~ maL + year + block/main plot, $P < 0.001$). Though the intercept for one block and one main plot differed significantly from the rest there was no overall significant effect of the block or main-plot structure (ANOVA $P = 0.699$ and 0.197, respectively) and regression coefficients without accounting for the differences between blocks were reported below (Table 20 and Figure 35). Yet again, this relationship predominantly reflected the differences in mean IGC and mean maL between cultivars, and within cultivars maL was a poor predictor of IGC, illustrated by

the *c.* 18-30 range in number of main axis leaves in plots which achieved *c.* 10 000 % days IGC observed in Expt 1 (Figure 35a).

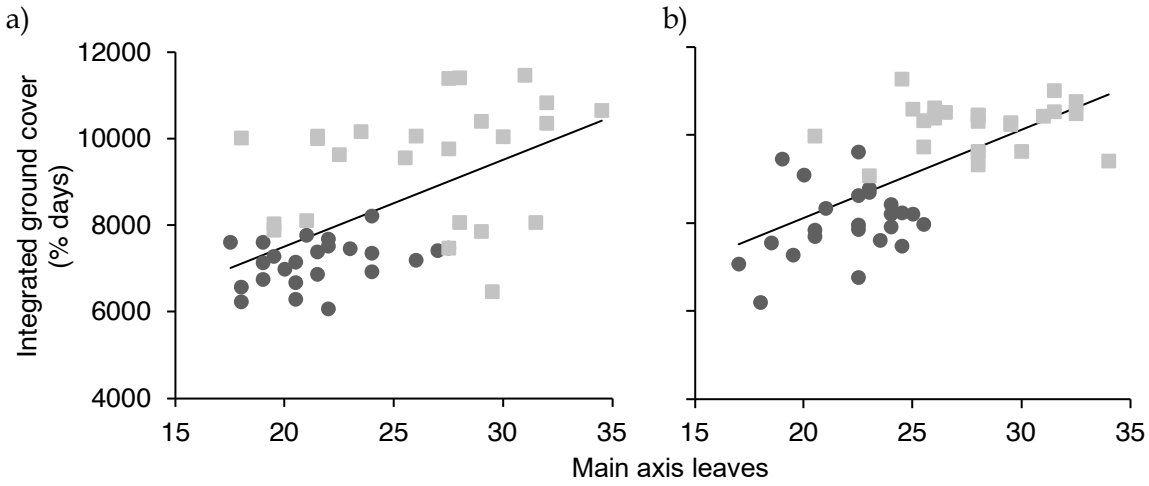

Figure 35. Relationship between number of leaves on the main axis (maL) and integrated ground cover (IGC) in (a) Expt 1 and (b) Expt 3. Estima, ●; Maris Piper, ■. R^2 = 0.410, see Table 20 for details of multiple linear regression.

Table 20. Relationship between integrated ground cover (IGC), number of leaves on the main axis (maL) and experiment (Expts 1 or 3). IGC = β0 + β1*maL + β2*Expt 3.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	3510	680	< 0.001
1	maL	200	27.5	< 0.001
2	Expt 3	610	237	0.012

4.3.4.5 Whole plant leaf appearance rate

Whole plant leaf appearance rate (pLA) was estimated by multiplying leaf appearance rate for an intermediate stem (msLA) by the number of stems produced by the plant, to examine the relationship between leaf production and canopy expansion. Average pLA was faster in Expt 1 than in Expt 3 (2.7 and 1.5 leaves/day/plant, Figure 36). In Expt 1, pLA was slowest in the April planting (2.3 leaves/day/plant) and fastest in the June planting (3.2 leaves/day/plant, P = 0.010, Figure 36a), whilst in Expt 3 there was no difference in pLA between planting dates (Figure 36b). Maris Piper had a faster pLA than Estima in Expt 1 (3.2 and 2.1 leaves/day/plant respectively, P < 0.001, Figure 36a). There was no effect of cultivar on pLA in Expt 3, (Figure 36b) due to the limited differences between cultivars in stems per plant in Expt 3 (Figure 9b). Applied nitrogen had contrasting effects on the rate of whole plant leaf appearance in Estima and Maris Piper in Expt 1, reducing pLA in Estima (2.3 to 2.0 leaves/day/plant at 0 and 250 kg N/ha, respectively), yet increasing pLA in Maris Piper (3.2 to 3.8 leaves/day/plant at 0 and 250 kg N/ha, respectively, P = 0.009). There was no interaction between cultivar and nitrogen rate in Expt 3, likely due to the limited

differences in and stem number (Figure 9) between cultivars. There was no overall effect of applied nitrogen on pLA in either experiment.

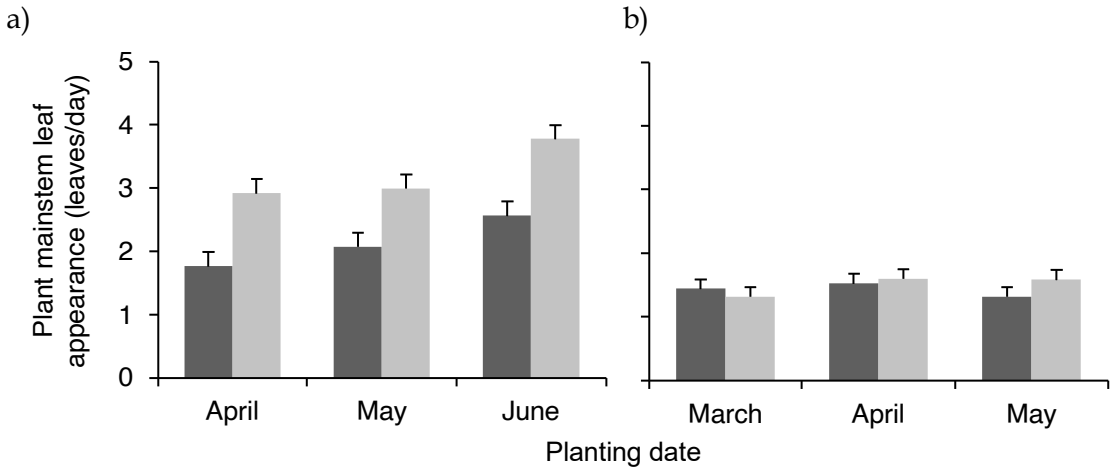

Figure 36. Effect of planting date and cultivar on rate of mainstem leaf appearance across the whole plant in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (23.99 D.F. (a), 10.96 D.F. (b)). Data presented are a mean of nitrogen treatments.

Whole plant rate of leaf appearance increased with number of stems in both experiments by 0.34 leaves/day for each additional stem produced by the plant (Figure 37). Stems per plant (S) explained 79.5 % of the variation in pLA, once variation between experiments and experimental blocks were accounted for (multiple linear regression; pLA ~ S + year + block/main plot, $P < 0.001$). Though neither the effect of block structure, nor the interaction between blocks and main plots was significant (ANOVA, $P = 0.063$ and $P = 0.465$), estimating block intercepts inflated the global intercept and regression coefficients without accounting for the differences between blocks were reported (Table 21 and Figure 37). Slower msLA in plants with a high number of stems was partially compensated for by number of stems, as shown by faster pLA in plants with more stems (Figure 37). However doubling the number of stems did not double the rate of whole plant leaf appearance due to the decreased rate of leaf appearance on an individual stem as number of stems per plant increased (Figure 29).

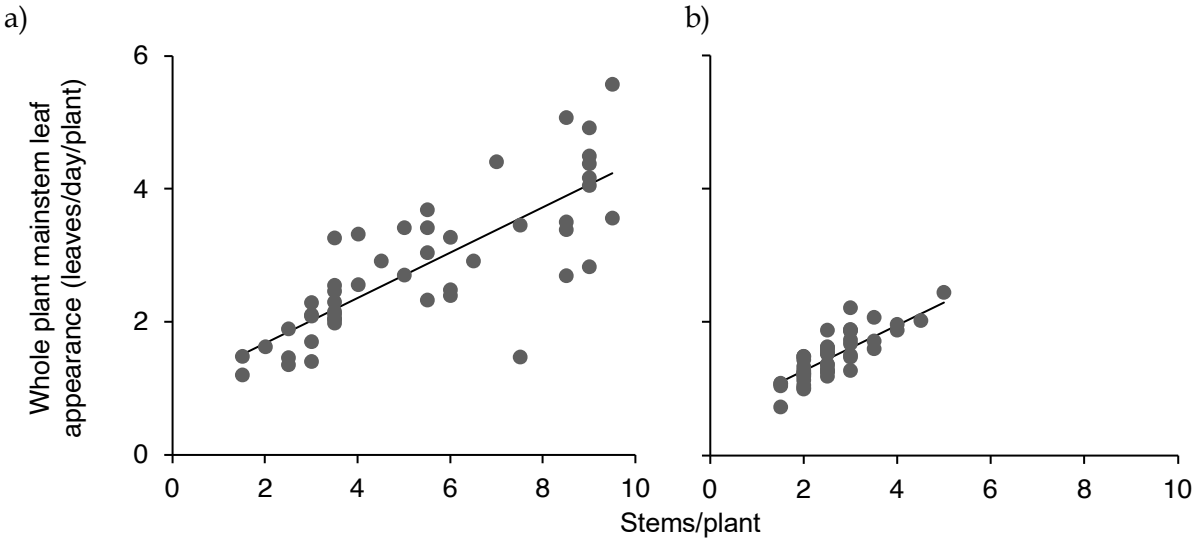

Figure 37. Relationship between number of stems per plant (S) and rate of whole plant leaf appearance (pLA) in (a) Expt 1 and (b) Expt 3. R^2 = 0.785. See Table 21 for details of multiple linear regression.

Table 21. Relationship between rate of whole plant mainstem leaf appearance (pLA), number of stems per plant (S) and experiment (Expts 1 or 3). msLA = β0 + β1*S + β2*Expt 3.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	1.00	0.160	< 0.000
1	S	0.340	0.0268	< 0.001
2	Expt 3	-0.41	0.123	0.001

There was a weak positive relationship between pLA and rate of mid-season canopy expansion (GCRate2575) across both experiments (multiple linear regression; GCRate2575 ~ pLA + year + block/main plot, R^2 = 0.380, *P* < 0.001, Table 22, Figure 38). Yet in the individual experiments, pLA was not a significant predictor of GCRate2575 (multiple linear regression; GCRate2575 ~ pLA + block/main plot, ANOVA; *P* = 0.224 and *P* = 0.185 in Expts 1 and 3, respectively), which is unsurprising given the high degree of scatter around the relationship (Figure 38).

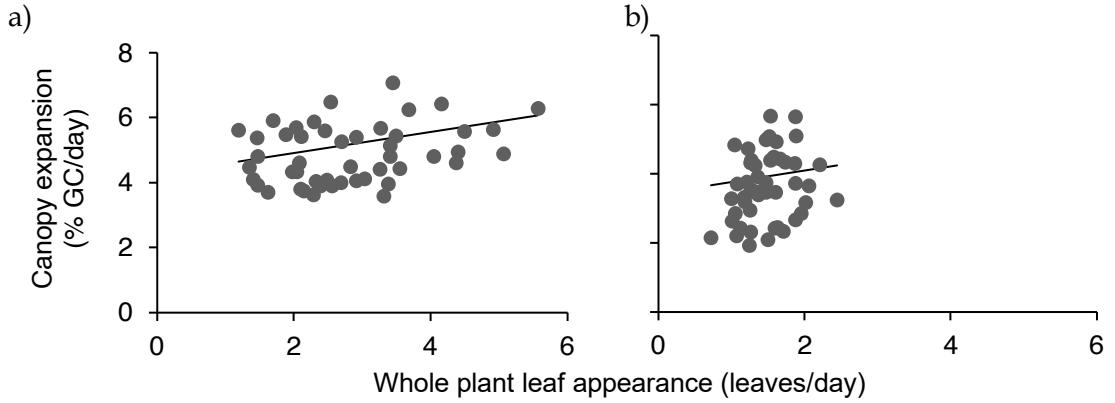

Figure 38. Relationship between rate of whole plant leaf appearance (pLA) and rate of mid-season canopy expansion (GCRate2575) in (a) Expt 1 and (b) Expt 3. R^2 = 0.380. See Table 22 for details of multiple linear regression.

Table 22. Relationship between rate of rate of mid-season canopy expansion (GCRate2575, whole plant leaf appearance (pLA) and experiment (Expts 1 or 3). msLA = β0 + β1*S + β2*Expt 3.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	4.26	0.523	< 0.001
1	S	0.33	0.124	0.010
2	Expt 3	-0.82	0.246	0.001

4.3.4.6 Sympodial branch leaf appearance

Rate of sympodial branch leaf appearance (sbLA), which occurred after the appearance of the first flower, was on average slightly faster in Expt 1, (0.279 leaves/day) than Expt 3, (0.254 leaves/day). In Expts 1 and 3, 9 and 1 % of stems measured, respectively, did not produce a sympodial branch, the majority of which were Maris Piper stems at 0 kg N/ha, and sbLA was recorded as a missing value for relevant plots. In Expt 1 sbLA was greater at the April planting (0.306 leaves/day), slowest at the May planting (0.242 leaves/day) and was intermediate at the June planting (0.289 leaves/day, *P* = 0.002, Figure 39a). There was no effect of planting date on sbLA in Expt 3 (Figure 39b). In Expt 3, sbLA was faster in Maris Piper than Estima (0.271 and 0.238 leaves/day, respectively, *P* = 0.006), yet cultivar had no effect on sbLA in Expt 1.

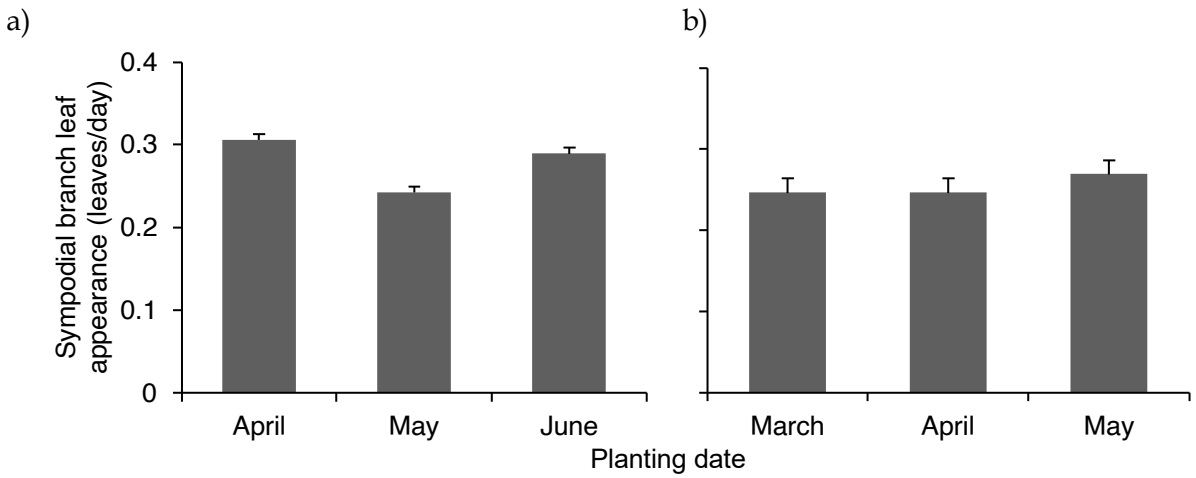

Figure 39. Effect of planting date on sympodial branch leaf appearance in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (6 D.F.). Data presented are a mean of cultivars and nitrogen treatments.

The differences in sbLA between the planting dates were not explained by variation in mean air temperature during the period of sympodial leaf appearance in either experiment (Figure 40). There were small but significant differences between the air temperatures in each planting date (Table 23), however temperature during sympodial leaf appearance varied somewhat within each planting date, likely resulting in the lack of relationship between sbLA and air temperature (Figure 40).

Table 23. Mean air temperature during the period of sympodial leaf appearance (°C) for each planting date treatment in Expts 1 and 3.

Expt	Planting date	Air temperature	S.E. (6 D.F.)
1	April	16.9	0.05
	May	18.1	
	June	18.3	
3	March	17.8	0.08
	April	17.6	
	May	17.1	

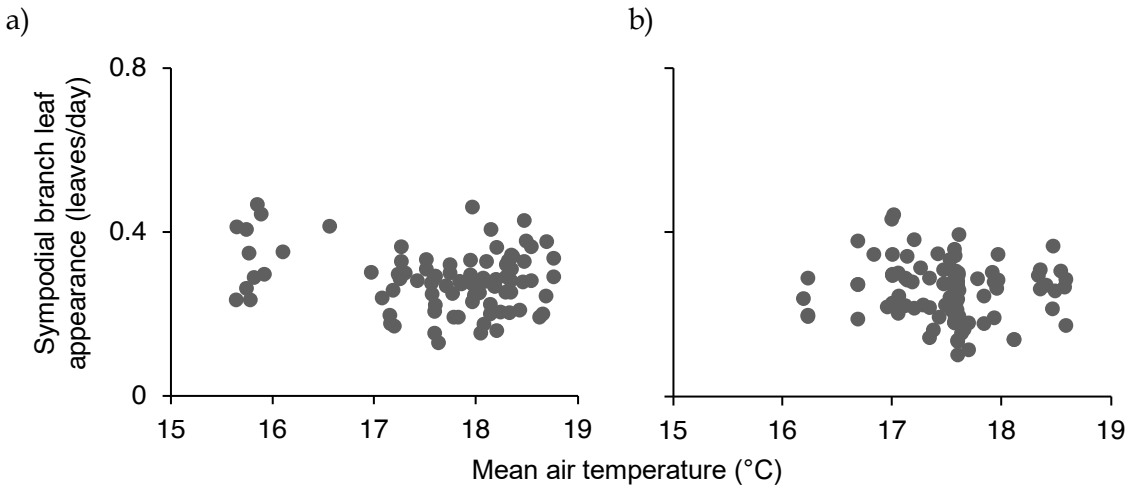

Figure 40. Sympodial branch leaf appearance rate plotted against mean air temperature during the period of sympodial leaf appearance in (a) Expt 1 and (b) Expt 3.

Sympodial branch leaves appeared at a faster rate at the high nitrogen rate than at the low nitrogen rate, with a greater difference observed in sbLA between 0 kg/N ha and 250 kg/N ha in Expt 3 (0.075 leaves/day, $P < 0.001$, Figure 41a) than Expt 1 (0.053 leaves/day, $P < 0.001$, Figure 41b).

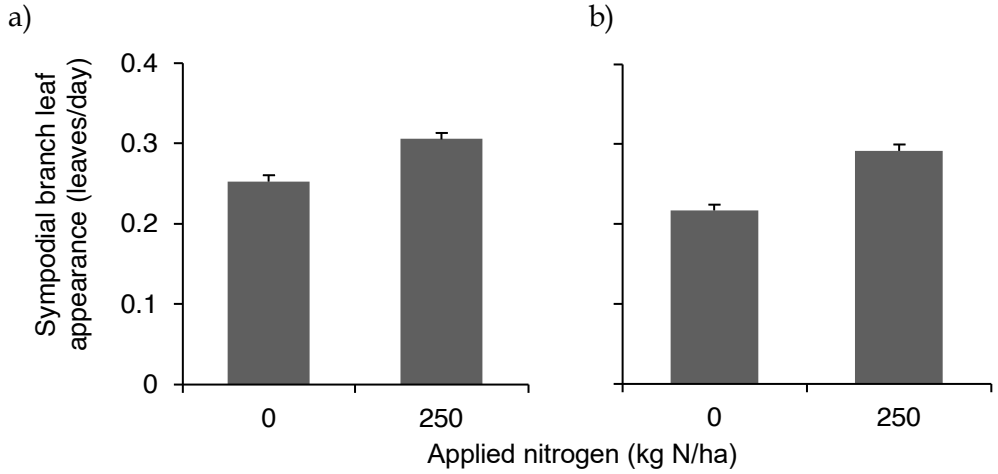

Figure 41. Effect of nitrogen on the rate of leaf appearance on the sympodial branches in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (27 D.F.). Data presented are a mean of cultivars and planting dates.

4.3.4.7 Key points: Leaf appearance

- Maris Piper produced more leaves before the first flower than Estima.
- msLA was faster in Estima than Maris Piper.
- msLA did not appear to vary with temperature as there was no correlation with temperature or pattern in response to varying planting date.
- Maris Piper leaf production tended to be slower in relation to thermal time than Estima (longer phyllochron) but this variation was not universal.
- Maris Piper produced more maL than Estima.
- There was more variation in maL with planting date in Maris Piper than Estima.
- On average four additional leaves were produced on the main axis at high nitrogen.
- pLA was greater in Maris Piper than Estima, when number of stems differed between the cultivars.
- pLA was faster at later planting dates (when there were more stems per plant).
- As expected, the pLA was greater when number of stems per plant was greater although the relationship was non-linear as rate of leaf production per stem was slower as stems per plant increased.
- Differences in pLA explained a limited amount of variation in GCRate2575.
- There was some variation in sbLA with planting date, but there was no clear pattern.
- sbLA was faster at 250 than 0 kg N/ha.

4.3.5 Leaf area index

Three harvests were carried out in each experiment at different stages of canopy development to quantify leaf area index (LAI) throughout the season. In Expt 1, harvests were carried out when average ground cover for each planting date reached *c.* 50 % and *c.* 100 % (H1 and H2 respectively) and senesced to *c.* 90 % (H3). In Expt 3 harvests were carried out at H2 and H3, but a later harvest, when the canopy had senesced to *c.* 50 % ground cover (H4) was carried out instead of H1 (Figure 42). The effects of all treatments and their interactions on LAI are reported in Appendix 10. The general pattern of LAI production throughout the season was described first, then effects of the three treatments on LAI at each harvest are described below. Interactions with other treatments were noted and main effects were detailed. Numerical differences are reported in H1 and H2, in Expt 1 since statistical analysis was

inappropriate due to the high proportion of zero values (where plots had produced neither axillary nor sympodial branches) and missing values (due to errors in data collection; 13 and 19 % of plots without axillary branch LAI (abLAI) and 8 and 21 % of plots without sympodial branch LAI (sbLAI) in H1 and H2 of Expt 1, respectively). Consequently, at H1 and H2 respectively, 17 and 54 % of plots had non-zero abLAI data, and 2 and 54 % of plots had non-zero sbLAI data. The proportion of missing data was lower at H3 in Expt 1; 8 and 4 % of plots lacked abLAI and sbLAI data, respectively. In Expt 3, missing values accounted for only 4 % abLAI H2 and 2 % sbLAI in both H3 and H4.

In Expt 1 total LAI (TotLAI) increased up to the onset of senescence (at H3), despite the reduction in mainstem LAI (msLAI) during complete canopy cover between H2 and H3 (Figure 42a). In Expt 3 the same pattern of increasing TotLAI despite decreasing msLAI was seen (Figure 42b). The proportion of TotLAI contributed by the mainstem decreased throughout the season in both experiments as axillary branch and sympodial branch leaves contributed more to whole plant leaf area (Figure 42). Mainstem comprised almost 100 % LAI at H1 (Figure 42a), to *c.* 50 % at H4 (Figure 42b). At H1 (Expt 1), 19 % of plots had axillary branch leaf material, which increased to 54 % at H2 and 92 % at H3, whilst in Expt 3. In both experiments maximal LAI was recorded at H3 (4.17 in Expt 1 and 4.76 in Expt 3).

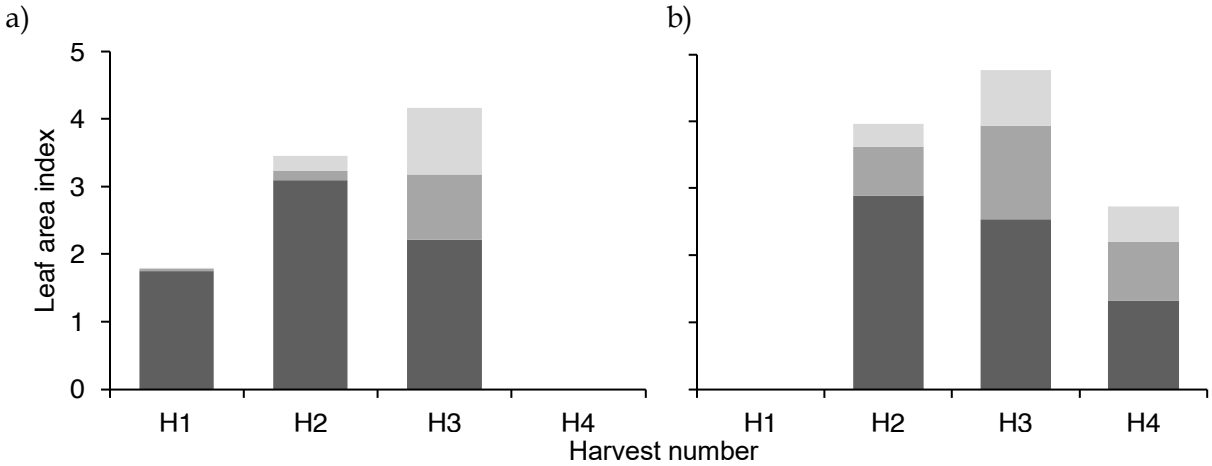

Figure 42. Changes to leaf area index (LAI) throughout the season by canopy component in (a) Expt 1 and (b) Expt 3. Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. H1, mid canopy expansion (GC~50 %); H2, early canopy closure (GC~100 %); H3, beginning of senescence (GC~90 %), H4, mid-senescence (GC~50 %). Data shown are a mean of cultivars, nitrogen treatments and planting dates.

4.3.5.1 Planting Date and LAI

Total LAI varied with planting date at most harvests throughout both experiments. At H1 in Expt 1, TotLAI was greatest in June, followed by April and May (2.06, 1.73 and 1.53, $P = 0.015$, Figure 43a), however this variation was likely due to differences in the

timing of harvest relative to canopy development of each planting date treatment, which, though designed to occur at 50 % GC, occurred at 52, 45 and 85 % GC in April, May and June, respectively. As few branches had been produced by H1, the differences observed in TotLAI were also found in msLAI across planting dates (P = 0.010, Figure 43a).

At H2 in Expt 3, msLAI was greater at later planting dates in Maris Piper, whilst Estima msLAI was greatest at the April planting (P = 0.007, Figure 43b). At H2, in Expt 3, abLAI varied with planting date and was greatest in the April planting followed by the May and March plantings (0.91, 0.71 and 0.54, respectively, P = 0.018) and these differences were reflected in TotLAI (4.48, 4.11 and 3.30, respectively, P = 0.042, Figure 43b).

At H2, Expt 1 the difference in sbLAI between 0 and 250 kg N/ha was numerically smallest at the May planting (0.27, 0.04 and 0.38 in April, May and June plantings, respectively, Figure 43a). The difference in sbLAI between cultivars also varied with planting date and in April Maris Piper produced greater sbLAI than Estima (a numerical difference of 0.14, Figure 43a), yet in May and June Estima produced a numerically greater sbLAI than Maris Piper (0.10 and 0.13, respectively, Figure 43a). Overall, sbLAI production was limited at canopy closure (100 % GC, H2), though was numerically greater in the April and June plantings (0.31 and 0.29 LAI, respectively) than in the May planting (0.05, Figure 43a).

At H3, Expt 3, Estima produced greater msLAI than Maris Piper when planted in March and April (difference of 1.06 and 0.69, respectively), but in the May planting Maris Piper produced greater msLAI (0.82, P < 0.001, Figure 43b). Axillary branch LAI also varied with planting date and cultivar at H3, in Expt 3, and was *c.* three times greater in Maris Piper than Estima in the March planting, *c.* twice as large, in Maris Piper than Estima in the April planting and equivalent, in the May planting (differences were 1.41, 1.46 and 0.02 in the respective planting dates, P < 0.001, Figure 43b). At H3, Expt 3, the range in abLAI produced between planting dates was greater at 250 than 0 kg N/ha (1.21 and 0.59, respectively P = 0.042), and abLAI was greatest in the April planting, followed by the March and May plantings (1.84, 1.38 and 0.94, respectively, P < 0.001, Figure 43b). Additionally at H3, Expt 3, there was a smaller range in sbLAI between planting dates at 0 than 250 kg N/ha (0.24 and 0.67, respectively P = 0.034) and sbLAI was greatest in March, decreasing with delay in planting, irrespective of applied nitrogen (1.09, 0.93 and 0.48, in March, April and May

plantings respectively, $P < 0.001$, Figure 43b). Similarly to the earlier harvest, at H3, Expt 1, sbLAI was lower at the May planting (0.74) than at the April and June plantings (both 1.11, $P = 0.017$, Figure 43a).

TotLAI also varied with planting date at H3 in both experiments, and in Expt 1 was greatest in the April planting followed by the June and May plantings (4.58, 3.96 and 3.72, respectively, $P = 0.006$, Figure 43a). In Expt 3, TotLAI was greatest in the April planting, followed by the March and May plantings (5.29, 4.85 and 4.13, respectively, $P = 0.040$, Figure 43b).

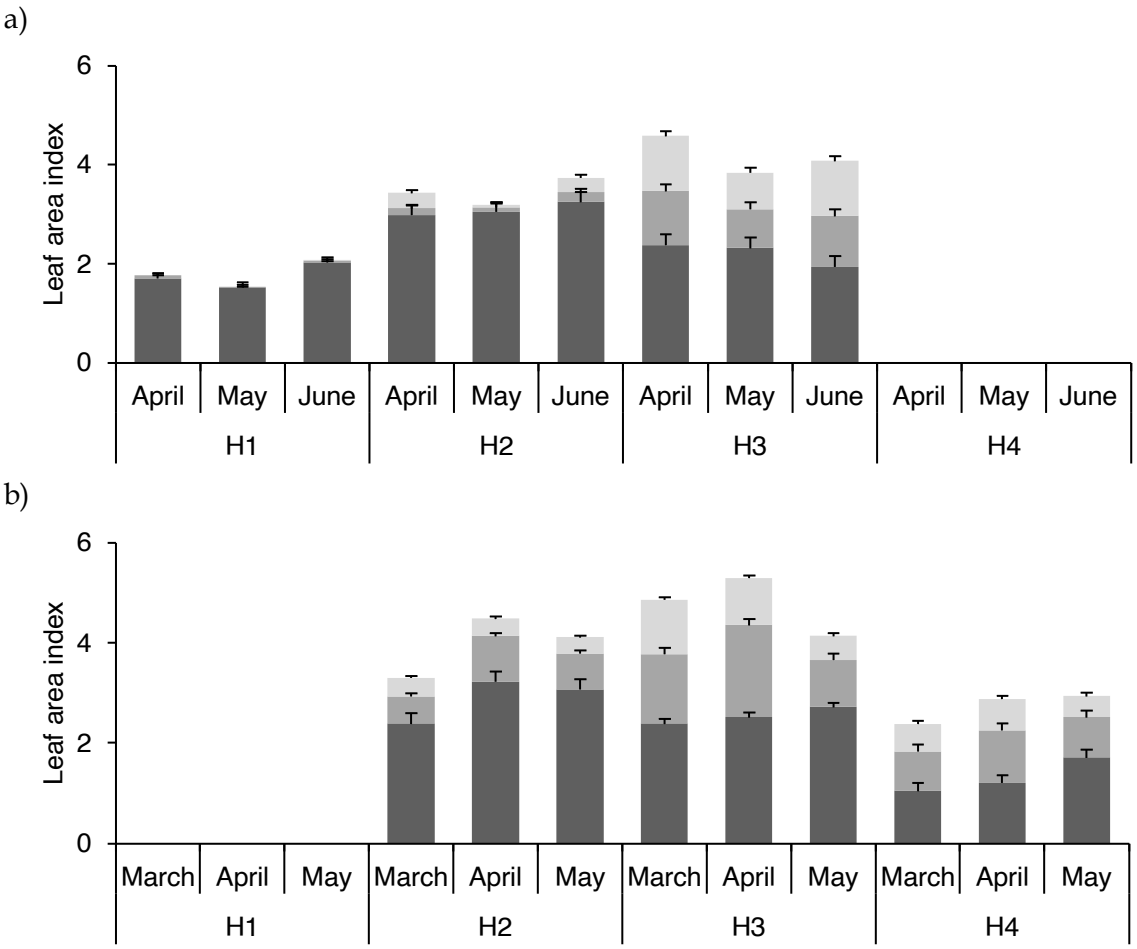

Figure 43. Effect of planting date on total LAI throughout the season in (a) Expt 1 and (b) Expt 3)). Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. H1, mid canopy expansion (GC~50 %); H2, early canopy closure (GC~100 %); H3, beginning of senescence (GC~90 %), H4, mid-senescence (GC~50 %). Bars represent S.E. (6 D.F.). Data presented are a mean of cultivars and nitrogen treatments.

4.3.5.2 Cultivar and LAI

Total LAI was similar for both cultivars in both experiments, with the only significant difference at H3 where Maris Piper produced a greater LAI than Estima in both experiments (a difference of 2.06 in Expt 1, $P < 0.001$, Figure 44a, and 0.72 in Expt 3, $P = 0.003$, Figure 44b). Yet there were differences within canopy components,

suggesting that axillary branch production occurred later in Maris Piper than Estima. In Expt 1, at H1 and H2, axillary branch LAI was numerically greater in Estima than Maris Piper (difference of 0.04 and 0.21, respectively, Figure 44a). Subsequently, at H3, Maris Piper produced greater abLAI than Estima overall (0.71, $P < 0.001$) and the difference in abLAI between cultivars was greater at 250 than 0 kg N/ha (1.34 and 0.63, respectively, $P = 0.002$, Figure 44a). Whilst in Expt 3 there was no difference in abLAI between cultivars at H2, at H3 Maris Piper produced a greater abLAI in response to additional nitrogen than Estima (2.22 and 1.06, respectively, $P < 0.001$), and Maris Piper abLAI was *c.* 1 greater than Estima ($P < 0.001$, Figure 44b). Finally, at H4, Expt 3, abLAI was 1.6 times greater in Maris Piper than Estima ($P = 0.004$, Figure 44b).

Between-cultivar differences in sympodial branch LAI appeared to follow a similar, though less distinct, pattern. Although there was no significant difference in sbLAI at H1 and H2 in Expt 1, at H3 the difference in sbLAI between cultivars was greater at 250 than 0 kg N/ha (0.90 and 0.42, $P = 0.003$), and Maris Piper produced greater sbLAI than Estima (0.66, $P < 0.001$, Figure 44a). In Expt 3, sbLAI was greater in Estima than Maris Piper at H2 ($P < 0.001$, Figure 44b) and the difference between the cultivars at 250 kg N/ha was double that at 0 kg N/ha (0.34 and 0.15, respectively, $P = 0.006$). At H3, sbLAI in Expt 3 was similar between cultivars, though numerically marginally greater in Maris Piper than Estima (0.06) and sbLAI decreased with delay in planting in both Estima and Maris Piper, though the range in sbLAI was greater in Maris Piper than Estima (0.85 and 0.37, respectively, $P = 0.042$).

Distribution of LAI within the canopy varied more in response to additional nitrogen in Maris Piper than Estima (Appendix 11) as shown above in the differences in axillary and sympodial LAI and at H3 in the greater difference between msLAI at high and at low available nitrogen in Maris Piper than in Estima in Expt 1 (1.30 and 0.66, respectively, $P = 0.038$) and in Expt 3 (2.22 and 1.06, respectively, $P < 0.001$). In both Expts 1 and 3, experiments Maris Piper msLAI was greater than Estima (0.69 and 0.97, respectively, $P < 0.001$, Figure 44).

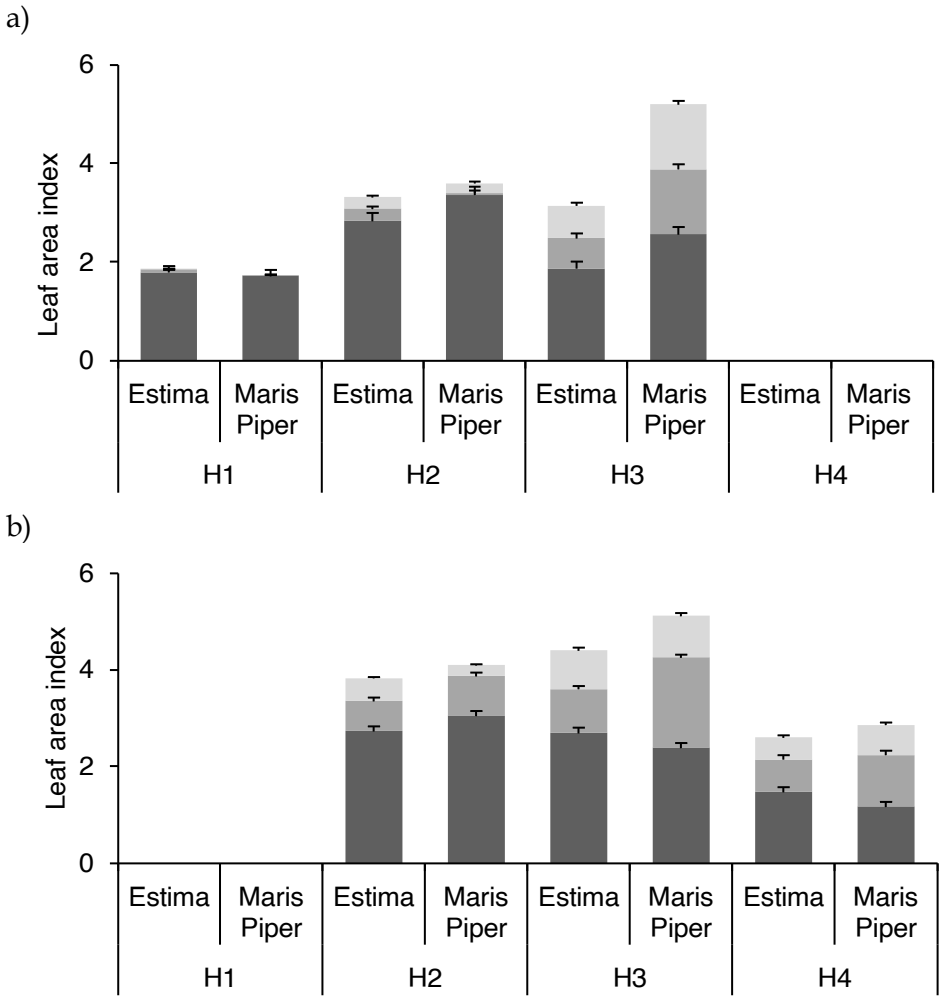

Figure 44. Effect of cultivar on total LAI throughout the season in (a) Expt 1 and (b) Expt 3. Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. H1, mid canopy expansion (GC~50 %); H2, early canopy closure (GC~100 %); H3, beginning of senescence (GC~90 %), H4, mid-senescence (GC~50 %). Bars represent S.E. (mainstem LAI, 27 D.F. at all harvests; axillary branch LAI, 21, 19 and 23 D.F. at H1, H2 and H3; sympodial branch LAI, 23, 18 and 25 D.F. at H1, H2 and H3, respectively in Expt 1. Mainstem LAI, 27, 27 and 24 D.F. at H2, H3 and H4; axillary and sympodial branch LAI, 27 D.F. at all harvests, in Expt 3). Data presented are a mean of nitrogen treatments and planting dates.

4.3.5.3 Nitrogen rate and LAI

In both experiments, total LAI was consistently greater at 250 kg N/ha than 0 kg N/ha, with the greatest differences when the canopy was harvested at near-complete GC. In Expt 1 the difference in LAI between the 0 and 250 kg N/ha plots was 0.36 at H1 (P = 0.009), 1.47 at H2 (P < 0.001) and 1.01 at H3 (P < 0.001, Figure 45a). In Expt 3, the difference in LAI between the 0 and 250 kg N/ha plots was 1.89 at H2 (P < 0.001), 1.99 at H3 (P < 0.001) and 0.37 at H4 (P = 0.009, Figure 45b), although TotLAI also varied with planting date and cultivar. At H4, TotLAI in Maris Piper was greatest in the May planting followed by the April and March plantings, though the range was greater at 250 kg N/ha than at 0 kg N/ha (1.16 and 0.31, respectively). Conversely in Estima, TotLAI was greatest in the April planting and smallest in the March planting at

0 kg N/ha, but greatest in the May planting and smallest in the April planting at 250 kg N/ha (P = 0.04).

At H1, Expt 1, msLAI was greater at 250 than 0 kg N/ha (0.36, P = 0.010), whilst sbLAI was numerically greater at 0 than 250 kg N/ha (0.03, Figure 45a). Mainstem LAI production was also greater at the higher nitrogen rate at H2 in both Expts 1 and 3 (1.23 and 0.61, respectively P < 0.001). At H2, Expt 3, Estima produced greater abLAI than Maris Piper at 0 N kg/ha (0.11) whilst at 250 kg N/ha the difference between the cultivars was reversed and Maris Piper produced greater abLAI than Estima (0.50, P = 0.011). In both Expts 1 and 3, abLAI was greater at 250 than 0 kg N/ha (0.17 and 0.92, numerical difference only and P < 0.001, respectively). At H2, in Expts 1 and 3, sympodial branch LAI was also greater at 250 than 0 kg N/ha (0.23 and 0.37, numerical difference only and P < 0.001, respectively). At 0 kg N/ha mainstem LAI increased until H3 in both experiments, whilst mainstem LAI at 250 kg N/ha was greatest at H2 (Figure 45). This suggests that either mainstem leaf production continued for longer at the 0 N treatment than at 250 N, or that at high N mainstem leaf senescence was faster than leaf production, reducing mainstem LAI earlier in the season.

At H3, in Expt 1, the difference in msLAI between nitrogen rates increased with delay in planting (0.61, 0.76 and 1.58 in March, April and May plantings respectively, P = 0.026), due to decreased msLAI with increasing lateness of planting at 250 kg N/ha, but slight increases at 0 kg N/ha. At H3, Expt 3, there was a small decrease in msLAI between 0 and 250 kg N/ha in Estima, but a greater decrease in Maris Piper (0.18 and 1.11, respectively, P = 0.005). In both experiments, msLAI was consistently greater without additional nitrogen at H3 (P < 0.001, Figure 45). LAI of axillary and sympodial branches at H3 in both experiments was greater at 250 than 0 kg N/ha (0.99 and 0.86, Expt 1, and 1.64 and 0.99, in Expt 3, respectively, P < 0.001, Figure 45b).

At H4, Expt 3 the distribution of LAI within the canopy was similar to that of H3; msLAI was greater without additional nitrogen (1.00, P < 0.001), whilst both axillary and sympodial branch LAI were greater at 250 than 0 kg N/ha (0.99 and 0.48, respectively, P < 0.001, Figure 45b). TotLAI decreased more rapidly in the higher nitrogen treatment compared to plots with no additional nitrogen in Expt 3 despite a larger canopy at the onset of senescence; at H3 the LAI of plots at 250 N were 50 % greater than those at 0 N and at H4, there was only a 20 % difference in LAI (Figure 45b).

Without additional nitrogen, axillary and sympodial branch LAI production was limited throughout the season in both experiments. At 0 kg N/ha in both experiments, the majority of the canopy consisted of mainstem leaves, ranging from 99 % at H1 to 90 % at H2 and 72 % at H3 in Expt 1 (Figure 45a) and from 86 % at H2 to 76 % at H3 and 73 % at H4 in Expt 3 (Figure 45b), although at H1 and H2 msLAI was greater at 250 than 0 kg N/ha (Figure 45).

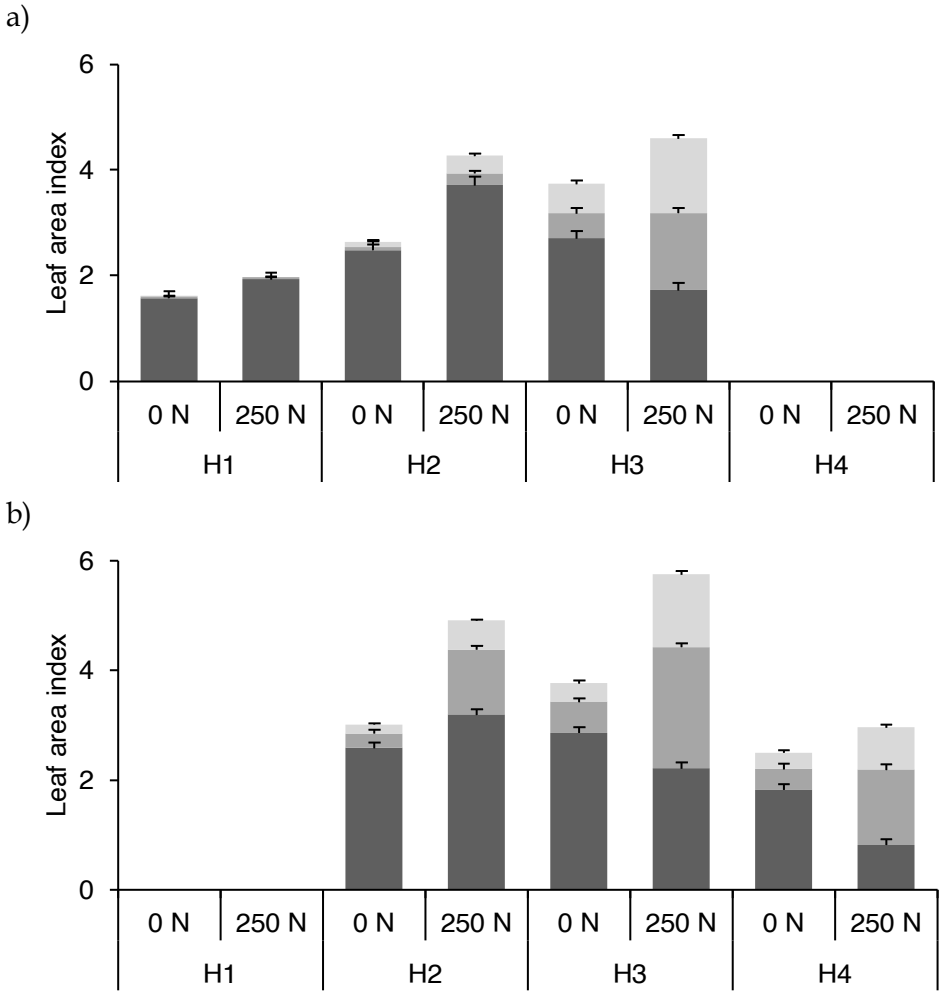

Figure 45. Effect of applied nitrogen on total LAI throughout the season in (a) Expt 1 and (b) Expt 3. Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. H1, mid canopy expansion (GC~50 %); H2, early canopy closure (GC~100 %); H3, beginning of senescence (GC~90 %), H4, mid-senescence (GC~50 %). Bars represent S.E. (mainstem LAI, 27 D.F. at all harvests; axillary branch LAI, 21, 19 and 23 D.F. at H1, H2 and H3; sympodial branch LAI, 23, 18 and 25 D.F. at H1, H2 and H3, respectively in Expt 1. Mainstem LAI, 27, 27 and 24 D.F. at H2, H3 and H4; axillary and sympodial branch LAI, 27 D.F. at all harvests, in Expt 3). Data presented are a mean of cultivars and planting dates.

4.3.5.4 Canopy cover and LAI

The relationship between ground cover (GC) and LAI was non-linear and highly variable in both Expt 1 and Expt 3 (Figure 46). Where LAI was ≥ 3, most plots had complete ground cover (Figure 46). Average LAI at 100 % GC was lower in Expt 1 (4.48) than Expt 3 (5.18). The relationship between ground cover and LAI was weaker

during senescence (H4, Figure 46b), than during canopy expansion, (H1, Figure 46a), and showed a wider range of LAI values at the *c.* 50 % GC harvest (Figure 46b).

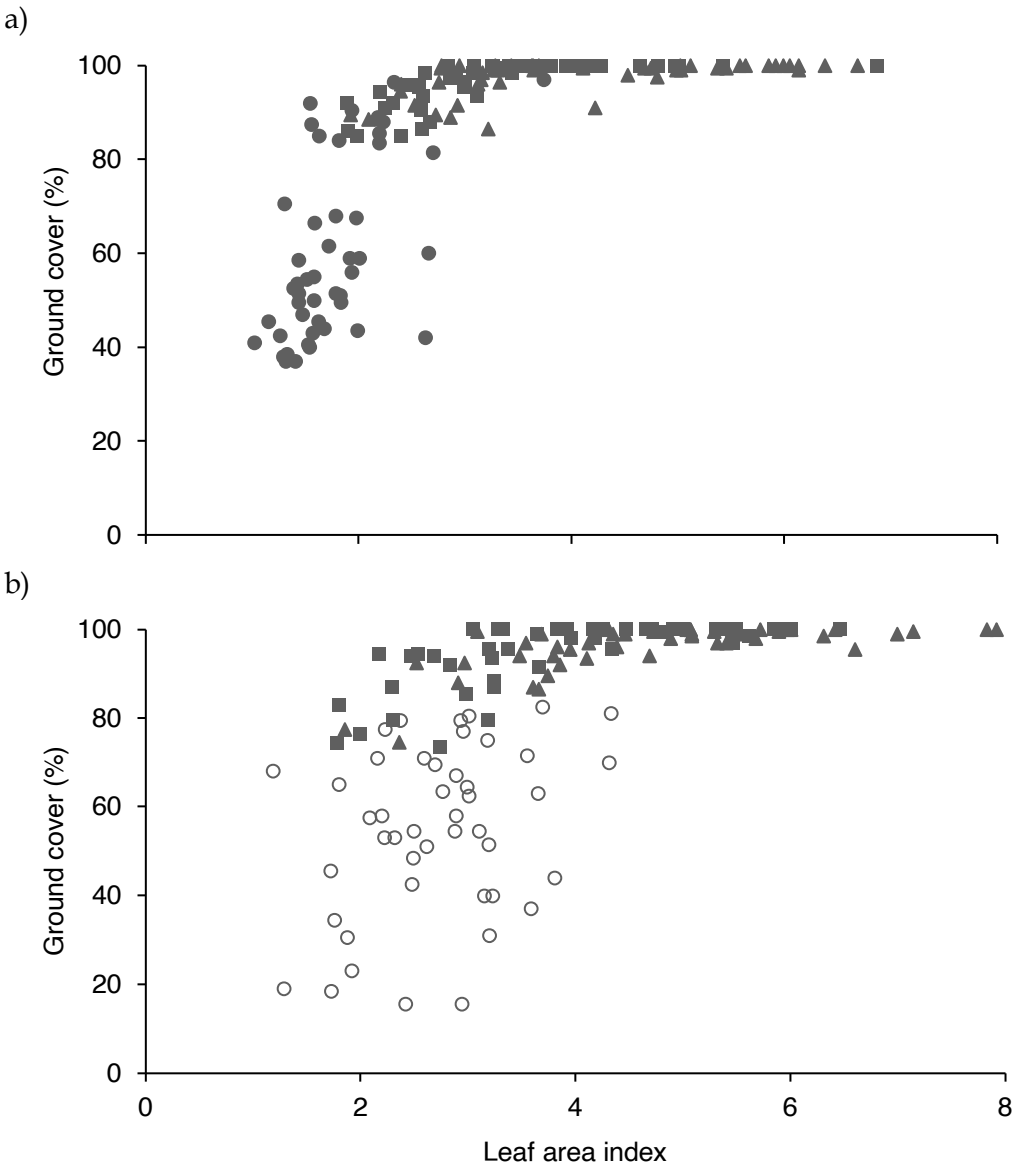

Figure 46. Relationship between leaf area index and percent ground cover, (a) Expt 1 and (b) Expt 3. H1, mid canopy expansion, GC~50 %, ●; H2, early canopy closure, GC~100 %, ■; H3, beginning of senescence, GC~90 %, ▲; H4, mid-senescence, GC~50 %, O.

Similarly, total LAI at the onset of harvest was a poor predictor of IGC and only explained 20.1 % of the variation in IGC once variation between experiments and blocks was accounted for (multiple linear regression; IGC ~ TotLAI + year + block/main plot, $P = 0.002$, Figure 47, Table 24). Incorporating cultivar in the model increased variation explained to 68.0 %, yet total LAI was no longer a significant predictor (ANOVA; $P = 0.178$) of IGC since cultivar also accounted for the differences in total LAI (multiple linear regression; IGC ~ cultivar + year + block/main plot, $P < 0.001$, data not shown). This indicates that the linear relationship between IGC and

TotLAI at the onset of senescence described above was derived from differences in mean IGC and TotLAI between the cultivars and was of limited predictive use, yet a better relationship might be found between IGC and peak TotLAI .

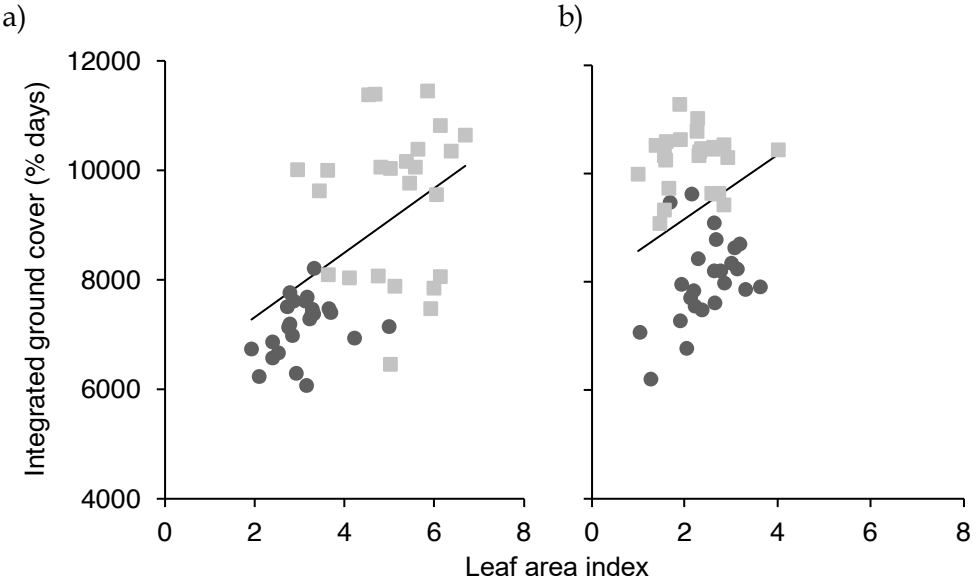

Figure 47. Relationship between leaf area index at the onset of senescence (H3) and integrated ground cover, (a) Expt 1 and (b) Expt 3. Estima, ●; Maris Piper, ■. R^2 = 0.201. See Table 24 for details of multiple linear regression.

Table 24. Relationship at H3 between integrated ground cover (IGC), total leaf area index (TotLAI) and experiment (Expts 1 or 3). IGC = β0 + β1*TotLAI + β2*Expt 3.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	6140	742	< 0.001
1	TotLAI	590	132	< 0.001
2	Expt 3	1850	358	< 0.001

4.3.5.5 Key points: Leaf area index

- Maximum LAI was recorded at H3, at the onset of senescence, in both experiments.
- There were limited differences in LAI between planting dates.
- Estima produced greater sympodial branch LAI at the early harvests.
- Maris Piper produced a greater total LAI than Estima throughout the season, but the difference was greatest at H3.
- Total LAI was greater at 250 than 0 kg N/ha across all harvests, initially due to greater mainstem LAI, but at H3 high N plots had lower mainstem LAI and much greater axillary and sympodial branch LAI.

- Additional nitrogen had a greater effect on the distribution of LAI in Maris Piper than Estima, with greater decreases in mainstem LAI and greater increases in axillary branch LAI.
- There was a non-linear relationship between LAI and percentage ground cover.
- Total LAI at the onset of senescence was a poor predictor of IGC.

4.3.6 Branch production

The distribution of leaves and branches along the mainstem and sympodial branches was recorded and described for the three destructive harvests in Expt 1 and Expt 3. Data from the earlier harvests (H1 and H2 in Expt 1) are not shown for all descriptive measures due to limited axillary and sympodial branch production at H1, and missing data resulting from an evolving harvest procedure (total stem length, TotLength, was only measured from the H2 harvest of the June planting, hence there was no TotLength data in the April and May plantings at H2 in Expt 1). The effects of all treatments and their interactions on branch production are reported in Appendix 12.

4.3.6.1 Branch production timing

The relative timing of branch production varied with planting date and at H1, in Expt 1, the June planting had a higher proportion of stems with at least one axillary branch, and a sympodial branch than the April and May plantings (pairwise comparisons using Fisher's exact test, axillary branches; April:June and May:June, $P = 0.049$ and $P = 0.007$, respectively and sympodial branches; April:June and May:June, both $P < 0.001$). Yet the relative timing of H1 varied between planting dates, as shown by the variation in % GC at harvest (52, 45 and 85 % GC in the April, May and June plantings, respectively), hence it is likely that the later stage of development of the June planting resulted in greater numbers of axillary and sympodial branches recorded as opposed to an inherent propensity of potatoes planted later in the season to produce branches earlier relative to canopy cover.

In Expt 1, at H2, the April and June plantings had twice as many stems with a sympodial branch as the May planting (pairwise comparisons using Fisher's exact test, $P < 0.001$), whilst in Expt 3 (at H2) the May planting had approximately 10 % fewer stems with sympodial branches than the April and June plantings (Table 25). There was no effect of planting date on proportion of stems with at least one axillary branch present at any harvest in Expt 3 (Table 25). There was less variation between the

planting dates in the timing of either axillary or sympodial branch production in Expt 3 than Expt 1.

Table 25. Percentage of stems with a minimum of one axillary branch or a sympodial branch present at harvest, by planting date (% presence). *P* values determined by Fisher's exact test.

Expt	Branches	Harvest	Planting date				*P*
			March	April	May	June	
1	Axillary	1	n/a	14.6	8.3	35.4	0.003
		2	n/a	85.4	37.5	87.5	< 0.001
		3	n/a	100.0	97.9	95.8	0.773
	Sympodial	1	n/a	0.0	0.0	37.5	< 0.001
		2	n/a	85.4	41.7	87.5	< 0.001
		3	n/a	100.0	95.8	97.9	0.773
3	Axillary	2	87.5	97.9	87.5	n/a	0.103
		3	95.8	97.9	91.7	n/a	0.503
		4	95.8	97.9	95.8	n/a	1.000
	Sympodial	2	97.9	97.9	85.4	n/a	0.020
		3	100.0	100.0	95.8	n/a	0.329
		4	100.0	100.0	97.9	n/a	1.000

Estima began axillary and sympodial branch production before Maris Piper as shown by the greater proportion of Estima stems with a minimum of one axillary branch or a sympodial branch (Fisher's exact test; $P < 0.001$, H1 and H2, Expt 1, Table 26). Earlier production of sympodial branches by Estima than Maris Piper was also observed in H2, Expt 3 (Fisher's exact test; $P = 0.033$). By H3 almost all stems had both axillary and sympodial branches, and there was no difference in branch presence between cultivars in either experiment (Table 26).

Table 26. Percentage of stems with a minimum of one axillary branch or a sympodial branch present at harvest, by cultivar (% presence). *P* values determined by Fisher's exact test.

Expt	Harvest	Axillary branches			Sympodial branches		
		Estima	Maris Piper	*P*	Estima	Maris Piper	*P*
1	1	36.1	2.8	< 0.001	25.0	0.0	< 0.001
	2	88.9	51.4	< 0.001	93.1	50.0	< 0.001
	3	98.6	97.2	1.000	98.6	97.2	1.000
3	2	93.1	88.9	0.563	98.6	88.9	0.033
	3	94.4	95.8	1.000	100.0	97.2	0.497
	4	94.4	98.6	0.366	98.6	100.0	1.000

In Expt 3, a smaller proportion of stems had either axillary or sympodial branches at 0 kg N/ha than at 250 kg N/ha at H2 (Fisher's exact test; $P = 0.002$ and $P = 0.033$, axillary and sympodial branches, respectively, Table 27). Whilst there was no difference in timing of the production of the first axillary branch or sympodial branch production between 0 and 250 kg N/ha in Expt 1 (Table 27), there were numerically fewer stems with axillary or sympodial branches at 0 N at H1 and H2 in Expt 1, supporting the hypothesis that mainstem growth, prior to branch production, continues for longer at 0 N than 250 N. At H3, 0 kg N/ha had 10 % fewer stems with

axillary branches than at the 250 kg N/ha treatment in Expt 3 (P = 0.013), whilst there was no difference between nitrogen treatments in sympodial branch production at either H3 or H4 (Table 27).

Table 27. Percentage of stems with a minimum of one axillary branch or a sympodial branch present at harvest (% presence), by nitrogen rate (kg N/ha). *P* values determined by Fisher's exact test.

Expt	Harvest	Axillary branches			Sympodial branches		
		0	250	*P*	0	250	*P*
1	1	13.9	25.0	0.140	9.7	15.3	0.451
	2	62.5	77.8	0.068	63.9	79.2	0.064
	3	95.8	100.0	0.245	95.8	100.0	0.245
3	2	83.3	98.6	0.002	88.9	98.6	0.033
	3	90.3	100.0	0.013	97.2	100.0	0.497
	4	93.1	100.0	0.058	98.6	100.0	1.000

4.3.6.2 Axillary branches

In Expt 1 there was a significant, but variable, effect of planting date on number of axillary branches (NoB) present at H1 and H2. At H1, in Expt 1 only April planted Maris Piper produced any axillary branches (0.2 NoB), whilst in Estima, the June planting produced more branches than either the April or May plantings (2.7, 0.6 and 0.4 NoB, respectively, P = 0.003, Figure 48a). Due to differences in the relative timing of H1 between the planting dates (as described above, 4.3.6.1), it is uncertain to what extent differences in NoB result from inherent differences between planting dates in the timing of axillary branch production. A similar pattern was observed at H2 in Expt 1, and the difference in NoB between cultivars was greatest in June (P = 0.008), with greatest mean axillary branch production also in June (followed by April and May, 3.9, 1.7 and 1.0 NoB, respectively, P = 0.004, Figure 48a).

The difference in NoB between nitrogen rates also varied with planting date in Expts 1 and 3 at H2; increasing with the delay in planting date in Expt 1 (1.0, 1.5 and 3.3, in April, May and June, respectively, P = 0.013) and in Expt 3 at 250 kg N/ha the number of axillary branches was greatest in the May planting (8.9, compared to 7.2 and 4.7 NoB in the April and March plantings, respectively) whereas at 0 kg N/ha NoB was greatest in the April planting (3.8, compared to 2.3 and 2.1 NoB in the March and May plantings respectively, P = 0.012). Overall, the March planting produced *c.* 2 fewer axillary branches than the April and May plantings at H2, Expt 3 (P = 0.030). At H3, in Expt 1, NoB varied between planting dates and was greatest in May, followed by April and June (5.1, 3.8 and 2.4 NoB, respectively, P < 0.001, Figure 48a).

Estima consistently produced more branches than Maris Piper at each harvest in Expt 1 (1.0, 2.4 and 1.1 more at H1, H2 and H3, $P < 0.001$, $P < 0.001$ and $P = 0.034$, respectively, Figure 48a), yet in Expt 3 the reverse was the case and Maris Piper consistently produced more branches than Estima (1.8, 3.0 and 1.9 more at H2, H3 and H4, $P = 0.004$, $P < 0.001$ and $P < 0.001$, respectively, Figure 48b). This variability between Expts 1 and 3 suggests that NoB is not an immutable cultivar characteristic.

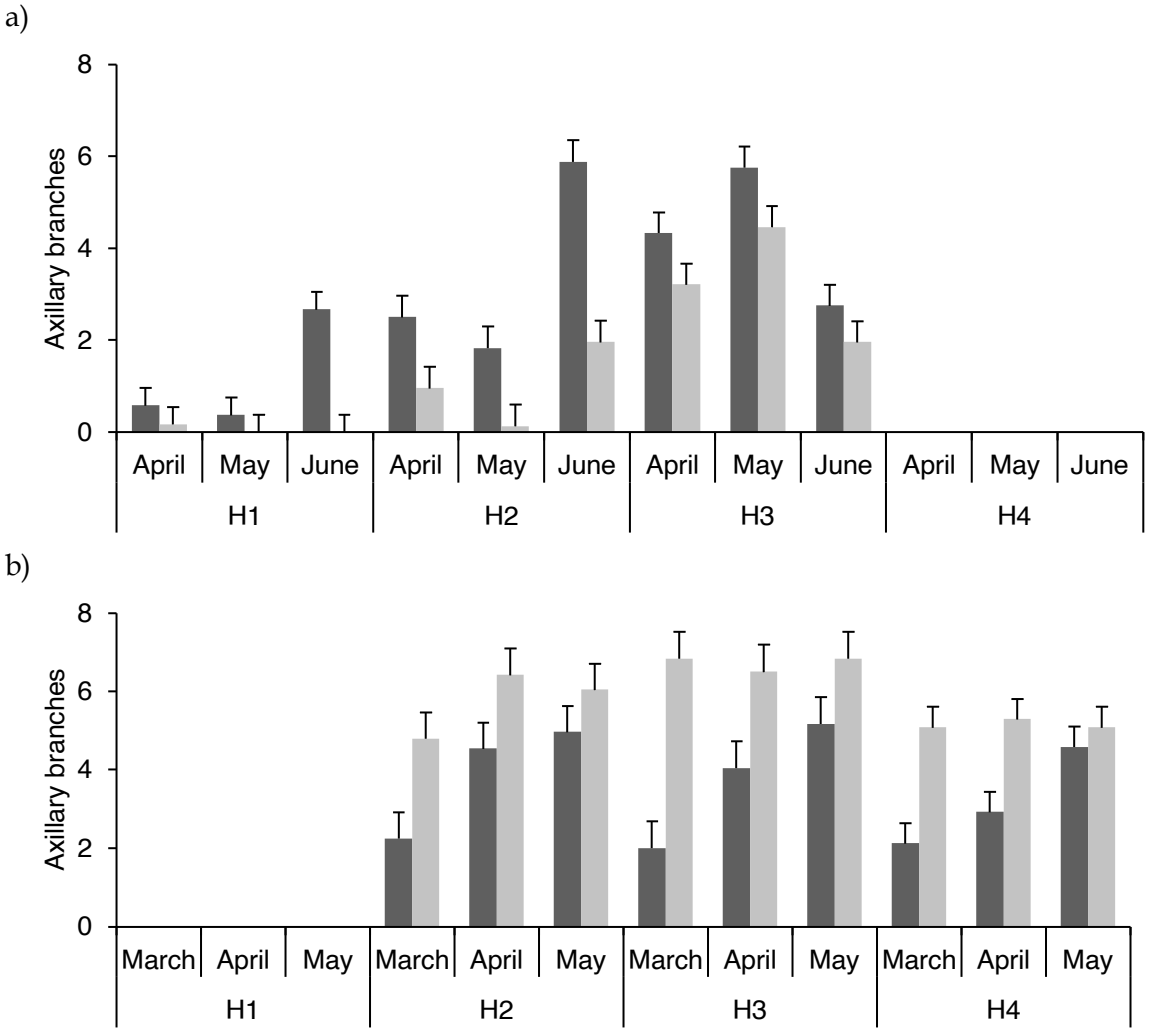

Figure 48. Effect of planting date and cultivar on number of axillary branches present in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (17.43, 13.13 and 33 at H1, H2 and H3 in Expt 1 and 23.38, 21.31 and 24.14 D.F. at H2, H3 and H4 respectively in Expt 3). Data presented are means of nitrogen rates.

In Expt 1, at H2, Estima produced an additional 2.7 axillary branches at high nitrogen, compared to an increase in NoB of 1.1 in Maris Piper ($P = 0.022$), indicating a greater axillary branch production response to additional nitrogen in Estima than Maris Piper. Yet the reverse was found in Expt 3 and Maris Piper showed a greater increase in NoB to additional nitrogen than Estima at H2 ($P = 0.003$). At H4, the difference in NoB between 0 and 250 kg N/ha was greater in the May planting (3.8 NoB) than in the

March and April plantings (both 0.8 NoB, $P = 0.020$). In both experiments, NoB was consistently greater at 250 than 0 kg N/ha across harvests, though the difference was only numerical at H1 in Expt 1 (1.9 and 1.7 at H2 and H3, in Expt 1, $P < 0.001$ and $P = 0.001$, respectively Figure 49a, 4.2, 2.6 and 1.8 at H2, H3 and H4 in Expt 3, respectively, $P < 0.001$, Figure 49b).

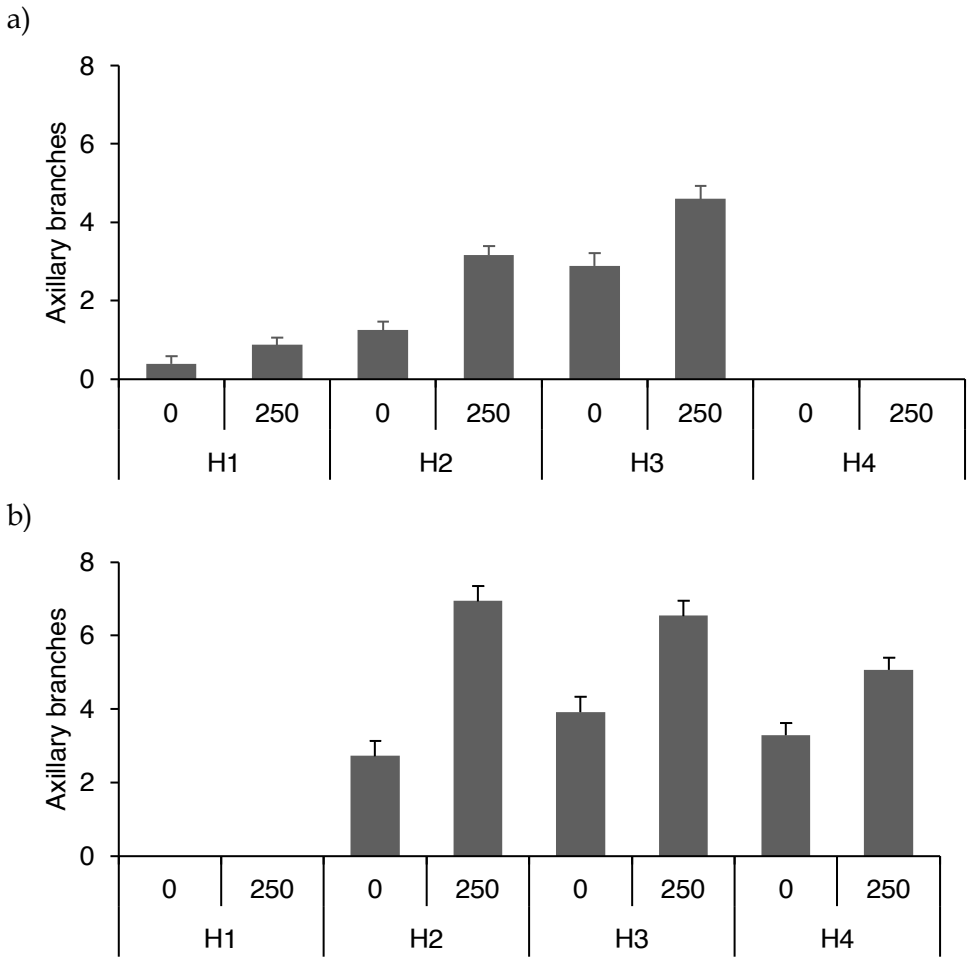

Figure 49. Effect of nitrogen rate on number of axillary branches present in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (27 D.F.). Data presented are means of planting dates and cultivars.

4.3.6.3 Axillary branch leaves

Average number of leaves per axillary branch (aveBLeaves) was not analysed in at H1, in Expt 1, since most (76 %) stems had not produced axillary branches by harvest. In Expt 3, at H2, aveBLeaves was lower in the May than the March and April plantings (4.0, 5.3 and 5.2 aveBLeaves, respectively, $P = 0.006$). At H3, Expt 1, aveBLeaves was greatest in the June planting, followed by the April and May plantings (7.1, 6.5 and 4.4 aveBLeaves, respectively, $P = 0.001$, Figure 50a). At H3, in Expt 3, there was a greater range in aveBLeaves in Maris Piper than in Estima (3.3 and 0.6 aveBLeaves, $P = 0.004$) across the planting dates, aveBLeaves was greatest at the April planting,

followed by the March and May plantings (6.5, 5.7 and 4.5 aveBLeaves, respectively, $P = 0.001$, Figure 50b). Similarly, at H4 in Expt 3, there was little difference in Estima aveBLeaves between planting dates (0.3 aveBLeaves), but fewer leaves were produced per axillary branch in the May than in the March and April plantings (4.7, 8.6 and 8.5 aveBLeaves, respectively, $P = 0.004$, Figure 50b). At H4, Expt 3, there was no difference in aveBLeaves between the March and April plantings and two fewer aveBLeaves in the May planting ($P = 0.011$, Figure 50b).

In Expt 1 Estima initially had more leaves present on each axillary branch than Maris Piper (1.3 more at H2, $P = 0.002$, Figure 50a). There was no difference between cultivars in number of leaves per branch at H2 in Expt 3. Whilst at later harvests Maris Piper had more leaves per axillary branch than Estima (2.6 more at H3 Expt 1, $P < 0.001$, Figure 50a; 1.0 and 2.0 more at H3 and H4 in Expt 3, $P = 0.003$ and $P < 0.001$, respectively, Figure 50b). In Expt 3 there were *c.* 5 leaves per axillary branch across all planting dates and harvests in Estima but aveBLeaves was more variable between planting dates in Maris Piper (Figure 50b).

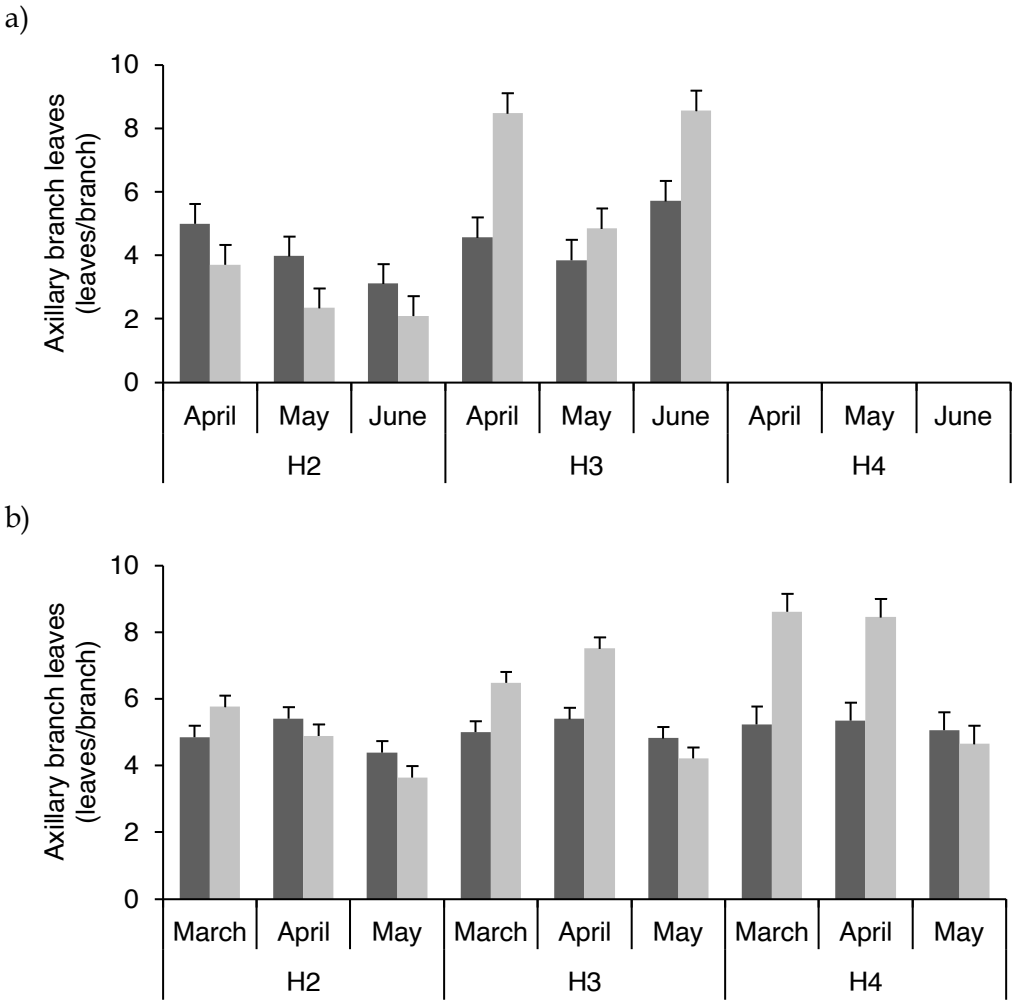

Figure 50. Effect of planting date and cultivar on mean number of leaves per axillary branch in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (10.53 and 20.79 D.F. at H2 and H3 respectively in Expt 1. 29.41, 27.44 and 22.17 D.F. at H2, H3 and H4 respectively in Expt 3). Data for H1, Expt 1, are not shown as only 19 % of stems measured had axillary branches. Data presented are means of nitrogen treatments.

At H2, Expt 1, there was little difference in aveBLeaves between nitrogen rates in the April and June plantings, but a large difference in the May planting (0.6, 1.0 and 3.1 aveBLeaves, respectively, $P = 0.024$). Throughout the season, aveBLeaves was greater at 250 kg N/ha than at 0 kg N/ha in both Expt 1 (1.5 and 3.1 aveBLeaves at H2 and H3, respectively, $P < 0.001$, Figure 51a) and Expt 3 (1.8, 1.7 and 4.1 aveBLeaves, $P < 0.001$, Figure 51b).

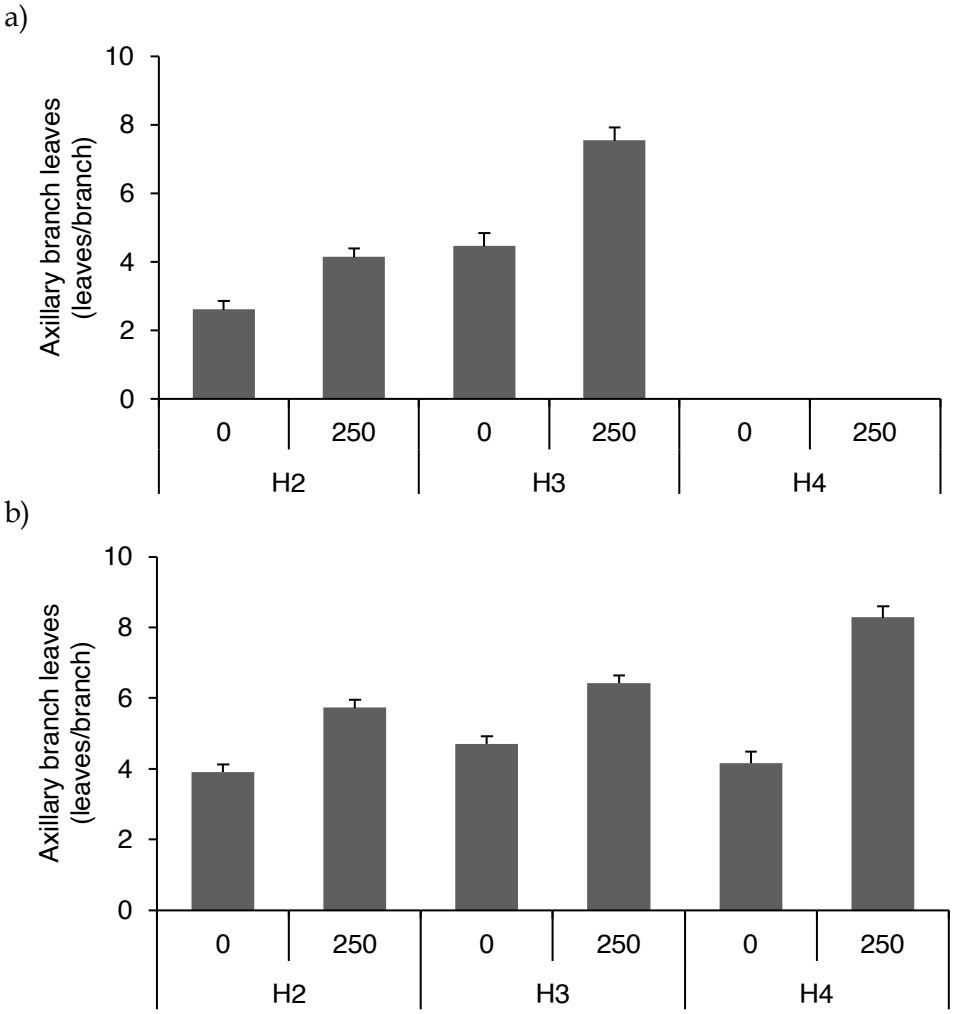

Figure 51. Effect of nitrogen on mean number of leaves per axillary branch in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (27 D.F.). Data for H1, Expt 1, are not shown as only 19 % of stems measured had axillary branches. Data presented are means of cultivars and planting date.

Axillary branch LAI increased linearly with total number of leaves on the axillary branches (BLeaves) in both experiments (multiple linear regression; abLAI ~ BLeaves * year + block/main plot, $P < 0.001$, $R^2 = 0.564$). Mean abLAI per leaf was greater at 250 than 0 kg N/ha and including nitrogen rate in the model increased variation in abLAI explained to 67.3 % (multiple linear regression; abLAI ~ BLeaves * year + nitrogen rate + block/main plot, $P < 0.001$, Table 28, Figure 52). Additional leaves in Expt 1 were associated with a greater increase in LAI than in Expt 3, as shown by the steeper gradient of the slope (see coefficients β1 and β2, Table 28), suggesting that branch leaves were larger in Expt 1 than in Expt 3.

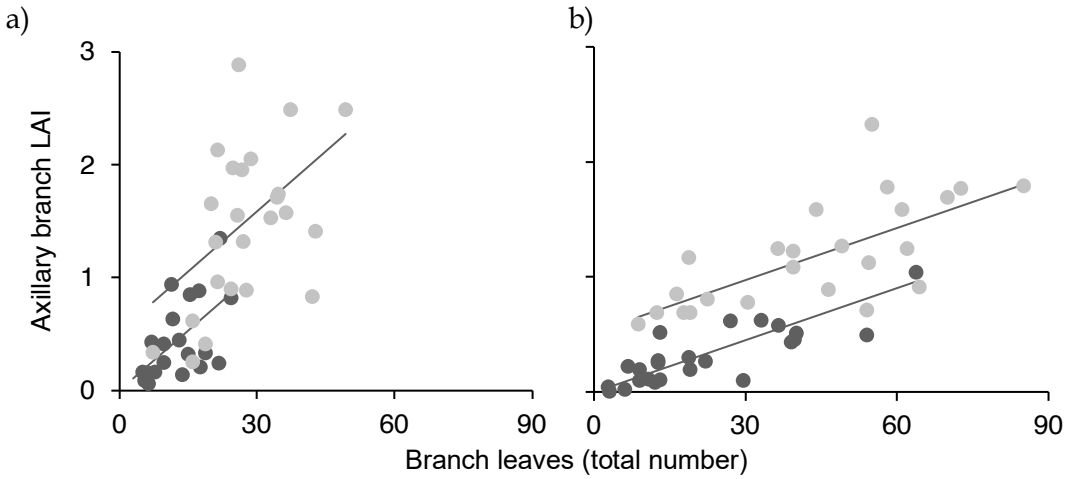

Figure 52. Relationship between total number of leaves on axillary branches (BLeaves) and axillary branch LAI (abLAI) at H3 with respect to nitrogen rate in (a) Expt 1 and (b) Expt 3. 0 kg N/ha, ●; 250 kg N/ha, ●. R^2 = 0.673. See Table 28 for details of multiple linear regression.

Table 28. Relationship at H3 between total number of leaves on axillary branches (BLeaves), axillary branch LAI (abLAI), nitrogen rate (0 or 250 N) and experiment (Expts 1 or 3). abLAI = β0 + β1*BLeaves + β2*Expt 3 + β3*250 N + β4*(BLeaves * Expt 3).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.06	0.202	0.766
1	BLeaves	0.0355	0.00653	< 0.001
2	Expt 3	0.03	0.168	0.876
3	250 N	0.53	0.101	< 0.001
4	BLeaves * Expt 3	-0.0204	0.00652	0.003

4.3.6.4 Sympodial branch insertion point and stem length

The effect of planting date on sympodial branch insertion point (SBInsert) varied with nitrogen rate at both H2 and H3 in Expt 1; at H2, not only was the range in SBInsert greater at 0 than 250 kg N/ha (89 and 20 mm, respectively), but SBInsert was greatest in the April planting at low N, and lowest in April at high N (*P* = 0.020). By H3, there was little difference in SBInsert between planting dates at 0 kg N/ha (12 mm), whereas at 250 kg N/ha the range between planting dates was greater (41 mm, *P* = 0.048), yet total stem length (TotLength) was more variable at 0 than 250 kg N/ha (83 and 41 mm, respectively, *P* = 0.049), suggesting that additional nitrogen reduced the differences in sympodial branch length between planting dates, although this was not replicated in Expt 3. At H2, Expt 3, at 0 kg N/ha, TotLength was greatest in the April planting, followed by the May and March plantings (742, 701 and 611 mm, respectively), whilst at 250 kg N/ha TotLength increased with delay in planting (753, 865 and 901 mm in March, April and May, *P* = 0.042), but the range in TotLength at 0 kg N/ha was similar to that at 250 kg N/ha (131 and 149 mm, respectively). In Expt 1, TotLength was not

recorded in one May planted Maris Piper plot, at 250 kg N/ha at H3 and was represented as a missing value. There was no overall effect of planting date on SBInsert at H2 or H3 and since TotLength was not recorded in the April and May plantings at H2 in Expt 1, the effect of planting date on TotLength was unknown (Figure 53a).

At each harvest in Expt 3, SBInsert was greater at later planting dates in Maris Piper, whilst in Estima, SBInsert was greatest in the April planting ($P < 0.001$, all harvests) and range of SBInsert between planting dates tended to be smaller in Estima (82, 64 and 90 mm at H2, H3 and H4, respectively) than in Maris Piper (258, 261 and 278 mm at H2, H3 and H4, respectively). At each harvest in Expt 3, the difference in SBInsert between Estima and Maris Piper became greater with delay in planting (mean difference across harvests of 83, 146 and 302 mm at the March, April and May plantings, respectively). There was no interaction between cultivar and planting date for total stem length in either experiment.

SBInsert was consistently greater at later planting across all harvests ($P < 0.001$, all harvests, Figure 53b), suggesting either that mainstem growth was faster following later planting, resulting in longer mainstem and greater SBInsert or that the sympodial branch production was delayed relative to planting date, again resulting in a longer mainstem and greater SBInsert. Overall at H2, TotLength was shortest in the March planting, but very similar in the April and May plantings (683, 804 and 801 mm, respectively, $P < 0.001$, Figure 53b). Whilst at H4, Expt 3, TotLength was greater in the April planting, than either the March or May plantings (999, 903 and 926 mm, respectively, $P = 0.004$, Figure 53b).

There was little growth of the mainstem between H2 and H4 (after the canopy achieved 100% GC) in all the plantings in both experiments (Figure 53) as shown by small increases in SBInserts between H2 and H3 in Expt 1 (37, 86 and 43 mm in the April, May and June plantings, respectively) and between H2 and H4 in Expt 3 (24, 36 and 49 mm in the March, April and May plantings, respectively). In Expt 3, sympodial branches were shortest in the May plantings, due to greater SBInserts and small increases in TotLegth (Figure 53b).

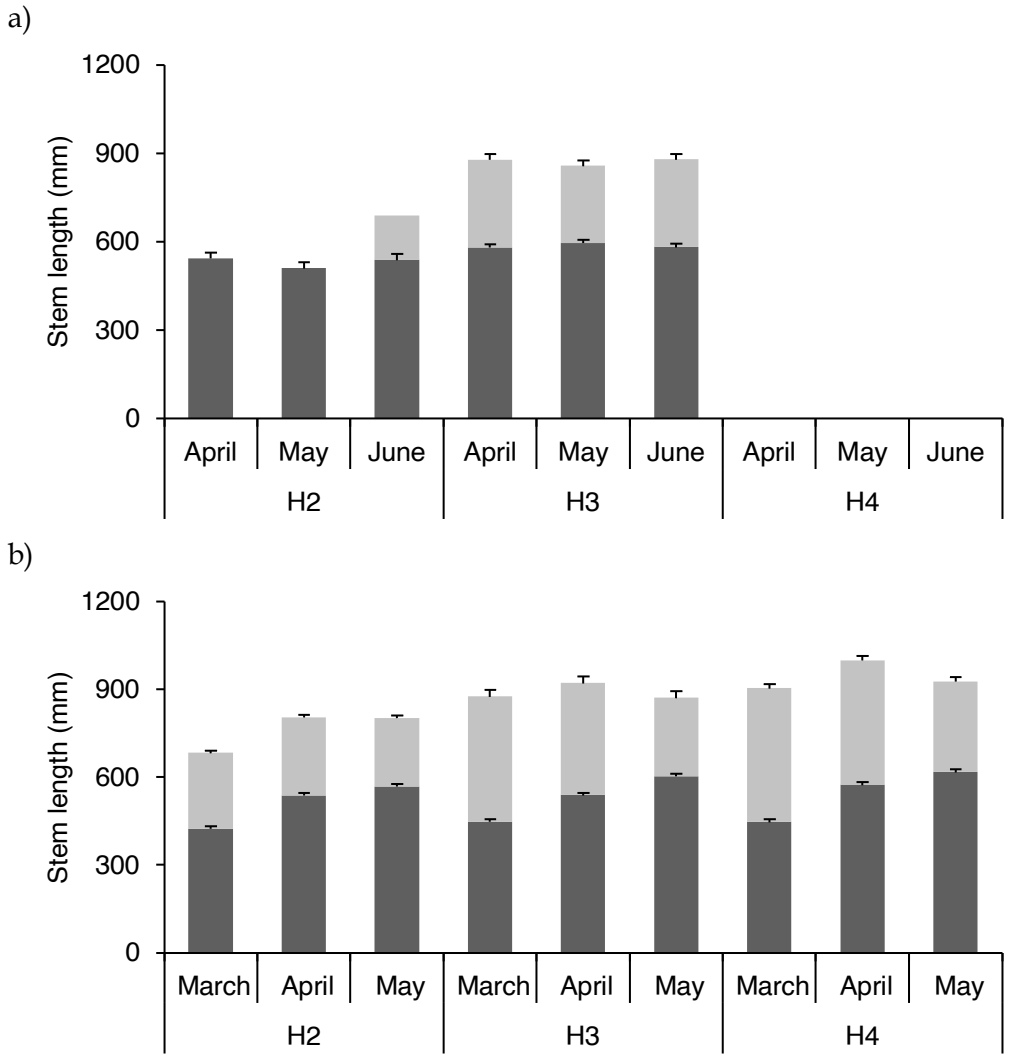

Figure 53. Effect of planting date on sympodial branch insertion point and total stem length in (a) Expt 1 and (b) Expt 3. Mainstem length, ■; sympodial branch length, ■. Bars represent S.E. (6 D.F.). Data for H1, Expt 1, are not shown as only 12 % of stems measured had sympodial branches. Total height was not measured for the April or May plantings at H2 in Expt 1. Data presented are means of cultivars and nitrogen treatments.

At both H2 and H3, in Expt 1, there was a greater increase in SBInsert in response to additional nitrogen in Maris Piper than Estima (129 and 34 mm, respectively, in H2, $P = 0.004$; 103 and 8 mm respectively, in H3, $P < 0.001$). Additionally, SBInsert in Maris Piper was greater than that in Estima at every harvest in both experiments, and the difference was typically greater at the later harvests (81 and 157 mm at H2 and H3, respectively in Expt 1, 177, 174 and 180 mm at H2, H3 and H4, respectively in Expt 3, $P < 0.001$ in all, Figure 54). At both H3 and H4, in Expt 3 the increase in TotLength in response to additional nitrogen was greater in Maris Piper than Estima (374 and 246 mm respectively at H3, $P = 0.001$, and 436 and 231 mm at H4, $P < 0.001$). There was no interaction between nitrogen rate and cultivar in TotLength in Expt 1 or H2 in Expt 3. There was no significant difference in TotLength between cultivars at H2, Expt 1, but at H3 and at each harvest in Expt 3 TotLength was greater in Maris Piper

than Estima, (180 at H3, Expt 1, 78, 217 and 305 mm at H2, H3 and H4, respectively, in Expt 3, all $P < 0.001$, Figure 54). At H2 in both experiments, the sympodial branch of Estima was longer than that of Maris Piper, but at subsequent harvests the Maris Piper sympodial branch was the longest (Figure 54).

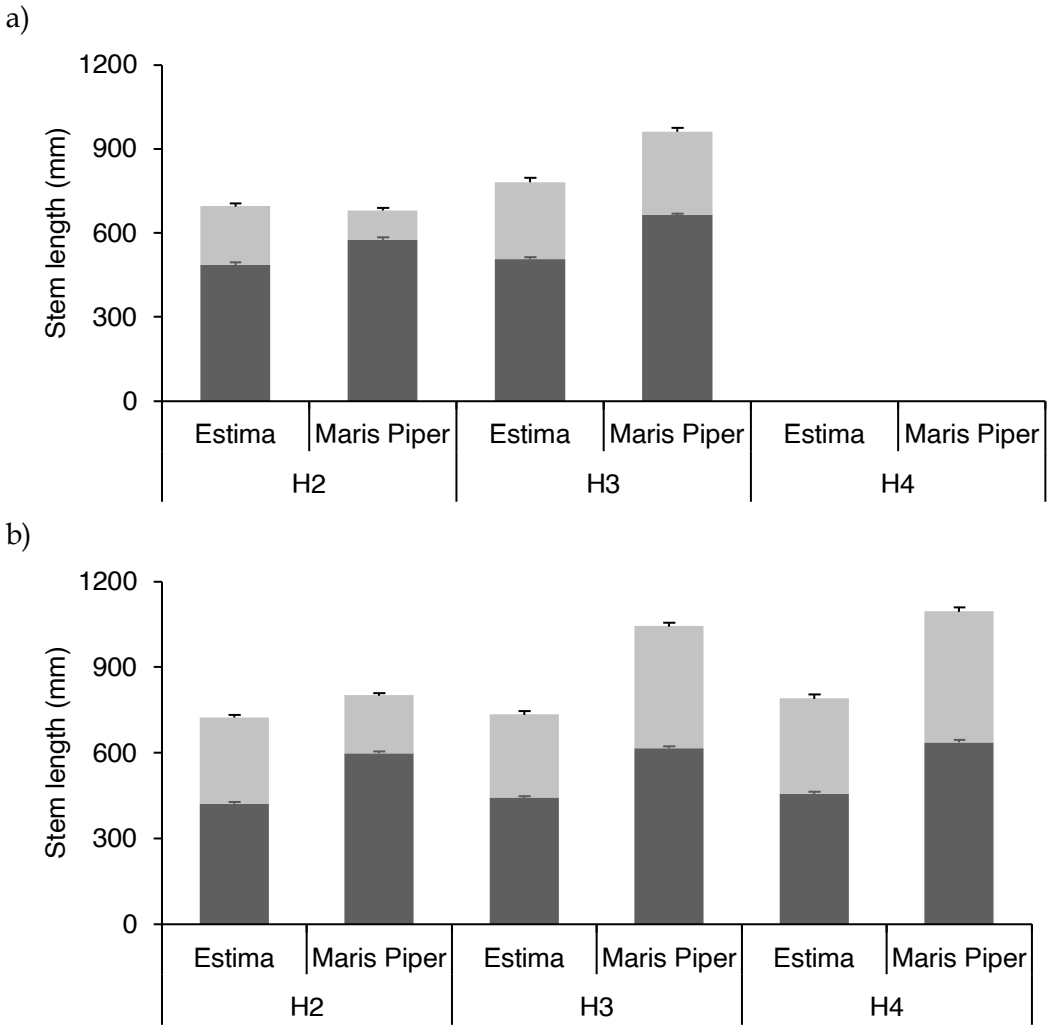

Figure 54. Effect of cultivar on sympodial branch insertion point and total stem length in (a) Expt 1 and (b) Expt 3. Mainstem length, ■; sympodial branch length, ■. Bars represent S.E. (27 D.F.). Data presented are means of nitrogen and planting date treatments. Expt 1 H2 total stem length data are from June planting date only due to missing total height data in the April and May plantings. Data for H1, Expt 1, are not shown as only 12 % of stems measured had sympodial branches.

At H3, Expt 3, there was a three-way interaction between nitrogen rate, cultivar and planting date and the greatest difference in SBInsert between nitrogen rates in Estima occurred in the March planting, but in the May planting in Maris Piper, where the difference in SBInsert between 0 and 250 kg N/ha was an order of magnitude greater than in earlier plantings for Maris Piper or any Estima plantings ($P = 0.043$). SBInsert and TotLength were greater at 250 kg N/ha than at 0 kg N/ha at both H2 and H3 in Expt 1 (all $P < 0.001$). The difference in SBInsert between nitrogen treatments

decreased between harvests (81 and 55 mm at H2 and H3 respectively), whilst the difference in TotLength increased (106 and 213 mm respectively, Figure 55a). SBInsert was also greater at 250 kg N/ha than at 0 kg N/ha at H3 and H4 in Expt 3, though the differences were small (37 and 46 mm at H3 and H4, $P < 0.001$ and $P = 0.001$, respectively, Figure 55b), though there was no effect of nitrogen on SBInsert at H2. TotLength was greater at the higher nitrogen treatment in all harvests and the difference increased throughout the season (differences of 106 and 213 mm at H2 and H3, respectively in Expt 1; and 155, 310 and 333 mm at H2, H3 and H4 respectively, in Expt 3, all $P < 0.001$).

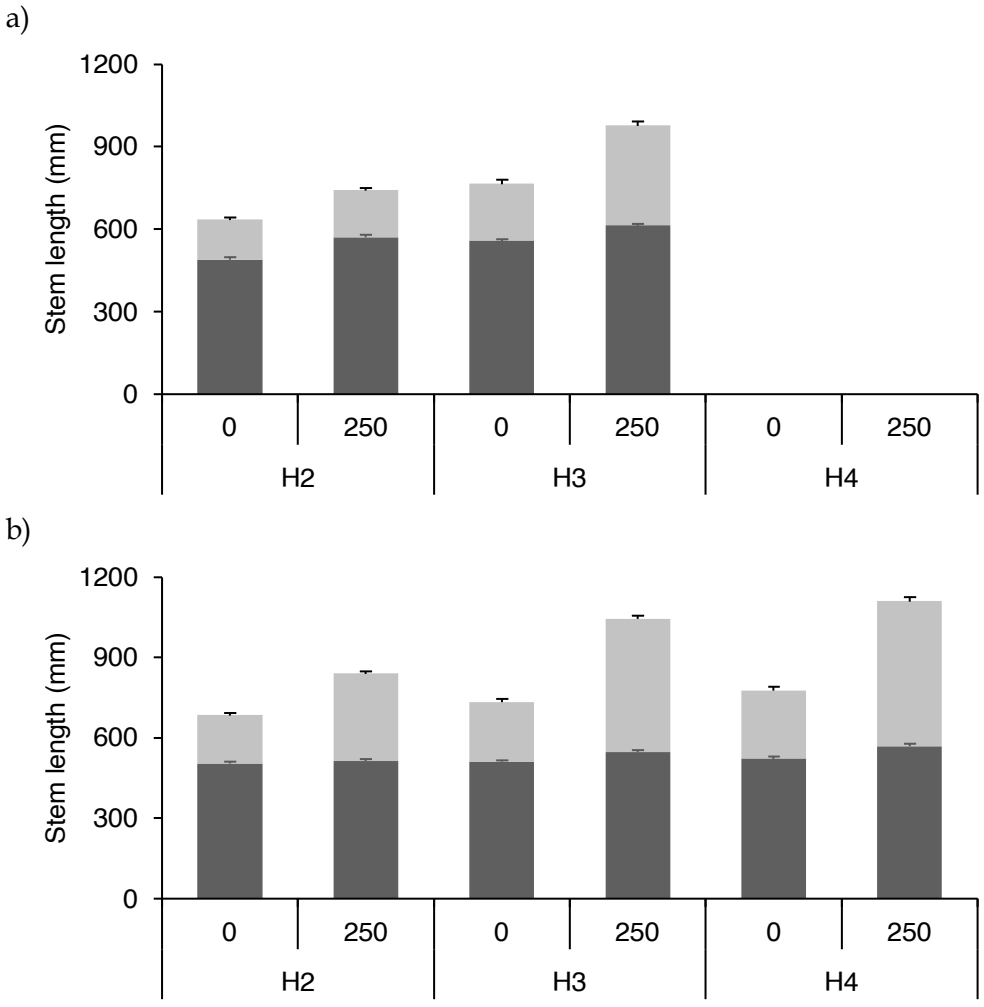

Figure 55. Effect of nitrogen on sympodial branch insertion point and total stem length in (a) Expt 1 and (b) Expt 3. Mainstem length, ■; sympodial branch length, ■. Bars represent S.E. (27 D.F.). Data presented are means of cultivars and planting dates. Expt 1 H2 total stem length data are from June planting date only due to missing total height data in the April and May plantings. Data for H1, Expt 1, are not shown as only 12 % of stems measured had sympodial branches.

4.3.6.5 Sympodial branch leaves

At each harvest in Expts 1 and 3 there was a greater range in SBLeaves between planting dates in Maris Piper than Estima (range of 3.1 and 1.5; and 7.5 and 4.5 SBLeaves, at H2 and H3, $P < 0.001$ and $P = 0.008$, respectively in Expt 1, Figure 56a; range of 2.7 and 0.4; 6.5 and 0.6; and 2.7 and 0.4 SBLeaves at H2, H3 and H4, all $P < 0.001$, respectively in Expt 3, Figure 56b). Additionally at H2, Estima produced more SBLeaves than Maris Piper in most, but not all, planting dates (the May and March planting dates were the exceptions in Expts 1 and 3, respectively, both $P < 0.001$, Figure 56). At H2, Expt 3, there was also a three-way interaction between planting date, cultivar and nitrogen rate; Estima produced more SBLeaves than Maris Piper with and without additional nitrogen at the April and May plantings, and in the March planting Maris Piper produced more SBLeaves than Estima, with a greater difference at 250 than 0 kg N/ha (1.4 and 0.3 SBLeaves, respectively, $P = 0.05$).

Whilst Estima produced a greater number of SBLeaves than Maris Piper at H2 (2.0 and 0.8 SBLeaves, in Expts 1 and 3, $P < 0.001$ and $P = 0.004$, respectively), in both experiments Maris Piper produced more SBLeaves than Estima later in the season (5.1 more SBLeaves at H3, Expt 1; 2.0 and 3.0 more SBLeaves at H3 and H4, respectively, in Expt 3, all $P < 0.001$).

Planting date had no overall effect on SBLeaves at H2 in Expt 1, but at H3, the April and June plantings produced *c.* four more sympodial branch leaves than the May planting ($P = 0.034$). Similarly in Expt 3, there was also no overall effect of planting date at H2, but at H3 and H4 number of sympodial branch leaves was greatest at the earlier planting dates ($P < 0.001$ and $P = 0.003$, respectively, Figure 56b).

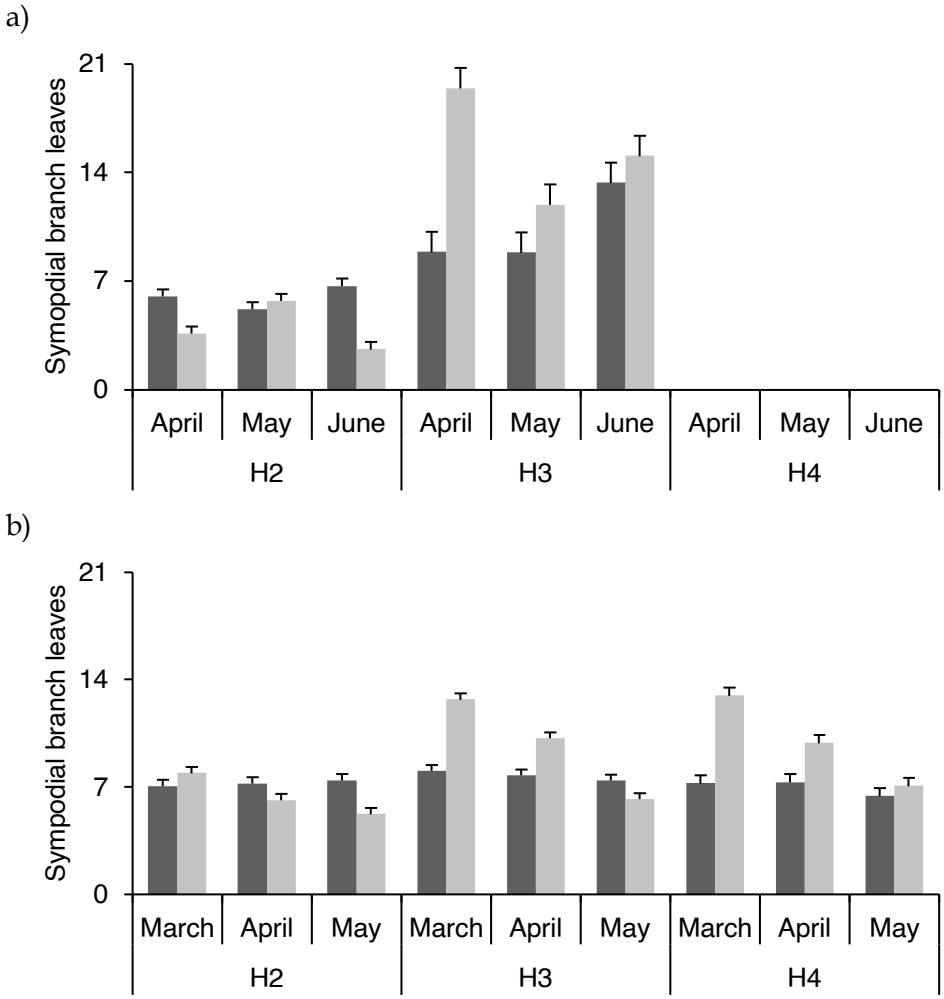

Figure 56. Effect of planting date and cultivar on number of sympodial branch leaves present at harvest in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (18.73 and 22.43 D.F. at H2 and H3 in Expt1. 11.03, 32.81 and 18.55 D.F. at H2, H3 and H4 respectively, Expt 3). Data for H1, Expt 1, are not shown as only 12 % of stems measured had sympodial branches. Data presented are means of nitrogen treatments.

At both H3 in Expt 1 and H2 in Expt 3 there was a greater range in the number of sympodial branch leaves between planting dates at 0 than 250 kg N/ha (7.1 and 4.3 SBLeaves at H3, Expt 1, $P = 0.020$; and 1.4 and 0.9 SBLeaves at H2, Expt 3, $P = 0.012$).

An average of 5.3 and 4.5 more sympodial branch leaves were present at 250 kg N/ha than at 0 kg N/ha in Expt 1 and 3 respectively (1.8 and 8.9 more at H2 and H3, respectively in Expt 1, both $P < 0.001$, Figure 57a; and 3.5, 5.1 and 4.9 more leaves at H2, H3 and H4 respectively in Expt 3, all $P < 0.001$, Figure 57b). The similar number of sympodial branch leaves at H3 and H4 suggests that sympodial leaf production did not continue after canopy senescence began at H3 (Figure 57b).

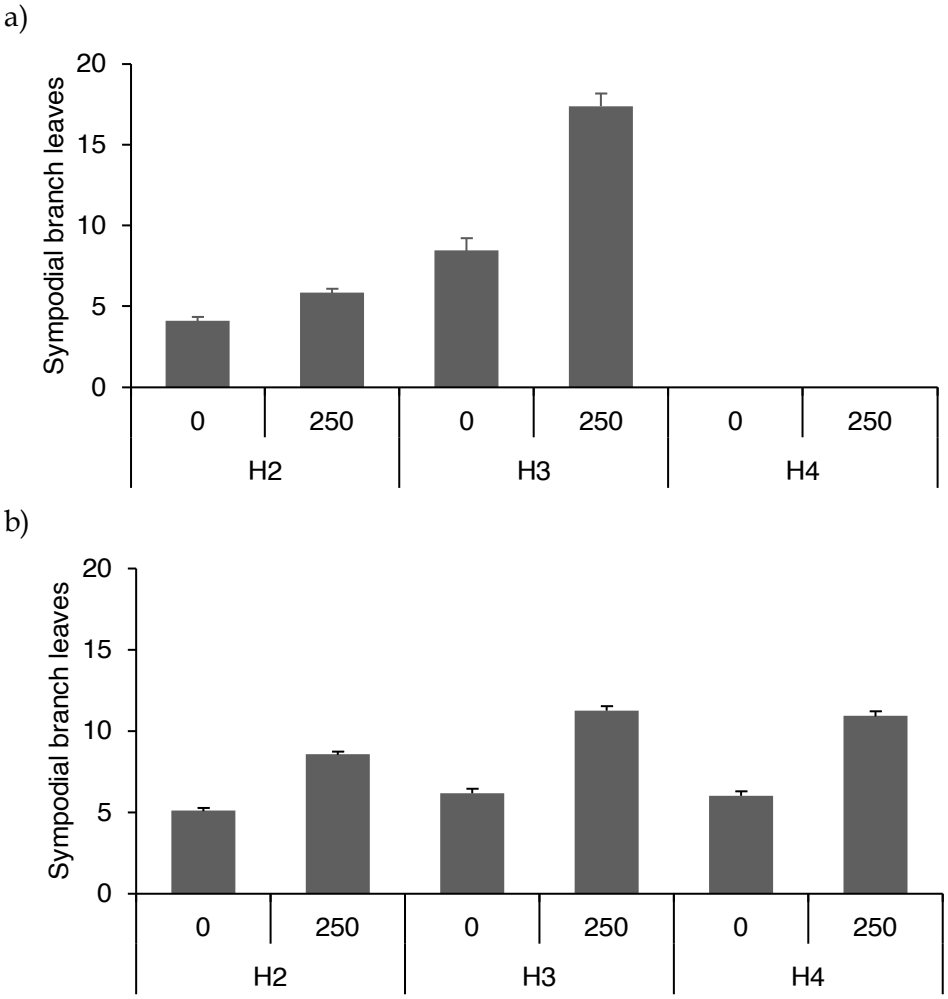

Figure 57. Effect of nitrogen on number of sympodial branch leaves present at harvest in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (27 D.F.). Data for H1, Expt 1 are not shown as only 12 % of stems measured had sympodial branches. Data presented are means of cultivars and planting date.

Sympodial branch LAI increased linearly with SBLeaves in both experiments (multiple linear regression; sbLAI ~ SBLeaves + block/main plot, $P < 0.001$, $R^2 = 0.683$). Mean sbLAI per leaf was greater at 250 than 0 kg N/ha and including nitrogen rate in the model, whilst also accounting for variation between experiments, increased the proportion of variation in sbLAI explained to 73.8 % (multiple linear regression; sbLAI ~ SBLeaves + year + nitrogen rate + block/main plot, $P < 0.001$, Table 29, Figure 58).

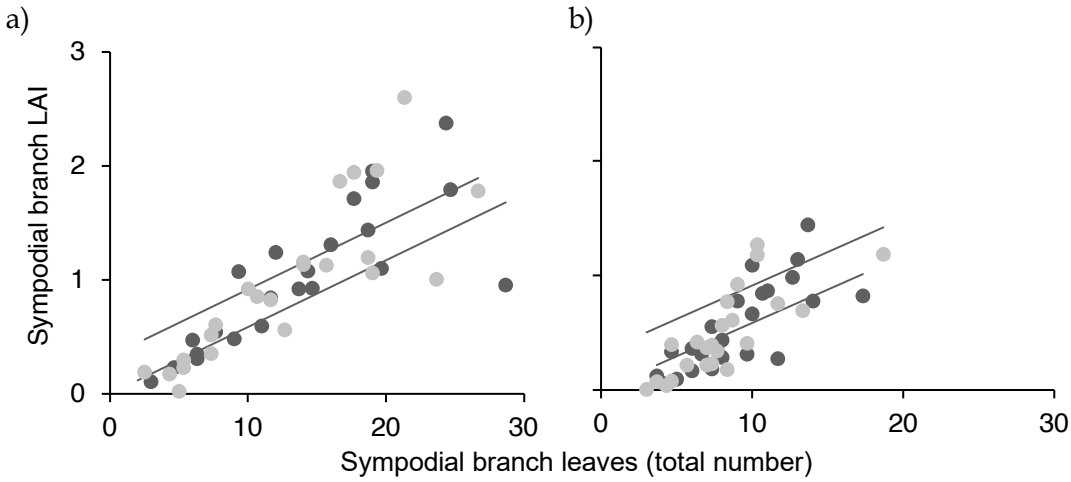

Figure 58. Relationship between total number of leaves on sympodial branches (SBLeaves) and sympodial branch LAI (sbLAI) at H3, with respect to nitrogen rate in (a) Expt 1 and (b) Expt 3. 0 kg N/ha, ●; 250 kg N/ha, ●. R^2 = 0.738. See Table 29 for details of multiple linear regression.

Table 29. Relationship at H3 between total number of sympodial branches leaves (SBLeaves), sympodial branch LAI (sbLAI), nitrogen rate (0 or 250 N) and experiment (Expts 1 or 3). abLAI = β0 + β1*SBLeaves + β2*Expt 3 + β3*250 N.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.15	0.144	0.314
1	SBLeaves	0.0586	0.00786	< 0.001
2	Expt 3	-0.189	0.0709	0.009
3	250 N	0.330	0.0804	< 0.001

4.3.6.6 Key points: Branch production

- Estima produced axillary and sympodial branches earlier than Maris Piper.
- Axillary and sympodial branches were produced slightly earlier at the higher nitrogen rate, though the differences were only significant in Expt 3.
- Differences in timing of axillary and sympodial branch production in response to planting date were probably the result of differences in the timing of harvests.
- Maris Piper produced more axillary branches per stem when number of stems per plant was equal, but when Maris Piper had more stems, Estima produced more branches.
- Estima axillary branch production varied in response to planting date more than Maris Piper and produced more branches at later planting dates in Expt 3.
- More axillary branches were produced at high nitrogen.
- More leaves were produced per axillary branch by Maris Piper than Estima, with a greater difference at later harvests, yet smaller difference at later plantings (Expt 3).

- More leaves were produced per axillary branch at high nitrogen.
- Increasing number of total leaves increased LAI in axillary and sympodial branches, but each sympodial branch leaf made a greater contribution to LAI than each axillary branch leaf.
- The mainstem was longer at flowering as sympodial branch insertion points were higher up the main axis, and sympodial branches were shorter at later planting dates in Expt 3.
- Estima mainstems were shorter at flowering (lower sympodial branch insertion points) than Maris Piper.
- Sympodial branches were longer in Maris Piper than Estima at the end of the season.
- The mainstem was shorter without additional nitrogen.
- Sympodial branches were longer at high nitrogen throughout the growing season.
- Number of sympodial branch leaves was more variable in Maris Piper than Estima and tended to decrease with lateness of planting date.
- More sympodial branch leaves were produced at high nitrogen.

4.3.7 Tubers

Tubers were graded, weighed, and dried at each harvest. Data from the final harvest only are shown here (except where stated otherwise) as tuber yield was not the main focus of the experiments. Fresh weight was not recorded in two plots (May planted Maris Piper, at 0 kg N/ha, in H2, Expt 1 and March planted Maris Piper, at 250 kg N/ha at final harvest, Expt 3), and was represented as missing values. Data from harvests 1-4 are in Appendix 13.

4.3.7.1 Number of tubers

Number of tubers greater than 10 mm in diameter varied with cultivar within planting dates and in Expt 1, May planted Maris Piper produced approximately 280 000/ha more tubers than either the April or June plantings, whilst the number of Estima tubers increased with delay in planting ($P < 0.001$, Table 30). Overall, the greatest number of tubers was produced at the May planting (884 000 compared to 700 000 and 750 000/ha produced by the April and June plantings, respectively, $P = 0.017$), a difference attributable to the large number of tubers produced by Maris Piper in May. In Expt 3, the number of tubers produced by Estima declined with delay in planting, yet in Maris Piper tuber number was greater at later than early planting dates ($P = 0.001$), hence

there was no main effect of planting date. Maris Piper produced more tubers greater than 10 mm in diameter than Estima in both experiments (90 % and 20 % more in Expt 1 and Expt 3, respectively, $P < 0.001$ in both experiments, Table 30). Nitrogen rate had no significant effect on number of tubers produced in either experiment.

Table 30. Number of tubers (tubers 000/ha) at final harvest in Expt 1 (12.42 D.F.) and Expt 3 (11.09 D.F.). Data presented are a mean of nitrogen rates.

		Cultivar		
Expt	Planting date	Estima	Maris Piper	S.E.
1	April	456	944	38.8
	May	560	1207	
	June	591	910	
3	March	489	479	31.0
	April	395	476	
	May	355	534	

4.3.7.2 Fresh tuber yield

In Expt 1 final fresh yield decreased with delay in planting ($P < 0.001$, Table 31). In Expt 3, Estima yield decreased with delay in planting, whilst final fresh yield of Maris Piper did not vary between planting dates ($P = 0.021$, Table 31) and there was no significant effect of planting date on fresh yield overall. There was no significant difference in fresh weight yield between Estima and Maris Piper at the final harvest in Expt 1 despite the production of a greater yield by Estima at H2 and H3 (Figure 59a). In Expt 3, Estima consistently produced a larger fresh weight tuber yield than Maris Piper (Figure 59b) and final fresh yield was significantly greater (65.6 and 58.5 t/ha in Estima and Maris Piper, respectively, $P < 0.001$, Table 31). In both experiments the difference in yield between cultivars was greatest at H3 (difference of 16.1 and 10.5 t/ha in Expt 1 and Expt 3 respectively) and the difference had decreased by the final harvest (difference of 1.9 and 7.1 t/ha in Expt 1 and Expt 3 respectively, Figure 59).

Table 31. Final harvest fresh weight tuber yield (t/ha) in Expt 1 (16.89 D.F.) and Expt 3 (9.42 D.F.). Data presented are a mean of nitrogen rates.

Expt	Planting date	Cultivar		S.E.
		Estima	Maris Piper	
1	April	69.3	72.2	2.53
	May	63.3	60.1	
	June	49.5	44.2	
3	March	71.2	58.7	3.44
	April	66.9	57.8	
	May	58.6	58.9	

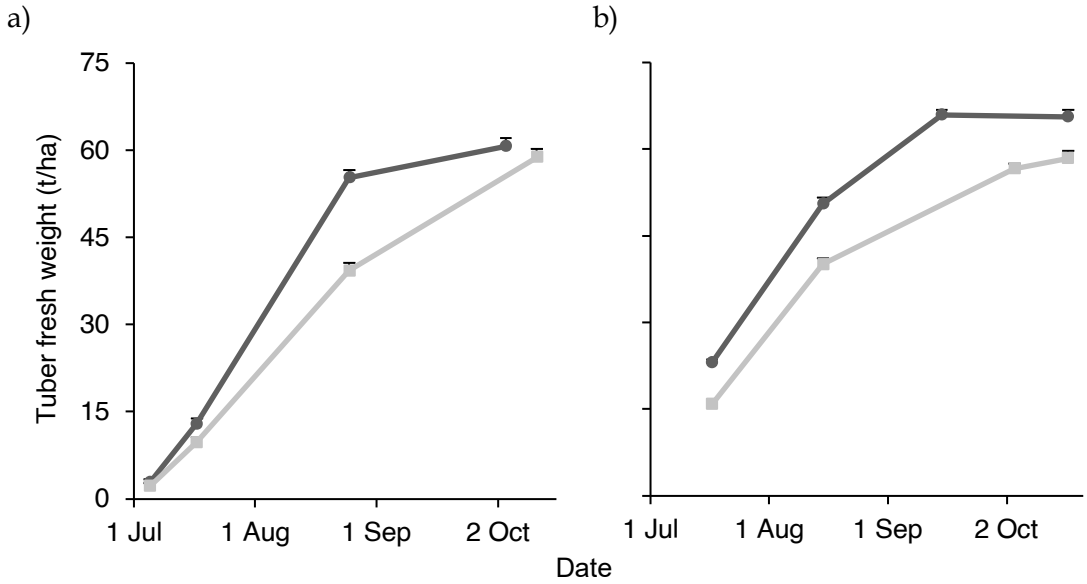

Figure 59. Fresh tuber yield at successive harvests in (a) Expt 1 and (b) Expt 3. Estima, ●; Maris Piper, ■. Data presented are a mean of nitrogen treatments and planting dates. Error bars represent S.E. (27 D.F. for all harvests in both experiments, except H2, Expt 1 and final harvest, Expt 3, both 26 D.F.).

At the final harvest, plots with 250 kg N/ha yielded a greater fresh weight than those without applied nitrogen (Table 32). The difference was slightly larger in Expt 1 (5.6 t/ha, $P = 0.007$) than in Expt 3 (5.4 t/ha, $P = 0.006$), though average tuber yield was similar in both experiments.

Table 32. Final harvest fresh weight tuber yield (t/ha) at different nitrogen rates in Expt 1 and Expt 3. Data presented are a mean of planting date treatments and cultivars.

	Nitrogen rate (kg N/ha)		S.E.
Expt	0	250	(27 D.F.)
1	57.0	62.6	1.37
3	59.3	64.7	1.28

4.3.7.3 Tuber percent dry matter

Percent tuber dry matter in Expt 1 varied little between planting dates in Estima (range of 0.8 %), whereas there was a range of 2.26 % dry matter in Maris Piper tubers between April and June plantings ($P = 0.021$). Tuber percent dry matter decreased with delay in planting in Expt 1 ($P = 0.004$), but not in Expt 3. Maris Piper produced tubers with higher percentage tuber dry matter than Estima at the final harvest in both Expts 1 and 3 ($P < 0.001$, Table 33). The difference in tuber dry matter between cultivars was greater in Expt 3 than Expt 1 (absolute difference of 4.03 and 3.50 % respectively).

Table 33. Tuber percent dry matter (% DM) for cultivars Estima and Maris Piper at each planting date in Expt 1 (21.39 D.F.) and Expt 3 (13.5 D.F.). Data presented are a mean of nitrogen rate treatments.

		Cultivar		
Expt	Planting date	Estima	Maris Piper	S.E.
1	April	21.48	25.85	0.279
	May	20.68	24.15	
	June	20.94	23.59	
3	March	19.98	24.46	0.241
	April	20.50	24.31	
	May	20.08	23.89	

In Expt 3, tuber percent dry matter was greater at 250 than 0 kg N/ha in Maris Piper, whilst there was no difference in tuber percent dry matter between nitrogen rates in Estima (interaction between cultivar and nitrogen rate; $P < 0.001$). Tuber percentage dry matter at final harvest was greater in the 0 kg N/ha treatment than where 250 kg N/ha was applied in both experiments ($P = 0.004$ and $P < 0.001$ in Expts 1 and 3, respectively, Table 34). In Expt 3, tuber percent dry matter was greatest at 0 kg N/ha, except in March-planted Estima and whilst tuber percent dry matter was typically lowest at the later planting dates March-planted Estima at 0 kg N/ha was again the exception ($P < 0.001$).

Table 34. Tuber percent dry matter (% DM) at final harvest in Expt 1 and Expt 3. Data presented are a mean of planting date treatments and cultivars.

Expt	Nitrogen rate (kg N/ha)		S.E.
	0	250	(27 D.F.)
1	23.15	22.41	0.401
3	22.54	21.87	0.315

Tuber dry weight yield (DMyield, calculated from tuber fresh weight yield and percentage dry matter data) was typically greater at greater IGC in both experiments. Increasing IGC by 1000 % days, equivalent to 10 days at 100 % GC, increased DWyield by 0.91 t/ha and 37.4 % of the variation in DMyield was explained by IGC once differences between experimental blocks were accounted for (multiple linear regression; DWyield ~ IGC + block/main plot, $P < 0.001$). Mean DWyield varied between experiment and cultivar, and explained 47.1 % of the variation when included in the model (multiple linear regression; DWyield ~ IGC + cultivar + year + block/main plot, $P < 0.001$, Figure 60, Table 35).

Similarly, FWyield increased with increasing IGC, though FWyield was more variable than DWyield (multiple linear regression; FWyield ~ IGC + cultivar + year + block/main plot, $P < 0.001$, $R^2 = 0.400$, data not shown).

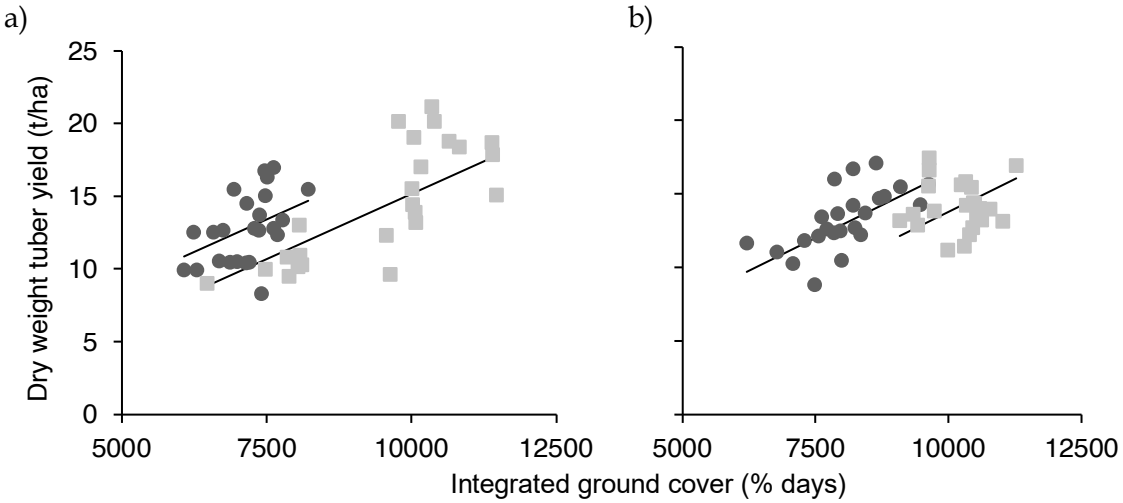

Figure 60. Relationship between tuber dry weight yield (DMyield) and integrated ground cover (IGC) for cultivars in (a) Expt 1 and (b) Expt 3. Estima, ●; Maris Piper, ■. R^2 = 0.471. See Table 35 for details of multiple linear regression.

Table 35. Relationship tuber dry weight yield (DMyield), integrated ground cover (IGC), cultivar (MP) and experiment (Expts 1 or 3). DWyield = β0 + β1*IGC + β2*MP + β3*Expt 3.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.0	2.12	0.997
1	IGC	0.00179	0.000264	< 0.001
2	MP	-2.71	0.721	< 0.001
3	Expt 3	-1.40	0.462	0.003

4.3.7.4 Harvest index

Harvest index (HI) varied between planting dates and the range was greatest at H1, although the extremely low HI in the May planting ($P < 0.001$, Table 36) was likely due to variation in relative harvest timing previously discussed (4.3.5.1, 4.3.6.1 & 4.3.6.2). Similarly, variations in timing of H2 (at 97, 94 and 98 % GC in the April, May and June plantings respectively, in Expt 1; and 91, 99 and 95 % GC in the March, April and May plantings respectively, in Expt 3) may have also resulted in the differences in HI in both experiments ($P = 0.019$ and $P = 0.046$, in Expts 1 and 3, respectively, Table 36). At H3, Expt 1, there was little variation in HI in Estima with planting date (range of 1 %), yet in Maris Piper HI was 7 % lower in the June than at either earlier planting (72, 73 and 65 % HI at the April, May and June plantings, respectively, $P = 0.001$, Table 36). Towards the end of the season, HI was typically greater following earlier planting and in Expt 1 was lowest in the June planting H3 and at final harvest (both $P < 0.001$), whilst in Expt 3, HI was greatest in the March planting ($P = 0.037$, Table 36).

Table 36. Dry matter harvest index (HI, %) at harvests throughout the season in Expts 1 and 3 (16 D.F.). H1, mid canopy expansion (GC~50 %); H2, early canopy closure (GC~100 %); H3, beginning of senescence (GC~90 %), H4, mid-senescence (GC~50 %); Final harvest, near-complete senescence (GC < 20 %, though GC was greater in Maris Piper, in Expt 1). Data presented are a mean of nitrogen rate treatments and cultivars.

		Harvest				
Expt	Planting date	1	2	3	4	Final
1	April	23.7	43.57	78.89	n/a	87.75
	May	3.0	41.43	78.52	n/a	85.73
	June	30.4	45.79	74.72	n/a	79.37
	S.E.	2.37	0.758	0.386	n/a	0.739
3	March	n/a	55.8	74.20	87.49	89.69
	April	n/a	47.3	71.73	85.17	86.61
	May	n/a	55.5	73.54	85.50	86.38
	S.E.	n/a	2.08	0.888	0.836	0.755

Applied nitrogen reduced tuber mass relative to haulm mass, resulting in a lower HI, early in the season in both cultivars ($P < 0.001$ in H1, Expt 1 and H2 and H3, Expts 1 and 3, Figure 61). The reduction in HI in response to additional nitrogen was greater in Maris Piper than Estima at H2, Expt 3 (11 and 16 % in Estima and Maris Piper, respectively, $P = 0.049$) and at H3, Expt 1 there was little difference in HI between nitrogen rates in Estima (< 2 %), but in Maris Piper HI remained *c.* 10 % lower at 250 than 0 kg N/ha ($P < 0.001$, Figure 61). Following the onset of senescence in September there was no significant difference in HI between nitrogen treatments (Figure 61). Harvest index was consistently lower in Maris Piper than Estima across all harvests ($P = 0.002$, in H1, Expt 1, $P < 0.001$ at all other harvests in both experiments, Figure 61).

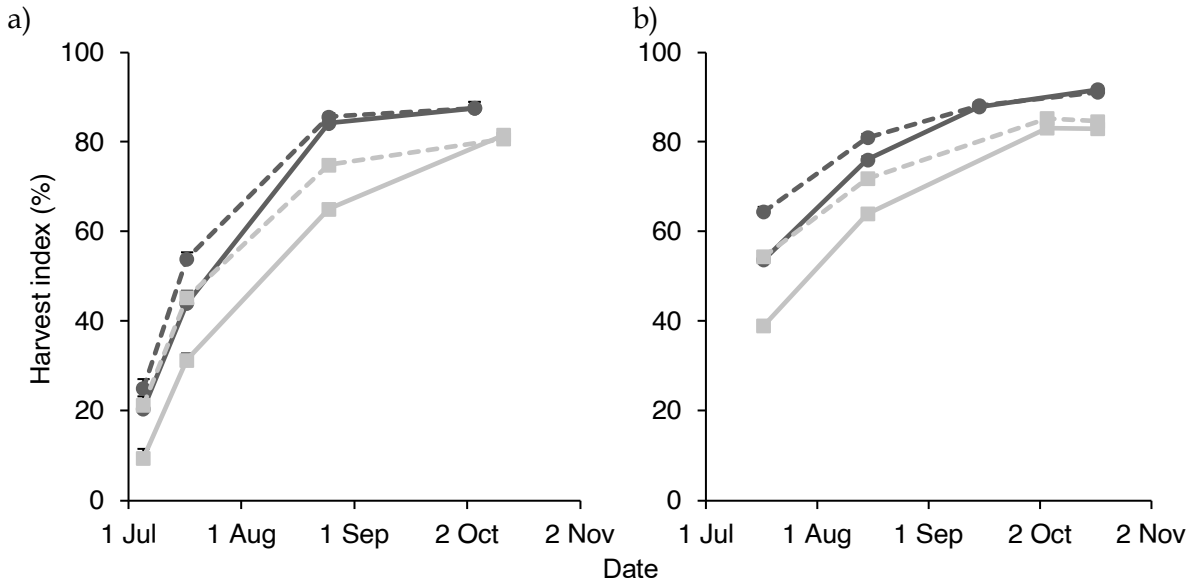

Figure 61. Change in dry matter harvest index (HI) at harvests throughout the season, for both cultivars, at differing nitrogen rates in (a) Expt 1 and (b) Expt 3. Estima, ●; Maris Piper, ■. 0 kg N/ha, – – – ; 250 kg N/ha, ——. Error bars represent S.E. (27 D.F. for all harvests in both experiments, except H2, Expt 1 and FH, Expt 3, both 26 D.F.). Data presented are means of planting date treatments.

4.3.7.5 Key points: Tubers

- Maris Piper tended to produce a greater number of tubers than Estima.
- Fresh tuber yield tended to decrease with lateness of planting date.
- Estima produced a greater yield throughout the season than Maris Piper, although the yield gap was smaller towards the end of the season.
- Fresh tuber yield was greater at 250 than 0 kg N/ha.
- Tuber percent dry matter was greater in Maris Piper than Estima.
- Tuber percent dry matter declined with lateness of planting date in Maris Piper but remained constant in Estima between planting dates.
- Tuber percent dry matter was *c.* 0.7 % (absolute value) lower at 250 than 0 kg N/ha.
- Dry weight tuber yield increased with increasing IGC, though the relationship was variable even when differences between cultivars and experiments were considered.
- Maris Piper partitioned a greater proportion of biomass to the haulm relative to tubers than Estima throughout the season.
- Additional nitrogen reduced HI before the onset of senescence and this reduction tended to be greater in Maris Piper than Estima.

4.4 Discussion

Planting date and applied nitrogen each can have a large influence over potato growth (4.1), yet differences in canopy development in relation to these agronomic factors are often overlooked and unrecorded. In experiments 1 and 3, variation in canopy growth in relation to the combined influences of planting date and nitrogen rate was successfully described using the CQ model, addressing thesis aim two. As stated in the chapter introduction (4.1.5), this work aims to consider the varying effects of temperature and light, with respect to planting date, and nitrogen application on canopy growth. In this discussion, the variation in both whole canopy growth, and canopy components, in response to variation in these agronomic factors will be explored, linking changes within the canopy architecture to changes in whole canopy growth (thesis aim three), and progressing chronologically through the season.

4.4.1 Early growth

4.4.1.1 Variation in early growth with planting date, temperature and daylength

Growth prior to emergence in Expts 1 and 3 primarily varied with planting date and the resulting differences in soil temperature and seed physiological age (Figures 7 & 8, in agreement with Bodlaender (1963), Bremner and Radley (1966), O'Brien *et al.* (1986), Firman *et al.* (1992) and Wang *et al.* (2015). Yet other factors influence sprout growth prior to emergence, illustrated by variation of *c.* 1 week in EmDAP over a narrow temperature range within a planting date (*c.* 0.6 °C, Figure 8). Date of emergence was predicted by Firman *et al.* (1992) using planting depth and sprout length at planting, in addition to soil temperature, whilst these predictions were typically *c.* 4 days earlier than field emergence, estimates were improved by including soil moisture, since dry soil conditions delay emergence (Firman *et al.* 1992). Additionally, seed size, seed tuber dormancy, seed health, seed age, soil fertility, cultivar and location of sprout on the seed tuber have all been reported to influence rate of emergence, as summarized by Pavek and Thornton (2009), illustrating the wide range of influences on the rate of emergence.

Planting date and the resultant variation in mean air temperature also appeared to be the primary influence upon initial canopy expansion and there was a general trend of decreasing duration between emergence and 25 % GC (TiE25) as mean air temperature increased (Figure 16). Yet, like EmDAP, TiE25 also varied within planting date treatments despite similar mean temperatures and there was a high degree of scatter in the relationship (Figure 16). This variation in early canopy growth between plots may be partially accounted for by within-field variation of soil texture, moisture and drainage which can explain within-field yield variation (Cambouris *et al.* 2006). Additionally, it is possible that the longer daylength at emergence which follows later planting (4.3.3.2) allowed greater cumulative daily photosynthesis, and therefore, in combination with warming temperatures, promoted more rapid early canopy growth. There is little in the literature to support or oppose this as most studies considering daylength focus on tuberization (Ewing & Struik 1992; Streck *et al.* 2007b) or compare highly contrasting photoperiods, with differences far in excess of the differences, < 1 h, reported here e.g. (Lorenzen & Ewing 1992; Wheeler 2006). Hence further work in which photoperiod is varied independent of temperature and seed age is required to clarify the influence of photoperiod on rate of early canopy development.

In summary, temperature had a strong influence over pre-emergence growth and early canopy expansion (chapter aim one) and small increases in daylength following later planting may be linked with the faster canopy expansion, but evidence limited (chapter aim four).

4.4.1.2 Influence of nitrogen rate and cultivar on early growth

Nitrogen rate had no effect upon the earliest phases of growth, as measured by EmDAP and TiE25, and additional nitrogen did not delay emergence as was reported by Firman (1987). This is not unexpected since initial potato growth, *c.* 40 days after planting and prior to emergence, potato growth is primarily dependent upon seed tuber resources (Pursglove & Sanders 1981), hence additional nitrogen should have little effect on the rate of growth. Whilst Firman *et al.* (1992) suggested that rate of pre-emergence growth may vary between cultivars, there was no difference in the duration between planting and emergence between Estima and Maris Piper. Similarly, Li *et al.* (2019) reported no difference in duration of emergence between cultivars, despite between-cultivar differences in percentage emergence. In summary, applied nitrogen and cultivar have little influence on early growth.

To conclude, mean daily temperature, of soil, then air, had the greatest influence on the rate of emergence and then early canopy growth (chapter aim one), whilst there was little variation between nitrogen rate or cultivar. Later planting will result in faster emergence due to warmer conditions and chronologically older seed (chapter aim five) and slow early growth due to earlier planting at cooler temperatures is the trade-off for a longer potential growing season.

4.4.2 Mid-season canopy expansion

4.4.2.1 Influence of temperature on mid-canopy expansion and leaf appearance

Whilst the rate of both mid-season canopy expansion and mainstem leaf appearance tended to increase at later planting dates, this variation was not associated with the differences in average temperature during these periods of canopy expansion (Figures 19 & 28, respectively). This contrasts with early canopy expansion (4.4.1.1) and a wide range of experiments in the literature which have shown a positive relationship between temperature and the rate of leaf appearance (Kirk & Marshall 1992; Cao & Tibbitts 1995; Firman *et al.* 1995). It is possible that the metric of mean temperature was too simplistic and masked variation in temperature which influenced growth. Yet, Firman *et al.* (1995) reported that mean air temperature explained 68.2

and 38.1 % of the variation in mainstem leaf appearance rate in Maris Piper and Estima, respectively, in the field, illustrating that mean temperature is able to account for variation in rate of leaf appearance.

Furthermore, it is also possible that the effect of temperature on leaf appearance rate was masked by variation from other factors varying between plots (4.3.4.2). For example, phyllochron varies with sowing date in sorghum (Clerget *et al.* 2008) and shorter phyllochrons have been reported with the delay in sowing date in oats (Chaves *et al.* 2016) and durum wheat (Riggi *et al.* 2017). Whilst in potatoes, Firman *et al.* (1995) reported that phyllochron was shorter in physiologically older seed, in some cultivars, including Estima. Hence, delayed planting and consequently older seed, a by-product of delaying planting, may have added to variability in mainstem leaf appearance rate between planting dates, independent of temperature. Yet, there was no significant difference in phyllochron between planting dates (4.3.4.3), suggesting that there was no systematic, non-temperature-related variation in leaf appearance between planting dates.

Another source of variation in leaf appearance is stem density and mainstem leaf appearance rate decreases at high stem densities under both glasshouse (Fleisher *et al.* 2011) and field conditions (Figure 29). Stem density is a function of stems per plant and plant spacing, and increases with increasing plant density, differs between cultivars (typically greater in Maris Piper than Estima, Figure 9) and increases with physiological seed age (increasing with delay in planting, Figure 9a). Stems per plant varied both within and between planting dates, increasing variability of the rate of leaf appearance at a given temperature, further obscuring the potential relationship between temperature and leaf appearance in the experiments here. The effect of stem density on leaf appearance is explored further in the Planting Density chapter (5.4.3.2).

Available nitrogen may also have a small effect on leaf appearance rate, with faster msLA in response to nitrogen in Maris Piper, though slower msLA in Estima (Figure 31). Vos and Biemond (1992) reported a marginal increase in in rate of leaf appearance with greater applied nitrogen and Firman *et al.* (1995) also reported a longer phyllochron in Maris Piper at low applied nitrogen. Together these results indicate that nitrogen rate has a small effect on rate of leaf appearance, and it is likely that the differing nitrogen rates in Expts 1 and 3 increased variability in msLA, contributing to noise around the relationship between temperature and leaf appearance.

Hence, there are multiple sources of variation in msLA which likely interact, generating noise around an anticipated relationship between temperature and leaf appearance. Indeed, this was illustrated by increased variation explained when number of stems per plant, in addition to mean temperature, was included in a model to explain variation in msLA, and the subsequent dropping of temperature from the model when planting date, nitrogen rate and cultivar were added as explanatory factors (Figure 29). There were also small, but potentially significant, experimental differences which may explain why Firman *et al.* (1995) reported a significant relationship and this work did not, under similar experimental conditions. Differences include a greater range of data (from seven experiments over five years, rather than two experiments in two years, as reported here) and a greater range in mean temperature (11-19 °C, compared to 15-20 °C) and likely contributed to allowing the relationship between mean temperature and mainstem leaf appearance rate to be quantified.

Further research indicates that other factors, in addition to temperature, affect leaf appearance rate and phyllochron, though they are not necessarily relevant here. Phyllochron varies with position of leaf on the main axis and lengthens after production of the first 20 leaves (Oliveira 2015) or after flowering (Firman *et al.* 1995). Yet, leaf appearance measurements in Expts 1 and 3 were not confounded by leaf position as measurements were taken on the mainstem only, prior to flowering, for all plots. Phyllochron has also been proposed to slow in relation to other demands for carbon within the plant and Oliveira (2015) reported an increase in phyllochron length after the onset of tuber bulking. Similarly, in peach trees the phyllochron was longer under a heavier crop load (Davidson *et al.* 2019). The influence of daylength on phyllochron appears variable between different crops; with longer daylength decreasing phyllochron in sorghum (Clerget *et al.* 2008) and wheat (Slafer Gustavo & Rawson 1997), whilst quinoa cultivars differed in phyllochron sensitivity to incident radiation, depending on cultivar origin (Bertero 2001). Yet differences between planting dates in daylength during mid-canopy expansion were small (< 1 h), and there was no significant difference in phyllochron between planting dates, likely the result of considerable phyllochron variability within each planting date, particularly in Expt 1.

In summary, differences in air temperature between the planting dates explained a limited amount of the variation in the rate of leaf appearance and canopy expansion.

Variation from number of stems and physiological age, which both vary with planting date (linking to chapter aim four), and nitrogen, together obscured any linear relationship between temperature and leaf appearance in Expts 1 and 3 (addressing chapter aims one and two).

4.4.2.2 Variation in canopy expansion in relation to nitrogen and cultivar

From mid-canopy expansion onwards both cultivars responded to greater nitrogen availability with faster canopy expansion (4.3.3.5) and faster sympodial branch leaf appearance rate (Figure 41), greater leaf production on both axillary and sympodial branches (Figures 51 & 57, respectively), more branches (Figure 49), greater LAI (Figure 45) and greater tuber yield (Table 32), in line with literature expectations (4.1.4).

There was little difference in the rate of mid-canopy expansion between Estima and Maris Piper, consistent with limited differences in rate of canopy expansion between cultivars reported by Oliveira *et al.* (2016). Both cultivars began axillary and sympodial branch leaf production before canopy closure (Table 26), though branch leaf production made a limited contribution to the rate of canopy expansion due to the relatively small leaf area produced by the branches before canopy closure (0.36 and 1.07 LAI at H2, in Expt 1 and 3 respectively, Figure 42). Determinate Estima began axillary and sympodial branch production earlier than Maris Piper (Table 26), but this difference in canopy composition was of little functional importance to canopy expansion. This is because total canopy leaf area is more important to light interception and photosynthesis than the relative proportions of mainstem and axillary branch leaves (Fleisher *et al.* 2006b) and total LAI did not differ between cultivars prior to canopy closure (Figure 44). So, despite differences in early branch production between cultivars, these results indicate that determinacy has a little effect on canopy expansion rate.

Whilst the differences in the rate of whole canopy expansion were small, leaf appearance on individual mainstems was significantly faster in Estima than Maris Piper (Figure 26). Between-cultivar differences in leaf appearance, described using phyllochron, have also been reported by Oliveira (2015) between Bondi and Fraser (27 and 34 °C days/leaf, respectively, base temperature; 2 °C), and Firman *et al.* (1995) between Maris Piper and Estima (31 and 34 K days/leaf, respectively, base temperature; 0 °C). Yet these differences were not replicated in this study, with phyllochrons of 39 and 27 °C days/leaf reported for Maris Piper and Estima, respectively (base temperature; 0 °C) in Expt 1 and no overall difference between

cultivars in Expt 3 (Figure 30), indicating that in potato phyllochron can be inconsistent and that other factors, in addition to temperature, have a high degree of influence on the rate of leaf appearance (4.4.2.1). Variation in stem density between experiments may partially account for between-experiment differences in phyllochron since rate of leaf appearance per stem slowed as number of stems per plant increased (Figure 29) and within-plant competition, initially for tuber resources, then for light, increased. Hence, the slower rate of mainstem leaf appearance in Maris Piper was both caused by, and partially compensated for by, the greater stem density of the cultivar (Figures 29 & 9). However, differing stem densities did not account for all variation in rate of leaf appearance between the cultivars, as leaves on Estima mainstems appeared at a faster rate than in Maris Piper in Expt 3, when there was no difference in stem density between the cultivars (Figure 9b). Furthermore, stem density did not explain any of the variation in rate of mid-season canopy expansion, despite accounting for *c.* 79 % of the variation in whole plant leaf appearance.

Whilst the response of leaf appearance rate to increased nitrogen differed between cultivars (increasing in Maris Piper and decreasing in Estima, Figure 27) this had no practical effect on canopy expansion, which increased in a similar fashion in both cultivars in response to additional nitrogen (Figure 18). Similarly, Ospina *et al.* (2014) reported that whilst the maximum rate of canopy expansion varied between determinacy groups (described as maturity types by Ospina *et al.*) across 189 cultivars, the increase in canopy expansion rate in response to additional nitrogen was similar in cultivars of differing determinacy. Furthermore, both cultivars produced *c.* 4 additional leaves on the main axis in response to applied nitrogen, supporting the theory that determinacy group has little effect on cultivar leaf production and canopy expansion responses to applied nitrogen, thus addressing aim seven.

In summary, mid-canopy expansion was faster at higher nitrogen rates, there was no difference in response of canopy expansion to nitrogen between cultivars, indicating that determinacy had little effect on early season growth, in spite of differences between the cultivars in the timing of branch production.

4.4.2.3 Relationship between mid-canopy expansion and leaf appearance rate

The rate of whole plant leaf explained a relatively low proportion of the variation in rate of ground cover expansion (38 %, when variation between experiments was also accounted for), answering chapter aim two. It is possible that calculating and including the rate of leaf appearance on the axillary branches would increase the

proportion of variation in ground cover expansion rate explained by whole plant leaf appearance since branches can make a large contribution to total canopy leaf area (Fleisher *et al.* 2006b). However, the additional variation explained may be modest, as whilst axillary branches were produced during mid-canopy expansion (Table 26), axillary branch contribution to leaf cover was small prior to canopy closure (Figure 42), and smaller still before reaching 75 % GC (at the end of mid-canopy expansion).

The rate of leaf appearance may additionally account for a limited proportion of the variation in canopy expansion rate as it records the incidence of new leaf production once longer than 10 mm in length, and additional leaves of this size will contribute little to canopy ground cover. Consequently, the expansion of existing leaves plays an important role in determining rate of canopy expansion (van Delden *et al.* 2000) and can explain further variation in rate of canopy expansion than rate of leaf appearance alone, although it was not measured in Expts 1 and 3. Mean temperature between emergence and flowering explained 64 % of the variation in final leaf size of 16 cultivars grown in the field, with leaf size decreasing as temperature increases (Escuredo *et al.* 2020). Additionally, rate of leaf expansion has been shown to occur more rapidly at higher nitrogen in glasshouse experiments (Vos & Biemond 1992; Vos & van der Putten 1998), likely accounting for the faster canopy expansion observed at high nitrogen in these experiments (Figure 18). Furthermore, variation in leaf expansion in relation to water availability suggests that rate of canopy expansion is more heavily influenced by leaf expansion rate than leaf appearance rate. It is likely that the slower rate of individual leaf expansion which occurs under water stress (Jefferies 1993; Fleisher *et al.* 2008) is the cause of slower canopy expansion, since rate of leaf appearance on the mainstem does not vary under reduced irrigation (Fleisher *et al.* 2008). Rate of leaf expansion also varies between cultivars in the field (Jefferies 1993) and so may account for faster canopy expansion in Maris Piper than Estima (Figure 17b). Thus, including rate of leaf expansion in a canopy growth model may help to better predict the variation in whole canopy expansion between cultivars and at different rates of applied nitrogen, than rate of leaf appearance alone, partially addressing thesis aim four.

To conclude, mid-canopy expansion rate increased with applied nitrogen, though there was no difference in nitrogen-response between determinacy groups, despite inherent between-cultivar differences in the rate of mainstem leaf appearance. Other factors in addition to temperature—including stem density—influence the rate of leaf

appearance in potato and obscured the expected positive effect of temperature on leaf appearance in Expts 1 and 3. Moreover, leaf appearance rate explained a limited proportion of the variation in canopy expansion rate, which is likely explained by variation in leaf expansion, addressing chapter aim two.

4.4.3 Canopy duration

Variation in canopy duration (≥ 90 % GC, GCDur90) and the structure of the canopy is explored herein to better understand how planting date, additional nitrogen and cultivar influence canopy duration and the changes in leaf and branch production which are the underlying mechanisms of these whole canopy variation, thus addressing thesis aim three.

4.4.3.1 Variation in canopy duration with planting date

Sources of variation in the duration of canopy cover can be partitioned between environmental variables and the differences in season length that delay in planting results in, thus chapter aims one and four, and five, respectively, will be addressed in turn.

4.4.3.1.1 With respect to environmental variables

There were slight, yet significant differences in both mean temperature and mean daylength during near-complete ground cover (Appendix 8 and 4.3.3.2). Yet it is unlikely that the small differences in mean temperature, < 2 °C, had any significant effect on duration of near-complete canopy cover between planting dates, since temperature differences between consecutive days were frequently greater (Appendix 14, Figure 146). Furthermore, it is difficult to distinguish temperature differences in field experiments which caused differences in canopy longevity, and differences in temperature which resulted from GCDur90 continuing until a later point in the season, when mean air temperature was lower, reducing mean temperature over the duration of near-complete canopy maintenance.

Greater increases in mean temperature can be expected to reduce total canopy leaf area, and under growth chamber conditions, maximum canopy area was found between *c.* 17-22 °C and lowest leaf area at *c.* 32 °C (Fleisher *et al.* 2006b). As despite more rapid leaf appearance (Kirk & Marshall 1992; Firman *et al.* 1995; Fleisher *et al.* 2006a), a greater number of leaves produced (Marinus & Bodlaender 1975), with a greater number of leaflets per leaf (Escuredo *et al.* 2020) at warmer temperatures, the duration of leaf expansion was shorter, resulting in lower leaf area (Kirk & Marshall

1992), comprised of smaller leaflets (Escuredo *et al.* 2020) and lower total leaf area (Fleisher *et al.* 2006b). In summary, the differences in temperature in Expts 1 and 3 were likely too small to affect canopy duration, and the relatively cool UK summer temperatures resulted in typically long-lived canopies (*c.* 2 months at near-complete canopy cover, Figure 20). Whilst daily temperature varies throughout the summer, it is unimportant which portion of the season near-complete canopy cover is maintained during due to the low range of mean UK summer temperatures between months, with little measurable effect on canopy longevity (Appendix 14).

Similarly, the relationship between GCDur90 and mean daylength during near-complete canopy cover was limited (Appendix 7) and GCDur90 tended to be shorter when dLength90 was greater. Yet it is likely that this is not a causative relationship, rather dLength90 was longer when GCDur90 was shorter because canopy senescence began earlier in the season, when daylength was longer and so variation in dLength90 resulted from variation in the timing of the onset of senescence as suggested by the strong relationship between the last date of 90 % GC and dLength90 (Appendix 7). Additionally, Streck *et al.* (2007b) found no relationship between mean photoperiod at tuber initiation and duration between tuber initiation and beginning of senescence. Furthermore, including photoperiod, in addition to thermal time, as a predictor of duration of potato developmental stages did not improve predictions (Streck *et al.* 2007b). It was suggested that using mean photoperiod oversimplifies any effect of photoperiod (Streck *et al.* 2007b), and this is supported by work in sorghum (Clerget *et al.* 2008), which showed that accounting for both photoperiod and the daily change in photoperiod, in addition to soil temperature, explained 40-50 % of the variation in initial phyllochron between planting dates. The effect of daily change in photoperiod merits further investigation to identify if lengthening photoperiod also increases the rate of leaf appearance in potato, as in sorghum, and if decreasing daylength prompts earlier onset of senescence relative to emergence (as suggested by McGrady and Ewing (1990)), shortening the duration of near-complete canopy cover. If present, the influence of daily change in photoperiod is likely to be greater in the UK than Mali, the site of the sorghum study (Clerget *et al.* 2008), due to larger step changes in UK than Malian photoperiod over a greater range in daylength (*c.* 10-15 h compared to *c.* 12-14 h, respectively).

4.4.3.1.2 With respect to season length

Cultivar ability to achieve maximum potential canopy duration, a function of determinacy and number of leaves produced on the main axis, is influenced by the length of the growing season (Allison 2020). Both duration of near-complete canopy cover and duration of whole-season canopy growth (from emergence until the point of senescence, at 90 % of maximum canopy cover) tended to decrease with delay in planting and the reduction was typically greater in Maris Piper than Estima (Figures 20 & 24). This reduction in canopy longevity was associated with a reduction in number of main axis (Figure 32), axillary branch (Figure 50b) and sympodial branch (Figure 56b) leaves. The number of leaves produced by Estima on the main axis, axillary and sympodial branches varied little from the cultivar mean values between planting dates, whilst there were significant reductions in number of leaves produced between the earliest and latest plantings in Maris Piper. Since Estima ended leaf production before Maris Piper it was less sensitive to delay in planting and subsequent reductions in season length, and this is reflected in the classification of Estima as a determinate cultivar, with a short-lived canopy (Naylor 2017).

Yet maximising leaf production does not guarantee a long period of near-complete canopy cover as shown by the short GCDur90 of the earliest planting (Figure 20b) in combination with high maL in Maris Piper (Figure 32b) in Expt 3 and also the limited relationship between the number of leaves produced on the main axis and GCDur90 (Figure 34). Whilst canopy longevity is thought to be the result of continued leaf production (Firman *et al.* 1995), which maintains canopy cover after senescence of leaves lower within the canopy has begun (Millard & MacKerron 1986), leaf area and lifespan is also important and can shorten canopy duration if reduced. Examples from nitrogen response (Biemond & Vos 1992; Vos & van der Putten 1998) and drought (Jefferies 1993) studies show that potatoes respond to environmental stress by reducing leaf expansion, not leaf number. Hence the shorter canopy duration in the March planting may indicate leaf expansion limited by stress, potentially related to likely compaction following sub-optimal soil cultivations in Expt 3, as compaction has been shown to reduce both canopy extent and duration (Stalham *et al.* 2007).

The consistent number of leaves per axillary and sympodial branch between planting dates in Estima (Figures 50b & 56b) indicated that Estima finished producing branch leaves before environmental changes associated with the end of the season (such as lower average temperatures, reduced radiation and daylength) retarded growth,

unlike Maris Piper, which continued branch leaf production later into the season and required longer to maximize leaf production potential. Estima, as the more determinate cultivar, began senescence after an average of 21 leaves had been produced on the main axis and hence completed leaf production earlier than Maris Piper. The determinacy of Estima was further reflected in the consistent number of axillary branch leaves (*c.* 5 leaves per branch) recorded at each harvest after canopy closure, which varied little between planting dates (Figure 50b). Axillary branch production in Estima also ended around canopy closure as there were similar numbers of axillary branches at each harvest within planting date treatments (Figure 48b).

There was a greater interaction of branch and leaf production with the environment in the more indeterminate Maris Piper, and the growth of Maris Piper was curtailed by the shortening of the growing season due to later planting in both experiments. There was little difference in canopy duration between the March and April plantings indicating that the inherent duration of growth for Maris Piper was approximately 114 days (Figure 24), during which a stem of intermediate size produced 30 leaves on average. As planting was delayed fewer leaves per stem were produced on the main axis, with an average of 24.7 leaves in the May plantings of both experiments and 25.7 leaves in the June planting in Expt 3 (Figure 32). Delay in planting was also associated with reduced sympodial branch length, as whilst sympodial branch length was similar between planting dates at canopy closure, growth continued during full canopy cover. Due to the shortened period of complete canopy ground cover in the May planting (Expt 3) sympodial branches were much shorter than those produced in the March and April plantings (Figures 20b & 53b).

Differences in axillary branch production between cultivars and planting dates were less consistent and number of branches did not decrease with delay in planting in either cultivar (Figure 48). Conversely, Figure 48b suggests that greater axillary branch production may follow later planting in Estima, potentially promoted by warmer conditions during branch production in the May planting, similar to the greater production of branch leaf area at *c.* 23 °C found by Fleisher *et al.* (2006b) under growth chamber conditions. Yet, this was only observed in Expt 3 and the differences were not significant hence further data is required to determine the influence of both planting date and temperature on axillary branch production in the field. Number of axillary branches is further influenced by stem density, decreasing as stem density increases (Vos 1995; Fleisher *et al.* 2011). The average number of axillary branches was greater in

Estima than Maris Piper in Expt 1, where Maris Piper stem density was double that of Estima, but greater in Maris Piper than Estima in Expt 3 when stem density was equal (Figures 48 & 9). These differences between the experiments suggest that whilst there are inherent differences between cultivars in the number of axillary branches produced, branch production was more heavily influenced by stem density than cultivar.

In summary, the reduction in number of main axis leaves, sympodial branch length and sympodial branch leaves with delay in planting in Maris Piper, but not Estima, suggests that foliage production in indeterminate cultivars was more sensitive to changes in length of growing season than determinate cultivars, thus addressing aim six. These differences in canopy components are the likely mechanism by which delay in planting reduced the duration of near-complete canopy in Maris Piper, though it is less clear how variation in axillary branch production affects canopy duration in either cultivar.

4.4.3.2 Influence of nitrogen and cultivar on canopy duration

The effect of additional nitrogen on near-complete canopy duration on Estima and Maris Piper was inconsistent between experiments, resulting in longer GCDur90 in Estima but shorter GCDur90 in Maris Piper in Expt 1, and longer GCDur90 in both cultivars in Expt 3 (Figure 21). It is plausible that there was a greater, positive GCDur90 response to additional nitrogen in Expt 3 than in Expt 1 as the additional nitrogen helped to mitigate the effects of a poor-quality, and potentially compacted, seed bed, which can limit rooting and increase the nitrogen requirement of the crop (Hamza & Anderson 2005). Whereas in Expt 1 it is possible that the high available soil nitrogen (Table 5) provided sufficient nitrogen for canopy development before fertilizer application, and that differences observed between the cultivars indicate the effect of excess nitrogen on canopy duration in canopies of differing determinacy levels. At lower rates of applied nitrogen, 180 compared to 250 kg N/ha, Ospina *et al.* (2014) identified a positive interaction between nitrogen rate and determinacy (described as maturity by Ospina *et al.*) in the duration of maximum canopy cover duration. Ospina *et al.* (2014) found that more indeterminate cultivars exhibited a greater increase in canopy duration in response to additional nitrogen than determinate cultivars across 189 cultivars. This difference may be explained by typically more limited canopy coverage, with the majority of plots not achieving 100 % GC, in the Dutch experiment (Ospina *et al.* 2014) than in Expts 1 and 3, with

mean maximum canopy coverage at the low nitrogen treatment (75 kg N/ha) *c.* 77 % GC and at high applied nitrogen (180 kg N/ha) *c.* 90 % GC, compared to 98 % GC and 100 % GC at 0 and 250 kg N/ha, respectively, indicating the plants were likely N-limited even at the higher nitrogen rate. One other difference may be that the high nitrogen treatment in Expts 1 and 3 supplied nitrogen in excess, resulting in greater branch production, creating more shade and promoting senescence lower in the canopy, as shown by Millard and MacKerron (1986), reducing lifespan of individual leaves and resulting in no net increase in canopy longevity.

In summary, the influence of cultivar and applied nitrogen on canopy duration appears to vary depending on total available nitrogen relative to cultivar nitrogen requirement. Below, variation in canopy components in relation to applied nitrogen and cultivar is explored to better understand how they relate to changes in canopy longevity.

4.4.3.2.1 With respect to branch production

Near-complete canopy duration tended to be longer at the higher nitrogen treatment, though the magnitude of the effect was smaller in Expt 1 than Expt 3 (Figure 21), despite a similar increase in number of additional main axis leaves in both years in response to additional nitrogen (Figure 33). This indicates that the influence of nitrogen on leaf longevity, branch production or leaf size can vary between years, although, when cultivars did not achieve 100 % GC, the positive effect of nitrogen on duration of maximum canopy cover was more consistent between years (Ospina *et al.* 2014). There was no difference in timing of either first axillary, or sympodial branch production or likelihood of producing a sympodial branch between nitrogen rates, reflecting the limited effect that applied nitrogen has upon the rate of leaf appearance (Vos & Biemond 1992; Vos & van der Putten 1998). However, more axillary branches were produced at 250 N than 0 N, with more leaves per branch, in agreement with glasshouse both glasshouse (Vos & van der Putten 2001) and field studies (Oliveira 2000). More axillary branches were produced in Expt 3 than Expt 1 in response to additional nitrogen (Figure 49) which may have contributed to the increase in canopy duration in response to additional nitrogen not found in Expt 1.

Cultivar responses to additional nitrogen differed and Maris Piper produced double the total number of axillary branch leaves at 250 N compared to the 0 N treatment, whilst Estima increased the total number of branch leaves in response to the high nitrogen treatment by 80 %, answering chapter aim eight. Yet differences in branch

number production did not correlate with differences in canopy duration. In Expt 1, the smaller increase in branches in Estima was associated with an increase in canopy duration, whilst GCDur90 decreased in Maris Piper, despite the large increase in branches produced in response to additional nitrogen, moreover in Expt 3, GCDur90 was greater at higher nitrogen in both cultivars, irrespective of branch number. Some of the variation in axillary branch number between experiments resulted from differences in stem number within cultivars as discussed above (4.4.3.1.2), partially accounting for the lack of relationship between number of axillary branches and duration of near-complete canopy duration. In summary, differences in branch production explains little variation in GCDur90.

4.4.3.2.2 With respect to number of main axis leaves

Cultivar was the only significant source of variation in mainstem leaf number (Figure 25), and Maris Piper produced more mainstem leaves than Estima. Whilst additional nitrogen had no effect upon the number of leaves on the mainstem, it was associated with four additional leaves on the sympodial branch (Figure 33) and later planting was linked to fewer sympodial branch leaves (Figure 56b), as discussed above, (4.4.3.1.2). This suggests that leaf production on the mainstem is genetically determined rather than responding to environmental conditions, or applied treatments, in agreement with Firman *et al.* (1991) who found that the number of above ground nodes on the mainstem varied with cultivar and was not affected by the degree of seed sprouting. In contrast, the number of leaves on axillary and sympodial branches was more variable, responding to changes in resources and environmental conditions. Hence, the difference in GCDur90 between cultivars may be linked to differences in number of mainstem leaves, whilst variation in GCDur90 in response to nitrogen rate and planting date may be associated with changes in the number of sympodial branch leaves, although the relationship between total number of leaves on the main axis and canopy duration is weak (Figure 34). Whilst continued leaf production is important to canopy longevity, as the mechanism by which applied nitrogen increases canopy lifespan (Millard & MacKerron 1986), shade cast by greater branch leaf production is associated with more rapid mainstem leaf senescence (Millard & MacKerron 1986; Fleisher *et al.* 2006b). This reduction in leaf lifespan lower within the canopy does not appear to affect canopy duration but may be linked to more rapid senescence rates observed at higher nitrogen (Figure 23).

4.4.3.2.3 With respect to leaf area index

Leaf area index provides further insight into the distribution of leaves within the canopy and a larger total leaf area was produced at greater nitrogen availability (Figure 45). The distribution of LAI between canopy components also differed between nitrogen treatments, with greater leaf area produced by axillary and sympodial branches at the higher nitrogen rate. After canopy closure, mainstem LAI in both cultivars declined more rapidly at high levels of nitrogen, as the thicker canopy, with more branch leaves (axillary and sympodial) shaded the lower mainstem leaves, decreasing leaf photosynthesis (Firman & Allen 1988) and increased the rate of senescence (Millard & MacKerron 1986; Fleisher *et al.* 2006b). Stems with a greater number of branches lost more mainstem LAI during complete canopy cover than those with fewer branches. Hence in Expt 1 there were greater reductions in mainstem LAI in Estima, with a greater number of axillary branches, than for Maris Piper, and in Expt 3 the opposite occurred as Maris Piper had more axillary branches than Estima (Figures 44 & 48). The difference between mainstem LAI at high and low available nitrogen was much greater in Maris Piper than in Estima. Similarly, whilst the proportional increase in axillary branch LAI in response to nitrogen was the same in both cultivars, the absolute difference was much greater in Maris Piper, decreasing the amount of light that penetrated to the lower levels of the canopy and the mainstem leaves. However, whilst decreases in Maris Piper mainstem LAI likely resulted from increased shading by branches (Niinemets 2007), axillary branch LAI compensated for those decreases and the differences in total LAI response between the cultivars to increased nitrogen were small (Appendix 11).

Leaf area, of both axillary and sympodial branch leaves, was greater at higher rates of applied nitrogen (Figures 52 & 58), reflecting the findings of Vos and Biemond (1992) who also reported that the area of individual leaves was sensitive to nitrogen, though found greater differences in leaf area between the low and high nitrogen treatments in mainstem, than axillary or sympodial branch leaves. Here, the increase in leaf size in response to nitrogen was greater in axillary branches than in sympodial branches, but the effects were consistent between years (Tables 28 & 29), confirming that additional nitrogen increases canopy leaf area by increasing the area of individual leaves, in addition to increasing the number of leaves produced. Axillary branch leaves were on average smaller than sympodial branch leaves and there were *c.* 21 and 44 leaves per unit of LAI in Expts 1 and 3, respectively (values mean of nitrogen rates, Figure 52)

compared to *c.* 13 sympodial branch leaves (mean of nitrogen rates, Figure 58). Whilst branch leaves met the minimum requirements to be recorded (length greater than 10 mm), many leaves produced on axillary branches did not grow to full maturity, likely due to the shade of the mainstem and sympodial branch leaves above, whereas the sympodial leaves developed at the top of the canopy in full sunlight, enabling them to fully expand, explaining the difference in the ratio of number of leaves to LAI between axillary and sympodial branch leaves.

Additional nitrogen may also increase leaf lifespan, and above the 10th leaf on the mainstem Vos and Biemond (1992) reported leaf lifespan was 3 weeks longer than without additional nitrogen, though increased shade likely reduced the lifespan of leaves below the 10th leaf, as discussed above. Whilst the large reductions in mainstem LAI suggest that leaf lifespan decreases on the mainstem at high nitrogen (Figure 45), it is not possible to determine if increased axillary and sympodial branch LAI was due to increased leaf production or lifespan, though likely it is a combination of both since the largest leaves tend to have the longest lifespans (Vos & Biemond 1992).

In summary, greater LAI was associated with longer near-complete canopy duration, though the relationship was weak. High nitrogen stimulated large changes in LAI distribution in both cultivars, promoting axillary and sympodial branch production at the expense of shorter leaf lifespan on the mainstem. The response was more extreme in Maris Piper than Estima due to the greater haulm production capacity of indeterminate, compared to determinate, cultivars. Despite promoting large changes in branch and leaf distribution within the canopy, the increase in total LAI to additional nitrogen was modest, with little functional impact due to the relative unimportance of leaf type to canopy light interception and photosynthesis (Fleisher & Timlin 2006).

To conclude, the canopy produced by Estima, as measured by number of axillary branches and axillary branch leaves and number of leaves on the main axis, was unaffected by the shortening growing season with delay in planting due to the determinate nature of the cultivar. In contrast, GCDur90 was shorter in indeterminate Maris Piper at later planting dates and fewer axillary and sympodial leaves per branch were produced, illustrating the interaction between determinacy level and season length, as determined by planting date. The production of axillary branches and axillary branch LAI decreased with increasing stem density yet the effect of varying branch production in response to stem density on canopy longevity remains unclear.

Additionally, whilst nitrogen had a large effect on the distribution of LAI between canopy components, particularly in Maris Piper, the higher rate of nitrogen had a surprisingly small effect on total LAI and the duration of near-complete ground cover.

4.4.4 Canopy senescence

Leaf senescence began during complete canopy cover in both cultivars, as leaves on the mainstem, shaded by the axillary branch leaves above, died in the process of progressive senescence (MacKerron & Davies 1986). Canopy senescence occurs after leaf production has finished, and since damaged leaves are not replaced, degradation and aging in individual leaves results in loss of canopy cover and whole canopy senescence. Whilst there was no effect of planting date on the rate of senescence, the different planting dates were associated with differences in environmental conditions at the onset of senescence and this will be explored below (4.4.4.1) and then differences in rate of senescence between cultivars at different nitrogen rates are explored (4.4.4.2), addressing aim four and partially addressing aim ten.

4.4.4.1 Influence of temperature and daylength on onset of senescence

At later planting dates mean weekly temperature and daylength decreased steadily in the three weeks prior to senescence and weekly reductions in temperature of 1 °C per week potentially hastened senescence of the June planting in Expt 1 and May planting in Expt 3 (Appendix 15). Cooler temperatures and lower light intensities have also been proposed as the cause of faster canopy senescence in canopies which senesce later in the season, though Ospina *et al.* (2014) provide no direct evidence for this. The lifespan of individual leaves appears strongly influenced by thermal time, with thermal time requirement before the onset of senescence initially increasing with leaf position, though the relationship between thermal time and leaf lifespan differed between cultivars (Oliveira 2015). Other research, focusing on the effect of temperature across the growing period, prior to senescence, found that whilst senescence of leaves lower in the canopy began earlier at higher temperatures (mean daily temperature 27 °C, compared to plants grown at 16 or 22 °C), plants were longer lived at higher temperatures due to prolonged leaf production (Marinus & Bodlaender 1975). Similarly, Hurtado *et al.* (2012) observed slower canopy senescence in the field following a warmer season (mean daily air temperature of 14.5 °C compared to 12.7 °C), in a diploid backcross potato population of 250 genotypes. Whilst ten quantitative trait loci (QTL) have been found to control the aging process (Hurtado-Lopez *et al.* 2015), QTL interactions with environmental conditions remain uncertain.

Hence, warmer temperatures throughout the growing season are associated with greater leaf production and delayed onset of canopy senescence, yet there the role of cooling temperatures at the end of the season in triggering senescence remains uncertain.

Similarly, shortening daylength during September may also have a role in slowing, then stopping leaf production before the main axis leaf production potential was met, as seen in the reduced number of main axis leaves and shorter duration of near-complete canopy cover in Maris Piper discussed above (4.4.3.1.2). Evidence for the role of photoperiod in hastening senescence is limited to a single study using cuttings as a model for whole plant response to short-days (McGrady & Ewing 1990). Shorter daylength has also been associated with restricted growth and 'accelerated maturation' in Dutch cultivars, bred under long-day conditions, (Hurtado-Lopez *et al.* 2015), yet again this is a difference observed between large differences in daylength in two contrasting locations (Ethiopia, *c.* 12 h and the Netherlands *c.* 13-17 h), as opposed to shortening daylength at the end of the season. The variability in daylength at the onset of senescence in Expts 1 and 3 suggests firstly that the onset of senescence is not dependant on daylength, and will begin once the plant produced the maximum number of main axis leaves based on the cultivar and available nitrogen (4.4.3.1.2). Then secondly, that the signal of decreasing daylength is responded to in combination with temperature related signals and internal plant development signals since there was no daylength 'cut-off' beyond which all plants begin to senescence. Although later planting dates are required to investigate when decreasing daylength becomes the overriding factor in initiating senescence.

4.4.4.2 Variation in rate of senescence with nitrogen rate and cultivar

Senescence was faster at the higher rate of nitrogen in both cultivars, though the increase in rate of senescence in response to additional nitrogen was greater in Estima than Maris Piper (Figure 23). Data from Expts 1 and 3 are mostly in agreement with the findings of a large field study, comparing the canopy development at differing nitrogen rates in 189 cultivars, which found that high levels of nitrogen delayed the onset of senescence, but that the rate of senescence was faster once started (Ospina *et al.* 2014). Differences in rate of senescence between cultivars were also consistent with other findings in the literature; Ospina *et al.* (2014) also found that the rate of senescence was faster in more determinate cultivars. Similarly, Hurtado-Lopez *et al.*

(2015) found that determinate cultivars (described as early genotypes) completed senescence more rapidly than indeterminate cultivars. It is likely that the greater LAI of indeterminate cultivars prolongs the duration of canopy senescence, as found here and in the literature, whilst the greater specific leaf area (SLA) at high nitrogen (Appendix 16) results in faster canopy senescence, since increases in SLA result in thinner leaves, associated with a shorter lifespan (Reich *et al.* 1997). Yet increases in SLA only accounted for 25 % of the variation in rate of senescence in the planting date experiments (Appendix 16). The variable nature of this relationship may be due to high variability in potato senescence in the field, potentially linked to stochastic damage from the weather. Lower SLA has also been linked to slower canopy senescence rate in the field (Oliveira *et al.* 2016), potentially explaining the differences in rate of senescence between cultivars.

In summary, cultivar and nitrogen rate had the greatest influence on the rate of senescence; potentially linked to the smaller total LAI of Estima at the onset of senescence and earlier senescence of mainstem leaves at the higher nitrogen rate.

4.4.5 Canopy size

Both maximum canopy ground cover and canopy longevity are incorporated in the summary statistic integrated ground cover (IGC) which reflects the capacity of a crop for light interception throughout the growing season. Similar variates to IGC, ground cover duration (Boyd *et al.* 2002) and A_{sum} (Tiemens-Hulscher *et al.* 2014) have been identified as good ($R^2 = 0.805$) or 'very good' predictors of yield, respectively, under a range of different management conditions. Here, the ability of canopy light interception capacity to predict crop yield, as per the hypothesis of Monteith (1977), is investigated under differing climatic conditions within the same season and different nitrogen regimes, addressing chapter aim three (4.4.5.3). The contribution of individual canopy components to IGC is explored, fulfilling thesis aim three (4.4.5.1) and the influence of delayed planting on IGC in cultivars of differing determinacy is also explored, addressing chapter aim six (4.4.5.2).

4.4.5.1 Relationship between canopy components and IGC

Variation in maximum canopy cover and duration, as measured by integrated ground cover, results from differences in the number, size, and longevity of canopy components. The number of main axis leaves (maL) accounted for *c.* 34 % of the variation in IGC (Figure 34), yet this relationship was the product of relatively

consistent differences in mean maL and IGC between the cultivars, and maL was a poor predictor of within-cultivar variation in IGC. Since both IGC and maL are indicators of determinacy (Allison 2020) they can be expected to covary, with more indeterminate cultivars producing a greater number of main axis leaves and a greater IGC. Yet this relationship is imperfect, with slight variations in cultivar determinacy ranking depending on the metric used (Allison 2020). Furthermore, IGC is influenced by environmental factors, such as drought, which can reduce leaf size and persistence without altering the number of leaves on the main axis (Jefferies 1993), and IGC can also be underestimated if harvest occurs prior to complete senescence. Hence, the number of leaves typically produced on the main axis provides a rough indication of potential IGC produced by a given cultivar, yet precise predictions are not possible due to the influence of variable environmental conditions. Alternatively, variation in IGC may be better explained by the maximum leaf area of the largest individual leaves on the mainstem, which is closely related to leaf lifespan and contribution to canopy longevity (Oliveira 2015). Leaf size systematically increases with leaf position on the mainstem, peaking between the 8th and 15th leaf (Vos & Biemond 1992; Oliveira 2015), varying with cultivar, and the largest 50 % of leaves contributed *c.* 80 % to canopy leaf area and longevity (Oliveira 2015).

Similarly, leaf area index (recorded at the onset of senescence) explained a limited amount of the variation in canopy duration (*c.* 30 %, data not shown) and integrated ground cover (*c.* 20 %, Figure 47) and was a limited predictor of percentage ground cover, particularly during senescence (Figure 46b). This is not unexpected since the strong relationship between GC and LAI deteriorates after canopy closure as LAI continues to increase whilst % GC does not (Khurana & McLaren 1982; Firman & Allen 1989a; Haverkort *et al.* 1991). Yet, Bremner and Radley (Bremner & Radley 1966) observed that whilst LAI 3 is the minimum requirement for complete canopy and maximal light interception, a greater LAI is necessary to maintain complete canopy cover due to continual leaf turnover within the canopy. This may suggest that high peak LAI could indicate prolonged canopy maintenance, since more individual leaves must senesce before whole canopy senescence begins, but increases in maximum LAI from *c.* 4.5-5.5 in *cv.* Ulster Torch did not result in a more long-lived canopy, although when peak LAI was lower in more determinate cultivars, there was greater variation in canopy duration with peak LAI (Bremner & Radley 1966). Similarly, *cv.* Majestic senesced *c.* one month before Ulster Torch, despite producing a slightly larger peak

LAI (Bremner & Radley 1966). The lack of relationship between peak LAI and canopy duration is likely due to variation in leaf longevity in canopies of different sizes. For example, when LAI is lower due to low nitrogen availability (Figure 45), the turnover of leaves is typically slower, as within-canopy shading is lower than in a more dense canopy, resulting in slower senescence in the leaves below (4.4.3.2.3). Similarly, lower LAI in the May planting in Expt 1 (Figure 43b) was not associated with a shorter duration of near-complete canopy cover (Figure 20), nor a significantly lower IGC (Figure 14). This illustrated that a less dense canopy, with a lower LAI, could maintain near-complete canopy cover for as long as environmental conditions permit. Hence, it is more important to model ground cover dynamics than LAI.

Infrequent measurements may also partially explain the lack of relationship found between LAI and canopy duration in the planting date experiment, as in Expts 1 and 3, relatively few LAI measurements were taken; three across the whole season, compared to weekly (Bremner & Taha 1966), twice or thrice weekly (Boyd *et al.* 2002), every 5 minutes (Firman & Allen 1989a) measurements elsewhere in the literature. Consequently, these measurements provided insight into LAI variation at discrete phases in canopy growth, as opposed to a complete record of LAI variation throughout the season, and may not have captured the maximum values of LAI since leaf senescence had begun prior to measurement of LAI, at the onset of canopy senescence. Boyd *et al*. (2002) reported a good relationship between ground cover duration (equivalent to IGC) and LAI throughout the season (Pearson's correlation coefficients 54-94 %), yet the strength of this relationship varies and depends, in part, on the duration of maximum GC and the variability of LAI within that period. Whilst more frequent measurements of LAI may allow identification of peak LAI and a more accurate assessment of the relationship between maximum LAI and IGC, Expts 1 and 3 suggest that increases in LAI may not result in increased IGC exemplified by the *c.* 1.5 increase in LAI at the higher nitrogen rate (Figure 45), yet the lack of difference in IGC between nitrogen regimes (Figure 14).

In summary, number of main axis leaves and leaf area index (at H3) explained little variation in IGC alone. Variation in main axis leaf production does not account for variation in leaf production on branches, leaf size varies independently of leaf number and leaves make unequal contributions to canopy cover and longevity and leaf level variation does not directly translate to canopy level variation. Similarly, LAI does not account for differences in leaf longevity and increases in LAI can result in reduced leaf

lifespan as increased branch leaf production increases shading of and nitrogen reallocation away from mainstem leaves.

4.4.5.2 Influence of delay in planting date on IGC in contrasting cultivars

Integrated ground cover typically decreased as planting date was delayed, though the relationship between IGC and planting date was variable, and the decrease in IGC with decreasing growing season length was greater in Maris Piper than in Estima in Expt 1, though not Expt 3 (Figure 14). Estima IGC varied little between planting dates, indicating that at each planting date there was sufficient time to complete the growth cycle of the determinate cultivar, unimpeded by shortened season length (Figure 14a). Yet, the similar responses between cultivars to delay in planting in Expt 3 suggests little between-cultivar difference in sensitivity to season length, since IGC in both cultivars was shorter in the May than the April planting (Figure 14b). The strong effect of planting date in Expt 1 may be partially attributed to differences in the relative timing of harvests, which occurred at increasingly high ground covers in Maris Piper with delay in planting (*c.* 19, 57 and 92 % GC in the April, May and June plantings, respectively, Figure 10). This truncation of IGC did not occur in Estima in either experiment, which senesced completely prior to each harvest, nor in Maris Piper in Expt 3, when canopy cover was < 21 % GC at the final harvest of each planting date (Figure 10). Whilst an artefact of experimental procedure, harvest timing relative to cultivar determinacy is agriculturally relevant since crops often must be harvested prior to complete senescence due to equipment-based logistics and anticipation of worsening weather conditions. The greater sensitivity of indeterminate cultivars to variation in season length was illustrated here and early harvest, prior to senescence, not only reduced crop light interception, but also reduced end-of-season reallocation of nitrogen within the plant from haulm to tubers (as described by Millard and MacKerron (1986)), reducing yields. Similarly, canopy growth of indeterminate cultivars was more likely to be terminated early (prior to senescence) by late-blight, than determinate cultivars (Tiemens-Hulscher *et al.* 2014). Furthermore, the difference in IGC between determinacy groups was smaller when the season was shorter, under organic conditions without blight protection, than when chemically protected, with a full growing season (Tiemens-Hulscher *et al.* 2014), indicating that a greater proportion of IGC was 'lost' by the indeterminate cultivars when the canopy was killed early than in determinate cultivars.

Additionally, Expts 1 and 3 illustrated that season length was not the only influence of planting date upon canopy longevity since the earliest planting did not result in the greatest IGC (Figure 14b). Whist not significant, the differences in IGC between cultivars in Expt 3 indicate that cultivars respond differently to earlier planting; in the March planting, Maris Piper IGC was slightly greater than that in the April planting, yet in Estima IGC in the March planting was smaller than in the April planting. This was similar to the increase in seasonal LAI distribution with delay in planting from March to May, observed in two determinate cultivars (Ulster Chieftain and Aran Pilot), but not found in the more indeterminate cultivar Ulster Torch (Bremner & Radley 1966). This suggests that very early planting has a detrimental effect on determinate cultivar canopy growth, a phenomenon potentially linked to cold soil at planting increasing effective determinacy (Naylor 2017). Nevertheless, the benefits of very early planting in the UK appear to be limited, even if the crop does not experience frost damage (Jones & Allen 1982).

The slower canopy expansion at early planting was not linked with reduced IGC across all the treatments (data not shown), though does account for the lack of difference in IGC between the March and April plantings in Expt 3. Despite the March planting emerging *c.* 2 weeks before the April planting, both achieved near-complete canopy cover within the same week, hence why earlier planting did not increase IGC in this case. Thus, whilst slow canopy expansion induced by stress, including compaction (Stalham *et al.* 2007) and drought (Jefferies & Mackerron 1987), is associated with reduced maximum canopy cover and reduced canopy longevity, slow canopy expansion resulting from earlier planting is not linked to reduced total canopy cover.

In summary, indeterminate cultivars are more sensitive to season length due to greater capacity for canopy maintenance and require more time to complete their growth cycle, than determinate cultivars, in answer to chapter aim six. The effect of a shorter season was greater when it resulted from harvest prior to senescence since both light interception and remobilisation of nitrogen from haulm to tubers was interrupted.

4.4.5.3 Relationship between IGC and yield

The relationship between IGC and fresh tuber yield was surprisingly poor, with only 47 % of the variation in tuber yield accounted for by IGC, in comparison to the strong relationship between capped leaf area duration (area under LAI curve when capped at LAI = 3, equivalent to IGC) in which 95 % of the variation was accounted for (Bremner & Radley 1966). Yet Zhou *et al.* (2017) also found a limited relationship (R^2 = 0.47)

between IGC (described as Sumfpar, ground cover duration) and biomass produced across 12 field experiments. It is possible that between-experiment variation can obscure the relationship between IGC and biomass, as occurred with the relationship between biomass produced and accumulated, intercepted PAR, which explained 80-95 % of the variation in individual experiments, but a limited amount across all 12 experiments (R^2 = 0.33, (Zhou *et al.* 2017)), where soil type, planting date and year of experiment varied. Similarly, variation within and between the planting date experiments, may explain the weak relationship between IGC and tuber yield found here.

Firstly, there were small differences in biomass partitioning between plating dates in Expts 1 and 3, and HI was greatest following earlier planting (Table 36). However, canopy efficiency, as described by the ratio of IGC to dry matter tuber yield, did not vary consistently with biomass partitioning (Appendix 17), indicating that there is variation, in addition to differences in HI, altering the relationship between IGC and tuber yield between planting dates. Furthermore, whilst there is little variation in mean radiation receipts between years (Monteith 1977; Allen & Scott 1980), differences in radiation received between years in an individual month can vary between 30-60 % (Allen & Scott 1980). Consequently, the radiation environment for a crop will vary with planting date as the canopy develops and is maintained during different portions of the season (Allen & Scott 1980) and mean radiation differed between planting dates by 1.5 and 1.9 MJ/day in Expts 1 and 3, respectively. Kooman *et al.* (1996a), Fahem and Haverkort (1988), and van der Zaag and Doornbos (1987) all found that calculating intercepted PAR explained greater variation in tuber dry matter yield than IGC alone, yet the relationship was not universal and not only the coefficients, but the strength of the relationship, differed between locations. Hence, differences in intercepted radiation can explain some of the variation in the relationship between IGC and yield, but as clearly illustrated by Zhou *et al.* (2017), tuber dry matter yield does not vary consistently with intercepted radiation between locations and growing seasons.

The relationship between IGC and yield may further be influenced by temperature differences, as indicated by the decreased biomass partitioning to the tubers when night temperatures were 4 °C warmer during tuber bulking (Kim & Lee 2019). However, in the planting date experiments mean temperatures did not exceed 22 °C, the temperature at which this negative effect was observed by Kim and Lee (2019). Similarly, van der Zaag and Doornbos (1987) found that the conversion efficiency of

intercepted radiation to yield, was *c.* 3 times lower in Israel than in the Netherlands or Italy, a difference attributed to high temperatures and high evapotranspiration, but again, the mean temperatures in Israel were far in excess of those in the planting date experiments. However, Zhou *et al.* (2017) found that an increase in mean temperature by 1 °C resulted in a 1.6 t/ha decrease in tuber dry matter yield, over a similar mean temperature range to the Planting Date experiments (*c.* 15-18 °C and *c.* 16-17 °C, respectively) due to decreased RUE with increased temperature (0.36 g/MJ decrease per 1 °C increase in mean temperature), indicating that small differences in mean temperature at relatively low mean temperatures, can have a significant effect on the relationship between IGC and tuber yield.

In summary, both mean daily radiation and mean daily temperature influence the relationship between IGC and tuber yield, and varied between planting dates, increasing variability of the underlying relationship.

Secondly, variability in biomass partitioning between haulm and tubers can account for further variation in the relationship between IGC and yield. The differences in HI between cultivars were consistent throughout the season and Maris Piper produced greater haulm biomass relative to tubers than Estima (mean HI; 83 and 90 %, respectively, Figure 61), as expected, given the greater leaf production capacity of indeterminate than determinate cultivars (Naylor 2017; Allison 2020). Consequently, dry matter yield was *c.* 3 t/ha greater in Estima than Maris Piper at the same IGC (Figure 60) and this is likely to be true for other comparisons of determinate and indeterminate cultivars. Though evidence from the literature on this is scant and whilst HI tended to be greater in Shepody, the more determinate cultivar, than the more indeterminate cultivar, Russet Burbank (mean HI; 77 and 75 %, respectively), the difference was only significant at two of six sites (Bélanger *et al.* 2001).

Thirdly, biomass partitioning, and therefore the relationship between IGC and tuber yield, also varies with nitrogen rate, though this appears to depend on the point of harvest in the season. In the first half of the season, HI was reduced by applied nitrogen and greater partitioning of biomass to haulm at 250 than 0 kg N/ha (Figure 61), as expected (Millard & Marshall 1986). This is because nitrogen, particularly when applied in excess (250 kg N/ha, (Millard & MacKerron 1986)) promotes leaf production (both number and area (Millard & Marshall 1986; Millard & Catt 1988; Millard *et al.* 1989), increasing LAI (Figure 45), with applied nitrogen initially accumulated in the canopy. Later in the season, as leaves senesce, nitrogen is

remobilized and transferred to the tubers (Millard & MacKerron 1986; Millard *et al.* 1989). In Maris Piper, Millard *et al.* (1989) reported that nitrogen remobilization occurred in the last 28 days of the growth, and by the end of the season there was little difference in DM partitioning between nitrogen treatments (Figure 61, (Millard & Marshall 1986)). Whilst a consistent reduction in HI following nitrogen fertilization throughout the season has been reported (Bélanger *et al.* 2001), this may be the result of relatively early harvest (as indicated by comparatively low end of season HI *c.* 76 %), before complete senescence and relocalization of nitrogen could occur. Hence, the effect of nitrogen on yield likely depends the timing of harvest relative to leaf senescence and nitrogen relocalization, since the benefits of increased light interception due to greater canopy size at high nitrogen are diminished by decreased biomass partitioning to the tubers earlier in the season, around the beginning of tuber bulking (Millard & Marshall 1986). Therefore, the relationship between IGC and yield may vary with nitrogen rate depending on the relative timing of harvest, with reduced DM partitioning to tubers at early harvests and reduced tuber yield associated with IGC.

Additionally, Expts 1 and 3 suggest that applied nitrogen can have a positive effect on yield which is distinct from increases in the duration of canopy cover as described by IGC, the primary mechanism by which nitrogen affects potato yield (Clutterbuck & Simpson 1978; Harris 1992). At 250 kg N/ha, fresh weight tuber yield was *c.* 5.5 t/ha greater than at 0 kg N/ha (Table 32), yet whilst LAI was greater (by *c.* 1.5, at H3), there was no increase in IGC associated with the higher nitrogen rate (Figure 14). A higher proportion of radiation was likely intercepted by the denser canopy at 250 kg N/ha, since total light interception at 100 % GC can be as low as 80 % (Firman & Allen 1989a). Firman and Allen (1989a) also suggest that calculating the efficiency of dry matter production using GC-based measures of light interception is likely to be inaccurate due to variation in radiation intercepted by canopies of different densities with the same ground cover. Although Firman and Allen (1989a) observed that the degree of inaccuracy is likely to be lower due to when considering PAR interception due to lower leaf transmission of PAR, relative to total radiation, through the canopy. Hence greater LAI within a canopy can result in greater light interception, further explaining variability in the relationship between IGC and yield.

Fourthly, the influence of applied nitrogen on biomass partitioning in Maris Piper and Estima differs depending upon season length and results in further variability in the relationship between IGC and yield. The duration of increased biomass partitioning to

the haulm, resulting from a higher rate of nitrogen, was shorter in Estima than in Maris Piper and when harvested near the onset of senescence in Expt 1 (H3), there was no reduction in HI associated with applied nitrogen in Estima, unlike in Maris Piper (Figure 61a). This was due to the smaller leaf production capacity of determinate cultivars, illustrated by a smaller increase in total LAI in response to additional nitrogen (Appendix 11). Differences in relative timing of harvest resulted in variation in cultivar HI, since in Expt 1 senescence had begun in Estima (mean GC, 95 %) but not in Maris Piper (mean GC, 100 %), whilst in Expt 3 there was little difference in HI between nitrogen rates in both cultivars, where the Maris Piper harvest was delayed to ensure that the canopy was senescing (Figure 61b). This indicates that at the onset of whole canopy senescence applied nitrogen ceases to reduce HI. This was further illustrated by Tiemens-Hulscher *et al.* (2014) who reported the same positive effect of nitrogen on both cultivars, providing that the growing season was long enough for complete or near-complete canopy senescence, whereas when the growing season was shortened by late blight, nitrogen only had a positive effect on the yield of determinate cultivars. Thus, since determinate cultivars, such as Estima, senesce earlier than indeterminate ones they are more likely to have maximised biomass partitioning to tubers prior to harvest, particularly in a shortened season.

Similarly, the point of harvest, relative to tuber bulking, will also affect the relationship between IGC and yield and the pattern of tuber bulking differs with determinacy. Tuber bulking appeared to be both more rapid and more brief in Estima than Maris Piper as indicated by the plateau in tuber fresh weight yield (Figure 59) which either was not present in Maris Piper (Expt1, Figure 59a) or occurred later (in Expt 3, Figure 59b). Likewise, Khan *et al.* (2019b) found similar differences between determinacy levels in the pattern of tuber bulking across 105 cultivars; the rate of tuber bulking was typically faster in determinate cultivars, occurring over a shorter period, whilst tuber bulking is slower in indeterminate cultivars, yet continues for a longer duration due to greater canopy persistence, hence resulting in a higher yield if season length permits. Consequently, tuber bulking of indeterminate cultivars is more sensitive to season length and yield relative to IGC diminishes with early harvest of indeterminate cultivars, especially when fertilized.

In conclusion, IGC is an imperfect proxy for light intercepted and explained almost 50 % of the variation in tuber yield within each cultivar, with differences in RUE at varying radiation levels between planting dates, mean temperature and nitrogen rate

generating noise around the underlying relationship, answering the third chapter aim. In a low nitrogen environment, applied nitrogen increases yield by lengthening the duration of canopy cover and increasing maximum canopy cover, consequently, increases in yield are proportional to increases in IGC. Yet under nitrogen replete conditions, as in Expts 1 and 3, there was little or no effect of additional nitrogen on IGC, yet light interception was greater due to increased LAI, weakening the link between IGC and yield. This work supports the findings of Kooman *et al.* (1996a) who stated that within the same radiation environment, IGC is a good indicator of total dry matter production, and that between contrasting sites, variation in radiation intensity, in combination with differences in IGC, accounts for further variation in biomass production.

In answer to chapter aim nine, biomass partitioning varies not only with cultivar and nitrogen rate but also the interaction between both factors. Determinate cultivars are expected to maintain a greater HI than indeterminate cultivars throughout the season, based on the consistent differences in partitioning between Estima and Maris Piper in Expts 1 and 3. Whilst applied nitrogen increases biomass partitioning to the haulm during the first half of the season, the difference in HI diminishes as tuber bulking continues and HI equilibrium between different nitrogen rates is reached earlier in determinate than indeterminate cultivars due to faster tuber bulking rates.

Although there was no significant three-way interaction between planting date, nitrogen rate and cultivar on either IGC or yield in Expts 1 and 3, the interaction between nitrogen rate and cultivar depend on season length, addressing chapter aim ten. When harvested prior to senescence, nitrogen has a positive effect on yield in determinate cultivars, yet often a negative one on indeterminate cultivars. However, if the season is long enough, as in Expts 1 and 3, nitrogen could either have a similar increase in yield between cultivar types or a greater positive effect on indeterminate types as their ability to continue branch and leaf production permits greater extension of season length by applied nitrogen. Yet the long seasons required for a positive effect of nitrogen on indeterminate cultivars are often not feasible in agricultural settings where very long seasons are often not possible or practical due to harvesting constraints.

In spite of variability in the relationship between IGC and tuber yield, IGC provides useful insight into variation in total dry matter production, even more useful when considered though the lens of determinacy and known differences in biomass

partitioning between cultivars, in a single, non-nitrogen replete, environment. The main differences in IGC were due to planting date and cultivar (similar to GCDur90): the canopy senesced after a shorter duration when planting was later, and indeterminate Maris Piper was able to produce more leaves and a larger, more persistent canopy than determinate Estima (4.4.3.2).

4.4.6 Modelling outlook and further questions

One of the aims of this research was to better understand the causes of variation in canopy development and be able to generate a predictive model for canopy development (thesis aim four). The Planting Date experiments have highlighted the need to know cultivar determinacy or the maximum number of main axis a cultivar is likely to produce, in order to estimate the duration of unrestricted canopy growth—a cultivar characteristic with high heritability (Khan *et al.* 2019a). Number of main axis leaves for each cultivar, planting date and rate of applied nitrogen can be used to parametrize a predictive model, enabling more accurate prediction of canopy development, duration, and subsequent tuber yield. Firstly, number of leaves allows approximation of canopy duration, based on cultivar determinacy (Allison 2020), though canopy duration may also be estimated using QTLs identified by Khan *et al.* (2019a). Secondly, planting date can be used to estimate the length of season available for growth before environmental signals slow, then stop leaf production resulting in canopy senescence, and future deterioration in weather conditions necessitate harvest. Thirdly, nitrogen rate influences the number of sympodial branch leaves produced, with higher rates of nitrogen associated with more sympodial branch leaves, greater branching, prolonged canopy growth and delayed onset of senescence. Whilst canopy longevity may also be predicted from the size of the largest leaves on the mainstem (Oliveira 2015), it is currently unknown how maximum leaf area varies between cultivars, determinacy groups and nitrogen availability, requiring extensive further research before it can be of practical use in predicting crop growth.

Whilst it is clear that the constituent parts of the canopy; number of leaves, branches, number of branch leaves and total stem length differed significantly between cultivars, and that differences in these were a key part of the different nitrogen responses of the contrasting cultivars Estima and Maris Piper, variation in the growth of individual canopy components does not clearly link to changes in whole canopy development, longevity and light interception. The limited relationships between discrete measurements of canopy component growth and whole canopy development indicate

that understanding the variation in leaf and branch production which results from varying agronomic conditions is not necessary to describe differences in whole canopy growth. This was exemplified by the inability of variation in leaf appearance and branch production to account for variation in whole canopy expansion rate, likely due to the importance of leaf expansion in increasing total leaf area and consequent ground covered. Additionally, since branch type has been shown to have little effect on whole canopy photosynthesis distinct from their leaf area contribution to total canopy leaf area (Fleisher *et al.* 2006b) it is both reasonable and most parsimonious to model whole canopy growth, rather than the development of individual components.

Experiments 1 and 3 have highlighted the influence of planting date on canopy development, with delayed planting both increasing the rate of early canopy expansion under warmer conditions, and reducing canopy duration as the length of the growing season shortens (Figure 10). Under UK conditions, the influence of temperature on canopy growth diminished as the season progressed, reflecting the findings of Kooman *et al.* (1996b), although the influence of variation in daylength is less clear. Whilst early planting was found to result in slower initial canopy expansion due to lower temperatures, this was not linked to slower growth later in the season, nor to reduced canopy duration. Therefore early growth can be treated as distinct from canopy duration and IGC within a predictive model, though this contrasts with the negative correlation found between slower canopy expansion, and duration of maximum canopy cover found by Khan *et al.* (2019a). Moreover, the importance of season length on the pattern of biomass partitioning in cultivars of differing determinacy at high and low nitrogen rates has been emphasised. Further experiments are required to determine the impact of truncating canopy duration on yield, how this varies between cultivars, and whether the impact of fewer days of canopy cover differs when the canopy senesces early due to reduced resource availability or desiccation and how this affects biomass partitioning. Additional agronomic factors, such as end market, could also be incorporated into the model, as required tuber size will alter the timing of harvest and determine the need for desiccation, thereby changing the desired crop canopy profile of the grower. Finally, it would also be advantageous when modelling crop canopy development to identify the causes of year-to-year variation, for example quantifying the effect of soil type and conditions on canopy development, to account for this additional variation which growers face when growing and trying to predict crop performance.

5 PLANTING DENSITY

5.1 Introduction

The planting density of a potato crop is of agricultural importance as it is one of the key variables which growers can control to influence tuber size and yield. It is of further importance due to the direct effect that seed rate has on production costs, since seed tubers can be amongst the more expensive inputs in less economically developed countries (Engels *et al.* 1993), and accounts for *c.* 14 % of main crop and 24 % of seed crop total production costs (and a higher proportion of the variable production costs) in the UK (D Almond, 2019, personal communication, 23 July). Allen and Wurr (1992) described and evaluated multiple methods of determining planting density including number of eyes (axillary buds, subtended by leaf scales on the tuber (Cutter 1992)) and sprouts, number of seed tubers, seed tuber surface area, seed rate (weight of seed per area) and stem density. It was concluded that stem density is the most useful metric to describe potato plant density due to links to tuber yield and the relative ease of measurement (Allen & Wurr 1992). Both mainstems and secondary stems are typically included in stem density counts as, although secondary stems do not always produce tubers (Allen & Wurr 1992), they contribute to plant light interception and, when included in the stem count, better correlations have been found between number of stems and stem number predictors (Wurr *et al.* 1992b). Stem density has not been adopted as a standard measure of plant density throughout the literature, but where possible it is used to compare the experimental treatments and findings below.

5.1.1 Stem population determinants

A range of factors contribute to stem density and key amongst them are seed spacing, seed size, seed age and cultivar. The practical importance of these factors is illustrated by their inclusion in the Agriculture and Horticulture Development Board (AHDB) seed rate recommendations (e.g. for Maris Piper (Potato Council 2009)).

Firstly, larger seed produce more stems (Allen & Scott 1980; Allen *et al.* 1992; O'Brien & Allen 1992) but the increase in number of stems with increasing tuber size diminishes as the tubers get progressively larger (Allen & Scott 1980; Wurr *et al.* 1992b; Engels *et al.* 1993). Although not all eyes on the seed tuber produce stems (Allen 1979), Wurr *et al.* (2001) and Mauromicale *et al.* (2003) both found that the number of eyes positively correlated with number of stems produced, whether eye-number was artificially varied

on a fixed size tuber-piece (50-60 g, (Mauromicale *et al.* 2003)), or as tuber size increased (from 20-25 mm to 50-55 mm, (Wurr *et al.* 2001)). Whilst larger tubers have a greater number of eyes, the relationship between tuber size and number of eyes is non-linear (Wurr *et al.* 2001) and the 'number of eyes per seed tuber increases with tuber size but at a decreasing rate' (Allen *et al.* 1992).

Secondly, plant population (the number of individual plants per hectare) can be manipulated by altering within-row spacing (between plants in the same row) or row width. Since seed spacing has no significant effect on the number of stems per plant (Bremner & Taha 1966; Lynch & Rowberry 1977; Oliveira 2000; Wurr *et al.* 2001; Mauromicale *et al.* 2003; Zebarth *et al.* 2006), increasing within-row spacing decreases stem density (Allen & O'Brien 1987; O'Brien & Allen 1992) and Love and Thompson-Jones (1999) reported that a 10-fold increase in plant spacing decreased stems per m^2 by a factor of 10. However, plant spacing can have an effect on canopy growth beyond influencing stem density, and when the desired stem density is achieved using large seed at wide spacing the clumped distribution of stems can be problematic, particularly if emergence is incomplete, creating large gaps in the whole crop canopy, as highlighted by Allen and Wurr (1992).

Thirdly, the conditions experienced by the seed during production and storage have been shown to affect the stem population and growth of the subsequent crop. Some of the effects have been attributed to chronological age (time from seed crop emergence to replanting (Firman 2014)) and physiological age (the thermal time, > 4 °C, experienced by the seed tubers after dormancy has broken, prior to planting (O'Brien *et al.* 1983)). Seed age, both chronological and physiological, affects the relationship between number of eyes, tuber size and stems, described above, by altering the extent of apical dominance; whereby the amount of sugar available for lateral bud growth is limited by the apical bud, suppressing lateral bud sprouting, as summarized by Danieli *et al.* (2018). The strength of lateral bud supression diminishes as the seed ages physiologically and more stems are produced after longer periods of storage (Eshel & Teper-Bamnolker 2012), though not all cultivars produce more stems from older seed (Blauer *et al.* 2013). However, as some, e.g. Eshel and Teper-Bamnolker (2012), have included chronological age within the determinants of physiological age it is difficult to distinguish the effects of chronological and physiological age within the literature.

Danieli *et al.* (2018) highlighted the importance of the duration of seed tuber storage to stem density, showing that stem density was greater after longer periods of seed

storage. This, however, appeared to be a function of chronological age since growing degree days (GDD) accumulated, either during storage or during growth of the seed in the field, had little and no effect respectively on stem density of the crop produced (Danieli *et al.* 2018). It is possible that increases in above-ground stem density (including both mainstems and secondary stems) with increasing physiological age are due to greater production of secondary stems; O'Brien *et al.* (1983) found that the proportion of mainstems decreased from *c.* 87 % when planted just after dormancy had broken, to *c.* 52 % with increasing physiological age (around 800 accumulated degree days > 4 °C).

Whilst delaying the planting date of the seed crop from spring to July, reducing the chronological age of the seed, reduced the number of mainstems produced in the subsequent ware crop, O'Brien and Allen (1992) reported that the effects on stem density were 'usually too small' to significantly affect canopy ground cover or yield. The same study also found limited effects of physiological age (generated using different storage regimes) on crop growth and tuber yields (O'Brien & Allen 1992). Alternatively, Wurr *et al.* (2001) suggested that weather conditions during seed tuber initiation may have a greater effect on the number of stems produced by the seed in the following season than precise planting date. It was reported that there was no consistent effect of seed planting date between years, but longer seed tubers, with more eyes, producing more stems, were initiated during the wetter, cooler periods of each year, potentially explaining why seed produced in different locations differ in the number of stems produced from the same seed weight (Wurr *et al.* 2001). Whilst it can be concluded that seed age and method of seed production effect the stem density of the subsequent crop, the precise mechanisms remain unclear as illustrated by varying results across the literature.

Lastly, number of stems has been shown to differ between cultivars by Firman (2014), who found that stems per 50 g tuber ranged from < 2 to > 5 across 14 cultivars. Ifenkwe and Allen (1978a) and Love and Thompson-Johns (1999) also noted that cultivars (Maris Piper and Désirée; and Russet Burbank, Frontier Russet, and Ranger Russet respectively) produced different average number of stems per seed tuber. These differences in stem number between cultivars may be linked to determinacy and Zebarth *et al.* (2006) also reported limited differences in average stem density between cultivars Atlantic and Shepody, which are both in determinacy group three. Additionally, the decreases in stem number per plant reported by Almekinders (1993)

in three Peruvian cultivars suggest that some cultivars respond to changing row spacing in a fashion contrary to the majority of European cultivars previously discussed, though it is also possible that stem production responds differently under different growing conditions as this experiment was conducted in the Peruvian highlands.

It is also possible that other factors, such as nitrogen availability and planting depth influence stem production. Mixed effects of increasing nitrogen availability on stem density have been reported; Lynch and Rowberry (1977) found no effect of increasing fertilization on mainstem production in *cv.* Russet Burbank, whilst Zebarth *et al.* (2006) reported slight increases in number of stems per plant in *cv.* Atlantic, though did not specify stem type recorded. Additionally, O'Brien and Allen (1992) observed that the number of secondary stems produced was greater at more shallow planting depths, suggesting that different planting practice between experimental sites may explain some of the variation in stem density between experiments.

In summary, stem density is determined by seed size (increasing as tuber weight increases), seed spacing (decreasing as within-row spacing increases) and seed age (tending to increase as seed ages), all of which are influenced by inherent differences in stem production capacity between cultivars.

5.1.2 Effects of stem density on the canopy

5.1.2.1 Canopy expansion

Allen and Scott (1980) showed that the rate of canopy expansion was faster at greater stem densities, achieved using either larger seed or seed planted at a higher density. Additionally, Engels *et al.* (1993) found that initial canopy expansion of small seed was slower than that of large seed, due in part to the lower stem density of smaller seed, but also the smaller energy reserves of the small seed tubers (microtubers, < 5 g). Conversely, Fleisher *et al.* (2011) found that leaf appearance on an individual stem was 0.1 leaves/day/stem faster on single-stem compared to three-stem plants under growth chamber conditions. From these results it is unclear how variation in leaf appearance in response to changing stem density links to changes in canopy cover. Therefore, it is necessary to quantify both leaf appearance and canopy expansion under field conditions to better understand how changes in leaf appearance affect whole canopy growth.

5.1.2.2 Canopy structure

Stem density can substantially affect the structure of the canopy and increases in axillary branching at lower stem densities and wider plant spacing have been reported in a range of papers. Ifenkwe and Allen (1978a) reported greater branching at wider plant spacing, with axillary branch leaves forming a larger proportion of total plant leaves at 61 cm compared to 20.3 cm spacing. Similarly, Lynch and Rowberry (1977) found that the number of axillary branches decreased as planting density increased. Furthermore, van der Zaag *et al.* (1990) found that a greater proportion of dry matter was partitioned to the branches at lower stem density, though the extent of this can vary between cultivars and climate as illustrated by the contrast between temperate and tropical potato growth. Whilst in a glasshouse experiment comparing plants with three stems to those with a single stem, Fleisher *et al.* (2011) also found that lower stem density promoted axillary branch production, longer axillary branches and faster leaf production on axillary branches (by 0.15 leaves/day), whereas at the higher stem density more leaves were produced on the two branches below the flower. Leaf size has also been shown to vary with stem density as the area of individual leaves on mainstems was greater at lower stem densities (Vos 1995; Oliveira 2000; Fleisher *et al.* 2011), though the difference varied with leaf position on the mainstem and was smaller in leaves at both base and apex of the mainstem (Vos 1995; Oliveira 2000). Hence, both branch production and mainstem leaf area are greater at lower stem densities, although the effect on canopy ability to intercept light is unclear.

Secondly, mainstem length has been shown to increase with increasing plant density (Ifenkwe & Allen 1978b). Vos (1995) similarly found that at higher stem densities the mainstem was on average 1.2 times (*c.* 10 cm) longer than at low stem densities (320 000 compared to 80 000 stems/ha). Additionally, Oliveira (2000) reported that maximum stem length was greater and achieved earlier at higher stem densities (15 cm compared to 30 cm within-row spacing). Yet in contrast, van der Zaag (1990) and Fleisher (2011) found limited differences in stem length between stem density treatments and it has been suggested (by Oliveira (2000)) that other factors, including nitrogen availability and cultivar, have a greater influence on stem length than between-stem competition for light. Regardless of stem length, Ifenkwe and Allen (1978a) found no difference in number of leaves produced on the mainstem between plant spacing treatments and Almekinders (1991) found that stem density had no effect on the onset or duration of flowering. The body of research suggests that higher stem

density promotes longer mainstems by increasing internode distances as opposed to producing more leaves, though the growth response varies between cultivar and location.

At extremely small seed sizes (< 5 g), Engels *et al.* (1993) reported that the minimum stem density to achieve full canopy cover was not met and maximum ground cover varied significantly with stem density. For example, the maximum ground cover produced at 40 000 stems/ha was less than half that at 95 000 stems/ha (Engels *et al.* 1993). Additionally, when different sized seed was planted to achieve the same stem density, the smallest seed (1-5 g) produced a smaller canopy throughout the season than the larger seed (5-20 g), suggesting that very small seed (< 5 g) are less capable of foliage production (Engels *et al.* 1993). Once above a stem density threshold, of *c.* 150 000 stems/ha (as suggested by the findings of Engels *et al.* (1993)), the functional importance of these structural differences between stem densities appears to diminish as the season progresses. Engels *et al.* (1993) found that similar ground cover was achieved (by the end of the growing season) by all stem density treatments greater than 150 000 stems/ha, as increased axillary branch leaf area compensated for the reduced mainstem leaf area at lower stem densities. Likewise, Firman and Daniels (2011) reported that three cultivars achieved the same maximum ground cover irrespective of stem density, though ground cover of plants at wider spacing peaked later in the season. Fleisher *et al.* (2011) similarly reported that there was no significant difference in total leaf area between plants with one or three stems, despite variation in the distribution of leaf area between the mainstem, axillary and sympodial branches. Whilst Bremner and Taha (1966) reported little difference in LAI between small and large seed, greater differences were observed between seed spacing treatments; with a slower increase in LAI and lower peak at 60 compared to 30 cm spacing in *cv.* King Edward (yet little difference in LAI throughout the season was observed in *cv.* Majestic). Both Lynch and Rowberry (1977), and Ifenkwe and Allen (1978a), reported that whilst maximum LAI was greatest at the highest stem densities, complete or near-complete ground cover was still achieved by canopies with lower stem densities. Additionally, no difference was found in intercepted radiation between stem density treatments after the first 23 days of canopy development (Fleisher *et al.* 2011). Although focusing on the effect of stem distribution (rather than stem density), Tarkalson *et al.* (2012) similarly reported smaller differences in light interception between more clumped and more even stem distributions across the whole season

(4-23 %) than early in the season (23-69 %). Hence, the effects of stem density on canopy growth are most apparent earlier in the growing season, with little variation reported in maximum ground cover, light intercepted and total LAI in relation to stem density. Yet the work of Bremner and Taha (1966) suggests that canopy size (as measured by LAI) is influenced by stem density in a cultivar-dependant manner, therefore it is important to quantify variation in canopy growth after canopy closure in relation to varying stem density, particularly with regard to differences between cultivars.

It was suggested by van der Zaag *et al.* (1990) that the ability of potato plants to respond to changing stem density depends on cultivar determinacy and environmental conditions and this hypothesis is supported by the work of both van der Zaag *et al.* (1990) and Fleisher *et al.* (2011). In field experiments, van der Zaag *et al.* (1990) found that increased branching at wider plant spacing did not compensate for lower stem densities in Katahdin, a determinate cultivar grown in temperate and tropical conditions, nor in Cosima and Berolina, indeterminate and determinate cultivars respectively, grown in the tropics (van der Zaag *et al.* 1990). Whereas Fleisher *et al.* (2011) found that the more indeterminate cultivar Kennebec maintained a similar total leaf area in single stemmed plants compared to plants with three stems, due to the production of additional branch leaves. Both van der Zaag (1990) and Engels (1993) found large differences in canopy cover within stem density treatments planted at different points in the season. They suggested that short-day conditions, either in the tropics (van der Zaag *et al.* 1990) or Mediterranean late autumn planting (Engels *et al.* 1993), promoted greater partitioning of dry matter to the tubers at the expense of the canopy due to earlier tuberization (although there is limited evidence for an effect of short photoperiods on tuber initiation in cultivars adapted for long days (O'Brien *et al.* 1998)). Fleisher *et al.* (2011) suggested that indeterminate cultivars tend to produce more, large axillary branches, allowing them to better compensate for low stem density with increased branch production. Tarkalson *et al.* (2012) also noted that uneven plant distribution had a greater effect on the light interception of determinate than indeterminate cultivars, which are more likely to achieve complete ground cover when stems are clustered unevenly. Russet Norkotah, a more determinate cultivar, with a more upright canopy, intercepted more light as stem distribution became more even, whilst Russet Burbank, a more indeterminate cultivar, with a vigorous, spreading canopy intercepted all available PAR 'regardless of planting configuration' (Tarkalson

et al. 2012). This suggests that the foliage production capacity of a cultivar influences crop ability to compensate for wide spacing and lower stem density, and hence, that determinate cultivars are less likely than indeterminate cultivars to close canopy gaps as stem density decreases with subsequent reductions in yield due to reduced intercepted light.

5.1.2.3 Canopy longevity and senescence

At lower stem densities a positive relationship between stem density and ground cover duration (equivalent to integrated ground cover (IGC)) was reported by Engels *et al.* (1993), suggesting that canopy longevity, as described by IGC, is only affected by stem densities below 150 000 stems/ha, when low stem densities are likely to limit ground cover. Engels *et al.* (1993) also showed that senescence occurred faster at higher stem densities, proposing that the reduced axillary branching at higher stem densities resulted in earlier senescence. Whilst experiments carried out by Firman and Daniels (2011) to develop seed rate guides, suggest that the effects of stem density on canopy persistence are cultivar specific. This was illustrated by slightly longer canopy persistence at lower stem densities in King Edward (80 compared to 31 and 19 cm spacing), but no difference in Russet Burbank or Pentland Dell or Marfona (Firman & Daniels 2011). Therefore, the relationship between canopy senescence deserves further attention, particularly in relation to the responses of cultivars of different determinacy levels.

In summary, lower stem densities are associated with slower canopy expansion, greater branch production and larger leaves on shorter mainstems. Once above the minimum stem density required to achieve complete ground cover, stem density appears to have a limited effect on light interception, but at low stem densities increasing the number of stems per plant positively correlates with IGC. Finally, the ability of potato plants to respond to changing stem density is affected by cultivar, particularly plant ability to continue leaf and branch production indicated by determinacy levels, and environmental conditions. Therefore, there is a need to investigate how differences in canopy expansion and structure, which result from variation in stem densities, affect canopy persistence and ability to intercept light throughout the season with regard to cultivar determinacy.

5.1.3 Stem population and yield

There are numerous ways to describe potato yield including gross biological yield (total mass of tubers produced), harvestable yield, (either fresh or dry total mass of tubers harvested), marketable yield (saleable tuber yield, classified by size and depending on end market—typically > 45 mm in diameter (Oliveira *et al.* 2017)) and tuber population (number of tubers per hectare). Each term, except harvestable yield, is used below and together provide useful information about the potential profitability of a given crop. Greater gross yields have been reported at higher stem densities (Bleasdale 1965; Allen & O'Brien 1987; Love & Thompson-Johns 1999). Yet marketable yield may be reduced at high stem densities since tuber population positively correlates with stem population, reducing average tuber weight (Ifenkwe & Allen 1978a; Allen & Wurr 1992; O'Brien & Allen 1992; Mauromicale *et al.* 2003; Tarkalson *et al.* 2011). At higher stem densities, between-stem competition for light reduces average tuber weight (Struik *et al.* 1990) and number of tubers per plant, although total tuber population is higher (Love & Thompson-Johns 1999). An increase in gross yield with increasing stem density has not been found in all studies as Lynch and Rowberry (1977) reported that there was no difference in gross yield across plant density treatments and marketable yield decreased with increasing stem density in Russet Burbank. Similarly Allen (1979) reported either no increase or a decrease in gross yield with increasing stem density and linear increases in tuber number with increasing stem number in cultivars King Edward and Majestic, but a plateau in tuber number above 130 000 stems/ha in *cv.* Pentland Crown.

As the relationships between stem density and both gross yield and tuber population have been shown to vary between cultivars (e.g. Allen 1979) a large proportion of the research into variation in stem density is concerned with finding the optimum stem and planting density for individual cultivars (e.g. O'Brien & Allen 1992; Wurr *et al.* 1992a; Firman & Daniels 2011; Ùanli *et al.* 2015). For example Love and Thompson-Johns (1999) reported that whilst highest total yields occurred at 8 cm plant spacing, the maximum marketable yields for Russet Burbank, Frontier Russet, and Ranger Russet, were predicted at 24.6, 23.6, and 20.8 cm, respectively. Optimum seed spacing, and therefore stem density, can also be considered from an economic perspective and work by Wurr *et al.* (1993) considered the economic optimum of seed density to occur when the difference between seed cost and yield price was greatest, and as seed became relatively more expensive to produce, optimum planting density decreased.

The economic optimum stem density will also vary over time as market demands change and differ between cultivars which can command a higher or lower price depending on quality and end-market.

In summary, whilst gross yield tends to be greater at greater stem densities, marketable yield often decreases due to reductions in mean tuber weight, but the relationship between stem density and yield varies with cultivar. As noted by Allen and Wurr (1992), it is important to understand the variation in canopy morphology in response to changing stem density to improve understanding of crop light interception capacity and the resultant differences in yield, particularly on differences in degree of response between cultivars.

5.1.4 Chapter aims

This chapter tests the overall thesis hypothesis in relation to varying stem density; that understanding variation in canopy growth with variation in stem density will provide greater insight into yield variability, than considering the effects of seed size, spacing and cultivar treatments upon yield directly. Hence, thesis aims two to four will be addressed in relation to planting density, to identify how changes in stem density affect canopy development and subsequent light interception and yield.

Firstly, the majority of the literature indicates that seed spacing and seed size have non-interacting effects on stem density, yet differences in stem distribution or clumping have been reported to alter canopy growth, structure and light interception. Thus, it was hypothesised that stem distribution (spacing in particular), in addition to stem density, will influence canopy growth prior to canopy closure. Hence, the ability of seed size and spacing, and stem density, to explain variation in canopy growth will be compared.

Secondly, the literature shows that the rate of canopy expansion is expected to increase with increasing stem density despite slower leaf appearance rates, however, these results were reported in separate experiments, under field and growth chamber conditions, respectively. Thus it is unknown if the negative relationship between leaf appearance and number of stems identified by Fleisher *et al.* (2011) under growth chamber conditions also occurs in the field and under with a wider range of stem densities, occurring naturally rather than by removal of stems from the seed tuber. Hence, there is a need to examine the relationship between whole canopy expansion and leaf appearance in the field by measuring both on the same plant.

Thirdly, further research is needed to better understand the links between the changes in canopy structure (including axillary branch production, mainstem length and LAI) which result from increasing stem density and the effect that these structural changes have on canopy longevity, senescence and ability to intercept light.

Fourthly, the literature also indicates that canopy growth responses to changing stem density vary between cultivars, and consequently, it is hypothesised that low stem densities are more likely to result in reduced maximum canopy cover, integrated ground cover and light interception in determinate, rather than indeterminate, cultivars.

Thus, the Planting Density chapter aims are as follows:

1. To determine if seed size and spacing have effects on canopy expansion (TiE25 and GCRate2575), maintenance (GCDur90 and IGC) and senescence (GCRate9050) distinct from their effects on stem density.
2. To quantify variation in canopy expansion and leaf appearance rate in the field and determine the relationship between the two descriptors of growth.
3. To quantify changes to canopy structure (including axillary branches, mainstem length and LAI) at differing stem densities and identify how these factors can explain differences in canopy ability to intercept light.
4. To quantify differences in canopy expansion, duration and senescence in cultivars of contrasting determinacy as stem density increases.

5.1.5 Chapter structure

This chapter focuses on the Planting Density experiments (Expt 2, Expt 4 and Expt 5) in which canopy growth was quantified throughout the season at a range of different stem densities, achieved by planting seed of different sizes at three spacings, in two contrasting cultivars as described below (5.2). Mid-season harvests were also carried out to capture structural differences in the canopy at varying stem densities to explain some of the variation with stem density in whole canopy growth. The growth of canopies from a ten-year series of seed size experiments was also quantified (5.2.4), increasing the number of cultivars included in the analysis to better illustrate the range of canopy responses to different stem densities across more UK cultivars. This archival data also provides context for Estima and Maris Piper results from the Planting Density experiments.

Results are reported in detail from, firstly, in season measurements of the Planting Density experiments relating to emergence (5.3.1), number of stems produced (5.3.2), percentage ground cover (5.3.3) and leaf appearance (5.3.4). Then secondly, data from the mid-season harvest in each experiment, concerning leaf area index (5.3.5) and branch production (5.3.6), are presented. Thirdly, end of season yield data is briefly shown (5.3.7), maintaining the focus of this work on the effects of stem density on the canopy. Fourthly, the ground cover variates from the Seed Size experiments are reported (5.3.8), illustrating the wide range in canopy growth responses to changing stem density between cultivars. The chapter finishes with a discussion (5.4), considering how the influence of stem density on canopy growth changes throughout the growing season, appearing to diminish in importance as the season progresses. The differing sensitivities of cultivars are highlighted, indicating the importance of cultivar specific data when attempting to include stem density in a predictive model of canopy growth.

5.2 Methods

Full details of methodology common to both Planting Date and Planting Density experiments are detailed in general methods (3), below are details specific to the Planting Density experiments.

5.2.1 Experimental details

5.2.1.1 Experimental design

Experiment 2 (Expt 2) was planted in 2016 and treatments consisted of all combinations of two cultivars (Estima and Maris Piper), two seed sizes (large and small, Table 37) and three within-row seed spacings (20, 40 and 60 cm) in a fully randomized block design with three replicates. Experiment 4 (Expt 4) was planted in 2017 with the same combination of randomized treatments as Expt 2 with slight differences in seed size (Table 37). Experiment 5 (Expt 5) was planted in 2018 with a similar design to Expts 2 and 4 but with an additional, intermediate seed size (Table 37). Mean seed mass for each seed size in all experiments is shown in Table 38.

Table 37. Planting details for each Planting Density experiment; planting date, plot length and seed size (mm). (E) and (MP) indicate cultivars Estima and Maris Piper respectively when seed size differed between the cultivars.

Expt	Planting date	Plot length (m)	Small	Medium	Large
2	19 April 2016	4.8	30-35 (E) 30-40 (MP)	n/a	50-55
4	10 April 2017	4.8	25-35	n/a	45-55
5	22 April 2018	6.0	25-35	35-45	45-55

5.2.1.2 Seed

Unsprouted seed was planted; size varied according to experimental design (Table 38). Chronological and physiological seed age were not included as experimental treatments however seed age may have differed between years due to variation in the agronomic conditions of seed production.

Table 38. Seed mass for Planting Density experiments, mean weight calculated from 200 tubers (g). Estima, E and Maris Piper, MP.

		Small		Medium		Large	
Expt	Cultivar	E	MP	E	MP	E	MP
2		24.9	30.5	n/a	n/a	87.8	89.0
4		26.1	15.9	n/a	n/a	98.3	96.8
5		28.7	23.6	41.5	49.3	80.4	85.2

5.2.1.3 Planting

Plots were fertilized with 150 kg N/ha (ammonium nitrate, broadcast fertilizer) in Expts 2 and 4, and 200 kg N/ha in Expt 5. Within-row spacing varied by plot according to experimental design and plots were longer in Expt 5 (Table 37).

5.2.1.4 Irrigation

Irrigation was carried out by boom, avoiding water deficit according to an irrigation scheduling model (Stalham & Allen 2004).

5.2.2 In-season measurements

5.2.2.1 Emergence counts

In Expts 4 and 5 the date of emergence of individual plants tagged for recording leaf appearance was recorded.

5.2.2.2 Ground cover

Percent canopy ground cover was measured with grids of two sizes, reflecting differences in plant spacing between plots (Table 39).

Table 39. Dimensions of handheld grid used to measure percentage ground cover in Expts 2, 4 and 5.

Seed spacing (cm)	Dimensions (cm)	Plants within grid
20	75 x 60	3
40	75 x 80	2
60	75 x 60	1

5.2.2.3 Harvest

In Expt 2 a mid-season harvest was carried out for Maris Piper at an average ground cover of 86 %. There was no mid-season Estima harvest due to advanced senescence of the Estima plots at the time of harvest. Final harvests were carried out for Estima and Maris Piper at near-complete senescence with average ground covers of 0 and 16 %, respectively.

In Expt 4 both cultivars were harvested at the onset of senescence with average ground covers of 92 and 95 % for Estima and Maris Piper, respectively. The final harvest was carried out at complete (0 % GC) and near-complete (12 % GC) senescence for Estima and Maris Piper, respectively.

In Expt 5 a mid-season harvest was carried out for Maris Piper at an average ground cover of 98 %. There was no mid-season Estima harvest, again, due to advanced senescence of the Estima plots at the time of harvest. Final harvests were carried out for Estima and Maris Piper after complete senescence at average ground covers of 0 and 2 %, respectively. See Table 40 for further details.

A harvest area of 1.2 x 1.5 m was dug per harvest, per plot, harvesting twelve, six or four plants according to plant spacing (20, 40 and 60 cm spacing, respectively).

Table 40. Harvest dates for experiments 2 (2016), 4 (2017) and 5 (2018).

Expt	Cultivar	Harvest date	
		Mid-season	Final
2	Estima	n/a	29 September
	Maris Piper	8 September	5 October
4	Estima	1 September	25 October
	Maris Piper	1 September	25 October
5	Estima	n/a	3 September
	Maris Piper	15 August	24 September

5.2.2.4 Leaf area index

Leaf area index was measured at one mid-season harvests, at the onset of senescence, in each experiment. LAI of Estima plots was not measured in either Expts 2 or 5, since the Estima canopy had senesced before the mid-season harvest was carried out.

5.2.2.5 Branch production

Number of branches was recorded on two stems per plot in Expt 2, and three stems per plot in Expts 4 and 5. Branch height on Estima stems was not measured in Expts 2 or 5, since the Estima canopy had senesced before the mid-season harvest was carried out.

5.2.3 Statistical analysis

The relationship between stem density and each canopy variate was determined using multiple linear regression (Faraway 2016), carried out in R. A full linear model was fitted, allowing for variation between experimental years and accounting for experimental block structure, with the basic form: lm(canopy variate ~ stem density * cultivar + year + block). Significance of predictors was determined using the 'Anova' command with type II sum of squares (from the 'car' package (Fox & Weisberg 2019)) and non-significant terms were then dropped from the model, though the blocking factor, describing the experimental blocks, was retained even if effects were non-significant to ensure that experimental structure was accounted for in the analysis (Faraway 2016). The R^2 of models with, and without, seed size and seed spacing were also compared to identify the additional variation which stem distribution (as described by seed size and seed spacing, Figure 62) could explain in addition to that already accounted for by stem density—lm(canopy variate ~ stem density * cultivar + year + block) vs lm(canopy variate ~ stem density * cultivar + seed size * seed spacing + year + block).

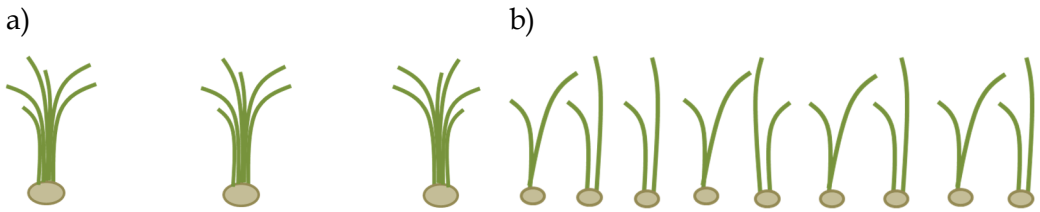

Figure 62. Illustration of varied stem distribution, resulting from different combinations of seed sizes and spacing at equal stem densities. (a) Highly clumped stem distribution, with few, large seed. (b) Even stem distribution, with many, small seed.

5.2.4 Seed Size experiments (archival data)

A series of seed size experiments was carried out by Cambridge University Farm (CUF) and NIAB CUF over ten years, from 2007 to 2016, as part of a commercial, and consequently unpublished, cultivar development programme. The programme was conducted at Cambridge University Farm, at 52 ° 13' N, 0 ° 05' E, on soils ranging from clay loams to sandy loams. The Seed Size experiments were carried out to determine

relationships between number of stems and seed weight and the methodology remained consistent with only minor adjustments between years.

5.2.4.1 Experimental methods

Six seed sizes were grown per experiment, increasing in 5 mm increments from 25-30 mm to 50-55 mm. Eight plants, at 30 cm spacing, were planted in 2.4 m long four-row plots in a randomised block design with four replicates per cultivar. Experiments were planted by hand. Emergence counts and ground cover measurements occurred weekly. Number of stems and plants in the whole plot were counted prior to harvest and stem density was calculated. Plots were harvested after the onset of senescence (< 90 % GC), with the majority harvested at complete senescence (< 10 % GC) and a length of 1.8 m was harvested in each of two harvest rows, consisting of a total of twelve plants. Tubers were graded at 10 mm intervals.

5.2.4.2 Cultivars

As the cultivar development programme was carried out on behalf of a commercial partner cultivars have been anonymized. Most cultivars were grown at least twice, with four cultivars only tested once and eight cultivars grown in three years (Table 41).

Table 41. Cultivar occurrence in each year of the Seed Size experiments.

	Cultivar number																			
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
2007																		●		
2008						●	●	●			●								●	
2009						●	●	●	●	●	●								●	
2010							●	●	●	●	●	●	●							
2011									●	●		●		●						
2012	●	●	●									●		●						
2013	●	●	●		●															●
2014	●		●		●										●					●
2015				●												●	●			
2016																●	●			

5.2.4.3 Statistical analysis

The canopy quantification (CQ) curve, as described in chapter 2 (2.3.2), was fitted to the ground cover data from each plot, generating the variates in Genstat. Further analysis was carried out in R (R Core Team 2019) using RStudio version 1.1.463 (RStudio Team 2015). Canopy variate responses to stem density, cultivar and year of experiment were determined using multiple linear regression. Differences between cultivars were identified using pairwise comparison of estimated marginal means (EMMs) using the 'emmeans' package in R (specifically the 'emtrends' function (Lenth 2019)) to indicate whether responses to changing stem density were similar or

dissimilar across the cultivars. Cultivars which showed no significant response to stem density for a particular variate (indicated by a 95 % confidence interval which included zero) were excluded from the EMMs analysis.

5.3 Results

5.3.1 Emergence

Within each experiment there was little variation in emergence date, with a range of three days or fewer between treatment means. Number of days between planting and emergence (EmDAP) did not vary between treatments in Expt 2 and averaged 35.5 days (Table 42).

In Expt 4, mean EmDAP was 46.3 days and there were small but significant differences between the treatments. On average, Estima emerged 50 days after planting, irrespective of seed size, whilst small Maris Piper seed emerged 2.6 days after the large seed (49.8 and 47.2 days, respectively, $P = 0.009$). Estima emerged an average of 1.5 days after Maris Piper ($P = 0.003$, Table 43). Whilst small seed emerged 1.3 days later than the large seed ($P = 0.009$, Table 45). EmDAP also varied in Maris Piper between seed spacings, with 20 and 40 cm spacings emerging 3 days earlier than seed at 60 cm spacing (47.5, 47.5 and 50.5 days, respectively, $P = 0.015$) possibly due to unintentionally deeper planting depth at 60 cm, yet there was no variation in EmDAP between seed spacings in Estima (50 days). The differences in Maris Piper resulted in longer on mean EmDAP at 60 cm spacing, with the 20 and 40 cm spacings emerging 1.5 days earlier ($P = 0.015$, Table 44).

With later planting in Expt 5 mean EmDAP was 29.7 days shorter than in Expts 2 and 4. Again Estima emerged later than Maris Piper, by 0.7 days ($P < 0.001$, Table 43), and small seed emerged 0.5 days later than the medium and large seed ($P = 0.008$, Table 45). There was no effect of seed spacing on EmDAP in Expt 5 (Table 44).

There was little variation in soil temperature, between planting and emergence, between the experiments (Table 42). The effects of all treatments and their interactions on emergence are reported in Appendix 18.

Table 42. Dates of planting and mean emergence, the delay between emergence and planting (EmDAP, days), and mean soil temperature between planting and emergence (°C) in Expts 2, 4 and 5.

Expt	Planting date	Emergence date	EmDAP	Soil temperature
2 (2016)	19 April	25 May	35.5	11.8
4 (2017)	10 April	29 May	49.3	12.8
5 (2018)	22 April	23 May	29.7	12.5

Table 43. Interval between emergence and planting (EmDAP, days) for each cultivar in Expts 2, 4 and 5. Data presented are a mean of seed size and seed spacing treatments.

	Cultivar			
Expt	Estima	Maris Piper	S.E.	D.F.
2	35.7	35.3	0.254	22
4	50.0	48.5	0.313	22
5	30.0	29.3	0.094	34

Table 44. Interval between emergence and planting (EmDAP, days) for each seed spacing in Expts 2, 4 and 5. Data presented are a mean of cultivar and seed size treatments.

	Seed spacing (cm)				
Expt	20	40	60	S.E.	D.F.
2	35.0	36.0	35.5	0.311	22
4	48.8	48.8	50.3	0.384	22
5	29.5	29.7	29.9	0.116	34

Table 45. Interval between emergence and planting (EmDAP, days) for each seed size treatment in Expts 2, 4 and 5. Data presented are a mean of cultivar and seed spacing treatments.

	Seed size				
Expt	Small	Medium	Large	S.E.	D.F.
2	35.5	n/a	35.5	0.254	22
4	49.9	n/a	48.6	0.313	22
5	30.0	29.6	29.5	0.116	34

5.3.1.1 Key points: Emergence

- Duration between planting and emergence varied little within experiments.

5.3.2 Number of stems

Number of above-ground stems (both main and secondary) per plant was recorded within the first month after emergence and mean number of stems per plant was 3.88, 2.82 and 2.94 in Expts 2, 4 and 5, respectively (Table 46). In Expt 5, in four plots (small Estima seed at 40 and 60 cm spacing, small Maris Piper seed at 20 cm spacing, and medium Maris Piper seed at 60 cm) stem number counts were unreplicated due to missing plants. The difference in stems per plant between small and large seed was

greater in Maris Piper than in Estima in Expt 2 (2.94 and 1.67 stems/plant, respectively, $P = 0.045$) and Expt 5 (2.82 and 1.20 stems/plant, respectively, $P = 0.003$). Large seed produced approximately 2 stems/plant more than small seed in each experiment (2.31, 1.98 and 2.01, Expts 2, 4 and 5, respectively, $P < 0.001$, Figure 63). Estima produced 2.19 and 1.09 fewer stems per plant than Maris Piper in Expts 2 and 5, respectively ($P < 0.001$, Figure 63a & c), but there was no difference between the cultivars in number of stems produced in Expt 4 (Figure 63b). As expected, number of stems per plant did not vary with seed spacing in any experiment, but stem density decreased in proportion to increasing seed spacing as seen in early and end of season stem counts (Tables 46 & 47). The effects of all treatments and their interactions on number of stems per plant are reported in Appendix 18.

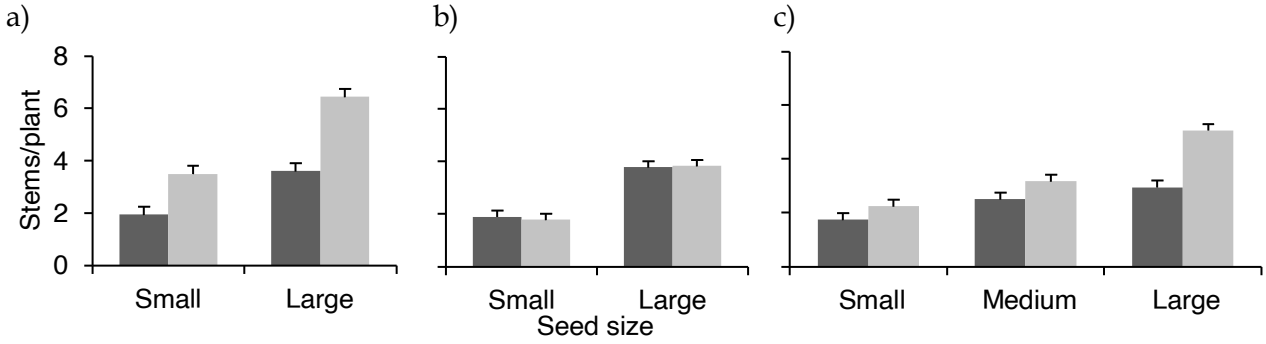

Figure 63. Effect of seed size on number of stems per plant, recorded in the first month after emergence, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 83 D.F.). Data presented are means of seed spacing treatments.

Table 46. The number of above-ground stems per hectare (000/ha), recorded within one month of emergence in two plants (0.3, 0.6 and 0.9 m² harvest area for 20, 40 and 60 cm spacings, respectively) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 3 (34 D.F.).

Expt	Seed size	Spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		100	72	48	278	109	63	22.8
	Large		200	128	102	422	183	141	
4	Small		133	67	37	133	56	37	31.7
	Large		256	122	89	300	100	89	
5	Small		133	67	30	144	72	52	19.8
	Medium		211	72	48	189	94	82	
	Large		167	100	74	344	156	119	

Table 47. The number of above-ground stems per hectare (000/ha), recorded at final harvest from 1.8 m² harvest area (twelve, six and four plants at 20, 40 and 60 cm spacing, respectively), for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 3 (34 D.F.).

Expt	Seed size	Spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		128	65	48	265	115	93	21.6
	Large		194	132	93	450	172	133	
4	Small		122	89	39	113	59	43	14.6
	Large		220	144	82	280	124	94	
5	Small		106	54	37	161	87	48	7.39
	Medium		152	89	43	269	119	69	
	Large		233	102	67	326	183	107	

Number of stems was also recorded at the final harvest (Table 47) and stem density tended to be lower at final harvest relative to the early season stem count (Figure 64), though mean stem density did not differ significantly between counts (paired t-test: t = 0.83, D.F. = 125, P = 0.406). Early season stem density (eS) explained 77.0 % of the variation in stem density at final harvest (fS, multiple linear regression; fS ~ eS + block, P < 0.001, Table 48) and the reduction in stem count did not differ between experiments (year; ANOVA, *P* = 0.804). The relationship between early and end of season stem density tended to be more variable at high stem densities (Figure 64). Early stem count data were used in subsequent analyses (despite a lower number of plants sampled than in the final harvest stem count) as the count was carried out on the plants used for the leaf appearance measurements. Using data from the same individual plants where possible should reduce noise from between-plant variation.

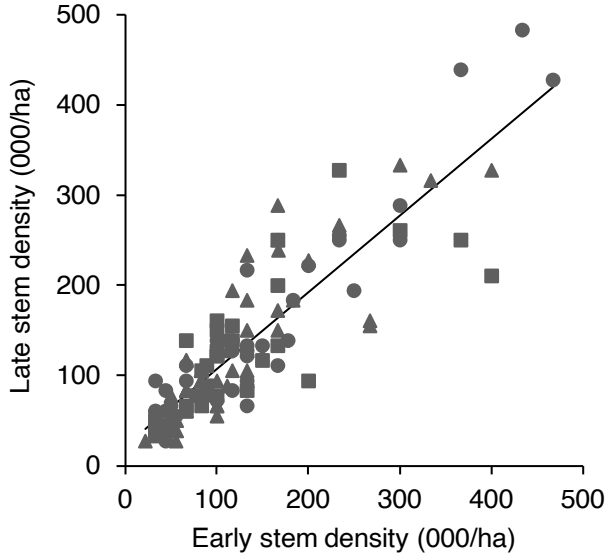

Figure 64. Relationship between early-season stem density (eS) and late-season stem density, at final harvest (fS), Expt 2, ●; Expt 4, ■ and Expt 5, ▲. R^2 = 0.770. See Table 48 for details of multiple linear regression.

Table 48. Relationship between early season stem count (eS) and final harvest stem count (fS). fS = β0 + β1*eS.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	22.4	6.56	0.001
1	eS	0.851	0.0415	< 0.001

5.3.2.1 Key points: Number of stems

- Larger seed consistently produced more stems per plant than smaller seed.
- As expected, seed spacing did not affect number of stems per plant but as within-row spacing increased, stem density decreased.
- Maris Piper tended to produce more stems than Estima.
- Number of stems was lower at final harvest than early in the season.

5.3.3 Ground cover growth patterns

Percentage ground cover (GC) was measured throughout the season and the canopy quantification (CQ) model fitted a curve to the raw data of individual plots, describing canopy growth throughout the season in relation to the interval after planting. Descriptive variates were then calculated from the curve as described in the modelling chapter (2.3.2). The effects of all treatments and their interactions on patterns of ground cover growth are reported in Appendix 19.

5.3.3.1 Season overview

Percent ground cover values were averaged for each seed size, seed spacing and cultivar treatment, and the CQ curve was fitted to the treatment mean GC data. The curves show the effect of each treatment on canopy growth throughout the season, until complete senescence in the Estima plots (all harvested at 0 % GC), and the curves illustrate the expected pattern of canopy senescence beyond the point of harvest in Maris Piper, which was harvested at *c.* 16, 15 and 2 % GC in Expts 2, 4 and 5, respectively. Variation in the CQ curve with respect to treatment interactions is reported in Appendix 20.

Early canopy growth was similar between Estima and Maris Piper with little difference in rates of canopy expansion within each experiment (Figure 65), but clear differences in canopy cover between cultivars were seen later in the season. Maris Piper maintained complete ground cover for longer than Estima, senescing later in all three experiments (Figure 65). The difference in canopy maintenance was greatest in Expt 5,

when Estima did not achieve 100 % GC (Figure 65c), and the difference between cultivars was smallest in Expt 4, as both Estima and Maris Piper began senescence at *c.* 245 ordinal days (Figure 65b). The rate of Maris Piper senescence was noticeably slower than Estima in Expt 4 (Figure 65b), though there was little difference in senescence rate between cultivars in Expts 2 and 5. These three experiments illustrated that whilst Maris Piper consistently produced a longer-living canopy than Estima, the differences were not fixed, instead varying between the seasons as growth was influenced by the different growing conditions in each year (Appendix 14). Treatment means were well represented by the CQ curves as shown by Willmott's index of agreement ≥ 0.998 and RMSE < 3.2 % GC across experiments and cultivars (Table 49).

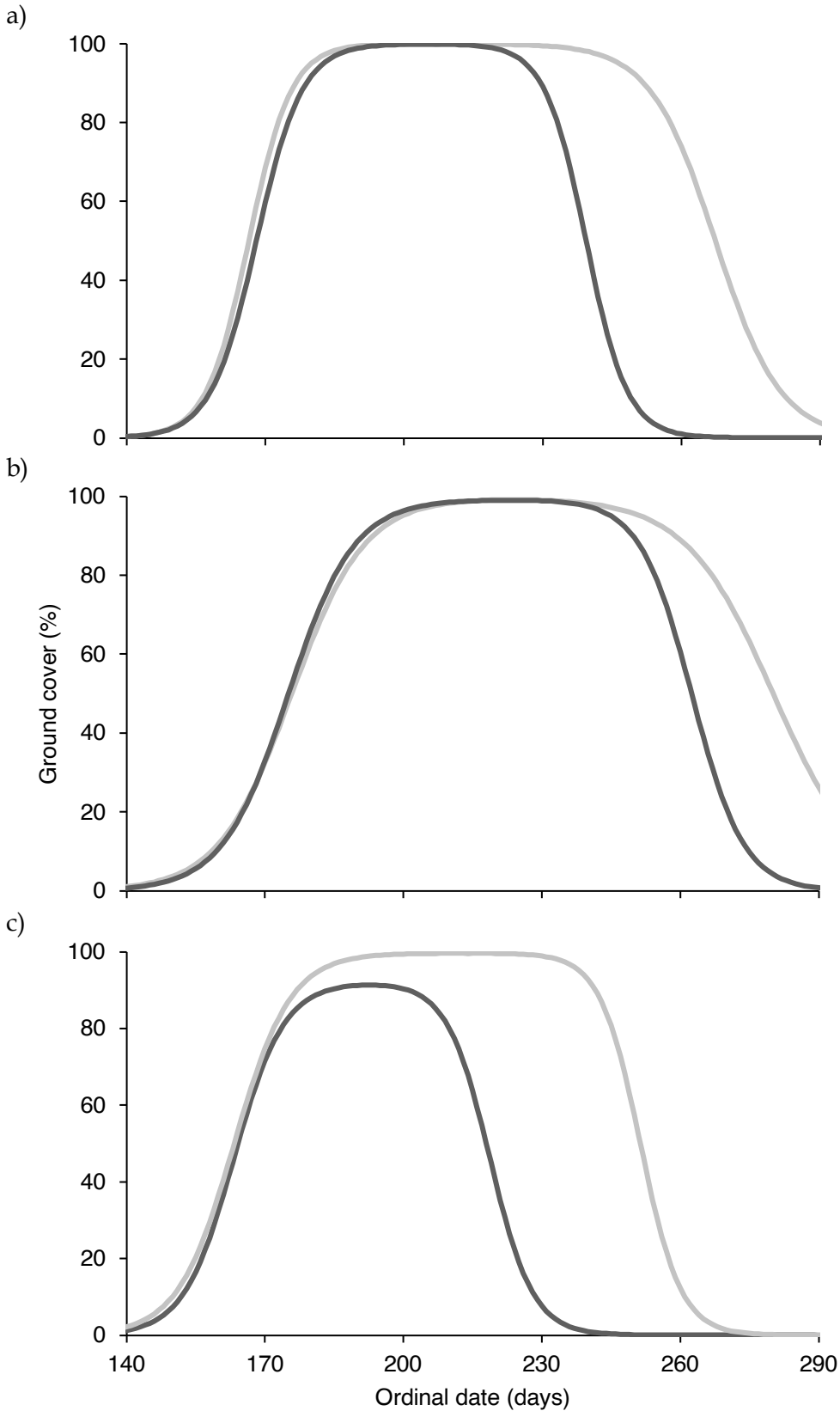

Figure 65. Average ground cover curve by cultivar, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, — ; Maris Piper, —. Data presented are means of seed size and seed spacing treatments. Goodness of fit for each curve is shown in Table 49.

Table 49. Goodness of fit scores for cultivar treatment means in Expts 2, 4 and 5. Goodness of fit measured using Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC).

		Goodness of fit score	
Expt	Cultivar	*d*	RMSE
2	Estima	0.999	2.58
	Maris Piper	0.999	2.04
4	Estima	0.999	2.94
	Maris Piper	0.999	2.46
5	Estima	0.998	3.14
	Maris Piper	0.999	2.22

Across all three experiments, increasing seed spacing delayed initial canopy growth, but rate of mid-season canopy was constant between seed spacing treatments (Figure 66). Hence, at 20 cm seed spacing maximum ground cover was achieved earliest, followed by the 40, then 60 cm spacing treatments. Duration of canopy and rates of senescence were similar across the spacing treatments (Figure 66). Mean seed spacing treatments were well represented by the CQ curves as shown by Willmott's index of agreement ≥ 0.993 and RMSE < 5.6 % GC across experiments and seed spacing treatments (Table 50), though goodness of fit varied between the experiments and was greatest in Expt 4 (d = 0.999, RMSE = 2.57 % GC) and least in Expt 5 (d = 0.994, RMSE = 5.07 % GC).

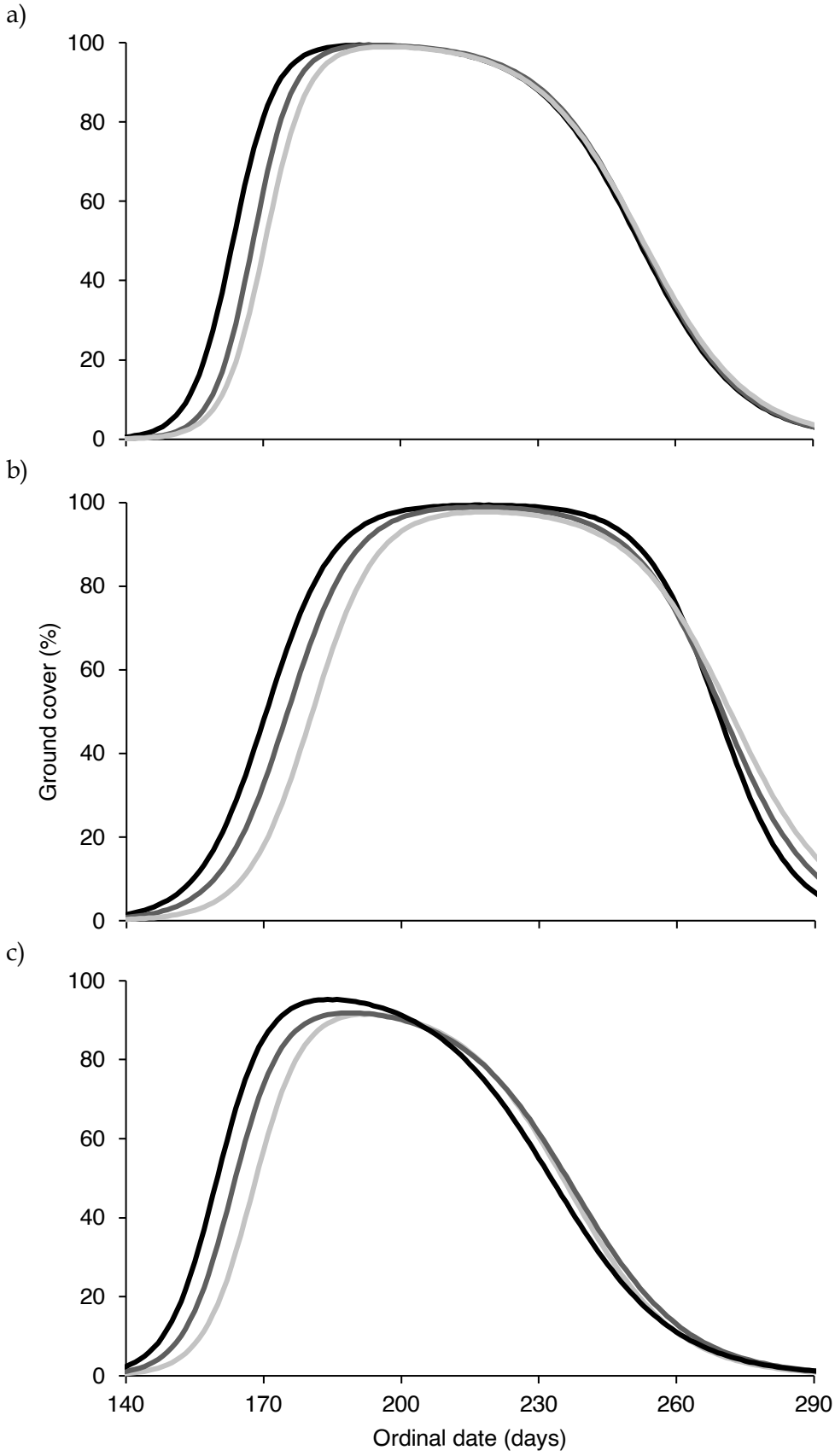

Figure 66. Average ground cover curve by seed spacing, (a) Expt 2, (b) Expt 4 and (c) Expt 5. 20 cm, —; 40 cm, —; 60 cm, —. Data presented are means of cultivar and seed size treatments. Goodness of fit for each curve is shown in Table 50.

Table 50. Goodness of fit scores for seed spacing treatment means in Expts 2, 4 and 5. Goodness of fit measured using Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC).

	Seed spacing	Goodness of fit score	
Expt	(cm)	*d*	RMSE
2	20	0.997	3.69
	40	0.997	3.97
	60	0.997	3.64
4	20	0.999	2.64
	40	0.999	2.14
	60	0.998	2.94
5	20	0.993	5.63
	40	0.994	5.08
	60	0.996	4.51

Canopies produced by large seed reached maximum ground coverage faster than those produced by small seed in each experiment (Figure 67). Canopies from small seed senesced at slightly slower rates than those from large seed in Expts 2 and 4, though the differences were marginal (Figure 67a & b). Maximum ground cover was both greater in (by a small margin in Expts 2 and 4), and was maintained for a longer duration by large seed than small, and the difference was greatest in Expt 5 (Figure 67c). Seed of intermediate size (35-45 mm, Table 37) produced an intermediate canopy in terms of both maximum ground cover and duration (Figure 67c). Mean seed size treatments were well represented by the CQ curves as shown by Willmott's index of agreement; ≥ 0.994, and RMSE; < 5.5 % GC, across experiments (Table 51). Again, goodness of fit varied between the experiments and was greatest in Expt 4 (d = 0.999, RMSE = 2.61 % GC) and lowest in Expt 5 (d = 0.995, RMSE = 4.99 % GC).

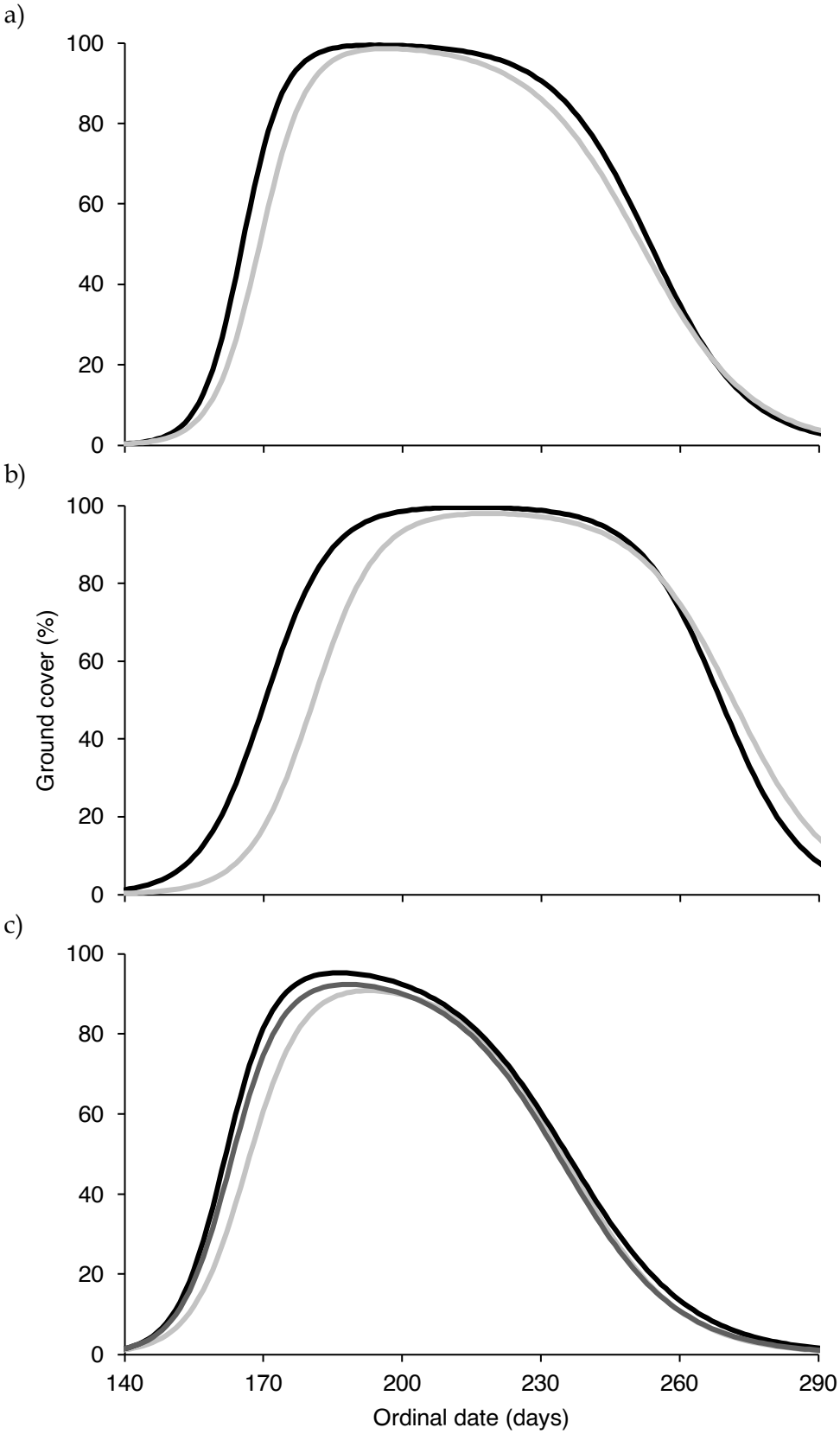

Figure 67. Average ground cover curve by seed size treatment, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Large seed, —; medium seed (Expt 5 only), —; small seed, —. Data presented are means of cultivar and seed spacing treatments. Goodness of fit for each curve is shown in Table 51.

Table 51. Goodness of fit scores for seed size treatment means in Expts 2, 4 and 5. Goodness of fit measured using Willmott's index of agreement (*d*) and root mean square error (RMSE, % GC).

		Goodness of fit score	
Expt	Seed size	*d*	RMSE
2	Small	0.997	4.04
	Large	0.997	3.62
4	Small	0.999	2.58
	Large	0.999	2.64
5	Small	0.995	4.54
	Medium	0.995	4.97
	Large	0.994	5.47

5.3.3.2 Integrated ground cover

Integrated ground cover (IGC, % days) combines whole season canopy cover and duration. Mean IGC was greatest in Expt 4 (9475 % days), followed by Expt 2 (8586 % days) and Expt 5 (6962 % days), equivalent to 94.8, 85.8 and 69.6 days at 100 % GC, respectively. In all three experiments the 20 cm spacing had a greater IGC than the 40 cm spacing (differences equivalent to 4.3 ($P = 0.009$), 4.2 ($P < 0.001$) and 1.9 ($P < 0.001$) days at 100 % GC in Expts 2, 4 and 5, respectively) and the 40 cm spacing IGC was greater than the 60 cm spacing (differences equivalent to 1.9, 4.6 and 5.6 days at 100 % GC in Expts 2, 4 and 5 respectively, Figure 68).

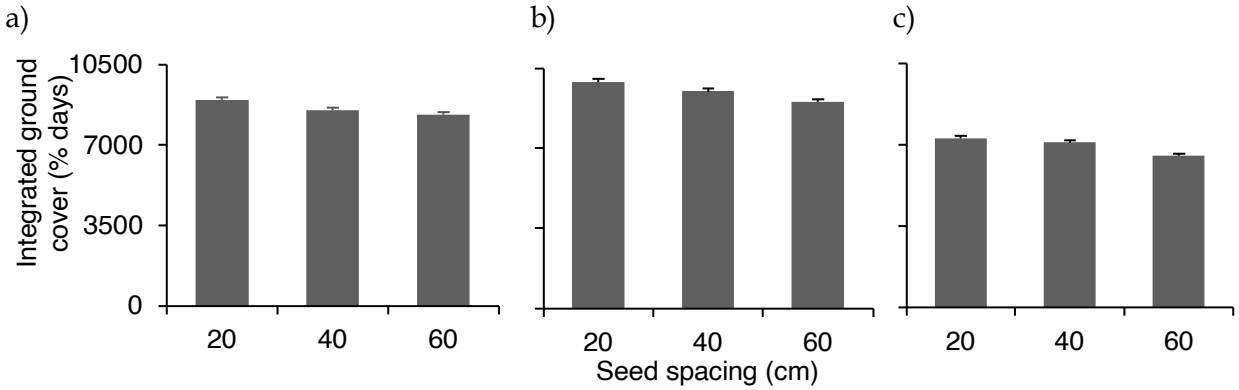

Figure 68. Effect of seed spacing on integrated ground cover in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of cultivar and seed size treatments.

Maris Piper had a greater IGC than Estima in each experiment, a difference equivalent to 29.3, 15.8 and 36.0 additional days at 100 % GC in Expts 2, 4 and 5, respectively ($P < 0.001$, Figure 69). IGC of large seed was the equivalent of 5.8, 8.5 and 8.0 days at 100 % GC greater than the IGC of small seed in Expts 2, 4 and 5, respectively ($P < 0.001$, Figure 69). In Expt 5, medium size seed produced an intermediate IGC, 446 % days smaller than the large seed and 355 % days greater than the small seed (equivalent to 4.5 and 3.5 days at 100% GC, Figure 69c). The difference between the IGC of small and

large seed in Expt 2 was greater in Estima than Maris Piper (9.5 and 2.2 additional days at 100 % GC, respectively, $P = 0.025$), however this was likely due to differences in size of the small seed between the cultivars; small Estima seed (24.9 g) was smaller than small Maris Piper seed (30.5 g) due to difficulties in sourcing the seed.

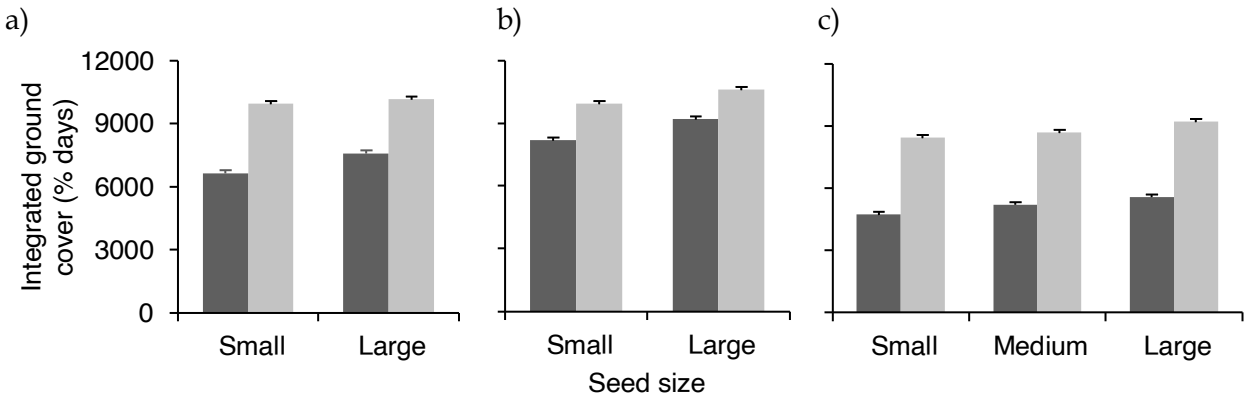

Figure 69. Effect of seed size and cultivar on integrated ground cover in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of seed spacing treatments.

IGC increased with increasing stem density in each experiment and both cultivars (Figure 70), though the degree of increase varied depending on combination of year and cultivar (multiple linear regression; IGC ~ stem density * cultivar + year + block, $P < 0.001$, Table 52). Mean IGC differed between experiments, and was lowest in Expt 5 (Figure 70c), whilst Estima IGC was more sensitive to increases in stem density than that of Maris Piper (Figure 70). Stem density alone explained a limited proportion of variation in IGC (multiple linear regression; IGC ~ stem density + block, $R^2 = 0.130$, $P < 0.001$). Stem distribution had little effect on IGC as indicated by the minimal increase in variation explained, from 87.7 to 89.1 %, by the inclusion of seed size and spacing in the model (multiple linear regression).

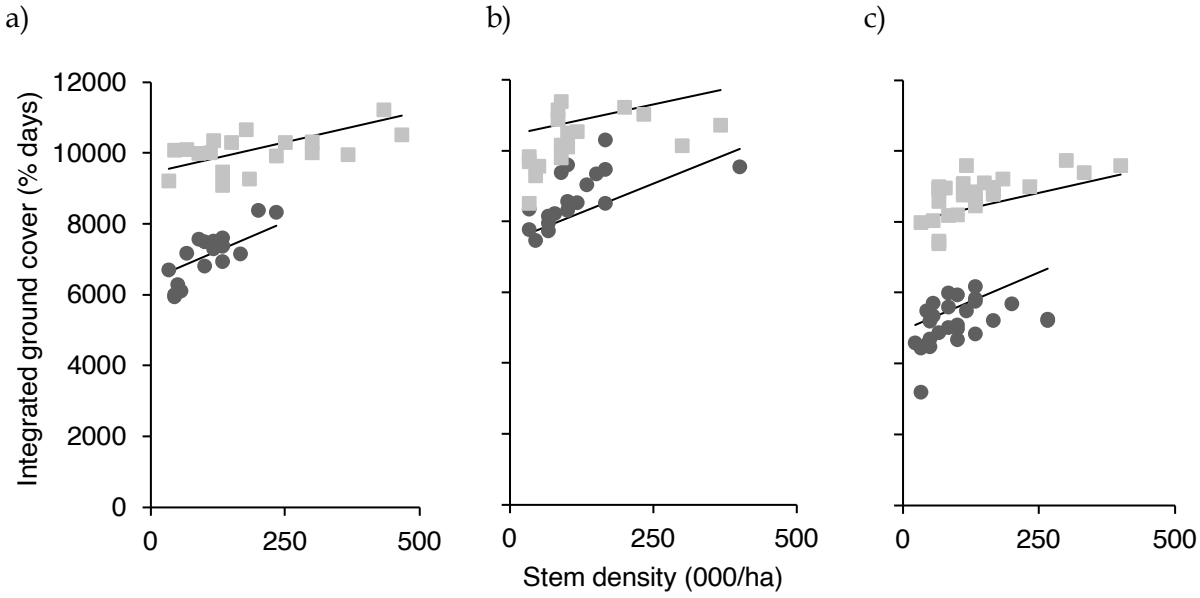

Figure 70. Relationship between integrated ground cover (IGC) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.877. See Table 52 for details of multiple linear regression.

Table 52. Relationship between stem density (S), integrated ground cover (IGC), cultivar (MP) and experiment (Expts 2, 4 or 5). IGC = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5 + β5*(S*MP).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	6439	31.0	< 0.001
1	S	6.5	5.07	< 0.001
2	MP	3012	13.5	< 0.001
3	Expt 4	1004.1	6.11	< 0.001
4	Expt 5	-1493.8	-10.02	< 0.001
5	S * MP	-3.1	-2.02	0.046

5.3.3.3 Duration of early canopy expansion

Duration of early canopy expansion, between emergence and 25 % GC (TiE25) was longest in Expt 4 (19.6 days), followed by Expt 2 (17.2 days) and was shortest in Expt 5 (15.2 days). As plant spacing increased, early canopy expansion slowed and 40 cm spaced plots took 3.8, 4.7 and 3.7 days longer to reach 25 % GC than 20 cm spaced plots in Expts 2, 4 and 5 respectively and TiE25 was 3.0, 5.1 and 3.4 days greater in 60 cm spacing than in the 40 cm spacing in Expts 2, 4 and 5 respectively ($P < 0.001$, Figure 71).

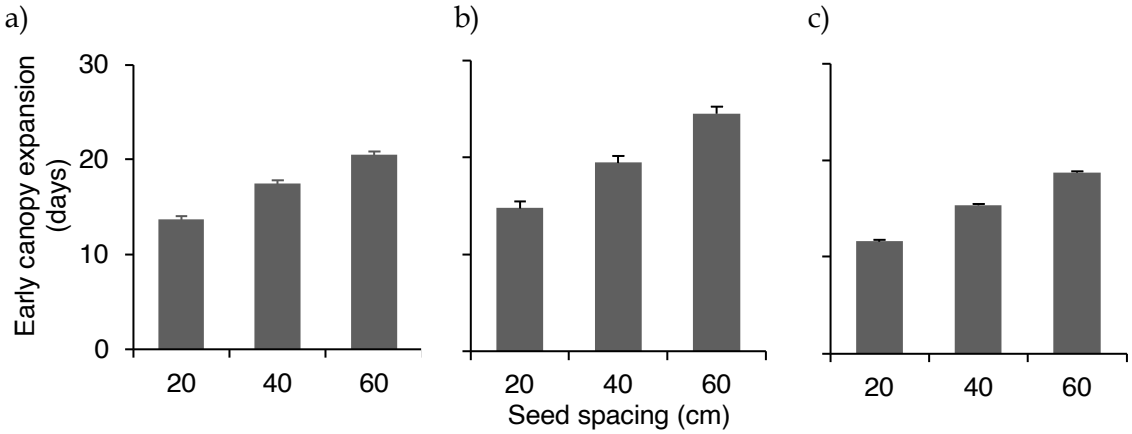

Figure 71. Effect of seed spacing on duration of early canopy expansion in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of cultivar and seed size treatments.

The rate of early canopy expansion (TiE25Rate) was calculated per plant to quantify the effect of spacing on individual plant canopy expansion, distinct from effects of plant and density. Rate of early canopy expansion per individual plant was greatest at the 60 cm spacing in each experiment ($P < 0.001$, Figure 72). The difference in early canopy expansion rate per plant between 20 and 40 cm spacings (0.10, 0.02 and 0.09 %/day/plant in Expts 2, 4 and 5, respectively) was smaller than between 40 and 60 cm spacings (0.51, 0.38 and 0.52 %/day/plant in Expts 2, 4 and 5 respectively), due to the greater reduction in between-plant competition at the widest spacing. Per plant rate of early canopy expansion was also greater in large, than small, seed by 0.16, 0.43 and 0.30 %/day/plant in Expts 2, 4 and 5, respectively ($P < 0.001$). The differences in TiE25Rate between cultivars were inconsistent between years and TiE25Rate was faster in Maris Piper than Estima in Expt 2 (by 0.05 %/day/plant, $P = 0.042$), faster in Estima than Maris Piper in Expt 4 (by 0.15 %/day/plant, $P = 0.02$) and did not differ between cultivars in Expt 5.

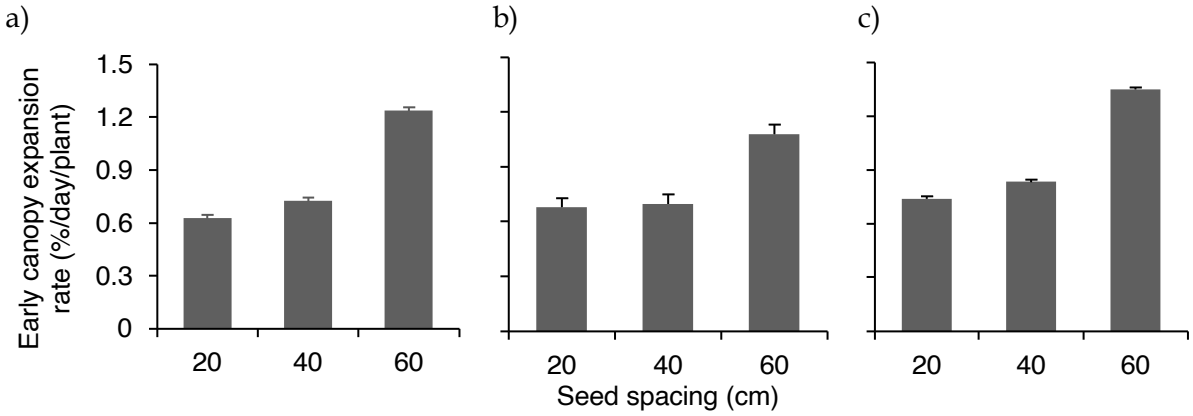

Figure 72. Effect of seed spacing on early canopy expansion rate per plant, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of cultivar and seed size treatments.

The difference in TiE25 between the cultivars in the small seed was almost double that of the large seed in Expt 2, partially due to the smaller seed size of the small Estima seed compared to Maris Piper (24.9 and 30.5 g respectively, $P = 0.031$, Figure 73a). There was no interaction between cultivar and seed size in either Expts 4 or 5 (Figure 73b & c), though there was a three-way interaction between cultivar, seed size and spacing in Expt 5 in which the range in TiE25 between seed sizes and spacing treatments was smaller in Maris Piper than Estima ($P = 0.017$). Early canopy expansion was slower for small than large seed and the difference was greater in Expt 4 (9.5 days, $P < 0.001$) than in Expts 2 and 5 (3.3 and 4.8 days, respectively, both $P < 0.001$, Figure 73). Early canopy expansion in the medium size seed was intermediate and TiE25 was 2.9 days shorter than the small seed and 1.9 days longer than the large seed (Figure 73c). Estima achieved 25 % canopy cover after Maris Piper in Expts 2 and 5 (1.2 and 0.5 days difference, $P = 0.014$ and $P = 0.028$, respectively, Figure 73a & c), whilst in Expt 4 early canopy expansion was faster in Estima than Maris Piper by 2.4 days ($P = 0.009$, Figure 73b).

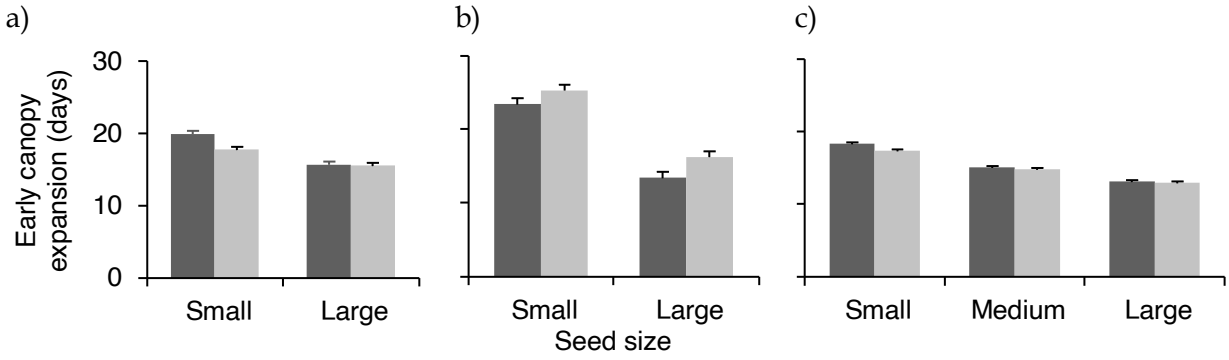

Figure 73. Effect of seed spacing on duration of early canopy expansion in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of seed spacing treatments.

TiE25 decreased with increasing stem density at a faster rate in Estima than Maris Piper (Figure 74 and Table 53) and 55.6 % of the variation TiE25 was explained by stem density and cultivar, whilst accounting for the random variation occurring in relation to experimental block and a shorter mean TiE25 in Expt 5 than in Expts 2 and 4 (multiple linear regression; TiE25 ~ stem density * cultivar + year + block, $P < 0.001$). Yet, 79.7 % of the variation was explained when seed size and spacing were included in the model (multiple linear regression, $P < 0.001$), indicating that TiE25 varied with stem distribution in addition to stem density.

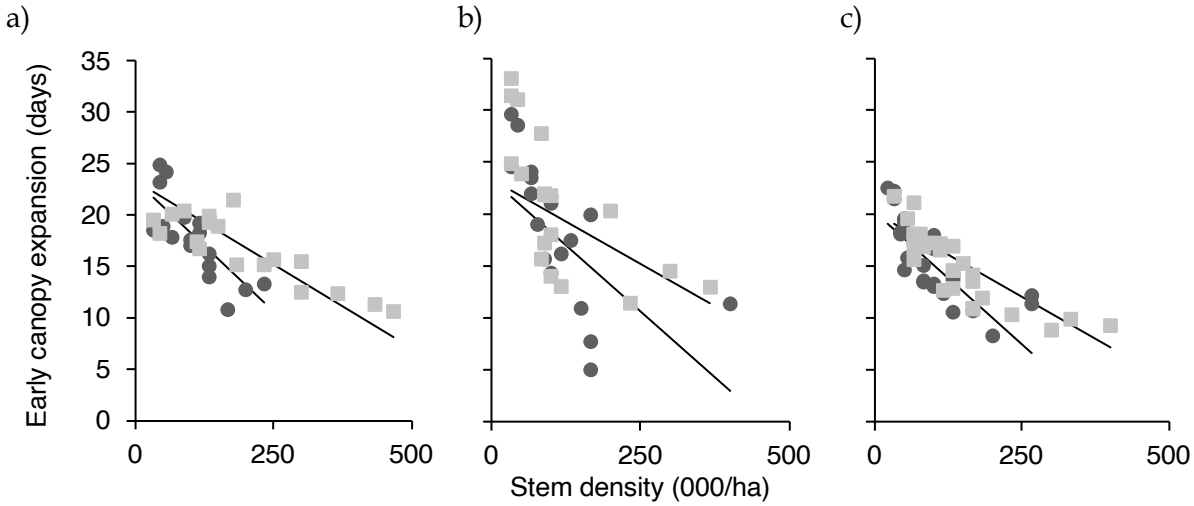

Figure 74. Relationship between duration of early canopy expansion (TiE25) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.556. See Table 53 for details of multiple linear regression.

Table 53. Relationship between stem density (S), duration of early canopy expansion (TiE25), cultivar (MP) and experiment (Expts 2, 4 or 5). TiE25 = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5 + β5*(S*MP).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	23.4	1.02	< 0.001
1	S	-0.0510	0.00637	< 0.001
2	MP	-0.4	1.10	0.714
3	Expt 4	1.26	0.811	0.124
4	Expt 5	-3.17	0.735	< 0.001
5	S * MP	0.0184	0.00756	0.017

5.3.3.4 Mid-season canopy expansion rate

In Expt 2, GCRate2575 decreased with increasing seed spacing in small seed, but increased in large seed (P = 0.013). Additionally in Expt 2, GCRate2575 was marginally faster in Estima than in Maris Piper at the 20 and 60 cm spacings (0.26 and 0.05 %/day, respectively), yet, at 40 cm spacing, Maris Piper canopy expansion was faster than Estima (1.19 %/day, P = 0.035). Mid-canopy expansion was faster in large seed than small seed in Expts 2 and 5 by 0.76 and 0.90 %/day respectively (both P = 0.003, Figure 75a & c) and rate of canopy expansion in medium seed was intermediate (Figure 75c). In Expt 5, maximum GC was 71 % for one Estima plot (small seed at 40 cm), consequently GCRate2575 could not be calculated and was represented as a missing value. Seed size had no effect on GCRate2575 in Expt 4 (Figure 75b) and there was no main effect of cultivar or seed spacing on mid-canopy expansion in any experiment (Figure 75).

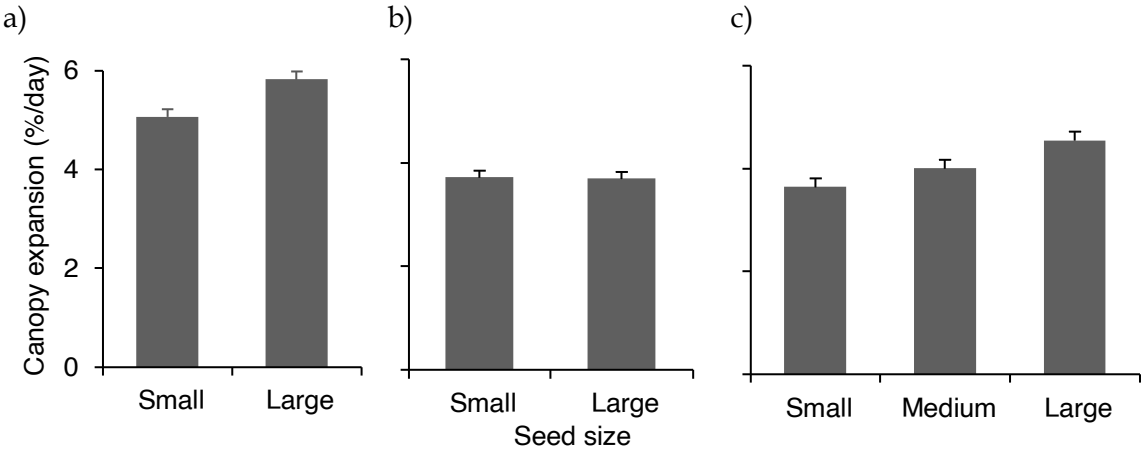

Figure 75. Effect of seed size on mid-season canopy expansion rate (GCRate2575) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of cultivar and seed spacing treatments.

There was no significant effect of stem density on GCRate2575 in either cultivar (multiple linear regression; GCRate2575 ~ stem density * cultivar + block, $P = 0.362$), though mean GCRate2575 differed between experiments (Figure 76), and differences between experiments alone explained 43.2 % of the variation in GCRate2575 (multiple linear regression; GCRate2575 ~ year + block, $P < 0.001$). Incorporating stem distribution in the model resulted in a modest increase in the variation in GCRate2575 explained (multiple linear regression; GCRate2575 ~ seed size * seed spacing + year + block, $R^2 = 0.504$, $P < 0.001$). Hence, mid-canopy expansion began earlier in the season at higher stem densities, due to decreases in TiE25 (Figure 74), but the rate varied primarily with experiment and seed size.

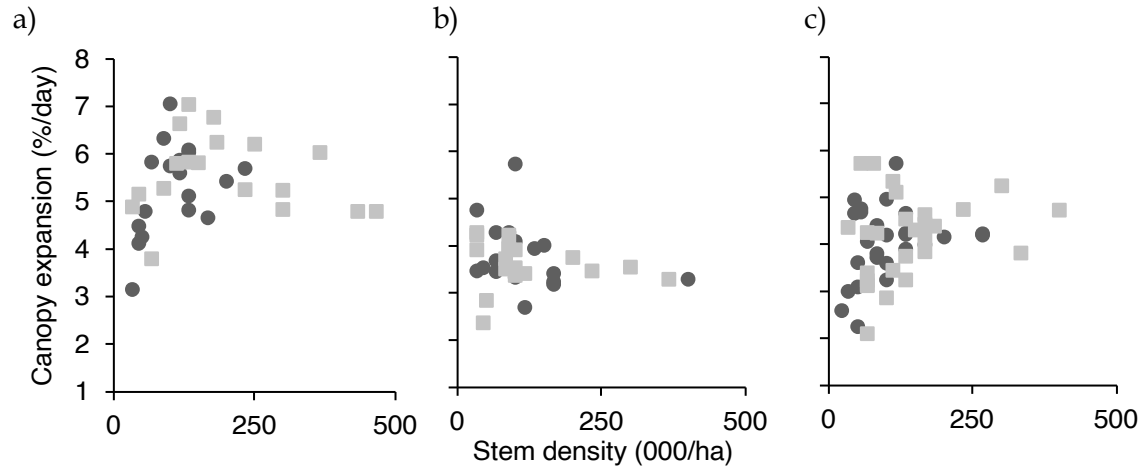

Figure 76. Mid-canopy expansion (GCRate2575) plotted against stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■.

5.3.3.5 Duration of near-complete ground cover

The duration of near-complete canopy cover (GC ≥ 90 %, GCDur90) was similar in Expts 2 and 4 (65.4 and 67.0 days respectively), but shorter in Expt 5 (46.8 days). In Expt 5, three plots of small seeded Estima (two at 40 cm spacing and one at 60 cm) did not achieve 90 % GC and GCDur90 was recorded as missing values. GCDur90 was shorter at wider plant spacing in each experiment, though the decrease was not significant in Expt 2 (Figure 77a). GCDur90 decreased by 6.2 and 3.4 days between 20 and 40 cm spacing in Expts 4 and 5 respectively, and decreased by 4.1 and 5.3 days between 40 and 60 cm spacing in Expts 4 and 5 respectively (P = 0.003 and P = 0.002, respectively, Figure 77b & c).

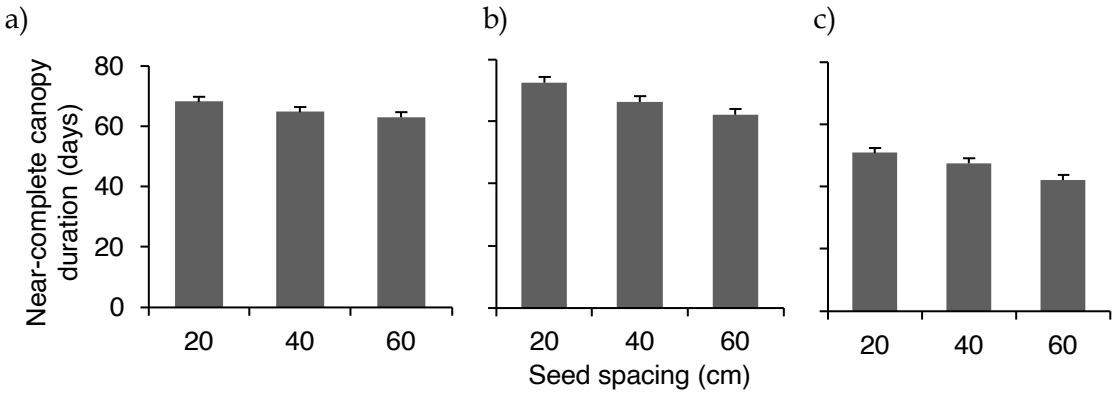

Figure 77. Effect of seed spacing on duration of near-complete ground cover in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 31 D.F.). Data presented are means of cultivar and seed size treatments.

Maris Piper maintained near-complete ground cover for longer than Estima in each experiment (P < 0.001, Figure 78) and the difference in GCDur90 was greatest in Expt 5 (39.6 days), followed by Expt 2 (23.7 days) and Expt 4 (11.4 days). GCDur90 was greater in large seed than in small seed in each experiment, with a difference of 7.4 (P = 0.001), 9.0 (P < 0.001) and 11.2 (P < 0.001) days in Expts 2, 4 and 5 respectively (Figure 78) and GCDur90 of medium seed was intermediate (Figure 78c). The difference in GCDur90 between small and large seed was greater in Estima (11.6 days) than in Maris Piper (3.2 days) in Expt 2, likely due to the difference in size of the small seed between the two cultivars (30-35 mm and 30-40 mm for Estima and Maris Piper respectively, P = 0.045, Figure 78a). There was no interaction between cultivar and seed size in either Expts 4 or 5 (Figure 78b & c).

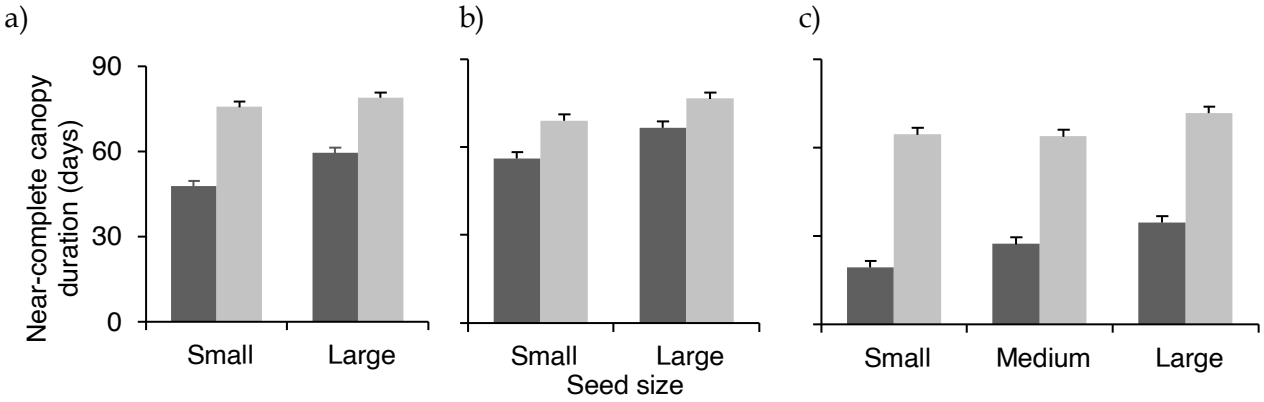

Figure 78. Effect of seed size and cultivar on duration of near-complete ground cover in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 31 D.F.). Data presented are means of seed spacing treatments.

Near-complete ground cover was a strong predictor of IGC, irrespective of cultivar and GCDur90 alone accounted for 92.0 % of the variation in IGC across all three experiments (multiple linear regression; IGC ~ GCDur90 + block, $P < 0.001$), Figure 79). Multiple linear regression showed that there were significant differences in the relationship between IGC and GCDur90 between the experiments (IGC ~ GCDur90 * year + block, $R^2 = 0.954$, $P < 0.001$), and the increase in IGC relative to GCDur90 was greater in Expt 2 than in Expts 4 and 5 (Table 54). Differences in mean ground cover above 90 % GC can explain the variation in relationship between GCDur90 and IGC. In Expt 5, few plots achieved 100 % GC, consequently each day above 90 % GC made a smaller contribution to IGC than days above 90 % GC in Expt 2, in which all plots achieved 100 % GC. Further variation is explained by including cultivar in the model (multiple linear regression; IGC ~ GCDur90 * year + cultivar + block), increasing the variance explained to 97.8 % ($P < 0.001$), as mean IGC was greater in Maris Piper than Estima (cultivar; ANOVA, $P < 0.001$).

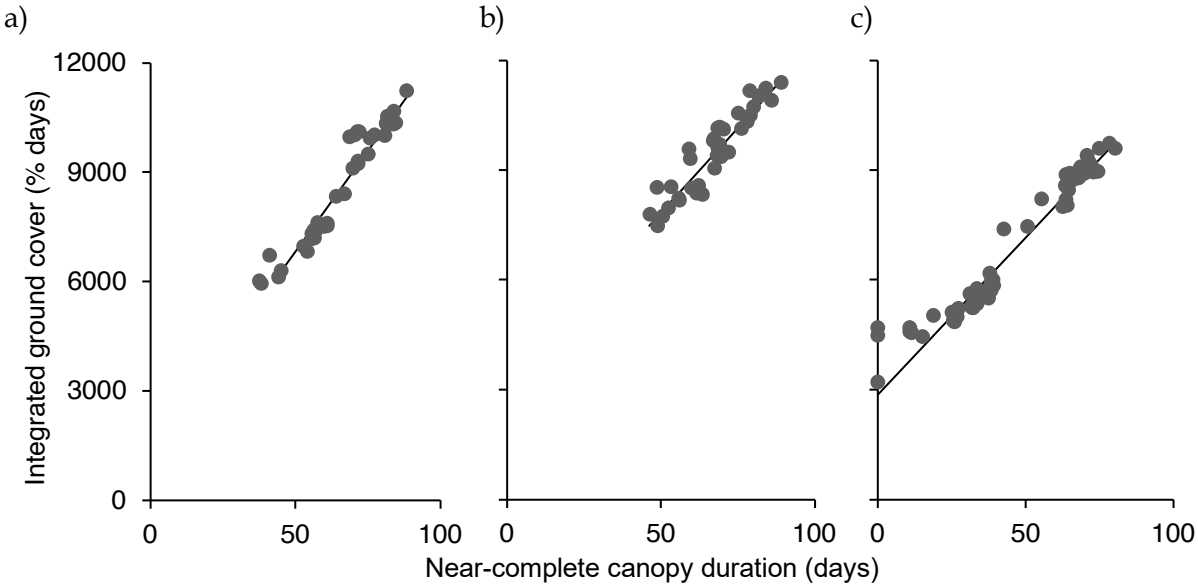

Figure 79. Relationship between near-complete ground cover and integrated ground cover in (a) Expt 2, (b) Expt 4 and (c) Expt 5. R2 = 0.954. See Table 54 for details of multiple linear regression.

Table 54. Relationship between integrated ground cover (IGC), duration of near-complete ground cover (GCDur90) and experiment (Expts 2, 4 or 5). IGC = β0 + β1*GCDur90 + β2*Expt 4 + β3*Expt 5 + β4*(GCDur90*Expt 4) + β5*(GCDur90*Expt 5).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	1370	321	< 0.001
1	GCDur90	109.5	4.78	< 0.001
2	Expt 4	1810	529	0.001
3	Expt 5	1490	351	< 0.001
4	GCDur90 * Expt 4	-16.4	7.84	0.038
5	GCDur90 * Expt 5	-23.4	5.50	< 0.001

Duration of near-complete canopy cover increased with increasing stem density in each experiment and the rate of increase was greater in Estima than in Maris Piper (Figure 80 and Table 55). Only 13.4 % of the variation in GCDur90 was explained by stem density alone (multiple linear regression; GCDur90 ~ stem density + block, $P < 0.001$). Greater variation, 74.7 %, was explained when cultivar and experiment were included in the model (multiple linear regression; GCDur90 ~ stem density * cultivar + year + block, $P < 0.001$, Figure 80 and Table 55). Yet this is likely the result of differences in mean GCDur90 between cultivars in each experiment (77.2, 72.7 and 66.7 days for Maris Piper, and 53.5, 61.3 and 27.0 days for Estima, in Expts 2, 4 and 5, respectively), indicating that GCDur90 is strongly influenced by cultivar and other agronomic conditions. Including stem distribution in the model (a 'seed size * seed spacing' term) resulted in a marginal increase in variation explained, from 74.7 to 76.6 %, indicating that stem distribution had a limited effect on near-complete canopy duration.

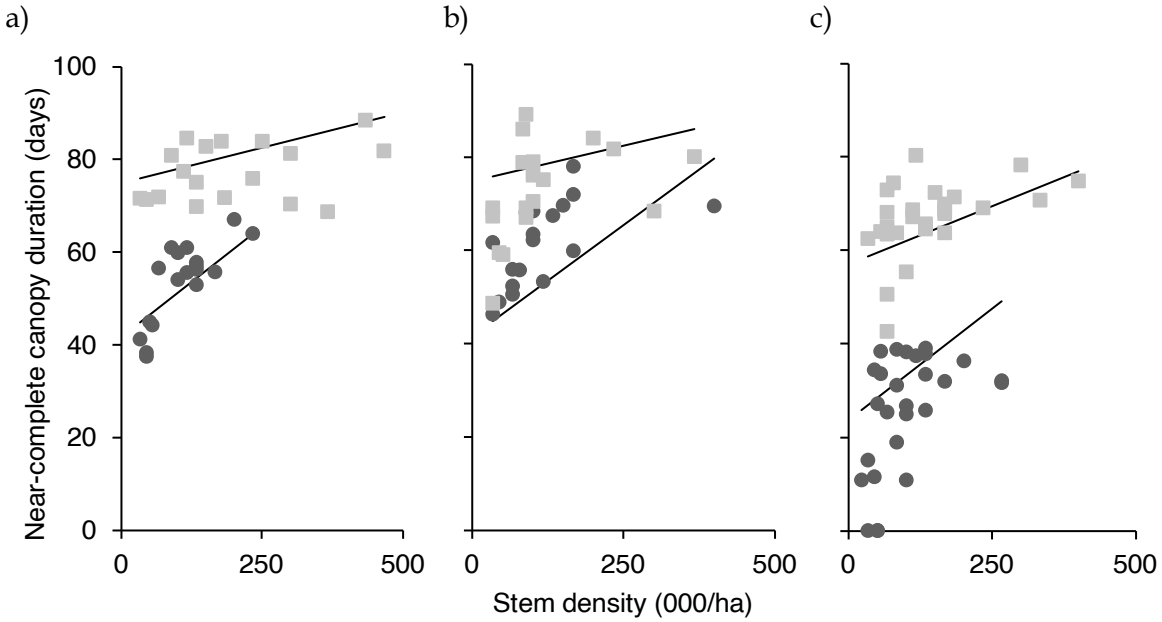

Figure 80. Relationship between duration of near-complete canopy cover (GCDur90) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.747. See Table 55 for details of multiple linear regression.

Table 55. Relationship between stem density (S), duration of near-complete canopy cover (GCDur90), cultivar (MP) and experiment (Expts 2, 4 or 5). GCRate2575 = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5 + β5*(S*MP).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	41.7	3.15	< 0.001
1	S	0.095	0.0196	< 0.001
2	MP	33.2	3.38	< 0.001
3	Expt 4	2.5	2.50	0.322
4	Expt 5	-17.9	2.27	< 0.001
5	S * MP	-0.065	0.0233	0.006

5.3.3.6 Ground cover senescence

In Expts 2 and 4, the rate of senescence between 90 and 50 % GC (GCRate9050) was greater in Estima than Maris Piper by 2.39 and 1.02 %/day, respectively (P < 0.001, Figure 81a & b), whilst in Expt 5 Maris Piper senesced more rapidly than Estima by 1.33 %/day (P < 0.001, Figure 81c). In Expt 5, GCRate9050 was recorded as missing values in three plots of small seeded Estima (two at 40 cm spacing and one at 60 cm) which did not achieve 90 % GC, and for which the rate of senescence could not be calculated. Seed spacing had no effect on rate of senescence in Expt 2 (Figure 81a) but in Expt 4, the wider spacing senesced at a slower rate (P = 0.011, Figure 81b). Whilst there was no overall effect of spacing on senescence rate in Expt 5, Maris Piper senesced more rapidly than Estima at the 40 and 60 cm spacing by 2.41 and 1.51 %/day respectively (P = 0.002, Figure 81c). There was an interaction between cultivar and seed size in Expt 5; as Estima seed size increased canopy senescence became more

rapid, whilst in Maris Piper, GCRate9050 slowed with increasing seed size (P = 0.003), consequently there was no overall effect of seed size on GCRate9050. Seed size had no effect on the rate of senescence in any experiment.

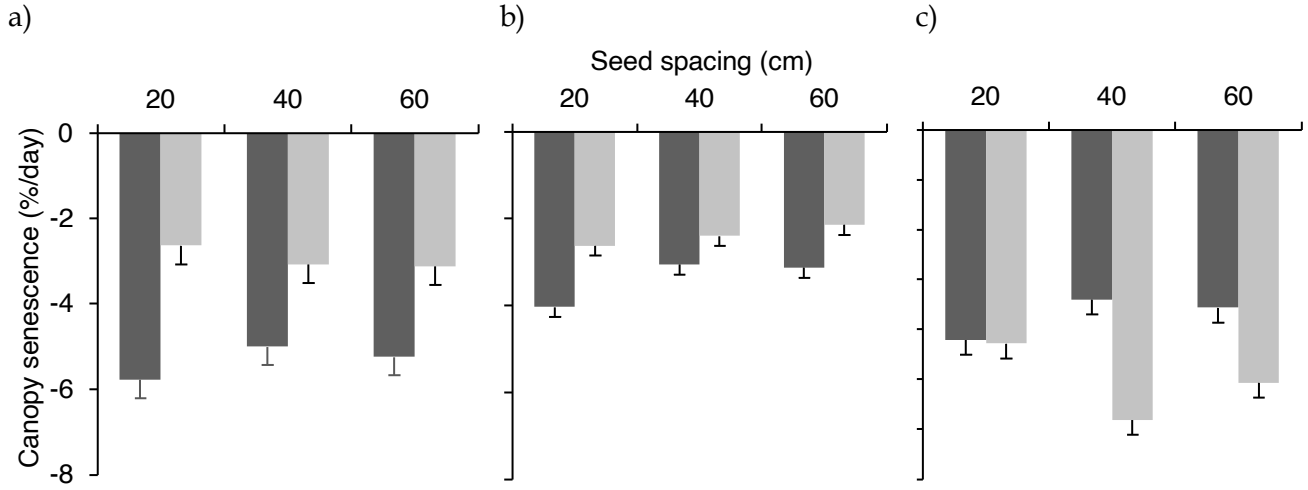

Figure 81. Effect of seed spacing and cultivar on rate of canopy senescence in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of seed size treatments.

There was no relationship between GCRate9050 and stem density alone (P = 0.589, Figure 82) and only 29.3 % of the variation in the rate of senescence was explained by stem density and cultivar, accounting for random variation between experiments (multiple linear regression; GCRate9050 ~ stem density * cultivar + year + block, P < 0.001, data not shown). Incorporating the effects of stem distribution, using the seed size and spacing treatments, explained no additional variation, indicated by a reduction in adjusted R^2 from 0.293 to 0.281, hence stem distribution had no effect on canopy senescence rate.

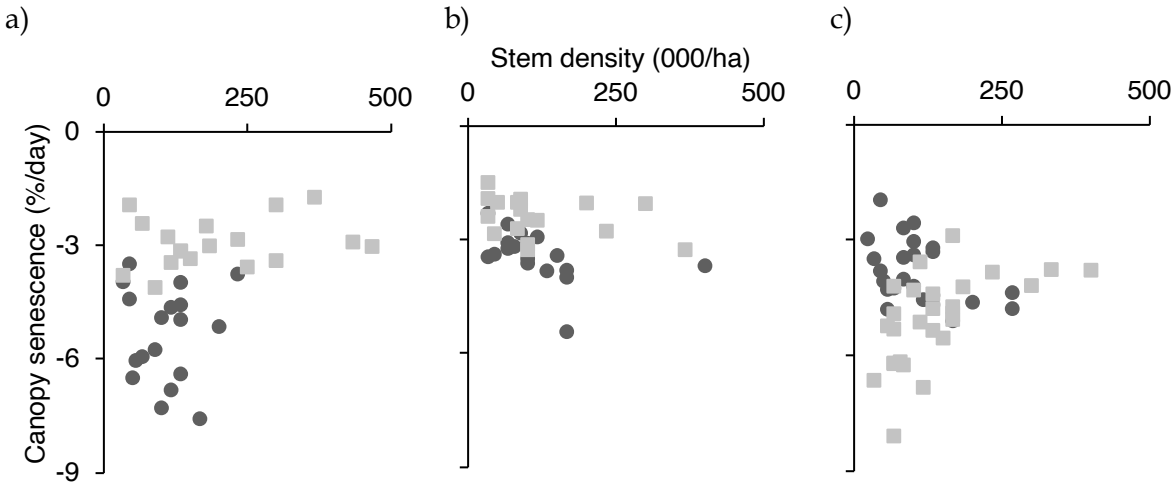

Figure 82. Rate of canopy senescence (GCRate9050) plotted against stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper (MP), ■.

Duration of canopy growth, between emergence and the onset of senescence (GrowDur), was greater in Maris Piper than in Estima in each experiment by 21.6, 14.3 and 34.8 days in Expts 2, 4 and 5 respectively ($P < 0.001$, Figure 83). In Expt 5, GrowDur of the 40 cm spacing was 3.5 days longer than the 20 and 60 cm spacing ($P = 0.007$), but there was no significant difference in GrowDur between spacing treatments in Expts 2 and 4 (data not shown). GrowDur did not vary significantly with seed size in either of the three experiments.

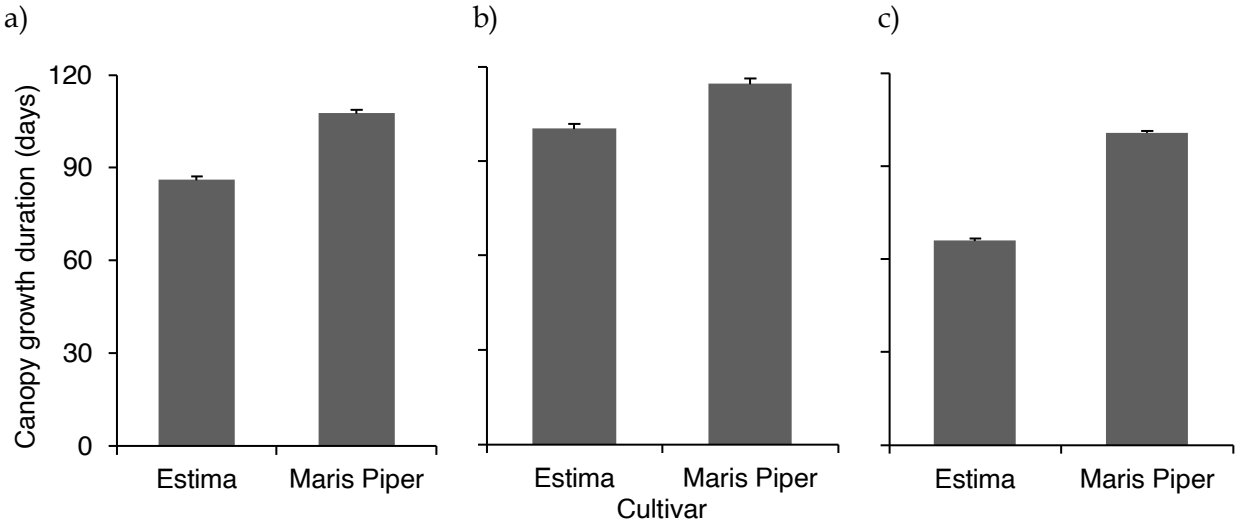

Figure 83. Effect of cultivar on duration of canopy growth in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of seed size and seed spacing treatments.

The duration of canopy growth did not vary significantly with stem density (Figure 84, $P = 0.240$), and cultivar and experiment alone explained 84.0 % of the variation (multiple linear regression; GrowDur ~ cultivar + year + block, $P < 0.001$).

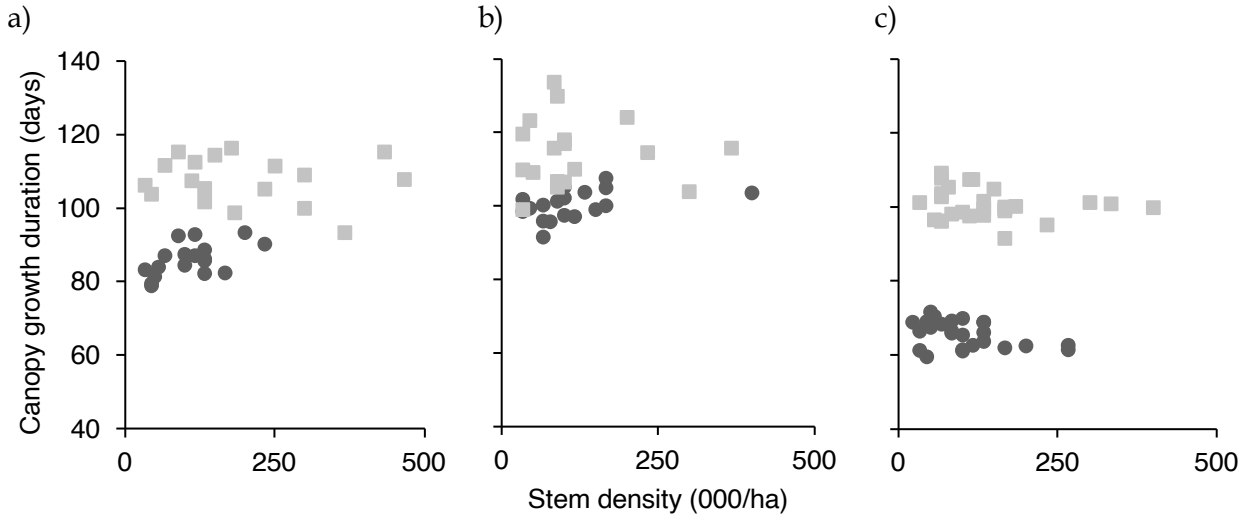

Figure 84. Duration of canopy growth (GrowDur) plotted against stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■.

5.3.3.7 Key points: Ground cover growth patterns

- IGC was greater in Maris Piper than Estima and at higher stem densities.
- TiE25 was slowest at the widest spacing due to the lower stem density and rate of early canopy expansion for individual plants was greatest at the widest spacing.
- TiE25 was shorter at higher stem densities in both cultivars, and differences between cultivars were small.
- GCRate2575 was faster in large than small seed in two of three experiments and there was no clear relationship between stem density and GCRate2575.
- The main effect of seed size and spacing was upon stem density, but stem distribution had a significant effect on early and mid-canopy expansion.
- GCDur90 was greater in Maris Piper than Estima, though the difference varied from *c.* 11 days to *c.* 40 days between experiments.
- GCDur90 was greater at higher stem densities (i.e. closer spacing and larger seed), although was more responsive to stem density in Estima than Maris Piper.
- GCDur90 was a good predictor of IGC.
- Differences in GCRate9050 between treatments and the response to increasing stem density were not consistent between experiments.
- GrowDur was greater in Maris Piper than Estima and varied little with increasing stem density in Maris Piper but increased in Estima.

5.3.4 Leaf appearance

The number of mature leaves on both the mainstem and sympodial branches was recorded throughout the season to better understand the influence of individual leaves on whole canopy growth. The effects of all treatments and their interactions on leaf appearance are reported in Appendix 21.

5.3.4.1 Mainstem leaves

Maris Piper produced on average 4.24 more leaves on the mainstem (msL) than Estima (3.58, 5.39 and 3.75 more leaves in Expts 2, 4 and 5, respectively, $P < 0.001$, Figure 85). Both cultivars produced a similar number of mainstem leaves in Expts 2 and 5, with means of 11.88 and 15.55 in Estima and Maris Piper respectively, and more msL were produced in Expt 4 by both cultivars (1.09 and 2.82 more leaves in Estima and Maris Piper respectively). Seed size and spacing had no effect on msL and there was also no

relationship between msL and stem density. Differences in mean msL between cultivars and experiments explained 76.0 % of the variation in msL, (multiple linear regression; msL ~ cultivar + year + block, $P < 0.001$, data not shown) with the majority (64.7 %) explained by cultivar.

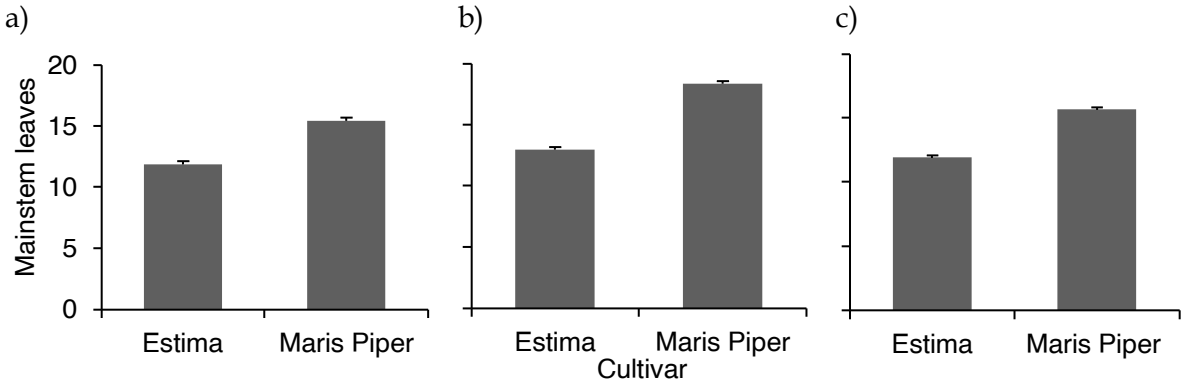

Figure 85. Effect of cultivar on number of leaves on the mainstem in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 85 D.F.). Data presented are means of seed size and seed spacing treatments.

5.3.4.2 Mainstem leaf appearance

The rate of mainstem leaf appearance (msLA) was faster in Estima than Maris Piper by 0.107 and 0.081 leaves/day stems in Expts 2 and 5, respectively ($P < 0.001$, Figure 86a & c), but there was no difference in msLA between cultivars in Expt 4 (Figure 86b). In Expt 5, sympodial branches were not produced by three measured Estima stems (two large and one medium sized seed, all at 20 cm spacing) and msLA was calculated between the 5th and 12th leaves (3.2.4). Rate of leaf appearance was fastest at 60 cm spacing in each experiment ($P = 0.004$, $P = 0.036$ and $P < 0.001$ in Expts 2, 4 and 5, respectively). In Expts 2 and 4 the difference in msLA between the 40 and 60 cm spacings was less than 0.020 leaves/day compared to the difference of 0.072 leaves/day in Expt 5, whilst there was little variation in the difference in msLA between the 20 and 40 cm spacings across the experiments (mean difference of 0.063 leaves/day, Figure 86).

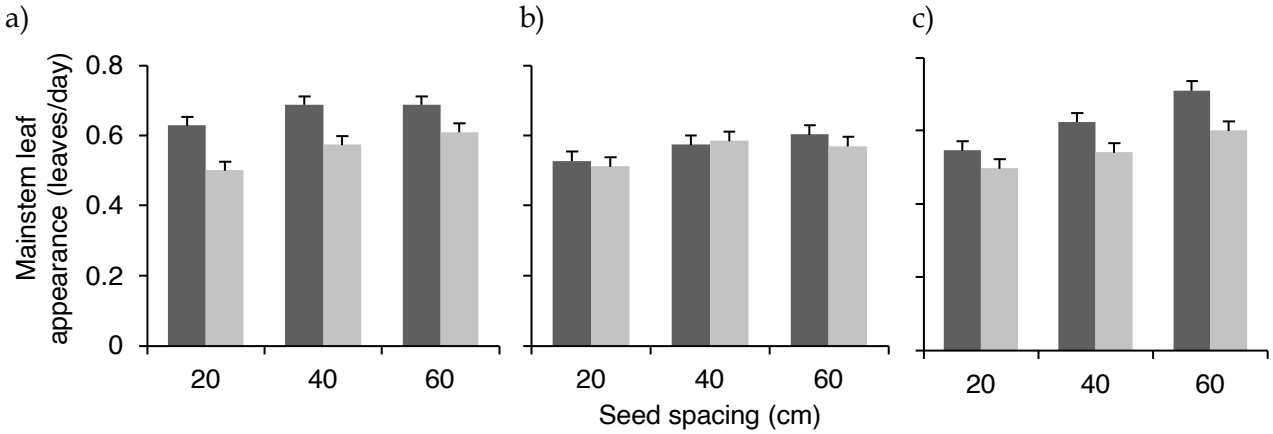

Figure 86. Effect of seed spacing and cultivar on rate of leaf appearance on the mainstem in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 85 D.F.). Data presented are means of seed size treatments.

Rate of mainstem leaf appearance was faster on small seed stems than large seed in each experiment, although the difference was greater in Expt 5 (0.093 leaves/day, $P < 0.001$) than Expts 2 (0.063 leaves/day, $P = 0.003$) or 4 (0.049 leaves/day, $P = 0.034$, Figure 87). In Expt 5, msLA of the medium seed was intermediate between the small and large (Figure 87c).

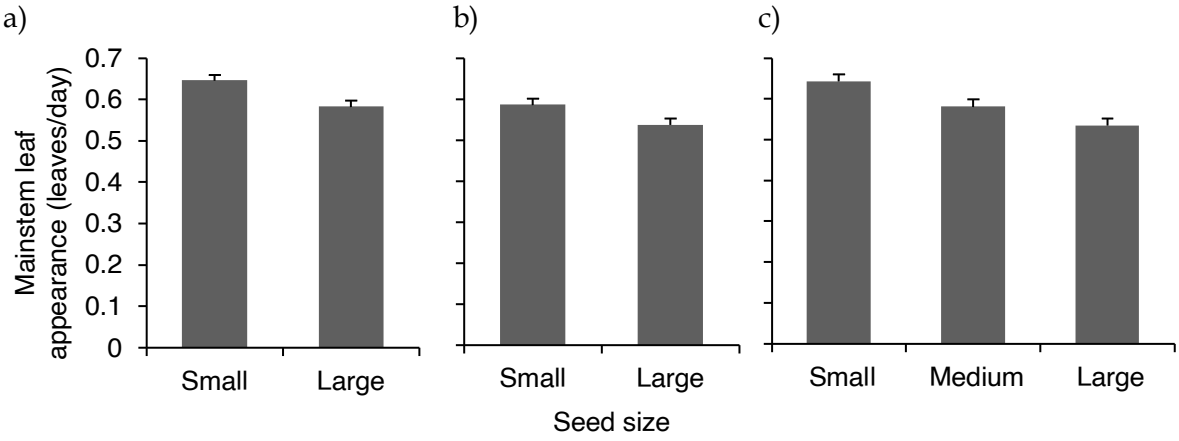

Figure 87. Effect of seed size on rate of mainstem leaf appearance in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 85 D.F.). Data presented are means of seed spacing and cultivar treatments.

In Expts 2, 4 and 5 the msLA decreased with increasing number of stems per plant (multiple linear regression; msLA ~ stem density + year + block, $P < 0.001$, Figure 88 & Table 54). Yet there was substantial variation in msLA at the same number of stems per plant (Figure 88), indicating the importance of other factors. Some of the variation may be linked to differences in stem mass, as despite attempting to select median stems for leaf appearance measurements stem diameter varied (data not shown) within those measured, which may have affected the rate of leaf appearance.

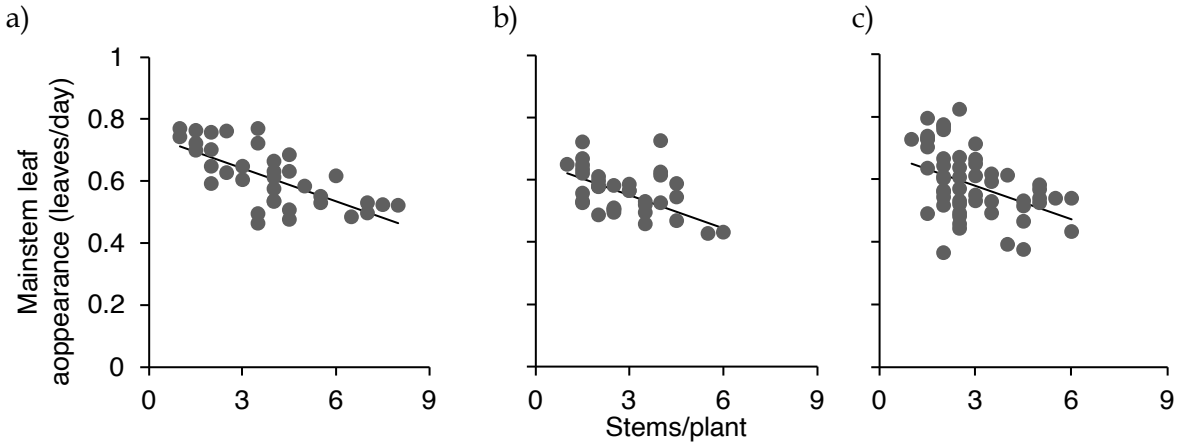

Figure 88. Relationship between number of stems per plant (stems) and rate of leaf appearance on individual mainstems (msLA), (a) Expt 2, (b) Expt 4 and (c) Expt 5. Data presented are means of seed size, seed spacing and cultivar treatments. R^2 = 0.292. See Table 56 for details of multiple linear regression.

Table 56. Relationship between rate of mainstem leaf appearance (msLA) and stems per plant (stems) and experiment (Expts 2, 4 or 5). msLA = β0 + β1*stems + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.747	0.0257	< 0.001
1	stems	-0.0354	0.00509	< 0.001
2	Expt 4	-0.091	0.0201	< 0.001
3	Expt 5	-0.062	0.0184	0.001

The rate of mainstem leaf appearance per stem was slower at higher stem densities (Figure 89) and there was a greater decrease in msLA in response to increasing stem density in Estima than in Maris Piper (Table 57). Stem density, cultivar and the interaction between the two explained 46.6 % of the variation in msLA (multiple linear regression; msLA ~ stem density * cultivar + year + block, $P < 0.001$, Table 57). Stem distribution had a small effect on msLA, and when the model included seed size and spacing, 50.6 % of the variation in msLA was explained ($P < 0.001$), hence highlighting the variability of msLA.

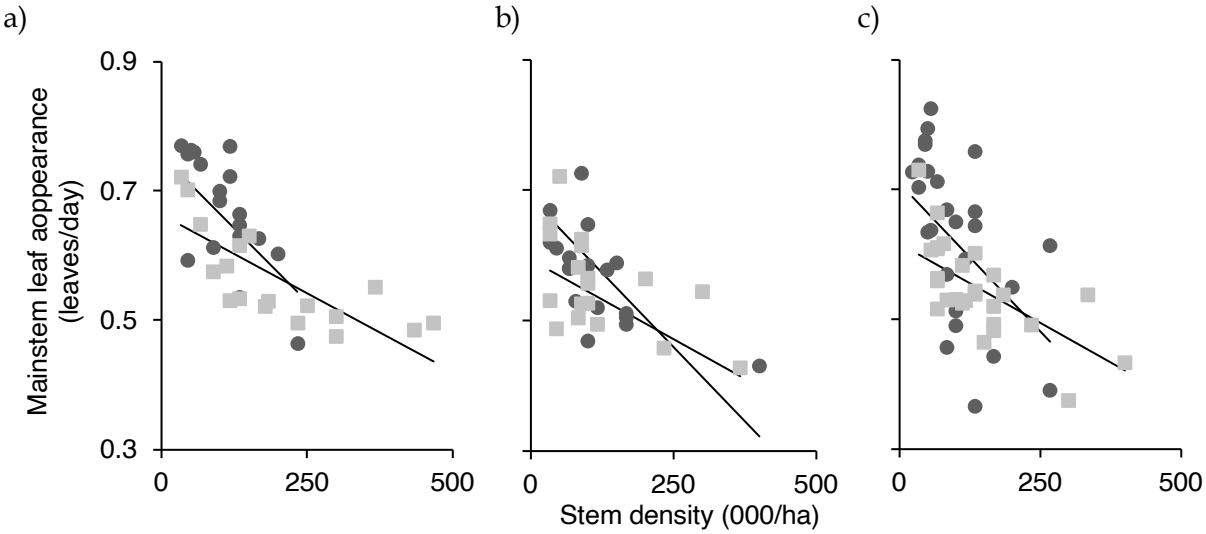

Figure 89. Relationship between the rate of mainstem leaf appearance (msLA) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.466. See Table 57 for details of multiple linear regression.

Table 57. Relationship between stem density (S), mainstem leave appearance rate (msLA), cultivar (MP) and experiment (Expts 2, 4 or 5). msLA = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5 + β5*(S*MP).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.756	0.0217	< 0.001
1	S	-0.00091	0.000135	< 0.001
2	MP	-0.093	0.0233	< 0.001
3	Expt 4	-0.069	0.0172	< 0.001
4	Expt 5	-0.047	0.0156	0.003
5	S * MP	0.00042	0.000161	0.009

5.3.4.3 Main axis leaves

On average the number of leaves on the main axis (maL) varied little between experiments and was 26.3, 26.7 and 25.3 in Expts 2, 4 and 5, respectively. There was less variation in Estima maL between spacing treatments than Maris Piper in each experiment, however this interaction was only significant in Expt 5 (P = 0.042, Figure 90c). Maris Piper produced an average of 7.4 leaves more than Estima on the main axis across all three experiments (7.1, 6.9 and 8.1 additional leaves in Expts 2, 4 and 5, respectively, P < 0.001, Figure 90). As spacing increased, maL increased (P = 0.005, P = 0.004 and P < 0.001 in Expts 2, 4 and 5, respectively), though the mean difference, across all other treatments and experiments, between the 40 and 60 cm spacings was less than half that of the difference between 20 and 40 cm treatments (0.7 and 2.1 leaves respectively, Figure 90).

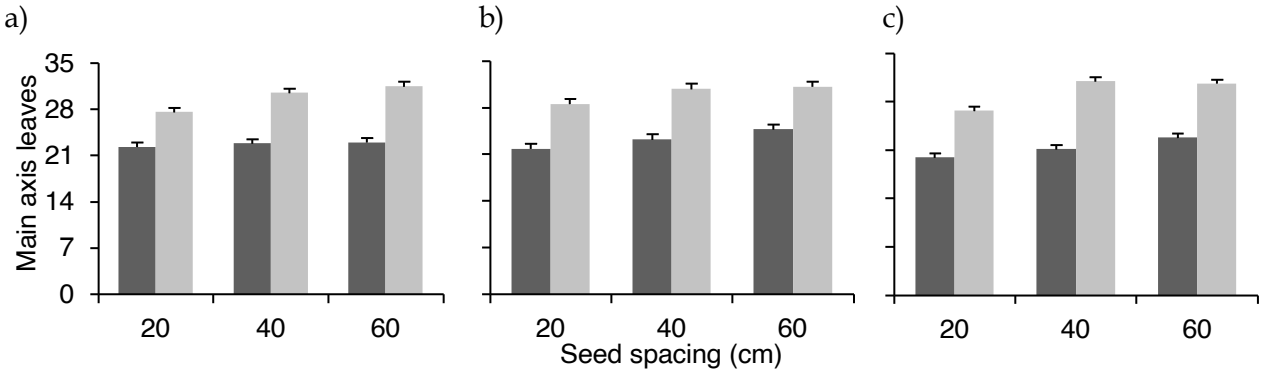

Figure 90. Effect of seed spacing and cultivar on total number of leaves on the main axis, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 85 D.F.). Data presented are means of seed size treatments.

Number of main axis leaves was greater in small than large seed by 1.7, 1.3 and 2.6 leaves in Expts 2, 4 and 5 respectively ($P = 0.004$, $P = 0.050$ and $P < 0.001$, respectively, Figure 91). The difference in maL between large and medium seed was smaller than the difference between medium and small seed (0.9 and 1.6 leaves respectively, Figure 91c).

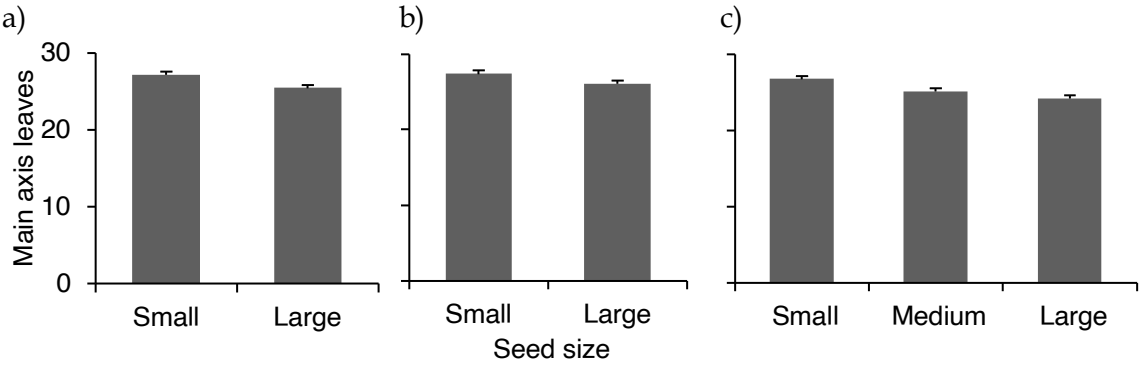

Figure 91. Effect of seed size on total number of leaves on the main axis, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 85 D.F.). Data presented are means of seed spacing and cultivar treatments.

Number of leaves on the main axis was a relatively weak predictor of near-complete canopy duration, explaining 36.2 % of the variation in GCDur90 (multiple linear regression; GCDur90 ~ maL + block, $P < 0.001$) yet greater variation in GCDur90 (69.6 %, $P < 0.001$) was explained by cultivar and experiment, without inclusion of maL in the model (multiple linear regression; GCDur90 ~ cultivar + year + block, Figure 92). Number of main axis leaves was closely linked to cultivar and the weak relationship between GCDur90 and maL appears to have resulted from the difference between the cultivars, illustrated by the high degree of scatter within each cultivar and thus why no relationship has been reported (Figure 92).

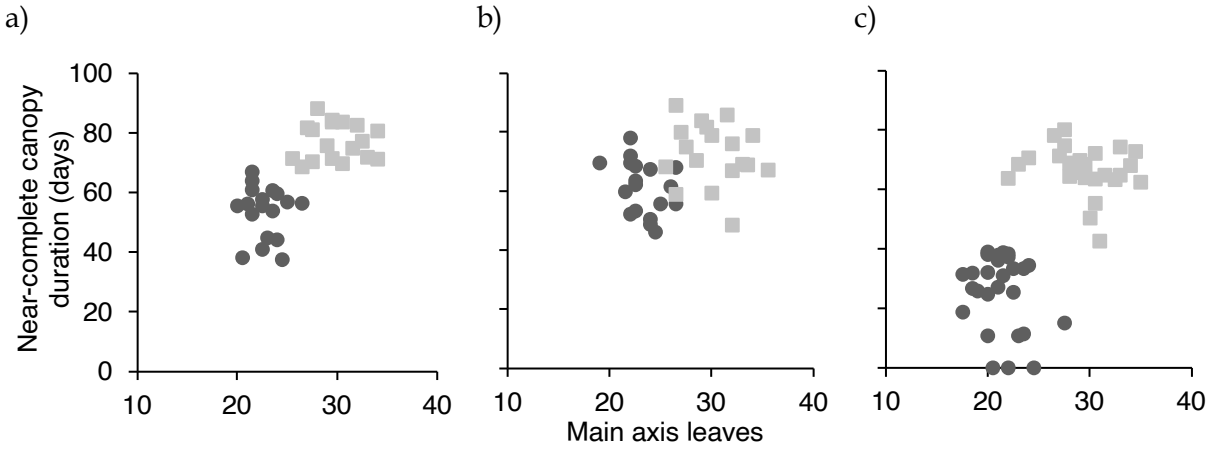

Figure 92. Relationship between number of leaves on the main axis (maL) and near-complete canopy duration (GCDur90), (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■.

Number of main axis leaves decreased with increasing stem density at the same rate in both cultivars (Figure 93), though Maris Piper produced an average of 8.26 maL more than Estima (Table 58). Stem density and cultivar, explained 79.8 % of the variation in maL once variation from experiment and experimental block were accounted for (multiple linear regression; maL ~ stem density + cultivar + year + block, $P < 0.001$, Table 58). Indicating that fewer rather than more leaves are produced as stem density increases. Stem distribution appeared to have a limited effect on maL and including it explained 81.3 % of the variation ($P < 0.001$).

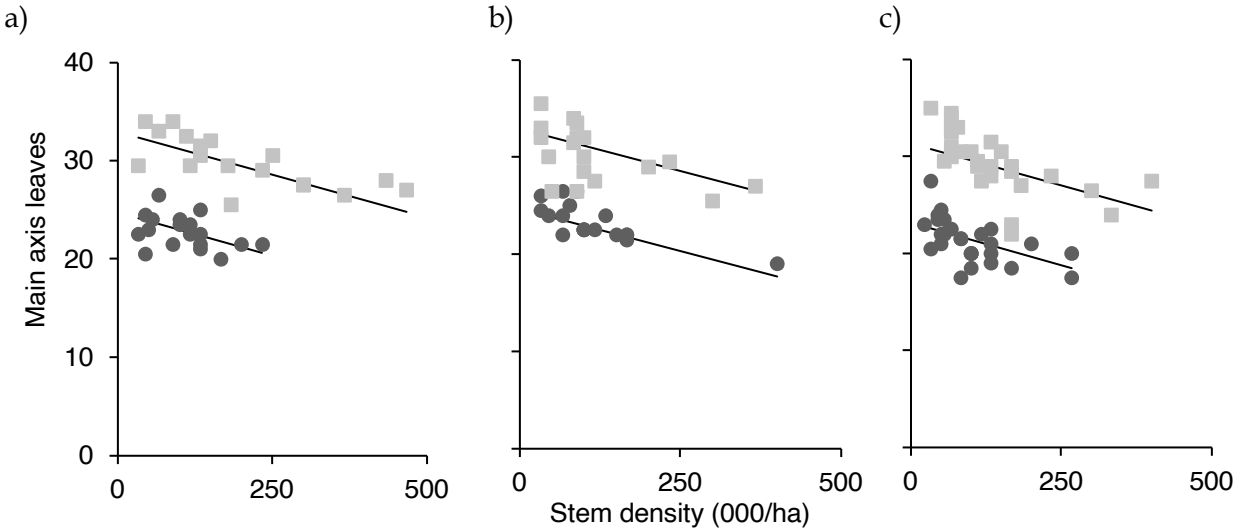

Figure 93. Relationship between number of main axis leaves (maL) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. $R^2 = 0.798$. See Table 58 for details of multiple linear regression.

Table 58. Relationship between number of main axis leaves (maL) and stem density (S), cultivar (MP) and experiment (Expts 2, 4 or 5). maL = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	24.68	0.539	< 0.001
1	S	-0.0173	0.00210	< 0.001
2	MP	8.26	0.377	< 0.001
3	Expt 4	-0.19	0.490	0.699
4	Expt 5	-1.54	0.448	0.001

5.3.4.4 Whole plant leaf appearance rate

Whole plant leaf appearance rate (pLA) was estimated by multiplying leaf appearance rate for a median stem (msLA) by the number of stems produced by the plant, to examine the interaction between number of stems, leaf production and canopy expansion. Average rate of whole plant leaf appearance (pLA) was greatest in Expt 2, followed by Expt 5 and Expt 4 (2.25, 1.64 and 1.53 leaves/day/plant respectively). In Expt 5, in four plots (small Estima at 40 and 60 cm spacing, small Maris Piper at 20 cm spacing and medium Maris Piper at 60 cm) stem number was recorded in only one replicate, consequently, plot pLA was unreplicated in those plots. In Expts 2 and 5, pLA was greater in Maris Piper than Estima by 0.40 and 1.00 leaves/day/plant respectively ($P < 0.001$, Figure 94a & c). In Expt 5, pLA was faster at 60 cm spacing than either 20 or 40 cm spacing (which did not differ significantly, 1.45 and 1.56 leaves/day/plant respectively) by 0.34 leaves/day/plant ($P = 0.012$, Figure 94c). There was no significant effect of seed spacing on pLA in Expt 2 (Figure 94a) and pLA did not differ significantly with either seed spacing or cultivar in Expt 4 (Figure 94b), reflecting the lack of variation in stem number between treatments in Expt 4 (Figure 94b). There was no significant interaction between seed spacing and cultivar in any of the three experiments.

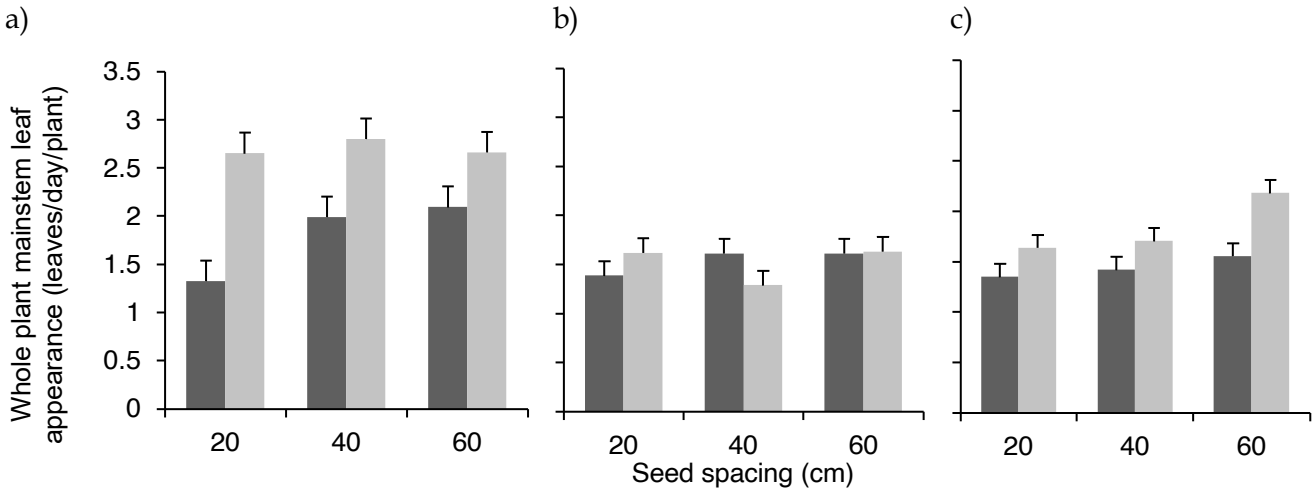

Figure 94. Effect of cultivar and seed spacing on rate of whole plant mainstem leaf appearance (pLA) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 83 D.F.). Data presented are means of seed size treatments.

In Expts 2, 4 and 5 the pLA of large seed was greater than small seed by 1.20, 0.98 and 0.85 leaves/plant/day respectively ($P < 0.001$, Figure 95). In Expt 5 the difference in pLA between small and large seed was three times greater in Maris Piper than Estima (1.27 and 0.50 leaves/plant/day difference, respectively, $P = 0.003$, data in Appendix 22). There was no interaction between seed size and cultivar in either Expts 2 or 4.

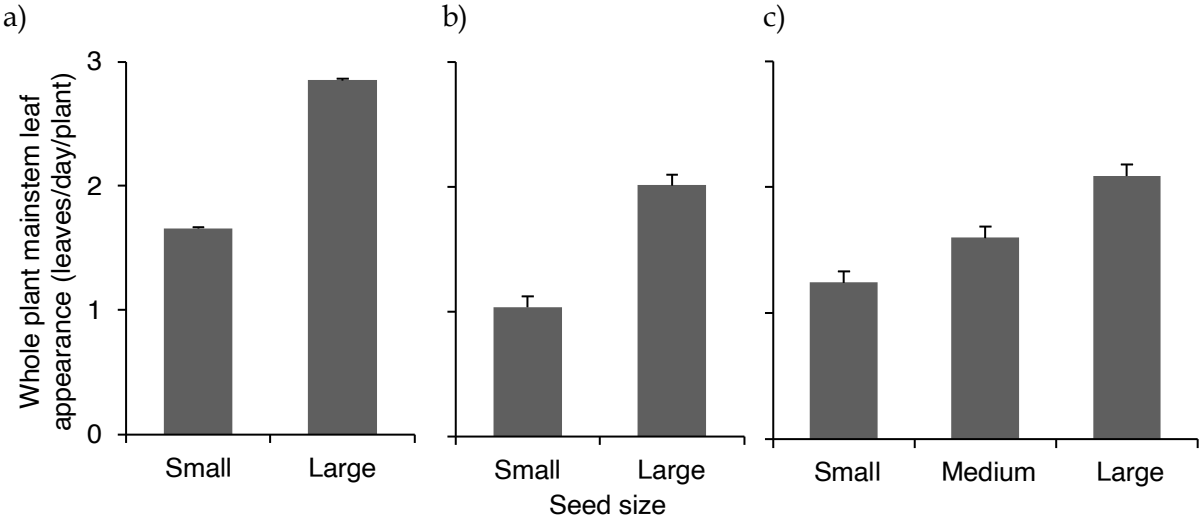

Figure 95. Effect of seed size on rate of whole plant mainstem leaf appearance (pLA) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 83 D.F.). Data presented are means of seed spacing and cultivar treatments.

As expected, rate of whole plant leaf appearance increased with number of stems per plant and the increase in pLA in response to additional stems was constant across cultivars (multiple linear regression; pLA ~ stems + year + block, $P < 0.001$, Figure 96, Table 59). Doubling stem number did not double rate of whole plant leaf appearance, since the rate of leaf appearance on individual stems decreased as number of stems per plant increased (Figure 88).

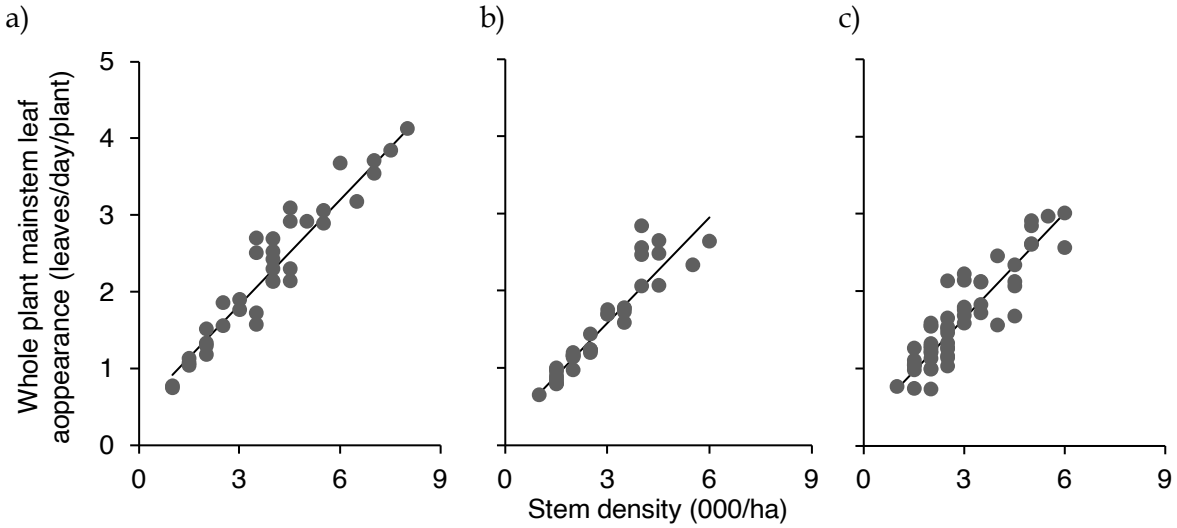

Figure 96. Relationship between number of stems per plant (stems) and rate of whole plant mainstem leaf appearance (pLA), (a) Expt 2, (b) Expt 4 and (c) Expt 5. R^2 = 0.887. See Table 59 for details of multiple linear regression.

Table 59. Relationship between rate of whole plant leaf appearance (pLA) and stems per plant (stems)and experiment (Expts 2, 4 or 5). pLA = β0 + β1*stems + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.464	0.0814	< 0.001
1	S	0.456	0.0161	< 0.001
2	Expt 4	-0.248	0.0638	< 0.001
3	Expt 5	-0.180	0.0581	0.002

GCRate2575 increased with increasing pLA in all three experiments, the relationship was the same in both cultivars and the different mean rates of canopy expansion between experiments were reflected in the different intercepts (Figure 97). The rate of whole plant leaf appearance explained 52.0 % of the variation in GCRate2575 when variation between experiments was accounted for (multiple linear regression; GCRate2575 ~ pLA + year + block, $P < 0.001$), yet there was a high degree of scatter in the relationship within each year, as other factors than pLA had a large influence on the rate of canopy expansion.

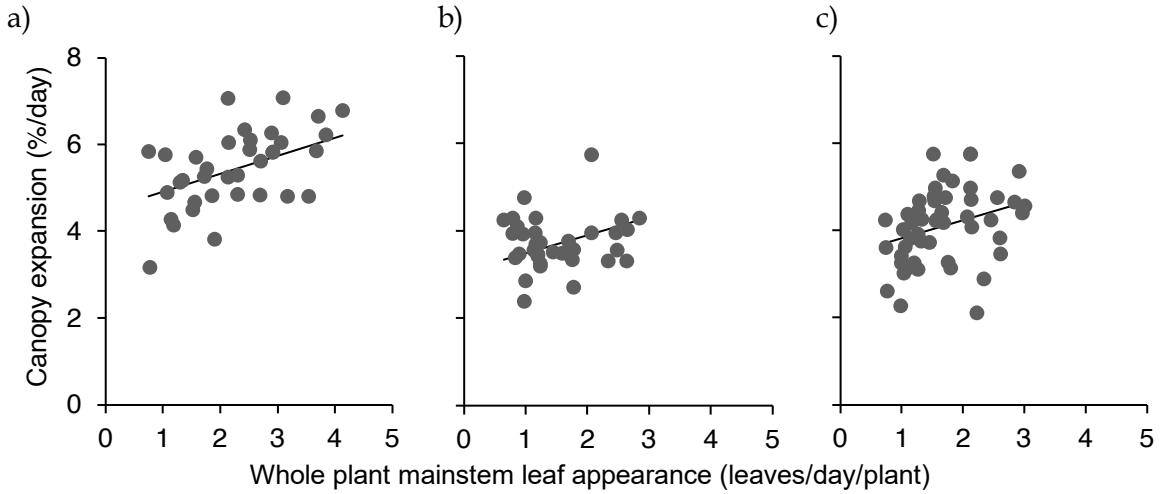

Figure 97. Relationship between rate of whole plant mainstem leaf appearance (pLA) and mid-season canopy expansion rate (GCRate2575), (a) Expt 2, (b) Expt 4 and (c) Expt 5. Data presented are means of seed size, seed spacing and cultivar treatments. $R^2 = 0.520$. See Table 60 for details of multiple linear regression.

Table 60. Relationship between mid-season canopy expansion (GCRate2575) and rate of whole plant leaf appearance (pLA) and experiment (Expts 2, 4 or 5). GCRate2575 = β0 + β1*pLA + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	4.31	0.317	< 0.001
1	pLA	0.64	0.157	< 0.001
2	Expt 4	-1.43	0.187	< 0.001
3	Expt 5	-1.08	0.168	0.002

The rate of whole plant leaf appearance increased with increasing stem density in both cultivars, but there was a high degree of variability (Figure 98). Stem density, cultivar and between-experiment variability explained a relatively small proportion of the variation (36.5 %) in pLA (multiple linear regression; pLA ~ stem density * cultivar + year + block, $P < 0.001$, Table 61). Incorporating stem distribution in the model (with a 'seed size * seed spacing' term) increased variation accounted for 84.3 % ($P < 0.001$), indicating that stem distribution had a strong influence on pLA. However, it is unsurprising that stem density—a measure of whole crop variation—explains a limited proportion of the variation in pLA, which is a measure of per plant variation.

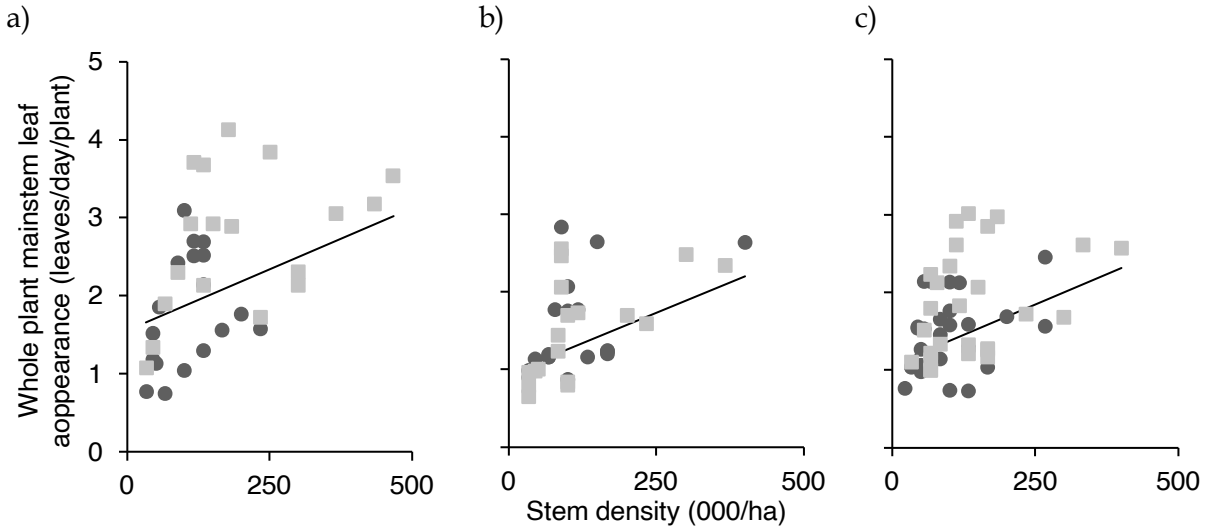

Figure 98. Relationship between rate of whole plant mainstem leaf appearance (pLA) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.342. See Table 61 for details of multiple linear regression.

Table 61. Relationship between rate of whole plant mainstem leaf appearance (pLA) and stem density (S), cultivar (MP) and experiment (Expts 2, 4 or 5). maL = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	1.56	0.191	< 0.001
1	S	0.0031	0.00119	0.009
2	MP	0.24	0.205	0.235
3	Expt 4	-0.60	0.151	< 0.001
4	Expt 5	-0.49	0.137	< 0.001

5.3.4.5 Sympodial branch leaf appearance

The influence of cultivar on rate of sympodial branch leaf appearance (sbLA) varied between experiments. In Expt 5, sbLA could not be calculated in three Estima plots (two large and one medium sized seed, all at 20 cm spacing) as sympodial branches were not produced, hence sbLA was represented as missing values. There was no significant effect of cultivar on sbLA in Expt 2 (Figure 99a). Maris Piper sbLA was faster than in Estima in Expt 4 by 0.06 leaves/day ($P < 0.001$, Figure 99b) whilst sbLA was faster in Estima than Maris Piper by 0.03 leaves/day in Expt 5 ($P = 0.008$, Figure 99c). Sympodial branch leaf production was faster at wider plant spacings than closer spacings in each experiment (Figure 99c). In Expt 4, sbLA increased steadily as spacing increased ($P = 0.003$), though there was little difference between sbLA of 40 and 60 cm spacings in Expt 2 ($P = 0.002$, Figure 99a) or sbLA of 20 and 40 cm spacings in Expt 5 ($P < 0.001$, Figure 99c). There was no interaction between effects of cultivar and seed spacing on sbLA (Figure 99).

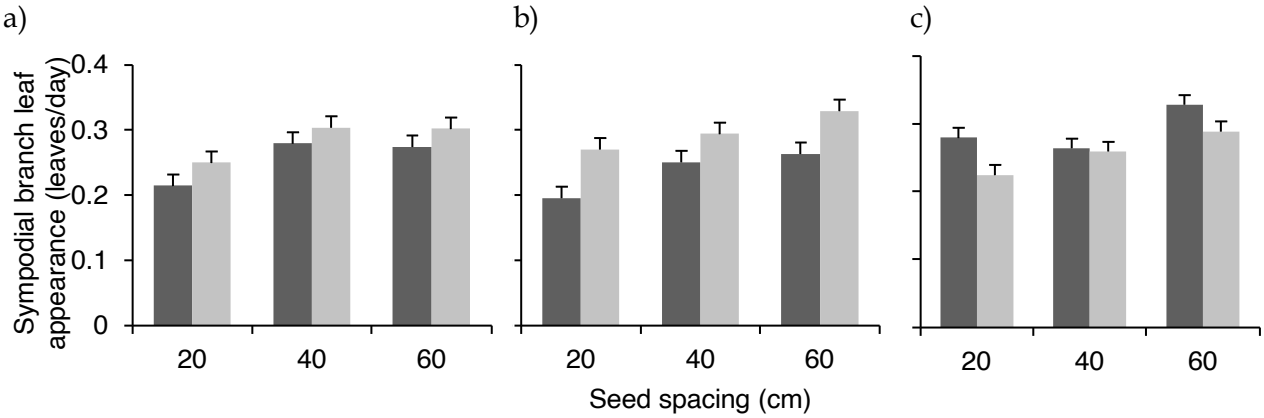

Figure 99. Effect of seed spacing and cultivar on rate of sympodial branch leaf appearance (sbLA) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 85 D.F.). Data presented are means of seed size treatments.

Seed size had no effect on the rate of sympodial branch leaf appearance in Expt 2 (Figure 100a), but sbLA was faster in small seed than larger seed by 0.04 leaves/day in Expts 4 and 5 (P = 0.017 and P = 0.008, respectively, Figure 100b & c). There was no difference in sbLA between medium and large seed in Expt 5 (Figure 100c).

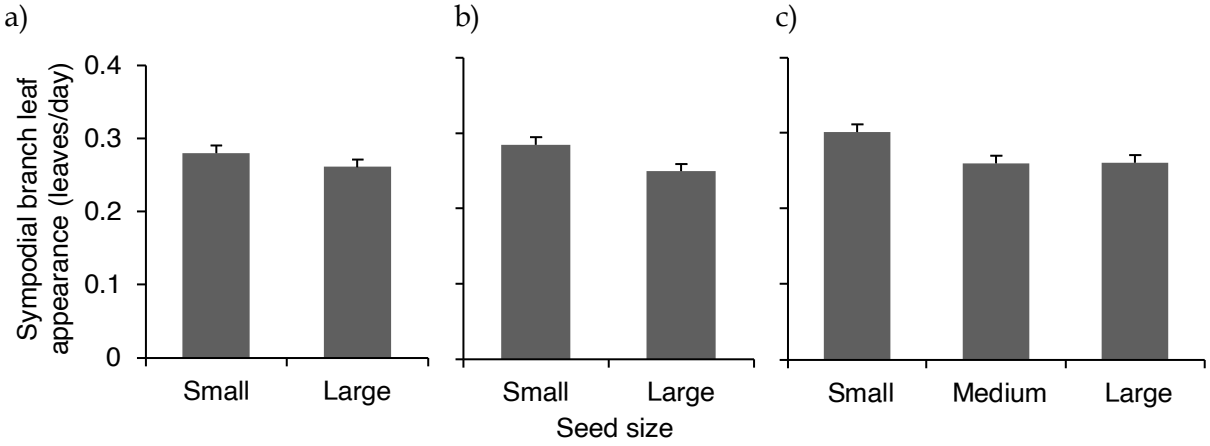

Figure 100. Effect of seed size on rate of sympodial branch leaf appearance (sbLA) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 85 D.F.). Data presented are means of seed size and cultivar treatments.

The rate of leaf appearance on sympodial branches decreased with increasing stem density in both cultivars (Figure 101), yet the relationship was weak, and stem density and cultivar explained only 17.3 % of the variation in sbLA (multiple linear regression; sbLA ~ stem density + cultivar + block, $P < 0.001$). The response of sbLA to stem density did not vary significantly between cultivars, although sbLA was on average faster in Maris Piper than Estima (Table 62). Stem distribution had a limited effect on sbLA and including seed size and spacing in the model resulted in a marginal increase in variation accounted for (R^2 = 19.4, $P < 0.001$).

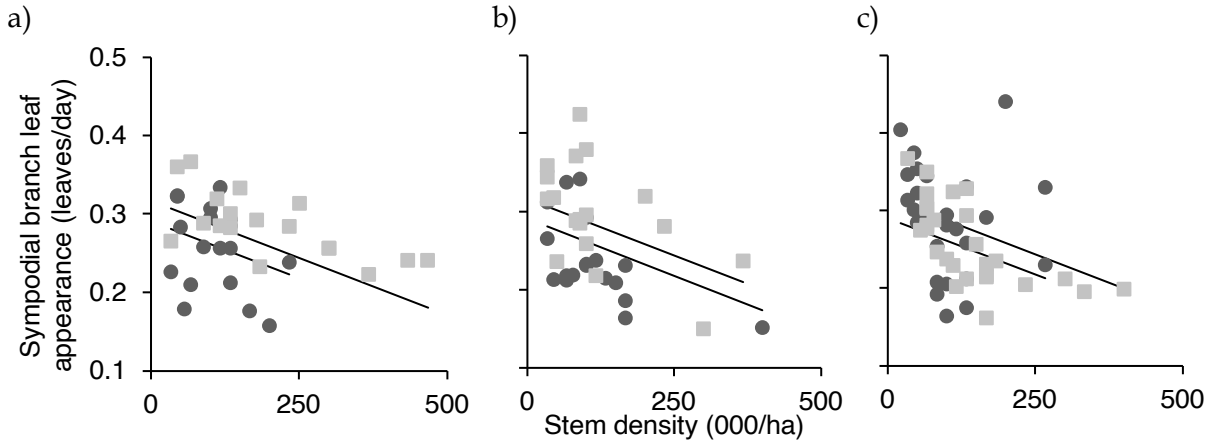

Figure 101. Relationship between rate of sympodial branch leaf appearance (sbLA) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.270. See Table 62 for details of multiple linear regression.

Table 62. Relationship between rate of sympodial branch leaf appearance (sbLA) and stem density (S) and cultivar (MP). maL = β0 + β1*S + β2*MP.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.291	0.0113	< 0.001
1	S	-0.00029	0.0000551	< 0.001
2	MP	0.026	0.0100	0.011

5.3.4.6 Key points: Leaf appearance

- Maris Piper produced an average of 4.2 more mainstem leaves than Estima.
- Leaf appearance on an individual mainstem was faster in Estima than Maris Piper, consistent with findings of the planting date experiments.
- Mainstem leaf appearance was faster when stem density was lower (i.e. at wider plant spacing and in smaller seed) but there was a high degree of scatter around the relationship.
- Maris Piper produced 7.2 more leaves on the main axis than Estima and number of main axis leaves decreased with increasing stem density in both cultivars.
- Whole plant leaf appearance was faster when the number of stems per plant was greater (i.e. with larger seed).
- GCRate2575 and pLA were positively correlated but with a high degree of scatter.
- Rate of sympodial branch leaf production tended to be faster at lower stem density (i.e. at wider plant spacing) but the relationship was weak.

5.3.5 Leaf area index

Mid-season harvests were carried out at the onset of senescence in each experiment, however in Expts 2 and 5 the harvest occurred after considerable senescence of the Estima canopy and only Maris Piper was harvested (5.2.2.3). In Expt 4 a mid-season harvest was carried out at the onset of Estima canopy senescence and both cultivars were included. Whilst each harvest was timed to occur at the onset of senescence, GC varied between plots; 60-95 % at the Maris Piper harvest in Expt 2, 83-97 % and 86-100 % in the Estima and Maris Piper harvests respectively in Expt 4, and 92-100 % in Maris Piper in Expt 5. In Expt 2, three plots had missing mainstem LAI (msLAI) values (all Maris Piper, small seed at 60 cm, large seed at 20 and 40 cm) and Expt 5, one plot was also missing msLAI (medium Maris Piper seed at 60 cm). The effects of all treatments and their interactions on LAI are reported in Appendix 23.

Mainstem LAI was smaller when seed was spaced further apart with a difference of 1.39, 0.48 and 0.78 between the leaf area index of 20 and 60 cm spaced plants in Expts 2 (P = 0.019), 4 and 5 (P = 0.006), respectively, however, the difference in Expt 4 was not significant (Figure 102). Sympodial branch LAI (sbLAI) was also smallest at the widest plant spacing and was 0.73 and 0.66 greater at the 20 cm than 60 cm spacing in Expts 4 and 5 (both $P < 0.001$, the difference was not significant in Expt 2). Axillary branch LAI (abLAI) was greatest at the widest plant spacing and was 1.28 and 1.64 greater at the 60 cm than the 20 cm spacing in Expts 4 and 5 (P = 0.006 and P = 0.002, respectively, the difference was not significant in Expt 2). There was no effect of seed spacing on total LAI (TotLAI) as the reduced mainstem and sympodial branch LAI at wider seed spacing was compensated for by increased abLAI which can be seen clearly in Expts 4 and 5 (Figure 102b & c). The differences in TotLAI between seed spacing treatments were also not significant in Expt 2, although the TotLAI was numerically 1.33 smaller at 60 than 20 cm spacing (Figure 102a).

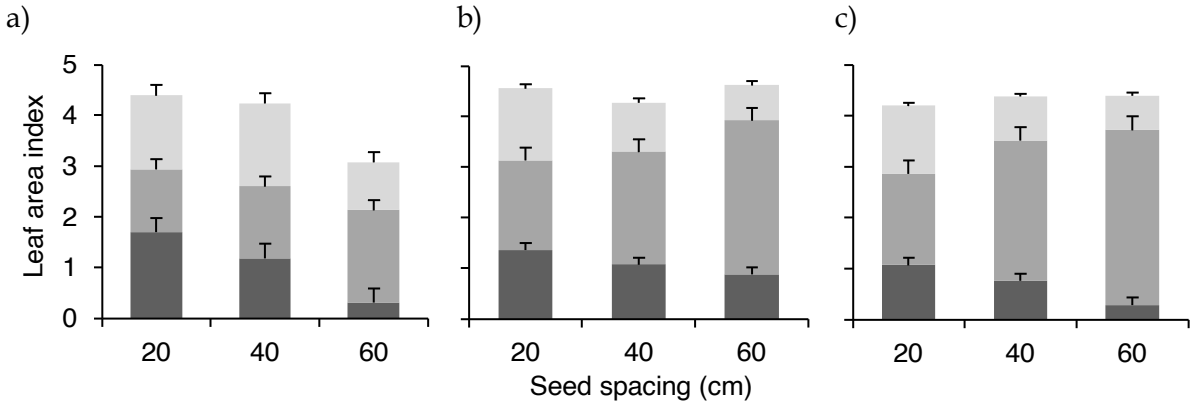

Figure 102. Effect of seed spacing on total LAI at onset of senescence, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. Data presented are a mean of seed size treatments and a mean of cultivars in (b), data from Maris Piper only in (a) and (c).

The influence of seed size on leaf area index of the different canopy components varied between the experiments. Mainstem LAI was 0.37 greater in large than small seed in Expt 4 (P = 0.034), though the difference was not significant in Expt 5. In Expt 5, small seed produced 1.25 abLAI more than the average of medium and large seed, which did not differ significantly from each other (2.32 and 2.17 LAI for medium and large seed respectively, S.E. 0.27, P = 0.006), whilst there was no significant difference in abLAI between seed sizes in Expt 4. Large seed produced 0.53 and 0.32 more sbLAI than small seed in Expts 4 (P < 0.001) and 5 (P = 0.005), respectively. In Expt 4, at 20 cm spacing small seed produced a slightly greater total LAI than large seed, but at 40 and 60 cm spacing, large seed produced LAI *c.* 1.1 greater than small seed (P = 0.020). On average, TotLAI of large seed was 0.58 greater than small seed in Expt 4 (P = 0.015, Figure 103b) whilst there was no significant difference in total LAI between seed sizes in Expt 5 (Figure 103c). Seed size had no significant effect on either total LAI or the LAI of individual canopy components in Expt 2 (Figure 103a).

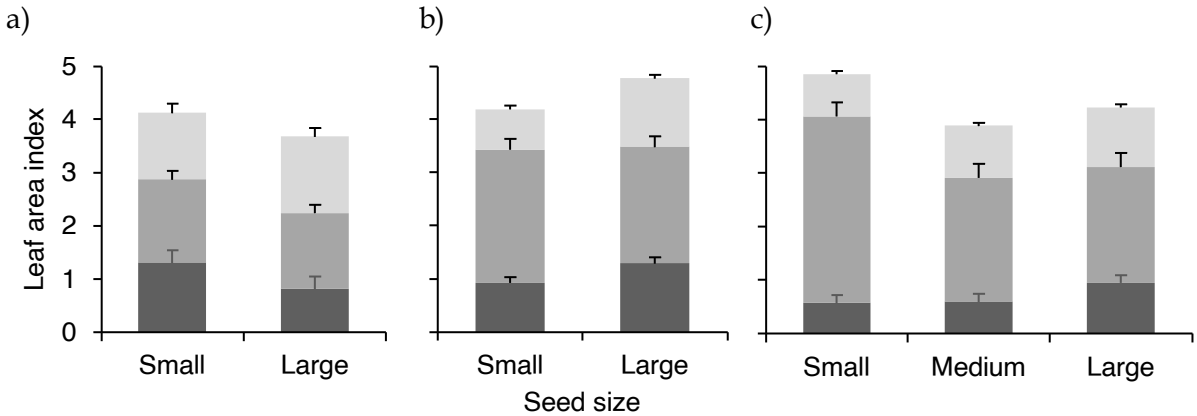

Figure 103. Effect of seed size on total LAI at onset of senescence, (a) Expt 2, (b) Expt 4 and (c) Expt 5. Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. Data presented are a mean of seed spacing treatments and a mean of cultivars in (b), data from Maris Piper only in (a) and (c).

In Expt 4, Maris Piper produced a larger total LAI than Estima, a difference equivalent to a complete additional layer of leaves ($P < 0.001$, Figure 104). In Maris Piper there was little difference in mainstem LAI between seed sizes, yet in Estima, there was a substantial increase in mainstem LAI with increase in seed size (0.8, $P = 0.014$). Whilst Maris Piper produced less mainstem LAI than Estima (0.85 compared to 1.37 LAI, respectively, $P = 0.004$), Maris Piper axillary branch LAI was approximately double that of Estima (3.11 and 1.58 LAI, respectively, $P < 0.001$). Both cultivars produced a similar sympodial branch leaf area (Figure 104).

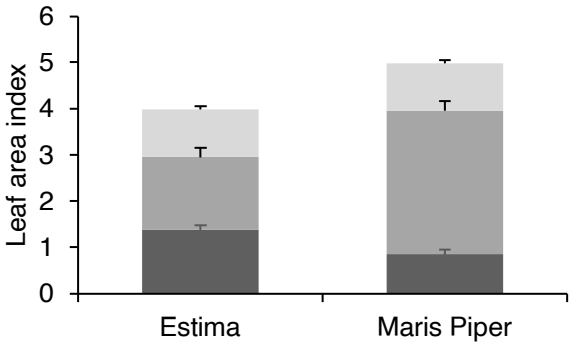

Figure 104. Effect of cultivar on total LAI at onset of senescence in Expt 4. Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. Data presented are a mean of seed spacing and seed size treatments.

At the onset of senescence there was no distinct relationship between LAI and percent ground cover (Figure 105). Whilst plots with near-complete ground cover were more likely to have a higher LAI (93 % of plots with ≥ 90 % GC had an LAI > 3), high LAI was not always associated with near-complete ground cover and 23 % of plots with LAI > 3 had < 90 % GC. This high degree of variability is probably the result of large plant to plant differences in senescence and the random effects of lodging on canopy cover.

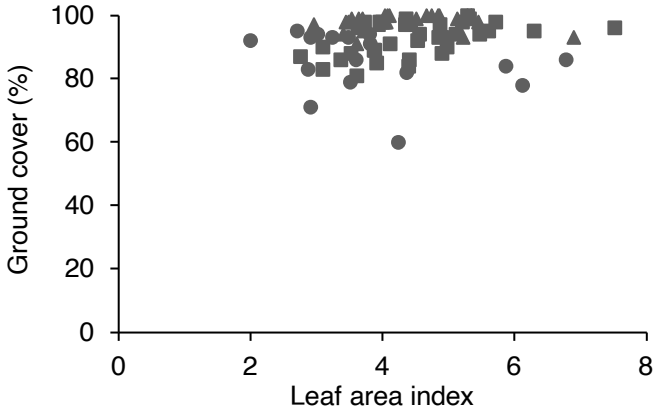

Figure 105. Relationship between leaf area index and percent ground cover at the onset of senescence. Expt 2, ●; Expt 4, ■ and Expt 5, ▲. Data from Maris Piper only in Expts 2 and 5, data from both cultivars in Expt 4.

There was a weak positive relationship between msLAI and stem density in each experiment, but since msLAI was highly variable within experiments (Figure 106a, b & c) stem density only explained 14.5 % of the variation in msLAI of Maris Piper across the experiments, after accounting for variation between experimental blocks (multiple linear regression; msLAI ~ stem density + block, $P = 0.007$, Table 63). Intercepts for each block differed significantly (block, ANOVA; $P = 0.039$), though regression coefficients without accounting for the differences between blocks were reported below for ease of interpretation (Figure 106 and Table 63). Axillary branch LAI decreased with increasing stem density in Maris Piper in Expt 5, but there was no response to stem density in Expts 2 and 4 (Figure 106f, d & e, respectively). Stem density explained 42.7 % of the variation in Maris Piper abLAI once variation between experiments and blocks was accounted for (multiple linear regression; abLAI ~ stem density * year + block, $P < 0.001$, Table 64). Sympodial branch LAI increased with increasing stem density (Figure 106g, h & i) and 47.0 % of the variation in Maris Piper sbLAI was explained by stem density and experiment (multiple linear regression; sbLAI ~ stem density * year + block, $P < 0.001$, Table 65).

Overall, Expt 4 suggests that LAI production in Estima responded to changing stem density in a similar way to Maris Piper (Figure 106b, e & h), and stem density explained 49.3 % of the variation in msLA ($P = 0.006$, (Figure 106b) once between block variation was accounted for, but the relationships between abLAI and sbLAI, and stem density were not significant.

There was no significant relationship between stem density and TotLAI in Maris Piper (data not shown), though 29.3 % of the variation in TotLAI was explained by stem

density in Estima (multiple linear regression; TotLAI ~ stem density + block, $P = 0.050$) and TotLAI increased with increasing stem density.

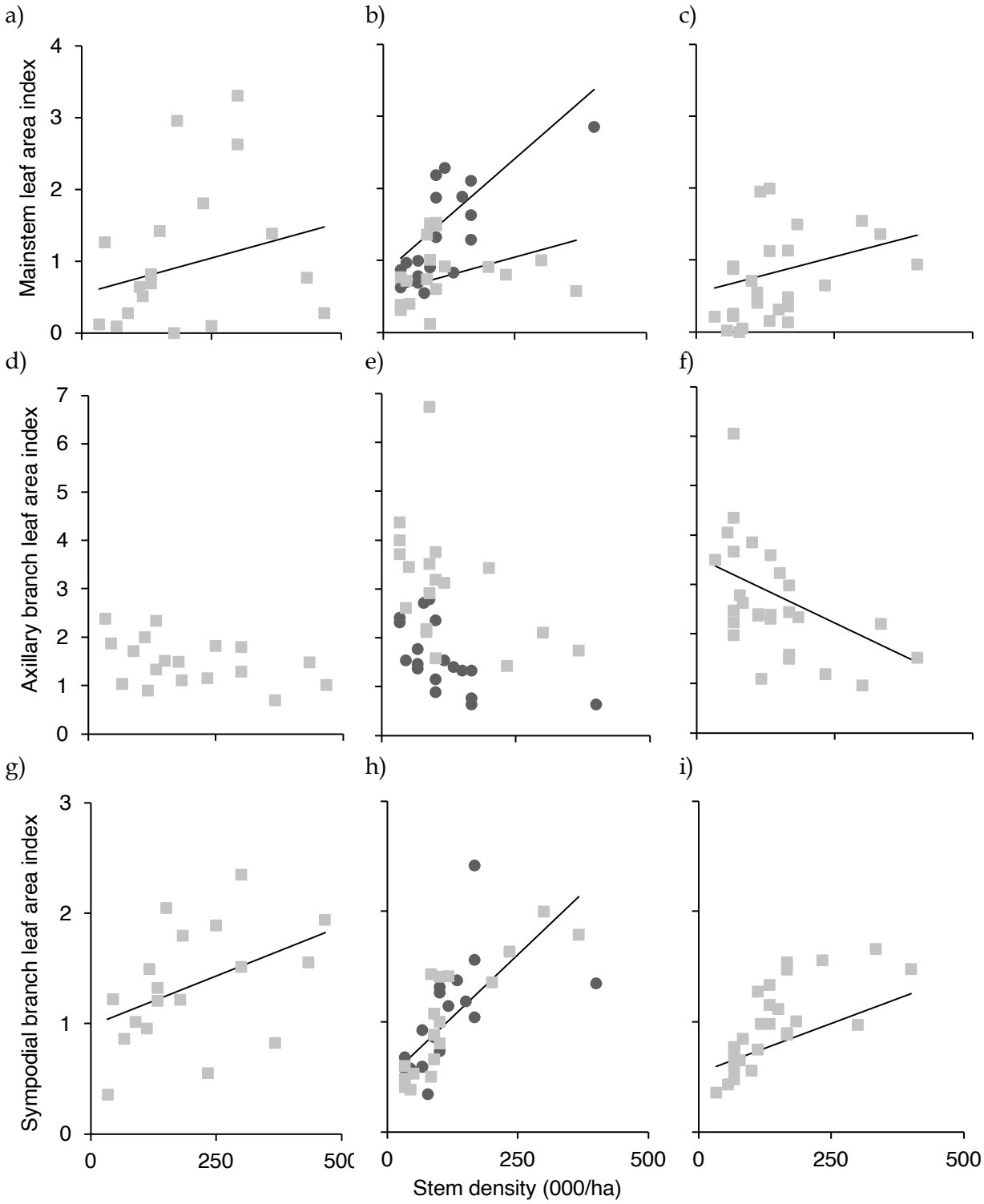

Figure 106. Relationship between leaf area index (LAI) components and stem density (S). Mainstem LAI; (a) Expt 2, (b) Expt 4 and (c) Expt 5, $R^2 = 0.128$, see Table 63. Axillary branch LAI; (d) Expt 2, (e) Expt 4 and (f) Expt 5, $R^2 = 0.427$, see Table 64. Sympodial branch LAI; (g) Expt 2, (h) Expt 4 and (i) Expt 5, $R^2 = 0.470$, see Table 65. Estima, ●; Maris Piper, ■.

Table 63. Relationship between mainstem leaf area index (msLAI) and stem density (S) and experiment (Expts 2, 4 or 5) in Maris Piper. msLAI = β0 + β1*S.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.55	0.149	< 0.001
1	S	0.00200	0.000807	0.016

Table 64. Relationship between axillary branch leaf area index (abLAI) and stem density (S) and experiment (Expts 2, 4 or 5) in Maris Piper. abLAI = β0 + β1*S + β2*Expt 4 + β3*Expt 5 + β4*(S*Expt 4) + β5*(S*Expt 5).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	1.76	0.429	< 0.001
1	S	-0.0018	0.00170	0.305
2	Expt 4	1.98	0.534	< 0.001
3	Expt 5	1.79	0.519	0.001
4	S * Expt 4	-0.0043	0.00289	0.145
5	S * Expt 5	-0.0053	0.002629	0.048

Table 65. Relationship between sympodial branch leaf area index (sbLA) and stem density (S) and experiment (Expts 2, 4 or 5) in Maris Piper. sbLAI = β0 + β1*S + β2*Expt 4 + β3*Expt 5 + β4*(S*Expt 4) + β5*(S*Expt 5).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	0.98	0.167	< 0.001
1	S	0.001791	0.000662	0.009
3	Expt 4	-0.51	0.207	0.018
4	Expt 5	-0.45	0.202	0.030
5	S * Expt 4	0.0028	0.001123	0.016
6	S * Expt 5	0.0012	0.001021	0.227

5.3.5.1 Key points: Leaf area index (mid-season)

- Stem density (and distribution) had no effect on TotLAI, as decreases in msLAI and sbLAI were compensated for by increases in abLAI.
- Stem density explained little of the variation in LAI of the different canopy components, likely due in part to variation in canopy coverage between plots at harvest.
- TotLAI was greater in Maris Piper than Estima, due to greater abLAI.

5.3.6 Branch production

Branch production was recorded at a single mid-season harvest, at the onset of senescence. In Expts 2 and 5, senescence was greatly advanced in Estima at the mid-season harvest, consequently only Maris Piper branch data was recorded. The effects of all treatments and their interactions on branch production are reported in Appendix 24.

5.3.6.1 Axillary branches

Number of axillary branches per stem (NoB) decreased as seed size increased (P = 0.031, P < 0.001 and P < 0.001 in Expts 2, 4 and 5, respectively, Figure 107) and the difference in axillary branch number between seed sizes was almost three times greater in Maris Piper than in Estima (P = 0.009, Expt 4, Figure 107b). In Maris Piper there were fewer axillary branches per stem in Expt 2 than Expts 4 and 5 (5.1, 9.1 and 8.7 NoB respectively (Figure 107)), though this may be a result of more advanced senescence on the mainstem and axillary branches at the comparatively late harvest in Expt 2 (at 86 % GC) compared to Expts 4 and 5 (95 and 98 % GC, respectively).

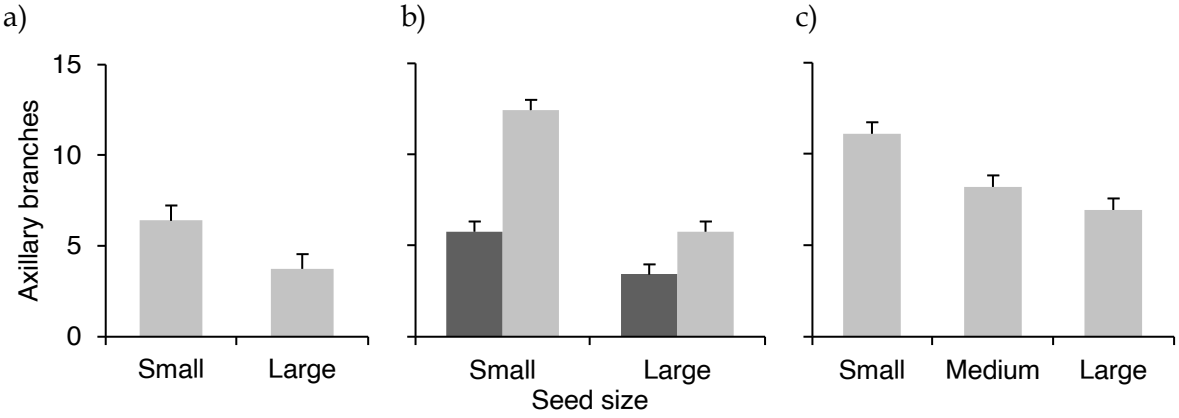

Figure 107. Effect of seed size on number of axillary branches in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F.). Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (c).

The range in number of axillary branches between large seed at 20 cm spacing and small seed at 60 cm spacing was 2.5 times greater in Maris Piper than in (P = 0.046, Figure 108b), indicating a greater branch production potential at lower stem densities in Maris Piper than in Estima. The difference in NoB between spacing treatments in Estima was greatest between 40 and 60 cm spacing, whereas in Maris Piper the difference was greatest between the 20 and 40 cm spacings (P < 0.001). Number of axillary branches per stem was greatest at the widest plant spacing (P < 0.001, Figure 108) and Estima stems had approximately half the number of axillary branches as Maris Piper at each spacing treatment (P < 0.001, Figure 108b).

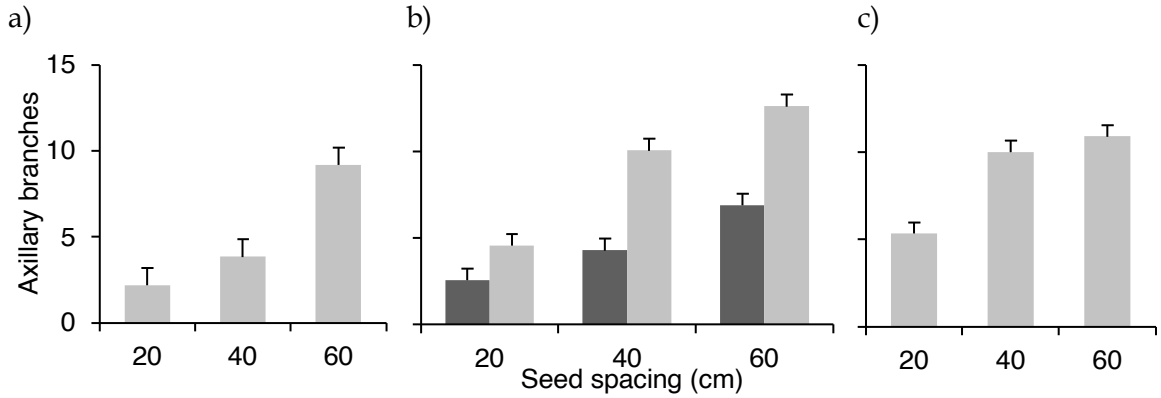

Figure 108. Effect of seed spacing on number of axillary branches in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F.). Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (c).

Number of axillary branches per stem decreased with increasing stem density in both Maris Piper and Estima (Figure 109). Stem density explained 56.3 % of the variation in NoB once differences in mean NoB between years were accounted for (multiple linear regression; NoB ~ stem density + year + block, $P < 0.001$, Table 66), whilst 41.3 % of the variation in Estima NoB was accounted for by stem density in Expt 4 (multiple linear regression, $P = 0.015$).

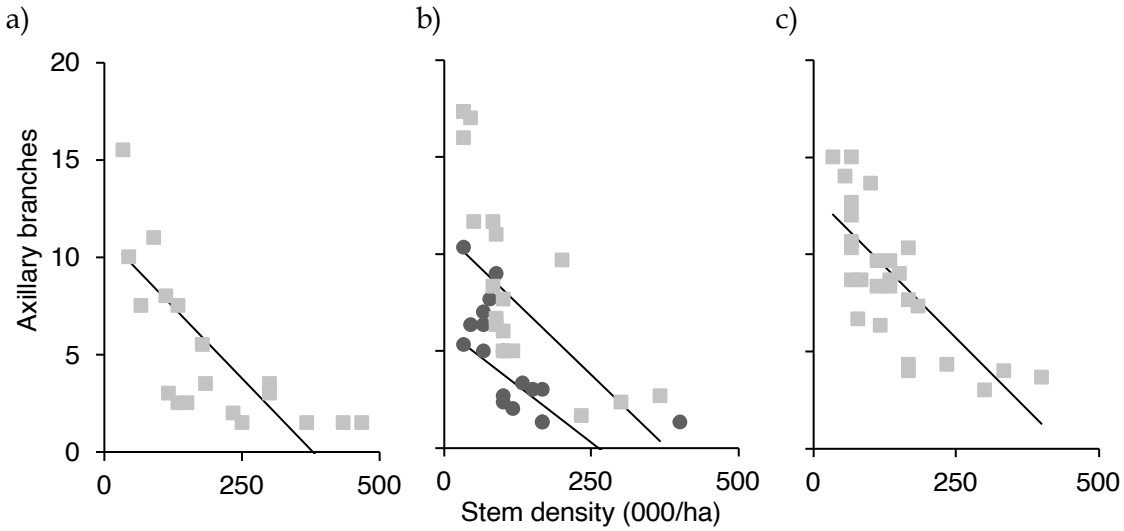

Figure 109. Relationship between number of axillary branches (NoB) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. For Maris Piper, $R^2 = 0.563$. See Table 66 for details of multiple linear regression. For Estima, $R^2 = 0.413$, NoB = -0.0235 (± 0.00628) * S + 6.12 (± 1.04).

Table 66. Relationship between number of axillary branches (NoB) and stem density (S), and experiment (Expts 2, 4 or 5) in Maris Piper (Expt 4 Estima data not included). NoB = β0 + β1*S + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	11.1	1.14	< 0.001
1	S	-0.0294	0.00371	0.002
2	Expt 4	1.7	1.03	0.1135
3	Expt 5	1.91	0.931	0.044

Duration of near-complete canopy cover was typically lower when stems produced a greater number of branches in both Maris Piper and Estima (Figure 110). Number of axillary branches explained 36.3 % of the variation in GCDur90 once differences in mean GCDur90 between years were accounted for (multiple linear regression; GCDur90 ~ NoB + year + block, $P < 0.001$, Table 67), whilst 31.7 % of the variation in Estima GCDur90 was accounted for by NoB in Expt 4 (multiple linear regression, $P = 0.040$, Figure 110b). The reduction in GCDur90 with increasing NoB reflects the changes in stem density; as stem density increased, branch production decreased (Figure 109), whilst GCDur90 increased (Figure 78).

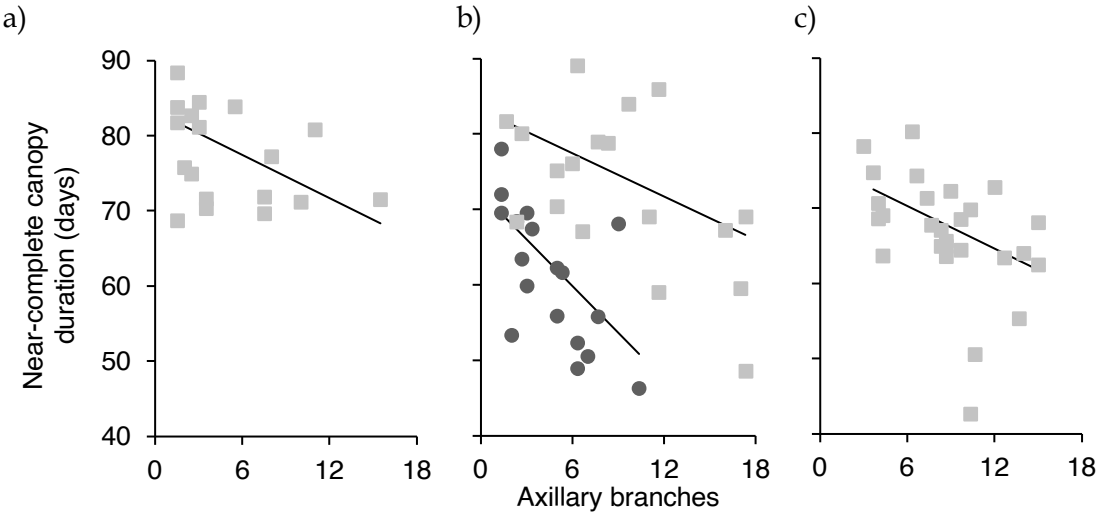

Figure 110. Relationship between duration of near-complete canopy cover (GCDur90) and number of axillary branches (NoB) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. For Maris Piper, $R^2 = 0.363$. See Table 67 for details of multiple linear regression. For Estima, $R^2 = 0.317$, GCDur90 = -2.07 (± 0.666) * NoB + 72.2 (± 4.01).

Table 67. Relationship between duration of near-complete canopy cover (GCDur90), number of axillary branches (NoB) and experiment (Expts 2, 4 or 5) in Maris Piper (Expt 4 Estima data not included). GCDur90 = β0 + β1*NoB + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	83.1	2.52	< 0.001
1	NoB	-0.950	0.2284	< 0.001
2	Expt 4	-0.7	2.64	0.784
3	Expt 5	-7.1	2.41	0.005

5.3.6.2 Axillary branch leaves

The mean number of leaves produced per axillary branches (aveBLeaves) in response to seed size varied between the experiments; there was no effect of seed size in Maris Piper in Expts 2 and 4 (Figure 111a & b) and large reductions with increasing seed size in Expt 5 ($P < 0.001$, Figure 111c). Results from Expt 4 suggested that there may be a differing response in branch leaf production to seed size between cultivars as the axillary branches of Estima small seed produced 3.4 more leaves per branch than large seed, whereas small seeded Maris Piper produced 2.2 fewer leaves than large seed ($P = 0.003$, Figure 111b). On average, Estima produced *c.* 3 fewer leaves per axillary branch than Maris Piper ($P = 0.002$).

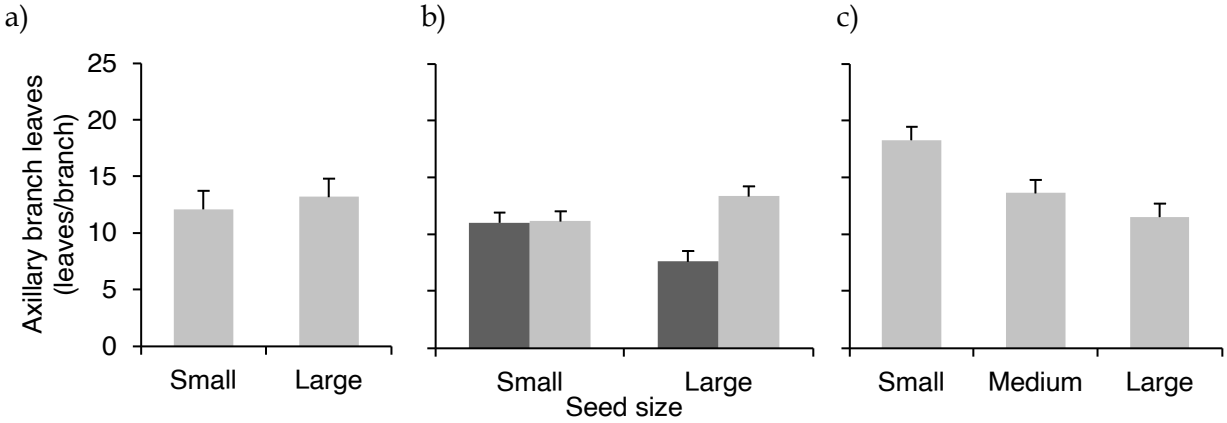

Figure 111. Effect of seed spacing on mean number of axillary branch leaves in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F.). Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (c).

Axillary branches at wider plant spacing tended to produce a greater number of leaves per branch than at closer plant spacing (Figure 112), though differences in number of leaves produced were not significant in Expts 2 or 4 (Figure 112 a & b, $P < 0.001$ in Expt 5, Figure 112c).

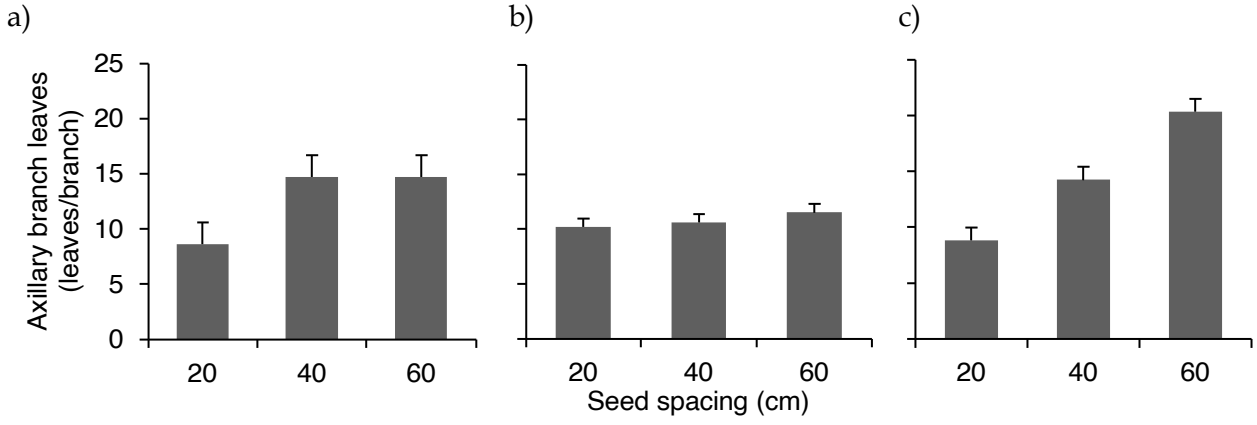

Figure 112. Effect of seed spacing on mean number of axillary branch leaves in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F.). Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (c).

The average number of leaves per axillary branch decreased with increasing stem density (Figure 113), but stem density only explained 15.9 % of the variation in aveBLeaves in Maris Piper once variation between experimental blocks was accounted for (multiple linear regression; aveBLeaves ~ stem density + block, $P = 0.004$, Table 68). There was no difference in mean aveBLeaves between experiments (Table 68). There was no significant relationship between aveBLeaves and stem density in Estima, in Expt 4, though fewer branch leaves tended to be produced at higher stem densities (Figure 113b).

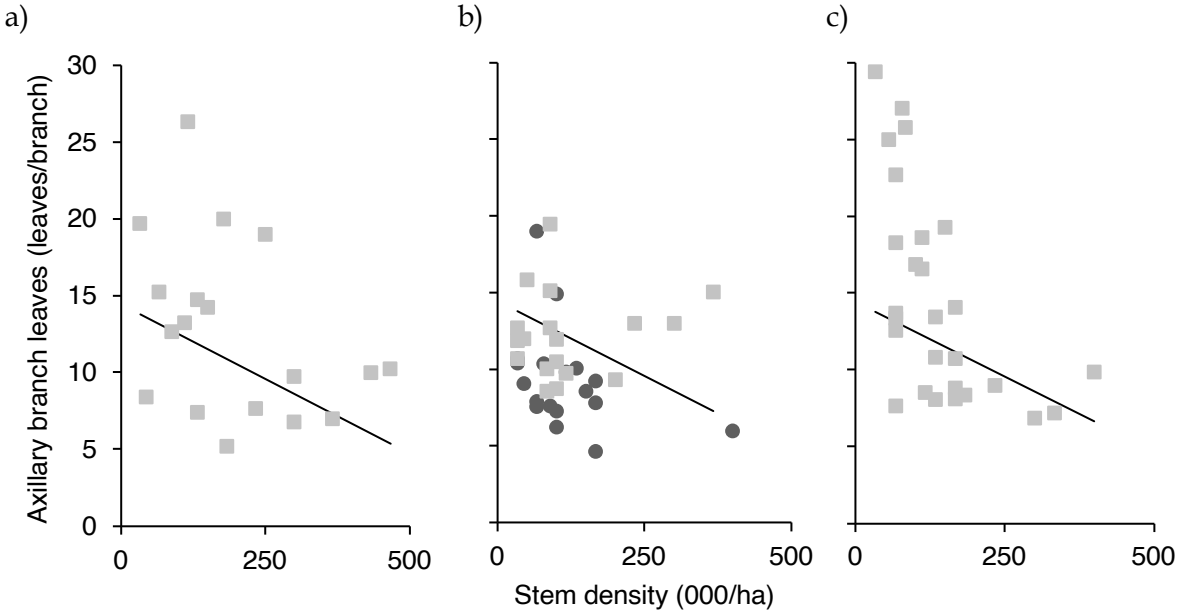

Figure 113. Relationship between mean number of axillary branch leaves and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. For Maris Piper, $R^2 = 0.159$. See Table 68 for details of multiple linear regression. The relationship was non-significant in Estima (b).

Table 68. Relationship between number of axillary branch leaves (aveBLeaves) and stem density (S), and experiment (Expts 2, 4 or 5) in Maris Piper (Expt 4 Estima data not included). aveBLeaves = β0 + β1*S.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	14.4	1.433	< 0.001
1	S	-0.0195	0.00610	0.003

5.3.6.3 Sympodial branch insertion point and stem length

Total stem length (combined length of mainstem and sympodial branch, TotLength) was greater in large seed than small seed by 96, 135 and 147 mm respectively in Expts 2, 4 and 5 ($P = 0.016$, $P < 0.001$ and $P = 0.016$, respectively, Figure 114). The mainstem, up to the sympodial branch insertion point (SBInsert), was longer in stems produced by large, rather than, small seed by 124, 109 and 174 mm respectively in Expts 2, 4 and 5 ($P < 0.001$, Figure 114). In each experiment a number of stems

measured produced no sympodial branches, hence SBInsert was recorded as a missing value in one plot in Expt 2 (small Maris Piper seed at 20 cm spacing), one in Expt 4 (large Estima seed at 20 cm spacing) and six in Expt 5 (all Maris Piper, small seed at 20 cm, two medium seed each at 20 and 60 cm, and one large seed at 60 cm). Sympodial branch length varied little between seed size treatments, with a range < 40 mm in each experiment, and was shortest in Expt 2, followed by Expt 4 and was longest in Expt 5 (363, 510 and 574 mm, respectively, Figure 114), suggesting that differences in total stem length result predominantly from differences in mainstem length.

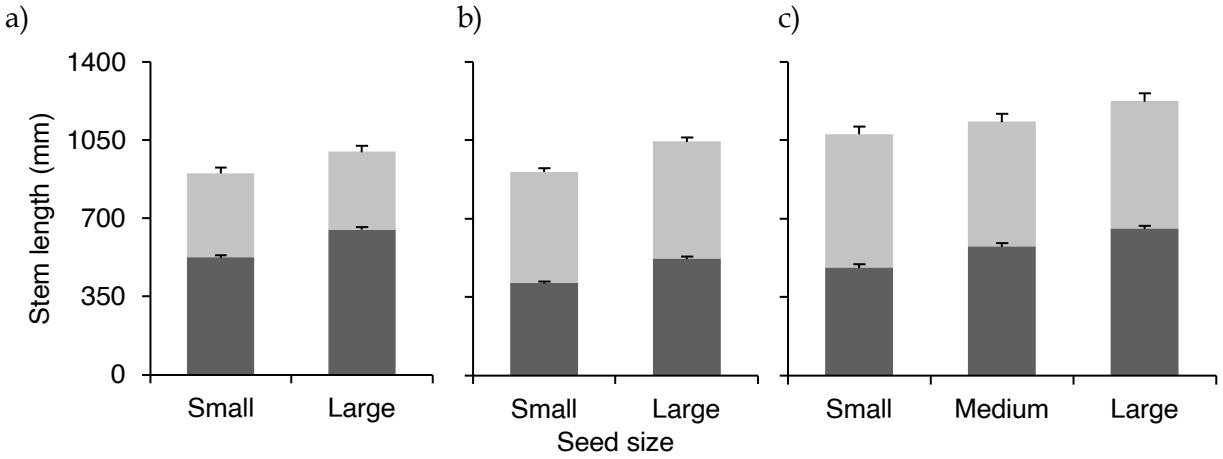

Figure 114. Effect of seed size on sympodial branch insertion point and total stem length in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Mainstem length, ■; sympodial branch length, ■. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F.). Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (c).

TotLength did not respond to seed spacing consistently across the three experiments. There was no difference in TotLength between seed spacing treatments in Expts 2 or 5 (Maris Piper only, Figure 115a and c). In Expt 4, 20 cm spaced seed produced stems 81 and 62 mm longer than 40 and 60 cm spaced seed respectively (P = 0.028, Figure 115b). At wider spacing the mainstem tended to be shorter (P < 0.001) and whilst there was little variation in sympodial branch length in Expt 4 (20 mm range), sympodial branch length increased as seed spacing became wider in Expts 2 and 5 (221 and 193 mm range, respectively).

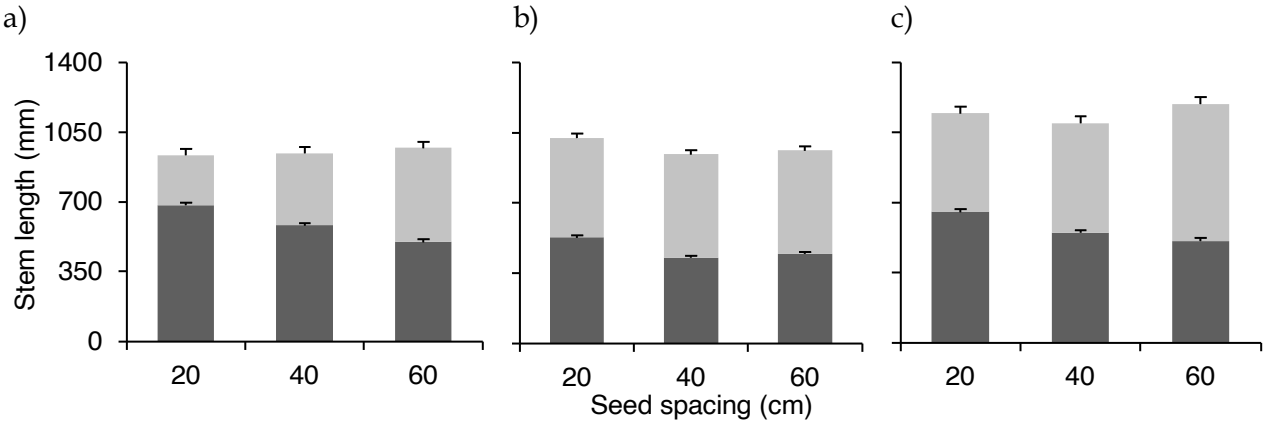

Figure 115. Effect of seed spacing on sympodial branch position and total stem length in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Mainstem length, ■; sympodial branch length, ■. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F. Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (b).

In Expt 4 both the mainstem and sympodial branch were longer in Maris Piper than Estima, by 170 and 110 mm respectively (both $P < 0.001$, Figure 116). In Expts 2 and 5 only Maris Piper was harvested during the season, so the cultivars could not be compared in these experiments.

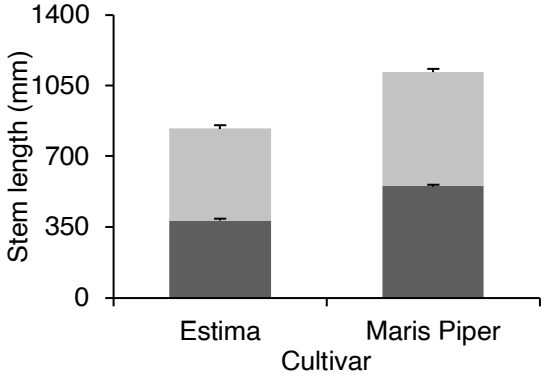

Figure 116. Effect of cultivar on sympodial branch insertion point and total stem length in Expt 4. Bars represent S.E. (94 D.F.). Mainstem length, ■; sympodial branch length, ■. Data presented are means of seed size and seed spacing treatments.

There was a small increase in total stem length as stem density increased in each experiment, though mean TotLength differed between experiments (Figure 117) and was much lower in Estima than Maris Piper (Figure 117b). In both cultivars and each experiment, SBInsert was greater at higher stem densities (Figure 117). In Maris Piper, stem density explained 31.1 % of the variation in TotLength and 58.6 % of the variation in SBInsert, once differences in mean TotLength between experiments and blocks were accounted for (multiple linear regression; TotLength ~ stem density + year + block, $P < 0.001$, Table 70; SBInsert ~ stem density + block, $P < 0.001$, Table 69). In Estima, Expt 4, TotLength did not differ significantly with stem density, though SBInsert

increased with increasing stem density which explained 37.4 % of the variation in SBInsert (P = 0.022, Figure 117b).

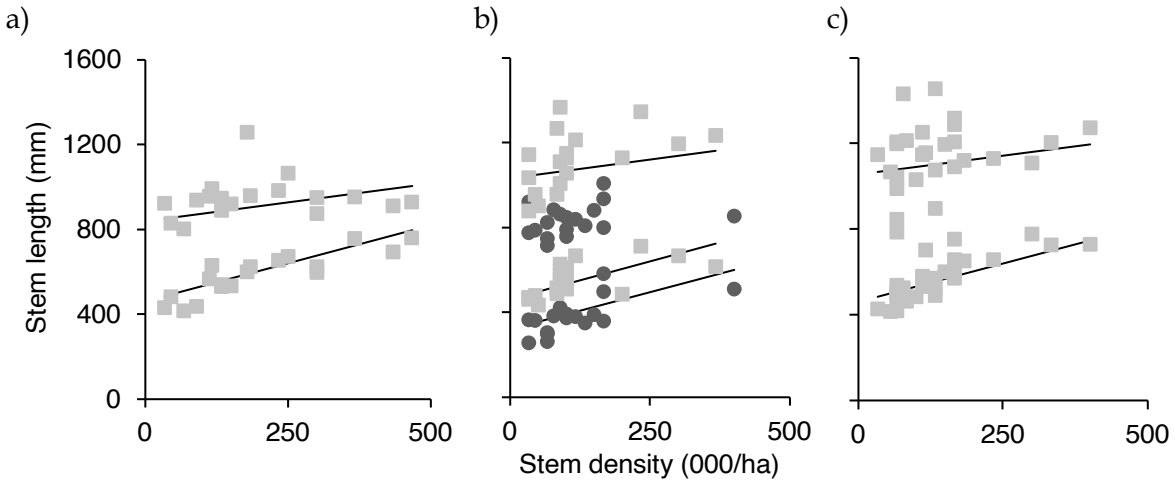

Figure 117. Relationship between mainstem length (SBInsert), total stem length (TotLength) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima; SBInsert, ●; TotLength, ■. Maris Piper; SBInsert, ●; TotLength, ■. For Maris Piper; SBInsert, R^2 = 0.586 and TotLength, R^2 = 0.311. See Tables 69 & 70, respectively, for details of multiple linear regression. For Estima, SBInsert R^2 = 0.374, SBInsert = 0.70 (± 0.195) * S + 320 (± 32.4), but the relationship between TotHeight and S was non-significant (b).

Table 69. Relationship between mainstem length (SBInsert) and stem density (S), and experiment (Expts 2, 4 or 5) in Maris Piper (Expt 4 Estima data not included). SBInsert = β0 + β1*S.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	462	17.7	< 0.001
1	S	0.718	0.0754	< 0.001

Table 70. Relationship between total stem length (TotLength) and stem density (S), and experiment (Expts 2, 4 or 5) in Maris Piper (Expt 4 Estima data not included). TotLength = β0 + β1*S + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	840	50.6	< 0.001
1	S	0.35	0.165	0.037
2	Expt 4	194	46.0	< 0.001
3	Expt 5	216	41.4	< 0.001

Duration of near-complete canopy cover was typically greater when mainstem length (as indicated by SBInsert) was longer in both Maris Piper and Estima (Figure 118). In Maris Piper, SBInsert explained 30.7 % of the variation in GCDur90 once differences in mean GCDur90 between years were accounted for (multiple linear regression; GCDur90 ~ SBInsert + year + block, P < 0.001, Table 71), whilst 57.8 % of the variation in Estima GCDur90 was accounted for by SBInsert in Expt 4 (multiple linear regression; GCDur90 ~ SBInsert + year + block, P = 0.002). The relationship between SBInsert and GCDur90 was weak as longer stems do not directly contribute to increases in canopy cover, nor canopy maintenance since number of mainstem leaves varies only with

cultivar, not stem density (Figure 85), instead likely acting as a weak proxy for stem density, since mainstem length tended to be greater at high stem density (Figure 117).

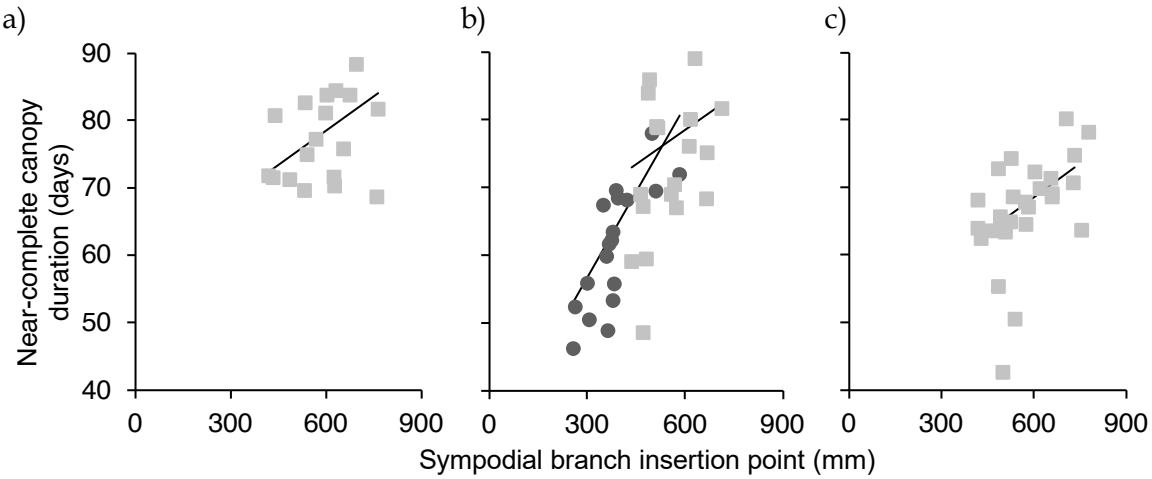

Figure 118. Relationship between sympodial branch insertion point (SBInsert) and duration of near-complete ground cover (GCDur90) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. For Maris Piper, R^2 = 0.307. See Table 71 for details of multiple linear regression. For Estima, R^2 = 0.578, GCDur90 = 0.085 (± 0.0172) * SBInsert + 31.3 (± 7.07).

Table 71. Relationship between sympodial branch insertion point (SBInsert), duration of near-complete ground cover (GCDur90) and experiment (Expts 2, 4 or 5) in Maris Piper (Expt 4 Estima data not included). GCDur90 = β0 + β1*SBInsert + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	58.2	6.32	< 0.001
1	SBInsert	0.034	0.0101	0.001
2	Expt 4	-3.3	2.61	0.206
3	Expt 5	-10.0	2.36	< 0.001

5.3.6.4 Sympodial branch leaves

In both Expts 2 and 5 Maris Piper tended to produce more leaves on the sympodial branch (SBLeaves) of small than large seed, though the difference was not significant in Expt 2 (Figure 119a), nor was the difference (1.9 leaves) between medium and large seed (Figure 119c). In contrast, for Maris Piper in Expt 4, 5.6 more sympodial branch leaves were produced by large than small seed, whilst the number of sympodial branch leaves did not differ between small and large seed in Estima (P = 0.008, Figure 119b). In each experiment a number of stems measured produced no sympodial branches, hence SBLeaves was recorded as a missing value in one plot in Expt 2 (small Maris Piper seed at 20 cm spacing), one in Expt 4 (large Estima seed at 20 cm spacing) and six in Expt 5 (all Maris Piper, small seed at 20 cm, two medium seed each at 20 and 60 cm, and one large seed at 60 cm). On average, *c.* 2 more sympodial branch leaves

were produced by large than small seed ($P < 0.001$) and Maris Piper produced 6.1 more leaves on the sympodial branch than Estima in Expt 4 ($P < 0.001$, Figure 119b).

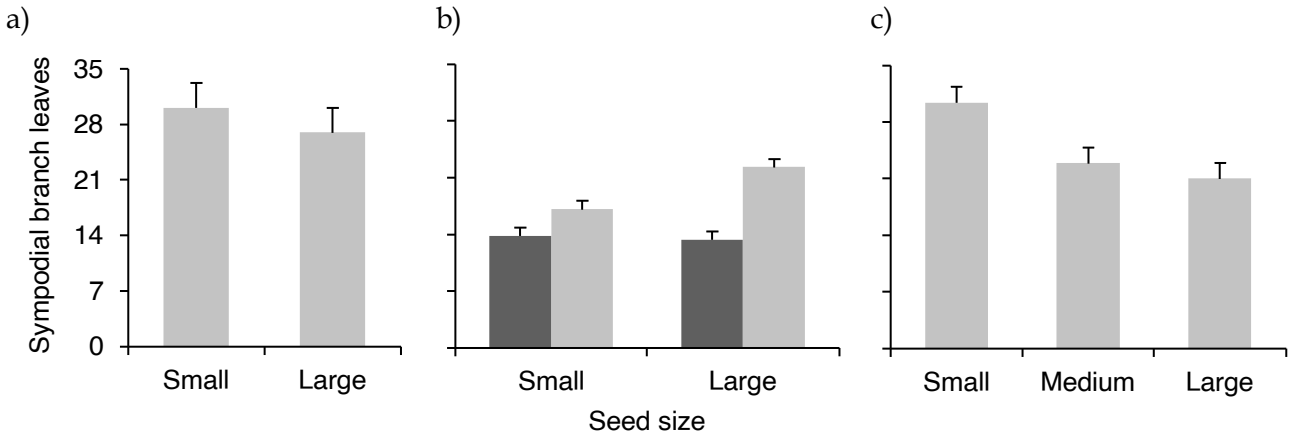

Figure 119. Effect of seed size on mean number of sympodial branch leaves in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ■; Maris Piper, ■. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F. Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (c).

At wider spacing, sympodial branches tended to produce more leaves than those at closer spacing (Figure 120), although in Expt 4 there was no difference in SBLeaves between seed spacing treatments (Figure 120b). The differences were also not significant in Expt 2, but 10.8 more SBLeaves were produced at 60 than 20 cm spacing (Figure 120a), whilst in Expt 5, the 60 cm spacing produced 2.2 more leaves than the 40 cm spacing, which produced 5.4 more leaves than the 20 cm spacing ($P = 0.022$, Figure 120c).

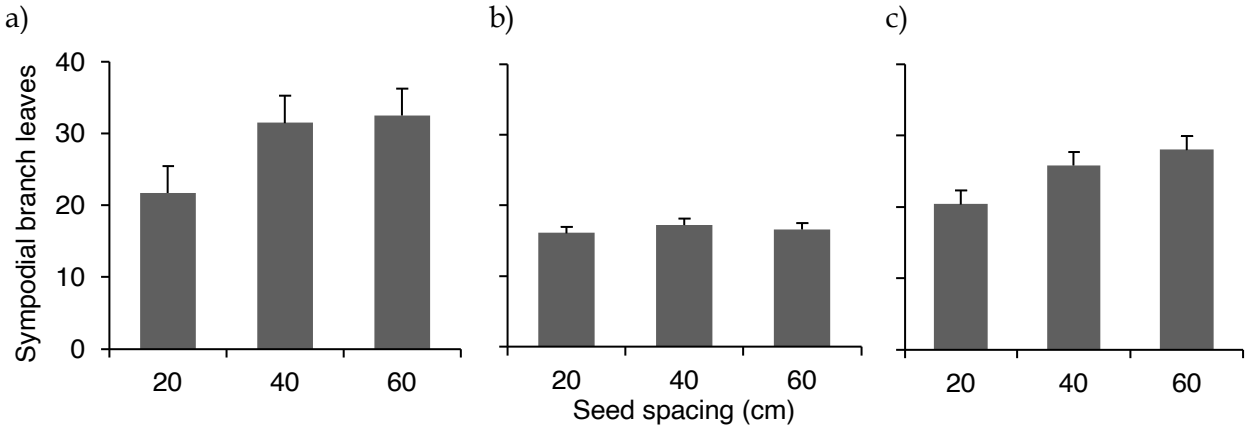

Figure 120. Effect of seed spacing on mean number of axillary branch leaves in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) 28 D.F. (b) 94 D.F. and (c) 70 D.F. Data presented are means of seed spacing treatments. Data from Maris Piper only in (a) & (c).

In Expts 2 and 5 the number of leaves per sympodial branch tended to decrease with increasing stem density (Figure 121a & c) but in Expt 4 there was a slight increase in SBLeaves with increasing stem density in Expt 4 (Figure 121b). The number of sympodial branch leaves was highly variable and just 23.2 % of the variation in

SBLeaves was explained by stem density and experiment (multiple linear regression; SBLeaves ~ stem density * year + block, *P* 0.003, Table 72) and there was no significant relationship in Estima. Figure 56 suggests that stem density was a very poor predictor of SBLeaves, particularly given the contrary slopes between Expts 2 and 5, and Expt 4.

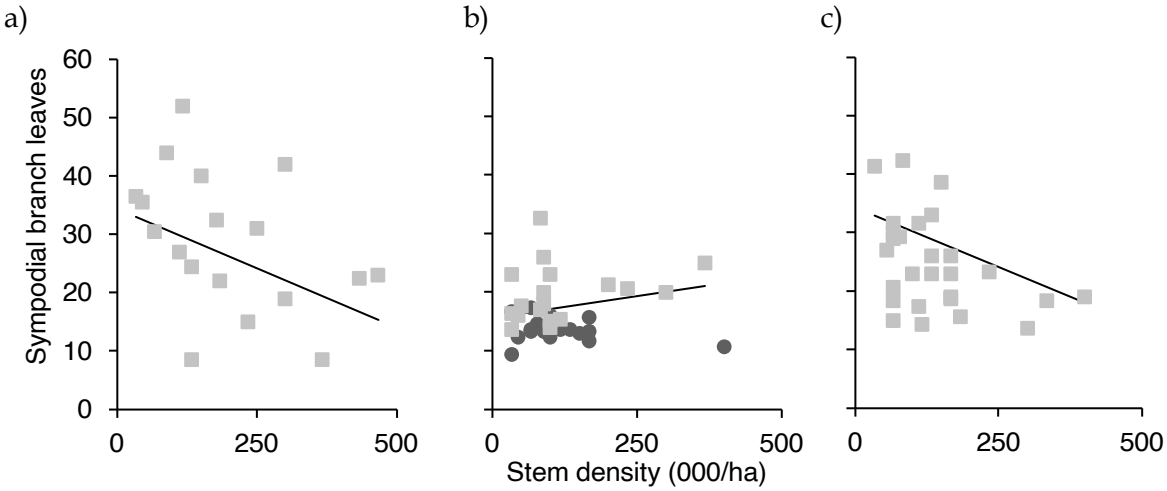

Figure 121. Relationship between number of sympodial branch leaves (SBLeaves) and stem density (S) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. For Maris Piper, R^2 = 0.232. See Table 72 for details of multiple linear regression. The relationship was non-significant in Estima (b).

Table 72. Relationship between number of sympodial branch leaves (SBLeaves) and stem density (S), and experiment (Expts 2, 4 or 5) in Maris Piper (Expt 4 Estima data not included). SBLeaves = β0 + β1*S + β2*Expt 4 + β3*Expt 5 + β4*(S*Expt 4) + β5*(S*Expt 5).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	34.3	3.81	< 0.001
1	S	-0.041	0.0151	0.009
2	Expt 4	-18.7	4.74	< 0.001
3	Expt 5	-6.5	4.61	0.166
4	S * Expt 4	0.055	0.0257	0.035
5	S * Expt 5	0.002	0.0233	0.947

5.3.6.5 Key points: Branch production

- There were more axillary branches per stem at lower stem densities (i.e. from small seed and at wide seed spacing).
- Mean number of leaves per axillary branch was typically greater at lower stem densities (i.e. from small seed and at wide seed spacing), although this relationship was only significant in Expt 5.
- Stem density had a limited effect on total stem length, but mainstem length was significantly greater at higher stem densities in both cultivars.
- Number of sympodial branch leaves may decrease with increasing stem density, but the relationship was weak and varied between experiments.

5.3.7 Tubers

Tubers were graded, weighed and dried at the mid-season and final harvests. Data from the final harvest only is shown here as tuber yield was not the primary focus of the experiments. Data from mid-season harvests are shown in Appendix 25 and the effects of all treatments, and interactions, on final tuber harvest are reported in Appendix 26, whilst the relationship between stem density and tuber variables are reported in Appendix 27.

5.3.7.1 Number of tubers

In Expts 2 and 5 Maris Piper produced 371 000 and 334 000 tubers/ha more than Estima respectively (both $P < 0.001$). In Expt 2 the difference between cultivars in number of tubers was greatest at 20 cm spacing (573 000 tubers/ha) and smallest at the widest spacing (246 000 tubers/ha) and the range in number of tubers produced between spacing treatments was greater in Maris Piper than Estima (472 000 and 145 000 tubers/ha, respectively, $P = 0.001$). Similarly, in Expt 5 there was a greater range in number of tubers produced by Maris Piper than by Estima between seed sizes (415 000 and 203 000 tubers/ha, respectively), with the greatest difference between cultivars found in large seed ($P = 0.007$). There was no difference in tuber number between the cultivars in Expt 4 (Table 73), potentially linked to the negligible differences between number of stems produced by each cultivar (Figure 63b).

Table 73. Number of tubers (000/ha) at final harvest by cultivar in Expt 2, Expt 4 and Expt 5. Data presented are a mean of seed size and seed spacing treatments.

	Cultivar			
Expt	Estima	Maris Piper	S.E.	D.F.
2	387	758	24.0	22
4	434	467	14.9	22
5	507	841	18.1	34

The number of tubers produced was greatest in the 20 cm spacing in each experiment ($P < 0.001$) and was on average 235 000 tubers/ha greater than at the 40 cm spacing. The difference between the 40 and 60 cm spacings was smaller; an average of 80 000 tubers/ha (Table 74). In Expt 4, large seed produced more tubers than small, but the difference between seed sizes diminished from 345 000 to 140 000 tubers/ha between 20 and 60 cm spacing ($P = 0.003$). There was no significant interaction between seed size and spacing in tuber number in either Expts 2 or 5. However, the combined effect of seed size and seed spacing in each experiment was illustrated by the effect of stem density in Appendix 27.

Table 74. Number of tubers (000/ha) at final harvest at different seed spacing in Expt 2, Expt 4 and Expt 5. Data presented are a mean of cultivar and seed size treatments.

	Seed spacing (cm)				
Expt	20	40	60	S.E.	D.F.
2	763	502	454	29.4	22
4	636	389	326	18.3	22
5	848	651	523	22.2	34

Large seed was associated with a greater number of tubers per hectare than small seed in each experiment ($P < 0.001$, Table 75).

Table 75. Number of tubers (000/ha) at final harvest at different seed sizes in Expt 2, Expt 4 and Expt 5.

	Seed size				
Expt	Small	Medium	Large	S.E.	D.F.
2	481	n/a	664	24.0	22
4	330	n/a	571	14.9	22
5	522	669	831	22.2	34

5.3.7.2 Fresh tuber yield

The effect of cultivar on fresh tuber yield varied between experiments. There was no effect of cultivar on fresh weight yield in Expt 2, but in Expt 4 the yield of Estima was 17.8 t/ha greater than that of Maris Piper ($P < 0.001$) whilst in Expt 5 the Maris Piper fresh yield exceeded that of Estima by 9.8 t/ha ($P < 0.001$, Table 76).

Table 76. Final harvest fresh weight tuber yield (t/ha) at final harvest by cultivar in Expt 2, Expt 4 and Expt 5. Data presented are a mean of seed size and seed spacing treatments.

	Cultivar			
Expt	Estima	Maris Piper	S.E.	D.F.
2	73.0	76.0	2.13	22
4	72.8	55.0	1.52	22
5	54.3	64.1	0.98	34

Fresh weight yield was greater at 20 than 60 cm spacing in each experiment, though the difference was not significant in Expt 2. There was an 8.5 and 9.4 t/ha difference in yield between the 20 and 60 cm spacings in Expts 4 and 5, respectively ($P = 0.009$ and $P < 0.001$, respectively, Table 77).

Table 77. Final harvest fresh weight tuber yield (t/ha) at final harvest at different seed spacing in Expt 2, Expt 4 and Expt 5. Data presented are a mean of cultivar and seed size treatments.

	Seed spacing (cm)				
Expt	20	40	60	S.E.	D.F.
2	78.7	75.0	69.8	2.61	22
4	69.1	62.1	60.6	1.86	22
5	64.7	57.6	55.3	1.20	34

On average fresh weight yield of large seed was 11.4 t/ha greater than the yield of small seed (10.3, 12.6 and 11.1 t/ha in Expts 2, 4 and 5, $P = 0.002$, $P < 0.001$ and $P < 0.001$, respectively, Table 78). Fresh weight yield also increased with increasing stem density (Appendix 27).

Table 78. Final harvest fresh weight tuber yield (t/ha) at different seed sizes in Expt 2, Expt 4 and Expt 5. Data presented are a mean of cultivar and seed spacing treatments.

	Seed size				
Expt	Small	Medium	Large	S.E.	D.F.
2	69.2	n/a	79.8	2.13	22
4	57.6	n/a	70.2	1.52	22
5	54.0	58.5	65.1	1.20	34

5.3.7.3 Tuber percent dry matter

Percent dry matter (% DM) was greater in Maris Piper tubers than Estima tubers in Expts 2, 4 and 5 with an absolute difference of 4.15, 3.40 and 3.82 % DM, respectively ($P < 0.001$, Table 79). Whilst there was no overall effect of seed size on tuber dry matter in any experiment, in Expt 4 tubers grown from large Estima seed had a numerically greater percent dry matter than tubers grown from small seed (21.20 and 20.69 % DM, respectively) whilst the opposite was true in Maris Piper with a higher tuber percent dry matter in small seed than large seed (24.77 and 23.92 % DM, respectively, P 0.020), this interaction was not present in either Expts 2 or 5. In Expt 2, tuber percent dry matter was greater at closer spacing, although the absolute difference between % DM at the 20 and 60 cm spacings was modest (1.35 % DM, $P = 0.008$). There was no effect of seed spacing on tuber percent dry matter in Expts 4 or 5. There was a slight increase in % DM with increasing stem density (Appendix 27).

Table 79. Tuber percent dry matter (% DM) at final harvest in Expt 2, Expt 4 and Expt 5. Data presented are a mean of seed size and seed spacing treatments.

	Cultivar			
Expt	Estima	Maris Piper	S.E.	D.F.
2	20.0	24.2	0.23	22
4	21.0	24.4	0.19	22
5	20.2	24.0	0.14	34

Tuber dry weight yield (DWyield) increased with increasing IGC and the degree of increase was the same in both Estima and Maris Piper, though mean DWyield varied between experiments (Figure 122). Integrated ground cover explained 59.2 % of the variation in DWyield, once differences between cultivars and experiments were accounted for (multiple linear regression; DWyield ~ IGC + cultivar + year + block, $P < 0.001$, Table 80). Dry weight yield was greater in Estima than Maris Piper at the same IGC, clearly illustrated in Figure 122b, reflecting the greater partitioning of dry matter to tubers than haulm in Estima relative to partitioning in Maris Piper. IGC alone is a limited predictor of DWyield, explaining 37.7 % of the variation in DWyield (multiple linear regression; DWyield ~ IGC + block, $P < 0.001$), hence cultivar or, perhaps, determinacy level, is necessary to predict the 'conversion rate' of canopy ground cover to yield due to variation in partitioning of biomass between cultivars of different determinacy.

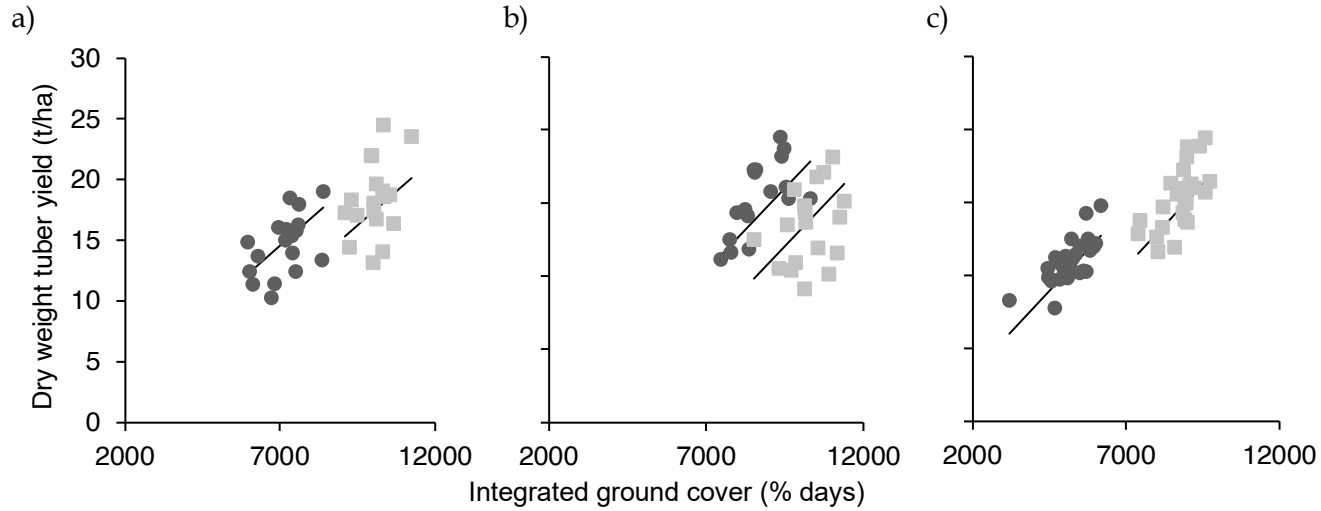

Figure 122. Relationship between integrated ground cover (IGC) and dry weight tuber yield (DWyield), (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. $R^2 = 0.592$. See Table 80 for details of multiple linear regression.

Table 80. Relationship between integrated ground cover (IGC), dry weight tuber yield (DWyield), cultivar (MP) and experiment (Expts 2, 4 or 5). DWyield = β0 + β1*IGC + β2*MP + β3*Expt 4 + β4*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	-1.2	1.80	0.517
1	IGC	0.002249	0.000241	< 0.001
2	MP	-3.95	0.777	< 0.001
3	Expt 4	-4.18	0.536	< 0.001
4	Expt 5	0.29	0.595	0.622

5.3.7.4 Key points: Tubers

- Maris Piper produced a greater number of tubers than Estima.
- Tuber number increased with increasing stem density (Appendix 27) and was greater at closer seed spacing and with larger seed.
- Effect of cultivar on fresh weight yield varied between experiments.
- Fresh weight yield was greater at higher stem densities (Appendix 27) and was higher at closer seed spacing and with larger seed.
- Tuber percent dry matter was greater in Maris Piper than Estima.
- Tuber dry weight yield increased with increasing IGC, but the intercept varied with cultivar.

5.3.8 Seed Size experiments (archival data)

Archival data from Seed Size experiments carried out by the research team at NIAB CUF between 2007 and 2016, are presented, illustrating canopy growth responses to varying seed sizes in a range of processing potato cultivars.

5.3.8.1 Stem density

Mean stem density, averaged over all seed size treatments, differed between cultivars and ranged from 69 700 to 241 000 stems/ha in *cv.* 9 and 18 respectively (Figure 123). The interquartile range (IQR) was 74 500 stems/ha, indicating a wide range in stem densities between cultivars at the same mean seed mass.

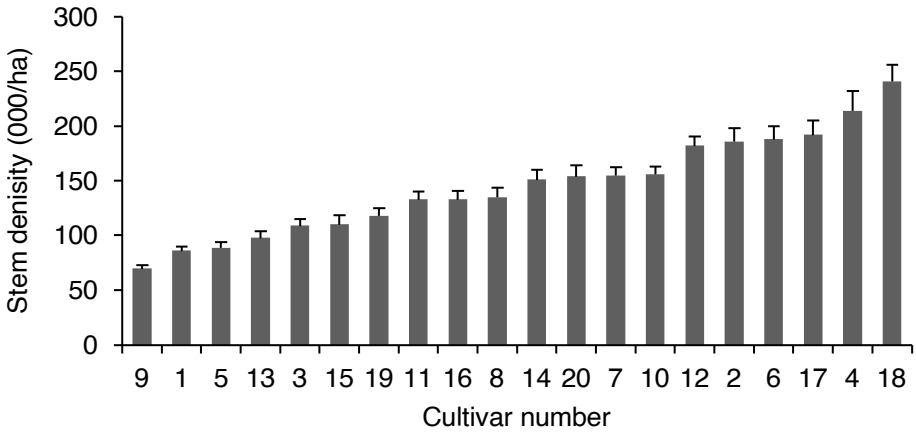

Figure 123. Mean stem density by cultivar, ranked from lowest to highest stem density. Bars represent S.E.

As expected, stem density increased as seed mass increased in all cultivars (Figure 124) although the gradient of the relationship differed between cultivars. The smallest response in stem density to increasing seed mass was found in *cv.* 9, with a gradient more than three times smaller than *cv.* 18, which showed the greatest increase (m = 0.81 and 2.47 respectively, Table 81). Small responses of stem density to seed mass were also found in *cv.* 1, 5 and 13 (m < 1.00). Greater sensitivity to seed mass was found in *cv.* 12, 17 and 20 (m > 2.00). Whilst there were differences in the gradient of the relationship between specific pairs of cultivars, there was, however, a high degree of overlap between the intermediate cultivars and few were significantly distinct from each other as indicated by the group analysis (Table 81). Seed mass, cultivar and their interaction explained 85.1 % of the variation in stem density (multiple linear regression; stem density ~ seed mass * cultivar, $P < 0.001$).

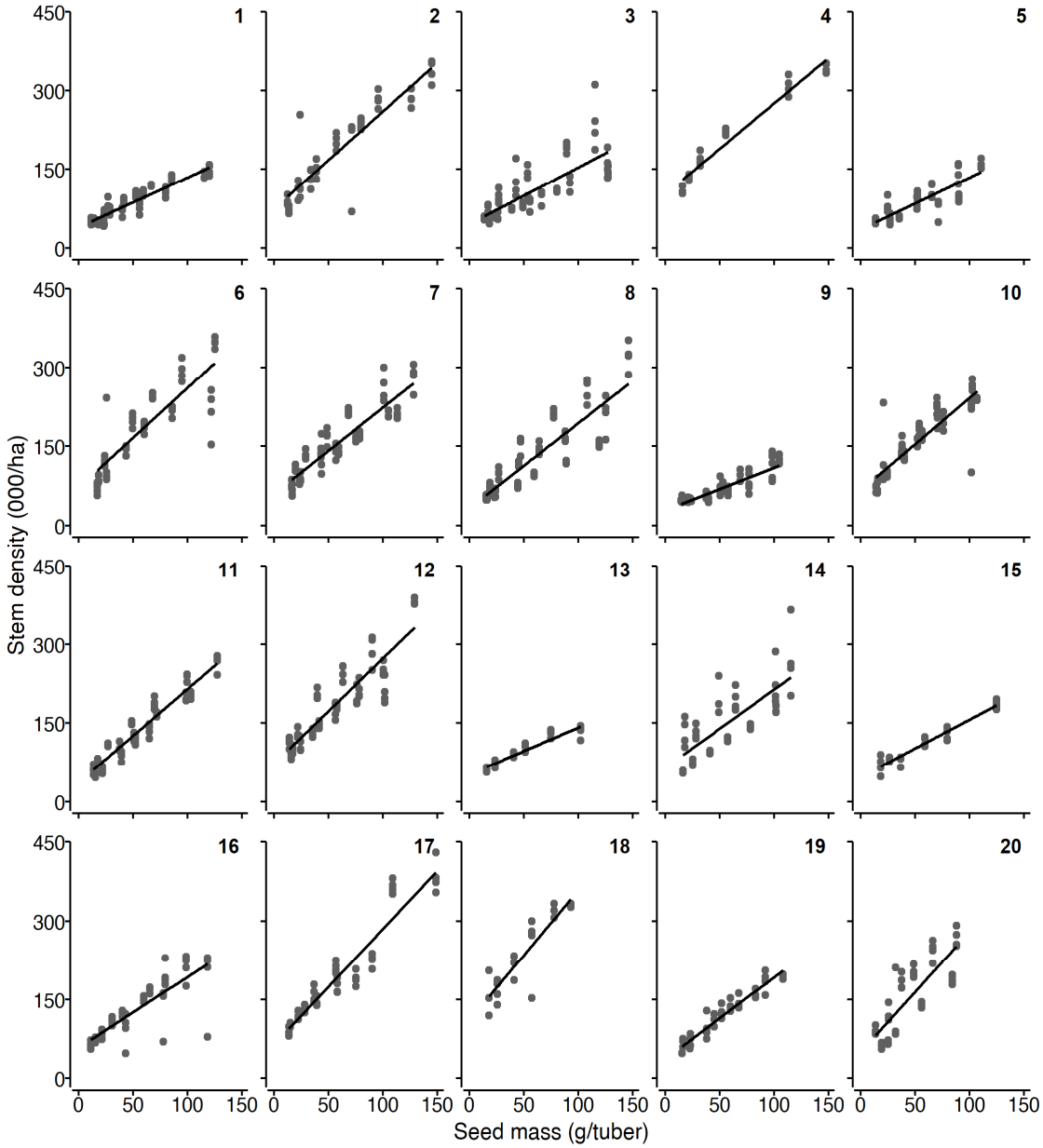

Figure 124. Relationship between seed mass (SM) and stem density (S) in 20 cultivars (C) from seed size experiments. Multiple linear regression; S ~ SM * C, R^2 = 0.851. Equations for each cultivar shown in Table 81.

Table 81. Relationship between stem density (S) and seed mass (SM) in 20 cultivars. Number of years of data varied between cultivars, see Methods (Table 41). Slopes of cultivars which did not differ significantly are grouped together, indicated by shared letters. Slopes which did not differ significantly from 0 were excluded from group analysis. S = m * SM + c.

Cultivar	m	S.E.	c	S.E.	Group
1	0.95	0.105	39.4	6.21	ab
2	1.85	0.144	75.0	9.52	efgh
3	1.08	0.140	45.8	8.93	ab
4	1.73	0.159	102	11.5	cdefgh
5	0.99	0.172	35	10.4	ab
6	1.89	0.154	71	10.2	efgh
7	1.64	0.144	59.7	9.13	cdefg
8	1.61	0.135	33.0	8.86	cdefg
9	0.81	0.156	28.5	9.20	a
10	1.76	0.154	66.4	9.09	cdefgh
11	1.78	0.146	36.3	8.96	defgh
12	2.01	0.146	72.4	8.98	fgh
13	0.90	0.225	52	13.3	abc
14	1.50	0.164	64	10.5	bcdef
15	1.10	0.193	47	12.6	abcd
16	1.36	0.166	58	10.3	abcde
17	2.20	0.149	64.7	9.63	h
18	2.47	0.244	112	14.3	gh
19	1.57	0.175	36	10.4	bcdefgh
20	2.29	0.207	51	11.0	fgh

5.3.8.2 Integrated ground cover

Integrated ground cover (IGC) varied with cultivar and was smallest in cultivar 18 and greatest in cultivar 3 (5205 and 10 204 % days respectively, Figure 125). The IGC of *cv.* 3 and 18 represent extremes and the range decreased from 4999 to 2353 % days when they were excluded (equivalent to 50 and 24 days at 100 % GC). IQR was 1092 % days, indicating limited variation within the middle-ranked cultivars.

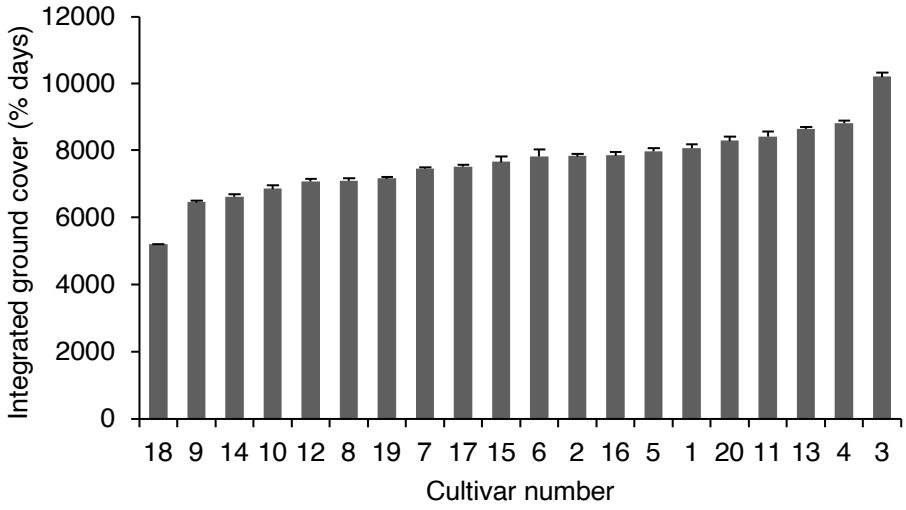

Figure 125. Mean integrated ground cover (IGC) by cultivar, ranked from lowest to highest IGC. Bars represent S.E.

Stem density alone had no significant effect on IGC, though the interaction between cultivar and stem density explained 64.5 % of the variation in IGC ($P < 0.001$, Figure 126). Accounting for variation in IGC between years in the multiple linear regression increased total variation explained to 76.4 % (IGC ~ stem density * cultivar + year, $P < 0.001$), indicating that IGC was sensitive to differences in environmental conditions between years. The relationship between stem density and IGC was significant in eleven of the cultivars in the seed size experiments but differed between cultivars (Table 82). In *cv.* 3, 11, 15 and 20, IGC showed negative correlations, of a similar order of magnitude, with stem density; m ranged from -3.5 to -11.6. In *cv.* 7, 9, 10, 12, 14, 16 and 17, IGC increased as stem density increased, with the strongest responses in *cv.* 9, 14, and 16 (Table 82).

Table 82. Relationship between integrated ground cover (IGC) and stem density (S) in 20 cultivars. Number of years of data varied between cultivars, see Methods (Table 41). Slopes of cultivars which did not differ significantly are grouped together, indicated by shared letters. Slopes which did not differ significantly from 0 were excluded from group analysis. IGC = m * S + c.

Cultivar	m	S.E.	c	S.E.	Group
1	0.9	2.71	7990	250	-
2	-1.7	2.99	8140	360	-
3	-5.1	3.21	10 770	325	ab
4	2.2	3.23	8350	478	-
5	-4.6	4.05	8390	382	-
6	-1.4	3.01	8090	368	-
7	3.1	3.06	6990	346	bcd
8	-0.3	2.96	7140	310	-
9	13.2	4.26	5540	350	d
10	3.5	3.08	6310	350	cd
11	-3.5	3.06	8890	326	abc
12	3.7	2.96	6410	342	d
13	0.1	6.09	8630	609	-
14	8.8	3.18	5290	372	d
15	-11.6	4.60	8940	503	ab
16	7.7	3.37	6830	381	d
17	4.9	2.95	6580	354	d
18	2.5	3.43	4600	586	-
19	3.1	3.52	6800	379	-
20	-6.9	3.17	9450	374	a

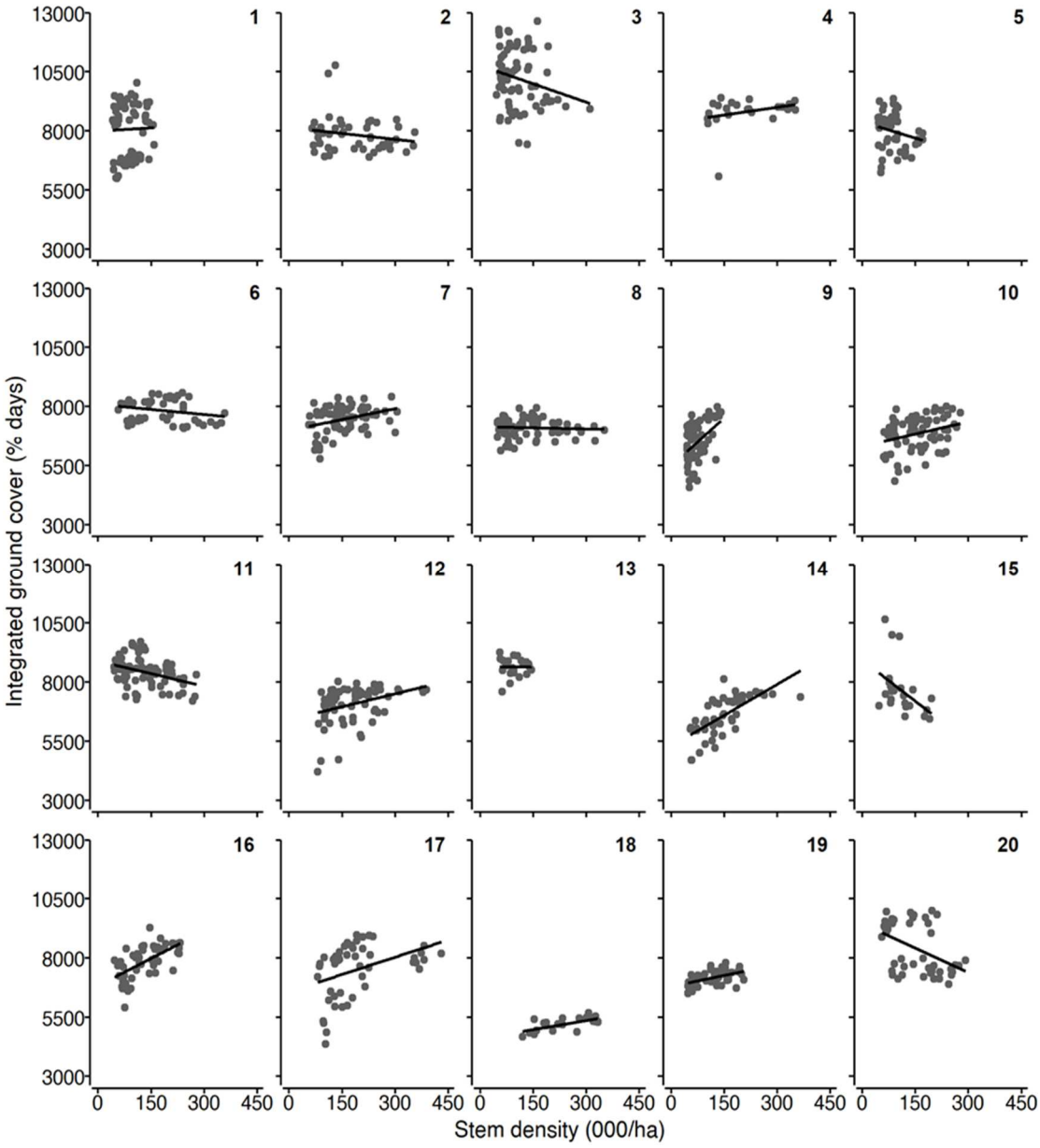

Figure 126. Relationship between stem density (S) and integrated ground cover (IGC) in 20 cultivars (C) from seed size experiments. Multiple linear regression; IGC ~ S * C, R^2 = 0. 645. Equations for each cultivar shown in Table 82.

5.3.8.3 Early canopy expansion

Duration of early canopy expansion (TiE25) varied with cultivar, with a range of 8.4 days between the shortest and longest mean TiE25 in *cv.* 18 and 4 respectively (Figure 127). When cultivars were ranked from shortest to longest TiE25, as in Figure 127, there was limited variation in TiE25 of the middle-ranked cultivars (*cv.* 13-17) as shown by the small IQR (1.85 days).

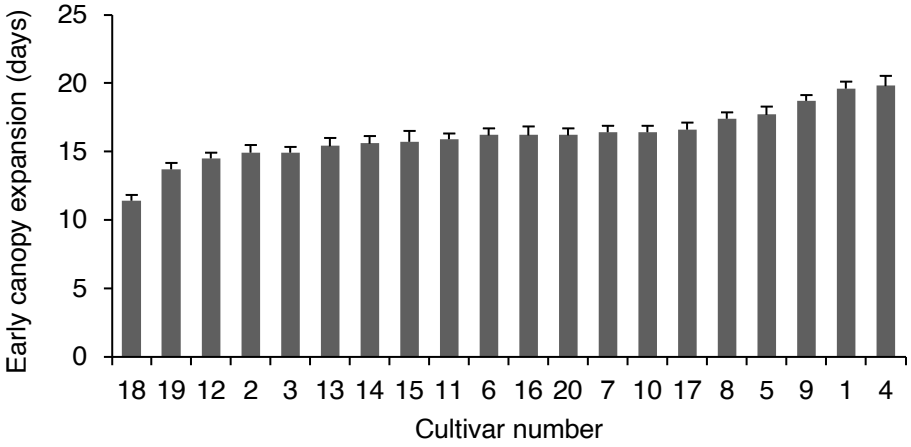

Figure 127. Mean rate of early expansion (TiE25) by cultivar, ranked from lowest to highest TiE25. Bars represent S.E.

Multiple linear regression showed that TiE25 decreased with increasing stem density across all 20 cultivars and together stem density, cultivar and their interaction explained 48.4 % of the variation in TiE25 ($P < 0.001$, Figure 128). Accounting for variation between year of experiment (multiple linear regression; TiE25 ~ stem density * cultivar + year) increased the proportion of variation explained to 53.0 % ($P < 0.001$). The relationship between stem density and TiE25 was similar across all 20 cultivars and the gradient (m) ranged from -0.020 and -0.070, excluding *cv.* 1 and 20 which respectively exhibited the greatest (m = -0.093) and the smallest (m = -0.017) reductions in TiE25 in response to increasing stem density.

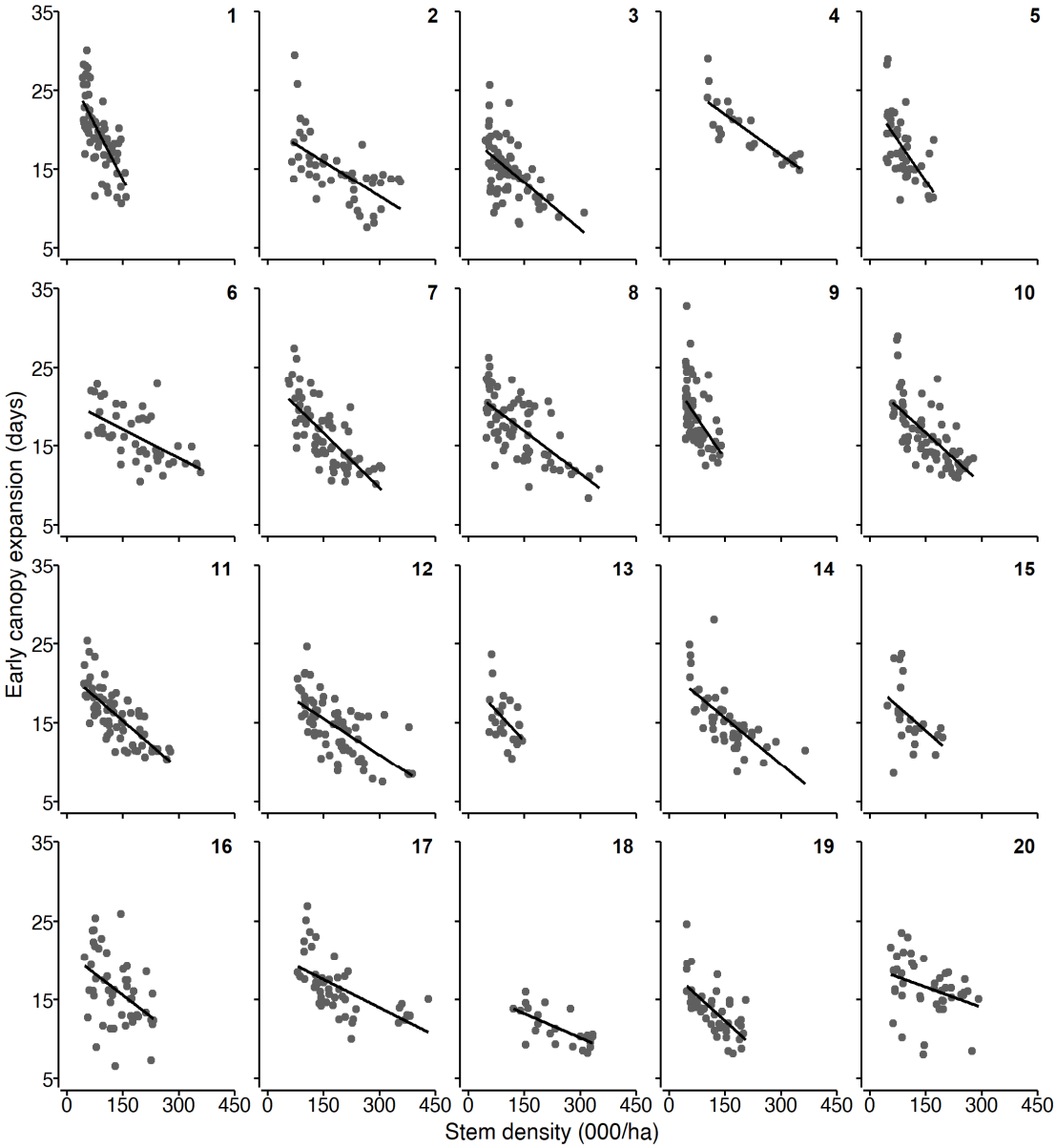

Figure 128. Relationship between stem density (S) and early canopy expansion rate (TiE25) in 20 cultivars from seed size experiments. Multiple linear regression; TiE25 ~ S * C, R^2 = 0.484. Equations for each cultivar shown in Table 83.

Table 83. Relationship between early canopy expansion duration (TiE25) and stem density (S) in 20 cultivars. Number of years of data varied between cultivars, see Methods (Table 41). Slopes of cultivars which did not differ significantly are grouped together, indicated by shared letters. Slopes which did not differ significantly from 0 were excluded from group analysis. TiE25 = m * S + c.

Cultivar	m	S.E.	c	S.E.	Group
1	-0.093	0.0107	27.61	0.984	a
2	-0.030	0.0118	20.4	1.42	bc
3	-0.040	0.0127	19.2	1.28	bc
4	-0.034	0.0127	27.1	1.88	bc
5	-0.069	0.0160	23.9	1.50	ab
6	-0.024	0.0119	20.7	1.45	bc
7	-0.046	0.0121	23.6	1.36	bc
8	-0.036	0.0117	22.2	1.22	bc
9	-0.070	0.0168	23.8	1.39	abc
10	-0.043	0.0121	23.2	1.38	bc
11	-0.041	0.0121	21.4	1.28	bc
12	-0.031	0.0117	20.1	1.35	bc
13	-0.051	0.0240	20.4	2.40	abc
14	-0.039	0.0125	21.5	1.47	bc
15	-0.041	0.0182	20.2	1.98	abc
16	-0.036	0.0133	21.0	1.50	bc
17	-0.024	0.0117	21.2	1.40	bc
18	-0.020	0.0135	16.3	2.31	bc
19	-0.043	0.0139	18.8	1.50	abc
20	-0.017	0.0125	19.2	1.48	c

5.3.8.4 Mid-season canopy expansion

Mid-canopy expansion rate varied with cultivar and was fastest in *cv.* 2 and slowest in *cv.* 4 (6.25 and 2.24 %/day, respectively, Figure 129). IQR was relatively small (1.09 %/day), although the range in GCRate2575 between centrally-ranked cultivars appeared to be greater than in TiE25 (Figure 127).

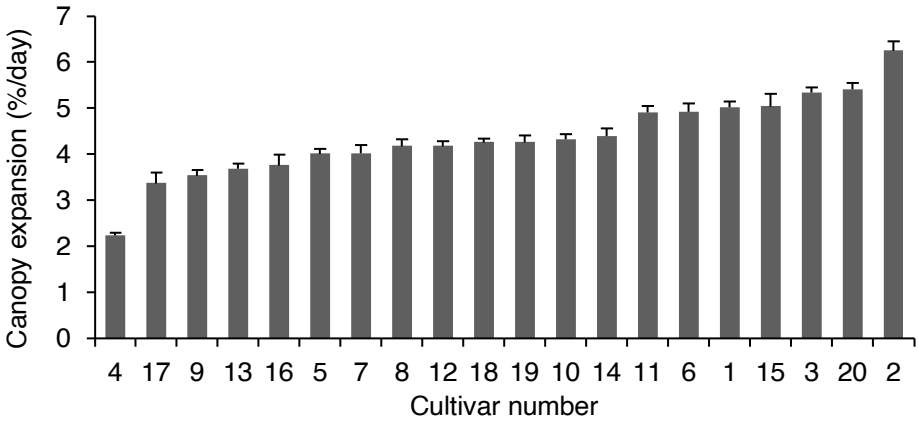

Figure 129. Mean rate of mid-canopy expansion (GCRate2575) by cultivar, ranked from slowest to fastest GCRate2575. Bars represent S.E.

In general, GCRate2575 tended to increase as stem density increased, however this was not the case across all cultivars and GCRate2575 did not vary with stem density in *cv.* 3, 4, 9, 10, 13, 17 and 18 (Figure 130). GCRate2575 increased at a faster rate in

response to increasing stem density in *cv.* 15 than *cv.* 2, 6 and 12 (Table 84), but the gradient of the relationship did not differ significantly between the other cultivars measured (Figure 130). Multiple linear regression showed that stem density, cultivar and their interaction explained 44.1 % of the variation in canopy expansion rate ($P < 0.001$). Accounting for variation between year of experiment (GCRate2575 ~ stem density * cultivar + year, $P < 0.001$) increased total variation explained to 72.9 %, indicating that the relationship between stem density and GCRate2575 varied with the different environmental conditions (including soil, temperature, radiation) between years.

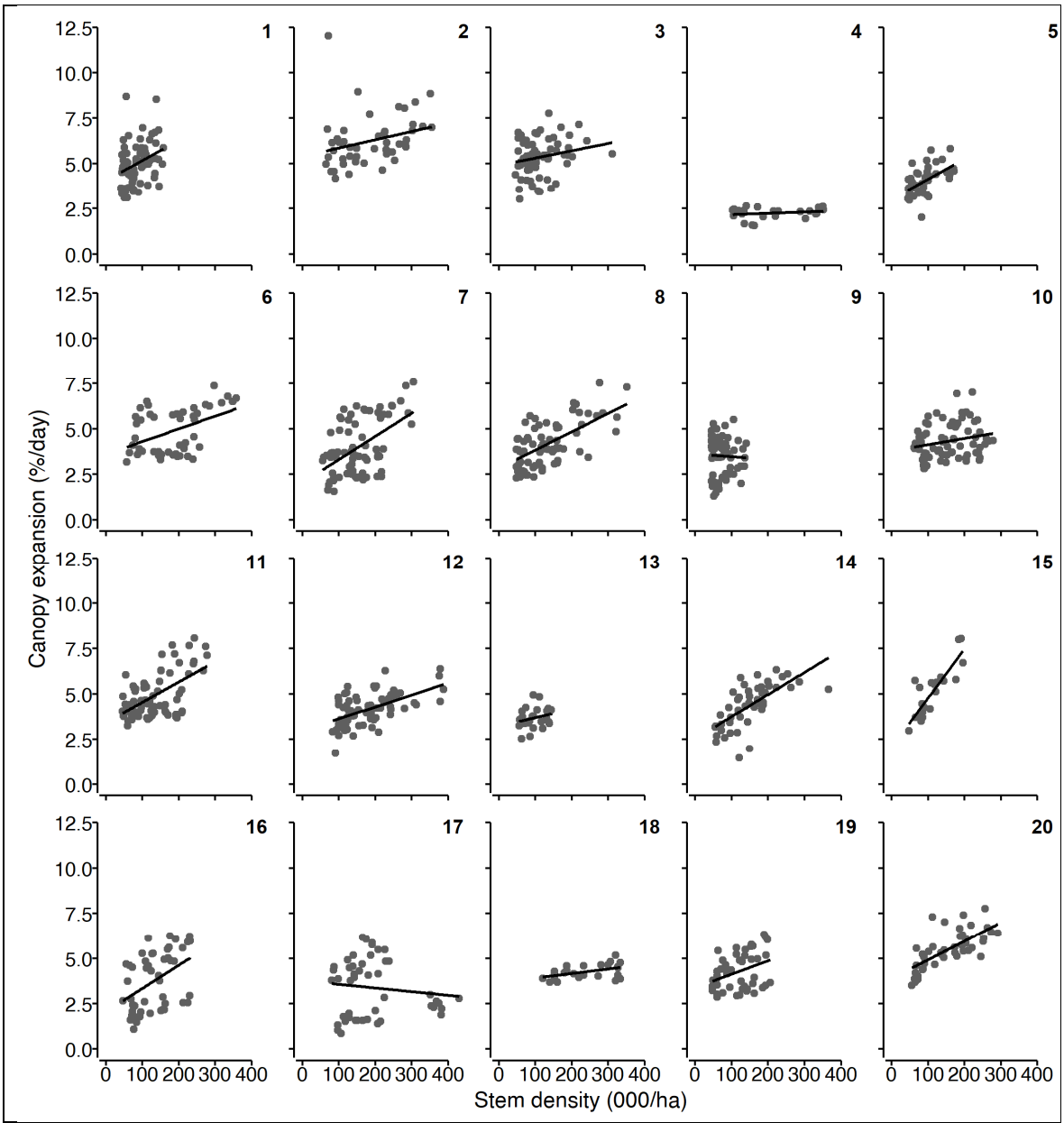

Figure 130. Relationship between stem density (S) and mid-canopy expansion rate (GCRate2575) in 20 cultivars (C) from seed size experiments. Multiple linear regression; GCRate2575 ~ S * C, $R^2 = 0.441$. Equations for each cultivar shown in Table 84.

Table 84. Relationship between mid-canopy expansion (GCRate2575) and stem density (S) in 20 cultivars. Number of years of data varied between cultivars, see Methods (Table 41). Slopes of cultivars which did not differ significantly are grouped together, indicated by shared letters. Slopes which did not differ significantly from 0 were excluded from group analysis. GCRate2575 = m * S + c.

Cultivar	m	S.E.	c	S.E.	Group
1	0.0111	0.00371	4.06	0.342	ab
2	0.0046	0.00173	5.40	0.493	a
3	0.0040	0.00235	4.90	0.445	-
4	0.0007	0.00241	2.08	0.654	-
5	0.0112	0.00413	3.02	0.522	ab
6	0.0070	0.00181	3.60	0.504	a
7	0.0128	0.00197	2.03	0.474	ab
8	0.0101	0.00163	2.82	0.424	ab
9	-0.0023	0.00450	3.70	0.480	-
10	0.0035	0.00201	3.78	0.479	-
11	0.0112	0.00194	3.42	0.446	ab
12	0.0066	0.00165	2.98	0.473	a
13	0.0047	0.00746	3.22	0.834	-
14	0.0122	0.00229	2.55	0.509	ab
15	0.0270	0.00510	2.08	0.689	b
16	0.0128	0.00275	2.05	0.523	ab
17	-0.0020	0.00164	3.77	0.490	-
18	0.0025	0.00289	3.67	0.803	-
19	0.0074	0.00308	3.39	0.520	ab
20	0.0104	0.00227	3.89	0.512	ab

5.3.8.5 Duration of near-complete canopy cover

Duration of near-complete canopy cover (GCDur90) varied with cultivar and was shortest in *cv.* 18 (37.7 days) and longest in *cv.* 3 (82.8 days, Figure 131). Values of GCDur90 measured in the Seed Size experiments were in some cases lower than 'true' GCDur90 for each cultivar, as in a small number of cases (< 5 %), cultivars were harvested before every plot had senesced past 90 % GC, truncating canopy longevity. Truncated GCDur90 typically only occurred in a small number of plots in each cultivar, though in one year (2014) most plots of *cv.* 3 were harvested at 100 % GC. The range of GCDur90 was reduced from 45.1 to 21.2 days when the two extreme cultivars (3 and 18) were excluded and the IQR was even smaller (8.4 days), highlighting lower variability in GCDur90 of the central cultivars when ranked shortest to longest GCDur90 (Figure 131).

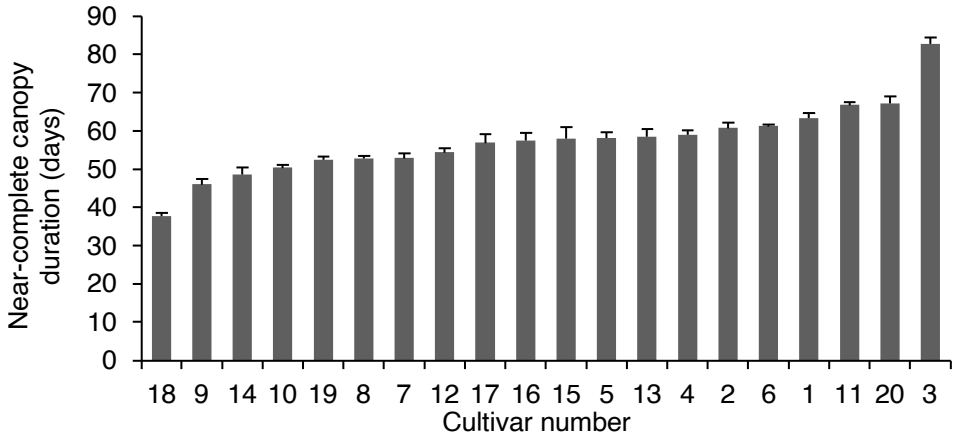

Figure 131. Mean near-complete canopy duration (GCDur90) by cultivar, ranked from shortest to longest GCDur90. Bars represent S.E.

The relationship between GCDur90 and stem density varied between cultivars and in over half of the cultivars increasing stem density had no significant effect on the duration of near-complete ground cover (Figure 132, Table 85). GCDur90 in *cv.* 14 and 16 exhibited a strong positive response to increasing stem density, whilst conversely GCDur90 in *cv.* 3 and 15 was shorter at higher stem densities. Across all the Seed Size experiments, 3.3 % of plots did not achieve 90 % GC. Failure to reach 90 % GC was more likely to occur at lower stem densities, but this varied between cultivars and year; *cv.* 9 and 17 were worst affected in years 2010 and 2015, respectively (Figure 132). Plots with no days of near-complete ground cover had the potential to heavily influence the relationship between stem density and GCDur90 and in *cv.* 17 the relationship changed from a positive to a negative slope when '0' values were removed. Stem density alone did not explain any variation in GCDur90 ($P = 0.405$), likely due to opposing responses of GCDur90 to stem density between cultivars, but in combination with cultivar it explained 46.6 % ($P < 0.001$, Figure 132), highlighting the strong influence of cultivar on GCDur90. When year of experiment was also accounted for (multiple linear regression; GCDur90 ~ stem density * cultivar + year) 64.8 % of the variation in GCDur90 was explained ($P < 0.001$), suggesting that GCDur90 was also sensitive to the environmental conditions which varied between years.

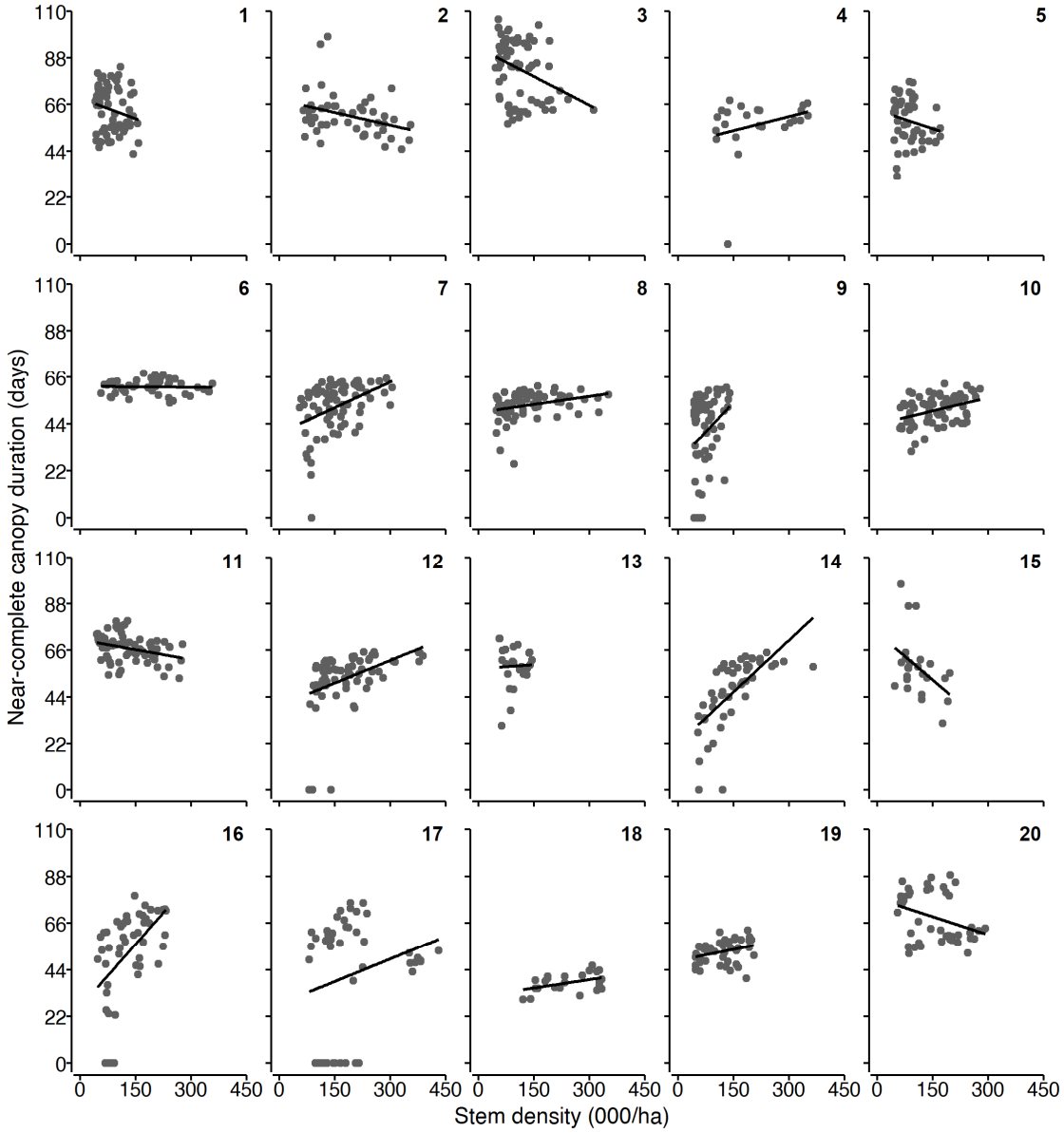

Figure 132. Relationship between stem density (S) and near-complete canopy duration (GCDur90) in 20 cultivars (C) from seed size experiments. Multiple linear regression; GCDur90 ~ S * C, R^2 = 0.466. Equations for each cultivar shown in Table 85.

Table 85. Relationship between near-complete canopy duration (GCDur90) and stem density (S) in 20 cultivars. Number of years of data varied between cultivars, see Methods (Table 41). Slopes of cultivars which did not differ significantly are grouped together, indicated by shared letters. Slopes which did not differ significantly from 0 were excluded from group analysis. GCDur90 = m * S + c.

Cultivar	m	S.E.	c	S.E.	Group
1	-0.064	0.0444	69.0	4.10	-
2	-0.040	0.0207	68.2	5.90	-
3	-0.090	0.0282	92.6	5.33	a
4	0.044	0.0289	47.1	7.83	-
5	-0.058	0.0494	63.3	6.26	-
6	-0.001	0.0217	61.6	6.04	-
7	0.080	0.0235	39.6	5.68	bc
8	0.025	0.0195	49.4	5.08	-
9	0.166	0.0540	28.6	5.75	abc
10	0.042	0.0240	43.8	5.74	-
11	-0.031	0.0233	71.0	5.34	-
12	0.071	0.0195	39.9	5.61	bc
13	0.012	0.0894	57.3	9.99	-
14	0.163	0.0274	21.9	6.10	c
15	-0.149	0.0611	74.3	8.25	ab
16	0.199	0.0329	26.3	6.25	c
17	0.071	0.0194	27.9	5.82	bc
18	0.027	0.0346	31.3	9.62	-
19	0.035	0.0369	48.3	6.22	-
20	-0.057	0.0272	77.6	6.14	ab

5.3.8.6 Duration of canopy growth

Duration of canopy growth, between emergence and start of senescence (GrowDur), varied between cultivars with a range of 46.1 days between the cultivars with the shortest (*cv.* 18; 65.9 days) and longest (*cv.* 4; 112.0 days) GrowDur (Figure 133). There was limited variation in GrowDur when the extremes were excluded, with a range of 16.3 days between the cultivars with the second shortest and third longest (*cv.* 14 to 11, Figure 133), similarly the IQR was relatively low (11.4 days). As with GCDur90, the duration of canopy growth was also truncated in some cultivars by early harvest and whilst this only occurred in 3.7 % of plots, some cultivars, such as *cv.* 3, were more affected than others. In all cases where the canopy did not senesce GrowDur was not calculated.

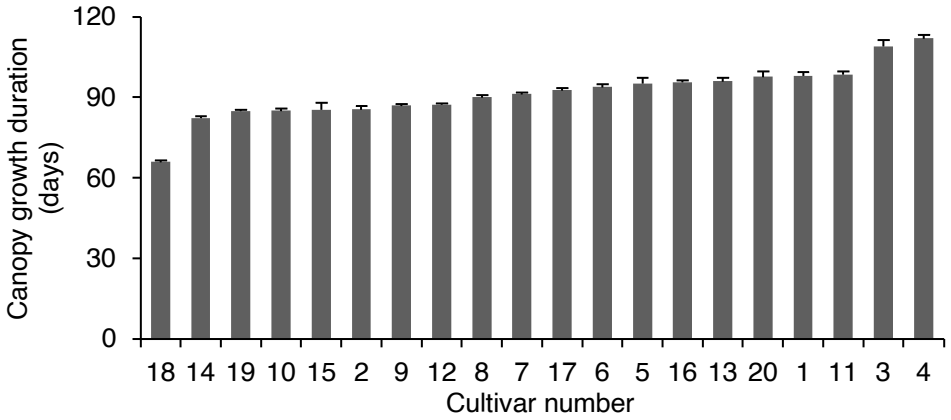

Figure 133. Mean duration of canopy growth (GrowDur) by cultivar, ranked from shortest to longest GrowDur. Bars represent S.E.

Stem density alone explained just 7 % of the variation in GrowDur ($P < 0.001$), but in combination with cultivar 56.1 % of the variation was explained ($P < 0.001$). Accounting for variation between years in the multiple linear regression (GrowDur ~ stem density * cultivar + year, $P < 0.001$) increased the proportion of variation explained to 73.0 %, indicating the relatively high variability of GrowDur between years. Stem density had a significant effect on GrowDur in half of the cultivars, with most cultivars showing a decrease in GrowDur as stem density increased (Figure 134). Duration of canopy growth decreased most in response to increasing stem density in *cv.* 1 and 15 (m = -0.181 and -0.223 respectively) and was five times more sensitive to stem density than the least responsive cultivar (*cv.* 7, m = -0.042), whilst *cv.* 14 showed a small, positive response of GrowDur to stem density (m = 0.036, Table 86).

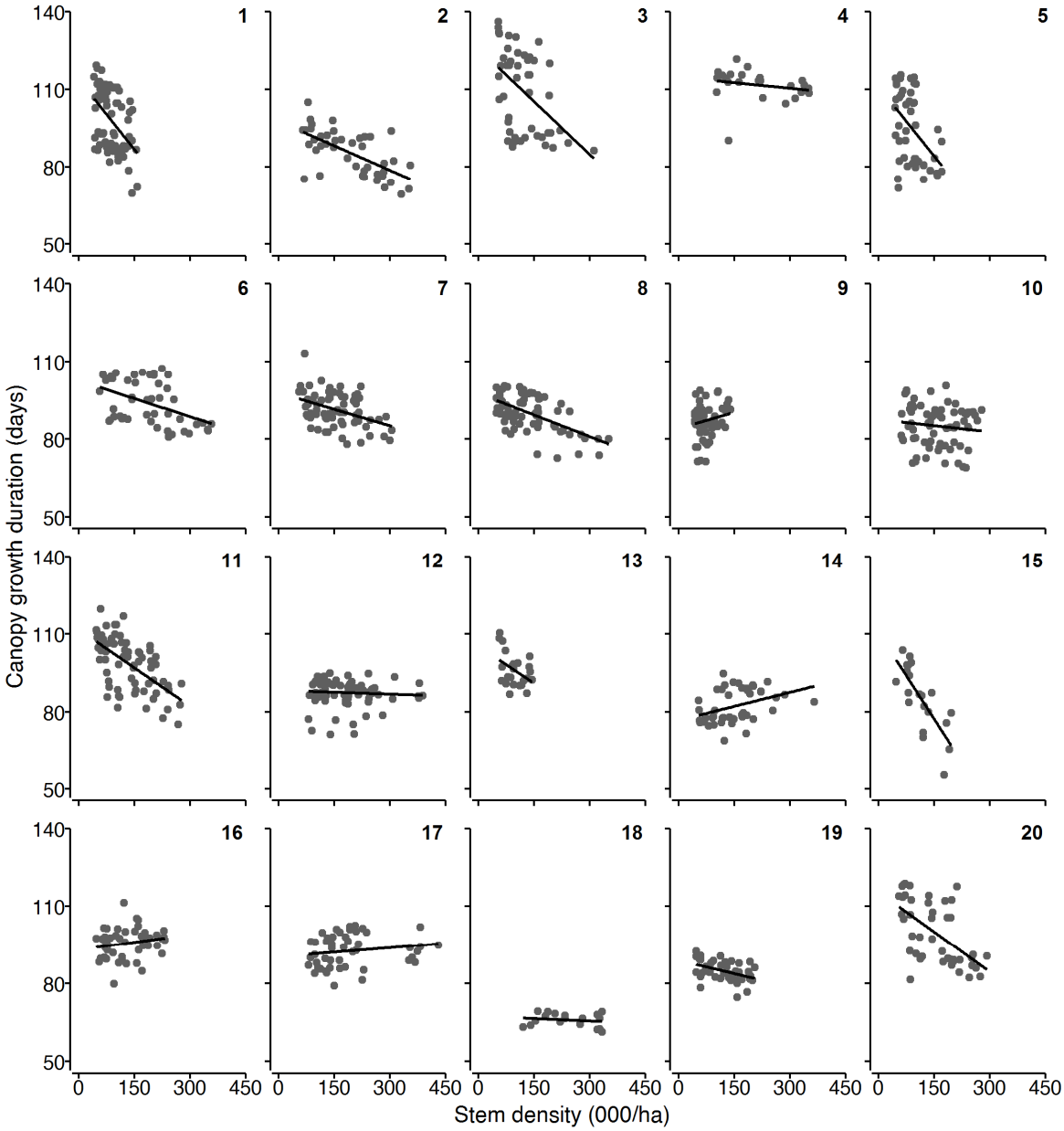

Figure 134. Relationship between stem density (S) and duration of canopy growth (GrowDur) in 20 cultivars (C) from seed size experiments. Multiple linear regression; GrowDur ~ S * C, R^2 = 0.561. Equations for each cultivar shown in Table 86.

Table 86. Relationship between duration of canopy growth (GrowDur) and stem density (S) in 20 cultivars. Number of years of data varied between cultivars, see Methods (Table 41). Slopes of cultivars which did not differ significantly are grouped together, indicated by shared letters. Slopes which did not differ significantly from 0 were excluded from group analysis. GrowDur = m * S + c.

Cultivar	m	S.E.	c	S.E.	Group
1	-0.181	0.0293	114.0	2.76	a
2	-0.063	0.0324	97.7	4.00	ab
3	-0.136	0.0355	125.7	3.86	ab
4	-0.014	0.0345	114.7	5.04	-
5	-0.179	0.0429	111.1	4.08	ab
6	-0.046	0.0323	102.5	3.94	b
7	-0.042	0.0329	97.8	3.71	b
8	-0.056	0.0318	97.5	3.37	ab
9	0.041	0.0453	84.0	3.81	-
10	-0.016	0.0330	87.4	3.75	-
11	-0.099	0.0329	111.8	3.54	ab
12	-0.005	0.0318	88.2	3.67	-
13	-0.096	0.0637	105.4	6.39	-
14	0.036	0.0340	76.7	3.97	-
15	-0.223	0.0497	110.7	5.59	a
16	0.019	0.0359	93.1	4.07	-
17	0.011	0.0318	90.4	3.80	-
18	-0.006	0.0388	67.4	6.99	-
19	-0.034	0.0374	89.0	4.05	-
20	-0.103	0.0340	115.5	4.00	ab

5.3.8.7 Canopy senescence

Rate of senescence (GCRate9050) varied greatly between cultivars, with a relatively even distribution of mean GCRate9050 between the slowest and most rapidly senescing cultivars (*cv.* 3 and 12, -2.82 and -9.11 %/day, respectively, Figure 135). There was also a relatively high degree of variability in senescence rate within each cultivar as shown by the large standard errors.

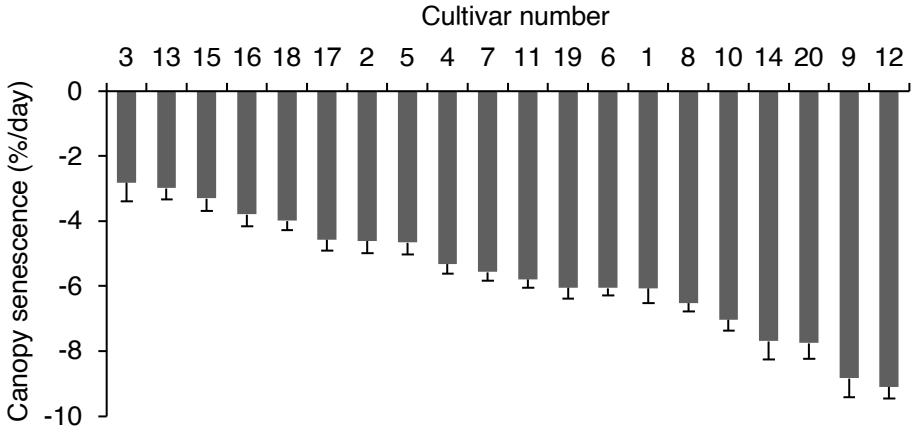

Figure 135. Mean rate of canopy senescence (GCRate9050) by cultivar, ranked from slowest to fastest GCRate9050. Bars represent S.E.

Stem density alone had no significant effect on the rate of canopy senescence (P = 0.102), though the interaction between cultivar and stem density explained 34.0 %

of the variation in GCDur90 ($P < 0.001$, Figure 136). Accounting for variation associated with year of experiment increased the variation explained to 48.5 % (multiple linear regression; GCRate9050 ~ stem density * cultivar + year, $P < 0.001$), highlighting that even when year to year environmental variation had been accounted for, senescence was a highly variable process. The relationship between stem density and GCRate9050 was significant in only four cultivars (1, 9, 14 and 20) and increases in stem density tended to reduce GCRate9050 (Table 87), but in *cv.* 14 GCRate9050 increased slightly (m = -0.016) with increasing stem density. The greatest increase in GCRate9050 in response to increasing stem density was three times greater than that of the least sensitive cultivar (*cv.* 9 and 20, m = 0.050 and 0.016 respectively).

Table 87. Relationship between canopy senescence rate (GCRate9050) and stem density (S) in 20 cultivars. Number of years of data varied between cultivars, see Methods (Table 41). Slopes of cultivars which did not differ significantly are grouped together, indicated by shared letters. Slopes which did not differ significantly from 0 were excluded from group analysis. GCRate9050 = m * S + c.

Cultivar	m	S.E.	c	S.E.	Group
1	0.0296	0.00945	-8.69	0.889	b
2	0.006	0.0104	-5.7	1.29	-
3	-0.002	0.0115	-2.0	1.24	-
4	-0.002	0.0112	-4.9	1.66	-
5	0.022	0.0138	-6.6	1.31	-
6	0.002	0.0104	-6.4	1.27	-
7	-0.001	0.0106	-5.4	1.21	-
8	0.005	0.0103	-7.3	1.09	-
9	0.050	0.0150	-12.1	1.28	b
10	0.011	0.0106	-8.8	1.21	-
11	0.004	0.0106	-6.3	1.14	-
12	-0.002	0.0103	-8.6	1.21	-
13	0.011	0.0205	-4.1	2.06	-
14	-0.016	0.0110	-5.2	1.31	a
15	-0.002	0.0160	-3.1	1.80	-
16	-0.006	0.0118	-3.0	1.37	-
17	0.006	0.0104	-5.8	1.36	-
18	0.004	0.0125	-4.8	2.25	-
19	0.006	0.0121	-6.7	1.31	-
20	0.016	0.0110	-10.6	1.29	b

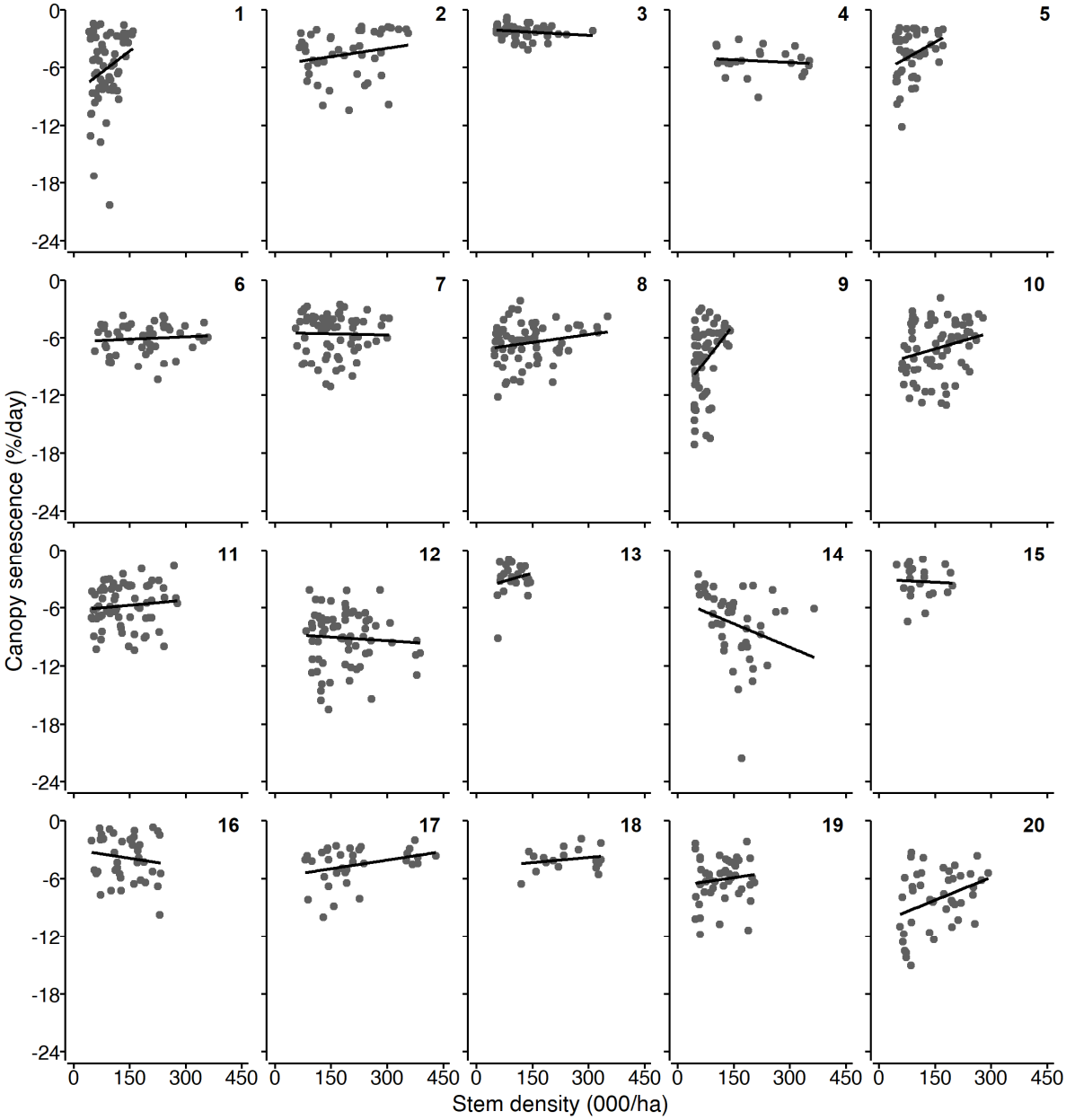

Figure 136. Relationship between stem density (S) and canopy senescence rate (GCRate9050) in 20 cultivars (C) from seed size experiments. Multiple linear regression; GCRate9050 ~ S * C, R^2 = 0.340. Equations for each cultivar shown in Table 87.

5.3.8.8 Key points: Seed size experiment

- The number of stems produced as seed weight increased varied significantly between cultivars and some cultivars were much more responsive than others.
- Overall, increasing stem density had a limited effect upon IGC in most cultivars.
- In all 20 cultivars TiE25 decreased as stem density increased, though the extent of the decrease in TiE25 varied between cultivars.

- GCRate2575 tended to increase with increasing stem density, though in some cultivars did not vary with, or showed a weak response to, increasing stem density.
- GCDur90 did not vary with stem density in the majority of cultivars, both increasing and decreasing in response to stem density when the relationship was significant.
- GrowDur decreased with increasing stem density in 50 % of the cultivars and showed no response to stem density in the other cultivars.
- Cultivars varied greatly in GCRate9050, but stem density had little effect on rate of senescence in most cultivars.

5.4 Discussion

Variation in planting density, and the consequent variation in stem density, has a substantial and well reported effect upon tuber population (5.1.3) and branch production within the canopy (5.1.2.2), yet few have reported how whole canopy growth varies with stem density. In experiments 2, 4 and 5, variation in canopy growth in relation to variation in seed size and spacing was successfully described using the CQ model, addressing thesis aim two. As stated in the chapter introduction (5.1.4), this work aims to quantify the varying effects of planting density on canopy growth in two cultivars of contrasting determinacy. In this discussion, the effects of the seed size and spacing treatments on both stem density and distribution are explored, then the resultant variation in both whole canopy growth, and canopy components, will be discussed, linking changes in canopy architecture to changes in whole canopy growth (thesis aim three), progressing chronologically through the season. Finally differing responses of cultivars of contrasting determinacy and the implications of varying stem density for modelling potato growth are considered.

5.4.1 Stem density and distribution

5.4.1.1 Between-treatment variation in stem density

The seed size and spacing treatments generated a wide range of stem densities and as expected, number of stems per plant was greater when seed was larger and unaffected by seed spacing, though stem density increased as seed spacing decreased (Tables 46 & 47).

Cultivar had a strong influence on stem density and there were large differences in stem production between cultivars, illustrated by the wide range of mean stem densities in the Seed Size experiment (from 69 700 to 241 000 stems/ha, Figure 123). The genetic basis for variation in stem production appears relatively weak due to the strong agronomic influence upon stem number, through seed size and age. Yet, a small proportion of variation in stem production is associated with a series of QTL (Hurtado-Lopez *et al.* 2015). Furthermore, whilst Maris Piper typically produced 1-2 stems more than Estima (Figure 63), suggesting that determinate cultivars produce fewer stems than indeterminate cultivars, Maris Piper also produced *c.* 2 stems more than Desirée (Ifenkwe & Allen 1978b), another indeterminate cultivar (Naylor 2017). This demonstrates that stem production does not vary consistently with determinacy level, or, if it does, that determinacy groups need to be more accurately assigned.

Additionally, the increase in stem production in response to increasing seed tuber mass varies between cultivars (Figure 124), in agreement with Allen and Scott (1980), and a 20 g increase in seed mass can result in between 0.37 and 1.15 additional stems per plant depending on cultivar (Table 81). The relationship between seed mass and stems produced can further vary with chronological age, as illustrated by a *c.* 1-4.5 stems range within 60 g Estima seed grown in different locations (Wales and Spain, (Firman *et al.* 2006)). However, seed age data is not routinely collected by seed producers and was not available in either the Planting Density or Seed Size experiments. Hence, reduced chronological age may explain why, in Expt 4, Maris Piper produced fewer stems than in Expts 2 and 5, resulting in similar numbers of stems per plant in both cultivars in Expt 4 (Figure 63b), but it is uncertain.

5.4.1.2 Variation in stem density throughout the season

Stem density tended to be lower at final harvest than at the early season stem count but the difference between mean stem densities at each harvest was not significant (Figure 64) and stem populations generally vary little between harvests (Firman 2019, personal communication). Similarly, Ifenkwe and Allen (1978a) reported that, after the first month following emergence, stem number varied little and was fairly consistent throughout the remainder of the season in Desirée and Maris Piper. Whilst the relationship between the early- and late-season stem counts appeared to be more variable at higher stem densities these differences are likely due to random, between-plant variation within relatively small samples at each harvest. There is no consistency in stem count methodology within the literature, varying in timing and number of

plants counted, making it difficult to compare details between experimental results, however, the general responses to increasing stem density reported within the literature typically show similar trends, and the results of the Planting Density experiments and the Seed Size experiments also reflect those trends.

5.4.1.3 Variation in canopy growth in relation to stem distribution

The combined effects of varied seed size and spacing on canopy development were well represented by the variation in stem density that these treatments precipitated, yet the spatial distribution of stems within the field was also varied, with greater clumping of stems when large seed was planted (Figure 62). As hypothesised, the effect of stem distribution, distinct from stem density, on canopy growth was most apparent during canopy expansion, addressing aim one. Changes in stem distribution explained an additional 24.1 % of the variation in TiE25, hence at the same density, early canopy expansion was slower both at wider plant spacing and in smaller seed. Also, when a given stem density was achieved by planting small seed at a higher planting density, the population of stems was more evenly distributed, resulting in more rapid canopy expansion than when large seed was planted at wide spacing and stems were more clustered. Surprisingly, there was no consistent effect of stem density on mid-canopy expansion (Figure 76), yet canopy expansion was typically faster when seed was larger and stem distribution explained an additional 7.2 % of variation in GCRate2575.

Whilst limited in Expts 2, 4 and 5, the influence of stem distribution on growth following canopy closure is expected to be greater in commercial crops, where missed-seed at planting or the failure of a plant to emerge is likely to have a greater effect on canopy cover at the wider spacing (Allen & Wurr 1992). Pavek and Thornton (2006) found that, even at optimum plant spacing (31 and 26 cm for Russet Burbank and Russet Norkotah, respectively), in-row neighbours of missing plants were only able to compensate for 71 and 60 % of the total yield of the missing plants in Russet Burbank and Russet Norkotah, respectively, likely due to reduced canopy cover. Therefore, it would be informative to carry out a similar study, recording the effect of missing plants on whole-plot canopy cover, across a range of stem densities. This could identify the stem density threshold at which reductions in canopy cover, as well as tuber yield, due to missing plants are compensated for. The work of Pavek and Thornton (2006) also suggests that sensitivity to missing plants varies between cultivars and this is discussed below (5.4.7).

Stem distribution also varies with row-width, in addition to the differences in within-row spacing explored in Expts 2, 4 and 5. Tarkalson *et al.* (2012) reported increased light interception, particularly early in the season before canopy closure, when the same planting density was achieved in 46 and 66 cm wide rows compared to 91 cm wide rows. Similarly, reducing row width from 90 to 60 cm whilst maintaining the same stem density, resulted in increased yield in both small (< 20 g) and larger (40-60 g) seed tubers (Wiersema 1989). In partial agreement, Ifenkwe and Allen (1978a) reported that the negative effect of wider rows (132 compared to 66 cm) on plant biomass was only apparent early in the season and that final yield did not differ between row width or was greater at the wider spacing. The contrasting effect reported by Ifenkwe and Allen (1978a) may result from substantially larger seed size planted (90-100 g compared to 1-60 g (Wiersema 1989)), producing more stems and enabling canopy gap filling later in the season.

In summary, stem distribution had the greatest influence on early canopy growth, incidentally when stem density also had the largest effect on canopy growth. The effect of stem distribution on whole-crop performance when plants are missing is unknown and stem distribution may have a greater influence on later stages of canopy growth under these circumstances. In most phases of canopy growth a similar level of variation in each canopy variate was described by either the combination of seed size and spacing or by stem density alone, thus, since differences resulting from stem distribution have been discussed here, this discussion will focus predominantly on stem density.

In conclusion, the main effect of varying seed size and spacing was upon stem density, with the differences generated in stem distribution only having a significant effect upon the rate of early canopy expansion. There were large differences between cultivars in mean number of stems per plant and the number of additional stems produced as seed mass increased, though these differences between cultivars were not constant across the years.

5.4.2 Early growth

Number of stems per plant had little effect on potato growth prior to emergence, illustrated by the small differences in EmDAP between small and large seed in each experiment (Table 45). This may be due to regulation of sprout growth, by apical dominance, initially supressing growth of all but the apical meristem (Eshel & Teper-

Bamnolker 2012), resulting in similar initial rates of sprout growth between tubers regardless of final stem number. Alternatively, since number of sprouts > 3 mm has been shown to increase linearly with tuber weight in *cv.* Home Guard (Allen *et al.* 1992), this limited variation in seed tuber 'resource availability per stem' across seed sizes may result in similar rates of sprout growth prior to emergence.

Early canopy expansion was consistently faster, illustrated by shorter TiE25, at higher stem densities in both Estima and Maris Piper, and the 20 cultivars in the Seed Size experiments (Figures 74 & 128). Cultivar TiE25 differed in sensitivity to increasing stem density, with reductions in TiE25 of 1.7 and 9.3 days in the least and most sensitive cultivars (*cv.* 20 and 1, respectively) as stem density increased from 100 000 to 200 000 stems/ha (Table 83). This may be due to variation in leaf morphology between cultivars, with broader leaves potentially linked to a greater increase in the rate of canopy expansion as stem numbers increase or a steeper response potentially indicating lower overlap between leaves produced on additional stems. Yet, Seijo-Rodríguez *et al.* (2017) found that leaflet shape and degree of overlap between leaflets varied within cultivars between years, and were not useful characteristics for distinguishing between cultivars. Similarly, Firman and Allen (1989) reported a predominantly consistent relationship between leaf length and leaf area across six cultivars (with only *cv.* Pentland Crown producing longer leaves relative to leaf area). Hence, it is unlikely that cultivar-specific differences in leaf shape were responsible for variation in the relationship between TiE25 and stem density between the cultivars. Furthermore, differences in leaf size and shape are more likely to be apparent later in the season when the leaves have matured, i.e. after the canopy has covered more than 25 % of the ground, which may explain why many cultivars had a similar mean TiE25 (shown by a small IQR, Figure 127) and similar responses inTiE25 to stem density, within the same order of magnitude (Table 83).

Nevertheless, differences in leaf production are associated with changes in mean temperature and more narrow leaflets are associated with warmer mean air temperature, with a more acute angle of divergence between stem and leaf, resulting in a more upright arrangement of leaves (Seijo-Rodríguez *et al.* 2017). Escuredo *et al.* (2020) also reported smaller leaflets, reducing leaf area when the growing season was warmer. Therefore it is possible that, in the Seed Size experiments, differences in temperature or other environmental factors between the years may have resulted in variation in TiE25, since each cultivar was grown in a small subset of years with a

different combination of environmental conditions, unique to that cultivar. In the more in-depth Planting Density experiments, TiE25 did not vary consistently with cultivar and between-cultivar differences could be explained by differences in mean tuber weight (Figure 73). Whilst the multiple linear regression (Table 53) indicated that the decrease in TiE25 with increasing stem density was greater in Estima than Maris Piper, fitting a curve which plateaus may better represent the relationship between TiE25 in Maris Piper and stem density, and reduce the difference between cultivars (Figure 74).

In summary, number stems per plant had no effect on pre-emergence growth, but early canopy expansion was faster at higher stem density, particularly when stem distribution was even.

5.4.3 Mid-season canopy expansion

5.4.3.1 Influence of stem density on mid-canopy expansion

The influence of stem density on mid-canopy expansion appeared to be cultivar dependant and in 13 of the 20 cultivars in the Seed Size experiments increasing stem density was associated with an increase in GCRate2575 (Figure 130 & Table 84). Although, there was no overall relationship between stem density and GCRate2575 in Maris Piper and Estima (Figure 76), GCRate2575 was typically faster in larger seed (Figure 75). Engels *et al.* (1993) also reported faster canopy expansion in large compared to small seed, although the clear difference in rate of canopy development between seed sizes reported is likely due to the negative effects upon canopy growth, distinct from stem population, of reduced tuber resources in the smallest seed (< 1 g, (Wiersema 1989)). Since the smallest seed size in the Planting Density was > 10 g—below which canopy growth appears to be limited by the extremely small size of seed (Wiersema 1989; Engels *et al.* 1993)—canopy production was likely unhindered by the effects of tuber resources, thus the differences in rate of canopy expansion between seed sizes were not as large. In some cases, cultivars 9 and 13, the lack of relationship found may reflect the limited variation in stem density (range < 100 000 stems/ha). Additionally, both Allen and Scott (1980) and Engels *et al.* (1993) noted that the effect of increasing stem density on canopy expansion duration was most apparent when stem density was lowest, hence the relatively large minimum stem density (> 100 000 stems/ha) may account for the lack of relationship in cultivars 4 and 18. Consequently, differences in the range of stem densities within cultivars may explain the limited response of GCRate2575 to increasing stem density in those cultivars.

Additionally, there was a wide range of GCRate2575 at any given stem density in both sets of experiments and this high degree of variability suggests that stem density has a minor role in determining mid-canopy expansion rate. The significant difference in GCRate2575 between experiments (Figure 76) highlights the influence of environmental variation on canopy expansion discussed in chapter four (4.4.2.1). Similarly, Khan *et al.* (2019) found that approximately half of the phenotypic variation in duration of canopy expansion was associated with environment variation. Moreover, Allen and Scott (1980) reported positive effects of increasing stem density on canopy expansion described by the time taken to achieve maximum GC (LAI of 3), encapsulating the effects of stem density on both early- and mid- canopy expansion. This difference in methodology may account for the differences in findings, as when the time to achieve 90 % GC was quantified, it was consistently shorter at higher stem densities (Appendix 28), similar to those reported by Allen and Scott (1980). Thus, crops grown with a higher stem density will achieve maximum canopy cover before those with lower stem densities, but these results suggest that that is mainly due to the shortened duration of early canopy expansion as illustrated the parallel slopes of the CQ of the different spacing treatments (Figure 66).

5.4.3.2 Relationship between mid-canopy expansion and leaf appearance rate

In large, relative to small, seed, the rate of mid-canopy expansion was greater, whilst leaf appearance rate on a single mainstem was slower (Figures 75 & 87, respectively), demonstrating that reductions in msLA with increasing stem density do not contradict reported increases in canopy expansion rate and occur concurrently in field grown potatoes, answering chapter aim two. The rate of leaf appearance on the mainstem slowed as stems per plant increased (Figure 88) and msLA on a plant with a single stem was *c.* 0.1 leaves/day faster than a plant with three stems, similar to the 0.1 leaves/day difference in leaf appearance rate on the main axis (mainstem and sympodial branch) between one- and three-stemmed plants found by Fleisher *et al.* (2011) under growth chamber conditions. Increasing stem density slowed leaf appearance on both the mainstem and sympodial branch (Fleisher *et al.* 2011), though Figure 101 shows a smaller and more variable reduction in sbLA in response to increased stem density. This was, however, not unexpected due to the greater variability in sbLA than msLA identified by Firman *et al.* (1995).

Yet, despite reductions in msLA with increasing stem density, the rate of whole plant leaf appearance increased as stems per plant and stem density increased (Figures 96

& 98, respectively). Whilst calculating the rate of leaf appearance on a per plant basis does not accurately reflect variation at the field level (with the resultant weak relationship between pLA and stem density, Figure 98), it is useful to consider how variation in a single stem affects whole plant growth. Similarly to the findings of the Planting Date experiments (Figure 38), pLA alone explained a limited proportion of the variation in GCRate2575 (< 30 %, Figure 97). It is likely that variation in mid-canopy expansion results from differences in leaf expansion (Firman *et al.* 1995), moderated by the degree of leaf overlap within the canopy (for further discussion see 4.4.2.3).

5.4.3.3 Relationship between early and mid-canopy expansion

Fast initial canopy expansion did not necessarily result in rapid mid-canopy expansion and the relationship between TiE25 and GCRate2575 was relatively weak across 20 cultivars, in the Seed Size experiments (Appendix 29, Figure 167), whilst there was no relationship between TiE25 and GCRate2575 in Expts 2, 4 and 5 (Appendix 29, Figure 166). Consequently, under unstressed conditions, slow initial canopy growth does not appear to result in slower subsequent canopy expansion.

In conclusion, the rate of canopy expansion increased with increasing stem density in some cultivars, but the relationship was highly variable and not universal, likely due to the influence of environmental factors. Rate of leaf appearance explained a relatively small proportion of the variation in canopy expansion, indicating again the importance of leaf expansion rate and environmental influences upon variation in canopy expansion.

5.4.4 Canopy duration

Canopy duration tended to be longer at higher stem densities (Figure 80), though this increase was not universal and differences in response between cultivars are discussed below (5.4.7). As identified in the literature review, changes in stem density can result in large structural changes within the canopy, yet it is unclear how these changes affect canopy light interception and longevity. Both Engels *et al.* (1993) and Ifenkwe and Allen (1978a) have proposed that differences in canopy structure may explain why there are differences in the onset of canopy senescence and canopy longevity, but the evidence supporting these suggestions is limited. Hence, differences in canopy components at the onset of senescence are discussed here to better understand variation in canopy duration with varying stem density, addressing chapter aim three.

5.4.4.1 Variation in branch production

Reduced axillary branch production is a consistent response to increasing stem density across a range of cultivars of differing determinacy levels including Estima (Figure 109b), Maris Piper (Figure 109, (Ifenkwe & Allen 1978b)), Desirée (Ifenkwe & Allen 1978b), Russet Burbank (Lynch & Rowberry 1977) and Kennebec (Fleisher *et al.* 2011). The increase in axillary branch production, with decrease in seed size and increased spacing, was greater in Maris Piper than in Estima (Figures 107 & 108), indicating the greater propensity of Maris Piper to continue branch production at lower stem densities. However, this difference may be between cultivars, as opposed to between determinacy types, since Maris Piper also produced more branches with decreasing stem density than Desirée, another indeterminate cultivar (Ifenkwe & Allen 1978b).

Ifenkwe and Allen (1978a) suggested that the indeterminate nature of stem and branch growth enabled canopies of similar functionality to be produced across a large range of spatial arrangements. Similarly, Lynch and Rowberry (1977) reported that a similar LAI was maintained across a wide range of plant densities, despite large increases in plant density and concomitant decreases in branch production. Yet, both the work of Engels *et al.* (1993) and the Planting Density experiments highlight the limits of flexible canopy production to adapt to low stem densities. Although increased branch production in extremely small seed (0.5-1 g) tended to result in later senescence, it did not compensate for reductions in maximum canopy cover and IGC at the lowest stem densities, which were much lower than in larger seed at the same stem density (Engels *et al.* 1993), though some of this may due to the negative effect of extremely small seed, with limited tuber resources discussed below (5.4.6.2). Moreover, there was a weak negative relationship between number of axillary branches and GCDur90 (Figure 110), indicating that at the widest plant spacing, with lower stem density, increased axillary branch production was unable to fully compensate for reduced plant population, as illustrated by the slightly restricted CQ curves for smaller seed (Figure 67) and widest plant spacing (Figure 66).

Fleisher *et al.* (2006) and Lynch and Rowberry (1977) found that the proportion of the canopy comprised of branches relative to mainstem leaf material did not significantly affect canopy photosynthesis or PAR intercepted at three layers throughout the canopy, respectively. Hence, providing that canopy closure can be achieved in a timely fashion, and that low stem density does not prevent formation of a complete

canopy, there is little effect of canopy composition and branch production on canopy functionality.

5.4.4.2 Mainstem length

Mainstem length increased with increasing stem density, as expected (Ifenkwe & Allen 1978b), in both Estima and Maris Piper (Figure 117) and internode spacing increased since mainstem leaf number varied only with cultivar, not stem density (Figure 85). Oliveira (2000) reported that competition for light at higher stem densities resulted in more rapid stem elongation, and this is likely the cause of longer mainstems in the Planting Density experiments. However, this increase in stem length was not universal and van der Zaag *et al.* (1990) reported little difference in either early or final plant height under in temperate conditions. It was suggested that resource availability has a stronger influence on plant height than stem density since, under tropical conditions, plant height was greatest at the widest plant spacing due to water stress experienced by the high stem density treatments (van der Zaag *et al.* 1990). In addition, Oliveira (2000) also suggested that nitrogen rate has a greater influence on stem length than competition for light, reporting a shorter but thicker mainstem at the highest rate of applied nitrogen (200 kg N/ha). It is, however, uncertain what effect an interaction between stem density and nitrogen rate has on stem length, since plants were only grown by Oliveira (2000) at the higher stem density at a single nitrogen rate, allowing no direct comparison between nitrogen rates. Together, these papers indicate that environmental factors can have a large influence on stem length, hence, mainstem length and plant height are not simply functions of stem density.

There was a weak positive relationship between mainstem length and GCDur90 (Figure 118). It is possible that the rate of light attenuation within the canopy was reduced in taller canopy, as has been shown in wheat (Miralles & Slafer 1997), due to more widely spaced leaves on the mainstem and the smaller number of axillary branches within the canopy (associated with greater stem density). This may have resulted in more long-lived mainstem leaves, as light levels were not low enough to trigger shade-induced senescence, as shown by Vos and van der Putten (2001) in an artificial shade experiment. Consequently, greater overall canopy longevity may be expected, since Oliveira (2015) reported that whole canopy longevity is closely related to the lifespan of the largest leaves on the mainstem. Yet, there is no direct evidence for this hypothesis and the weak relationship between mainstem length and GCDur90 may also be an artefact of the increases in both with increasing stem density.

Moreover, Lynch and Rowberry (1977) found no difference in light intercepted throughout the canopy between *c.* 156 000 and 388 500 stems/ha (40 000 and 111 000 plants/ha), despite decreased number of axillary branches within the canopy at the highest stem densities (though variation relative to mainstem height is unknown as it was not recorded). In short, whilst greater mainstem length may promote mainstem leaf longevity, and consequent canopy longevity, there is little evidence for this since light penetration through the canopy has not been found to vary with stem density.

The Planting Density experiments also provided no evidence to suggest that taller plant stands (indicated by greater SBInsert and TotLength) at higher stem densities, are more likely to lodge and begin senescence earlier (or later) than shorter canopies, as there was no relationship between either measure of canopy height and the onset of senescence (data not shown). Consequently, it remains unclear why Ifenkwe and Allen (1978a) found earlier lodging in plants 66 than 132 cm rows at the same density, despite shorter mainstem length and greater branch production in the narrower rows.

In summary, at higher stem densities mainstem length is longer, potentially promoting mainstem leaf longevity and increased near-complete canopy duration, although there is little evidence for this and no evidence that mainstem or total stem length affects the timing of senescence onset relative to emergence.

5.4.4.3 Leaf area index

Differences in stem density had the anticipated effect on distribution of leaf material within the canopy and greater stem population was associated with fewer axillary branches, fewer leaves per branch and lower axillary branch LAI, similar to the findings of Fleisher *et al.* (2011) under growth chamber conditions. Mainstem LAI, at the onset of senescence, was greater at higher stem densities, also akin to the findings of Fleisher *et al*. (2011). As discussed above (5.4.4.2), the smaller number of axillary branches (Figure 109) likely resulted in reduced shade intensity within the canopy, allowing greater mainstem leaf persistence due to less intense shade (Vos & van der Putten 2001). Despite large differences in canopy structure, total LAI did not vary with seed spacing and size or stem density, as increased axillary branch LAI was offset by reductions in mainstem and sympodial branch LAI (Figures 102 & 103), in agreement with the findings of Fleisher *et al.* (2011) and Lynch and Rowberry (1977). Very little variation in total LAI at the onset of senescence was explained by stem density and the relationship between stem density and canopy component LAI was also typically weak, partially due to variable degrees of senescence between plots, obscuring the

relationship between stem density and LAI. Yet the relationship between stem density and LAI differed between cultivars and stem density explained no variation in TotLAI in Maris Piper, but 29 % in Estima (5.3.5, Figure 106). Bremner and Taha (1966) also reported differences in LAI production in response to varying plant spacing between cultivars and the delayed increase in King Edward LAI at wide seed spacing was not observed in Majestic due to greater leaf production by Majestic, though this was not linked to differences in determinacy since both cultivars are indeterminate.

Above *c.* 156 000 stems/ha (at 40 000 plants/ha), Lynch and Rowberry (1977) found little variation in LAI at a wide range of plant densities, due to the increases in axillary branching with decreasing plant density. However, Ifenkwe and Allen (1978a), Oliveira (2000), and Bremner and Taha (1966) all reported that maximum LAI was greater at higher stem densities. This contrast is likely due to relatively high stem densities at which Russet Burbank (an indeterminate cultivar) was planted—*c.* 156 000 to 389 000 stems/ha, (Lynch & Rowberry 1977)—with stem densities greater than those at which canopy growth is limited and branch growth may not be able to compensate for reduced stem populations. The precise point of this threshold is unknown; the work of Engels suggests that the threshold is *c.* 150 000 stems/ha, and a positive response of LAI to increasing stem density was reported with minimum densities of *c.* 93-124 000 stems/ha in *cv.* Desriée and Maris Piper, respectively (Ifenkwe & Allen 1978b) but at *c.* 191 000 stems/ha in *cv.* Snowden (Oliveira 2000), suggesting that the threshold may vary between cultivars. Moreover, when LAI differed with stem density, differences in LAI tended to diminish as the season progressed (Bremner & Taha 1966; Ifenkwe & Allen 1978b; Engels *et al.* 1993; Tarkalson *et al.* 2012), likely due to continued branch production at lower stem densities. Hence, it is perhaps unsurprising that no differences in total LAI were found since the late season harvest in Expts 2, 4 and 5 did not capture peak LAI.

In summary, the effect of LAI upon light interception is unclear from these experiments, but changes in the ratio of mainstem, axillary branch and sympodial branch leaf material within the canopy have been shown to have a limited effect upon whole-canopy photosynthesis (Fleisher *et al.* 2006b), thus it is likely that changes in canopy leaf composition are of little functional importance. In addition, there was no relationship between total LAI and either GCDur90 or GrowDur (data not shown), illustrating that LAI at the onset of senescence does not vary consistently with duration of near-complete canopy cover. Yet, this is partially to be expected since plots were all

harvested at or close to the onset of senescence when gaps were forming in within the canopy and LAI was decreasing. Maximum LAI may be a more informative measure of both canopy size and potential longevity, with a larger LAI indicating canopy ability to persist in the face of high leaf turnover (Bremner & Radley 1966). Yet greater maximum LAI does not guarantee greater canopy longevity, as discussed in chapter four (4.4.5.1).

In conclusion, indeterminacy of potato stem and branch growth allows this crop to tolerate extreme spatial arrangements and canopies of similar overall effect can be produced (Ifenkwe & Allen 1978b), with similar canopy LAI reported over a wide range stem densities (Lynch & Rowberry 1977). Yet whilst branch production enables canopy closure at low stem densities, canopy closure is delayed at widest plant spacing, reducing IGC, light intercepted and subsequent yield. Hence, in answer to aim three, below a threshold, increasing stem density will result in increased canopy duration and increased light interception, but above it, whilst the proportions of canopy components can differ drastically but have little effect upon light interception and canopy growth. The point at which canopy growth in response to increasing stem density plateaus appears to be *c.* 150 000 stems/ha but is likely to be higher in determinate than indeterminate cultivars. More determinate cultivars may be more sensitive to reductions in stem density and extreme spacings, due to more limited leaf production relative to indeterminate cultivars, yet differences between cultivars are not always related to determinacy.

5.4.5 Canopy senescence

The influence of stem density on rate of canopy senescence varied between cultivars and experiments, reflecting the inconsistent results reported in the literature and the unpredictable nature of senescence due to both stem lodging and pathology at the end of the season. Stem density had no effect on either the onset or rate of senescence in Expts 2, 4 and 5, similar to the findings of Firman and Daniels (2011). Whilst at higher stem densities, slower senescence was observed in three cultivars and faster senescence in one cultivar in the Seed Size experiment, the rate of senescence did not vary consistently with stem density in the majority of cultivars (Figure 136). Engels *et al.* (1993) reported that increased axillary branch production at lower stem density was associated with delayed senescence (Engels *et al.* 1993), conversely, Ifenkwe and Allen (1978a) reported earlier stem lodging and senescence when plant distribution was more even (constant plant density in narrow (66 cm), relative to wide (132 cm) rows),

despite greater branch production. Moreover, variation in number of axillary branches explained no variation in the onset of senescence in Maris Piper and Estima (data not shown) despite the same trend of greater branch production by smaller seed tubers (Figure 107). Duration of senescence is expected to vary with both environmental variation (particularly available nitrogen), genotype and the interaction between the two (Khan *et al.* 2019a), though the influence of stem density on the rate of senescence remains uncertain. Khan *et al.* (2019) also noted that senescence is difficult to accurately model, consequently variation in model goodness of fit may have increased the variability in an already stochastics process, reducing the likelihood of identifying a relationship between stem density and, either the onset of, or rate of, senescence. Hence, increased branch production at lower stem density appeared to have little effect, if any, on the onset of senescence, similarly there was no clear effect of increasing stem density on the rate of canopy senescence.

5.4.6 Canopy size

5.4.6.1 Influence of stem density on integrated ground cover

The effect of stem density on integrated ground cover was modest, with typically small increases in IGC with increasing stem density in seven cultivars in the Seed Size experiments (Table 82), and in Estima and Maris Piper (Figure 70). Since increasing stem density hastens early canopy expansion (5.4.2), subsequent achievement of complete ground cover and has no effect on the timing of senescence (5.4.5), IGC could be expected to increase, with a longer duration of near-complete canopy cover, due to more rapid early canopy development. Yet increased IGC with increasing stem density was not universal; in the Seed Size experiments, IGC in nine cultivars did not vary with stem density, whilst IGC decreased with increasing stem density in four cultivars, reflecting differences in the relationship between GCDur90 and stem density (5.4.4 & Figure 132), since IGC is closely related to GCDur90 (Figure 79). The lack of consistency in the relationship partially results from variable final harvest timing relative to canopy cover in the Seed Size experiments; canopy cover varied from 0-100 %, and 4.8 % of plots were harvested whilst GC > 90 %, curtailing canopy duration and preventing potential IGC from being reached. Differences in environmental conditions between the experiments, including soil type, available soil nitrogen and meteorological variables, are a further source of variation in IGC, found by Khan *et al.* (2019) to account for *c.* 30 % of the variation in IGC (described by Khan *et al.* (2019) as A_{sum}). However, both Allen and Scott (1980) and Engels *et al.* (1993)

observed a diminishing influence of stem density on canopy growth variables with increasing stem density. Engels *et al.* (1993) reported a positive linear relationship between IGC between *c.* 40 000 and 150 000 stems/ha, yet as stem density increased to *c.* 320 000 stems/ha the influence of stem density on IGC diminished and the relationship was better described by a logarithmic, than linear, equation. Firman and Daniels (2011) also reported that stem density only reduced IGC, by delayed canopy closure, at the most extreme plant spacings, 25-44 000 stems/ha. Hence, future work should attempt to describe the influence of stem density on IGC, and other descriptors of canopy growth, using a non-linear approach, aiming to identify the threshold below which decreasing stem density negatively affects canopy growth and persistence.

5.4.6.2 Influence of seed size on canopy production

There was very little effect of seed size and spacing on IGC distinct from their effect on stem density (Figure 70). However, Engels *et al.* (1993) and Wiersema (1989) both suggest that, in extremely small seed, 1-20 g, tuber resources restrict canopy development despite equal stem densities. At similar stem densities, smaller seed, < 20 g, produced smaller canopies than those grown from larger seed (Engels *et al.* 1993). Similarly, canopy expansion was markedly slower in 1-5 g and 5-10 g seed, compared to 40-60 g seed, and the increase in rate of canopy expansion with increasing seed size was non-linear (Wiersema 1989). Consequently, Wiersema (1989) suggested that when seed size is very small, < 20 g, above-ground stems are no longer an appropriate unit of plant density due to the variation in leaf production with seed size. Whilst the smallest seed sizes in both the Planting Density and Seed Size experiments were < 20 g (16 and 11 g, respectively) there was no apparent canopy size penalty of the smallest seed, with canopy variates not significantly lower at the lowest stem densities (produced by the smallest seed). The impact of very small seed is likely observed when seed tubers are < 10 g as in the experiments of both Engels *et al.* (1993) and Wiersema (1989), or due to differences in daylength and air temperature between the UK, Egypt and Peru where the Planting Density and Seed Size experiments, those of Engels *et al.* (1993), and of Wiersema (1989), were respectively carried out, since van der Zaag *et al.* (1990) has shown that biomass partitioning to the haulm is reduced under tropical, relative to temperature conditions.

5.4.6.3 Relationship between integrated ground cover and yield

Total fresh weight yield increased with stem density, akin to the increases in IGC (Appendix 27). The modest increases in IGC between small and large seed, and the

20 and 60 cm spacing treatments were equivalent to an additional 7.4 and 7.5 days at 100 % GC, respectively (Figures 67 & 66, respectively), resulted in equally modest increases in dry weight tuber yield *c.* 1.7 t/ha. These increases in yield with increasing stem density were similar, though slightly lower than those reported by Collins (1977) and Love and Thompson-Johns (1999) with similar increases in stem density and between plant spacing (14 t/ha, and *c.* 12 t/ha, respectively compared to 8.9 t/ha; mean of Expts 2, 4 and 5, Table 77). Consequently, increasing stem density had the expected small effect on gross tuber yield, whilst resulting in large increases in number of tubers (Appendix 27) and subsequent reductions in average tuber size.

The effect of increasing stem density on gross yield may depend on cultivar determinacy, with greater increases in yield in determinate than indeterminate cultivars, due to greater responsiveness of IGC to stem density in determinate cultivars as discussed below (5.4.7). However, despite greater increases in IGC with increasing stem density than in Estima than Maris Piper (Figure 70), there was no difference in degree of increase in yield with increasing stem density between cultivars (Appendix 27).

Differences in plant distribution not considered here may also influence light interception and yield. Decreasing rectangularity of planting—the ratio of row width to within-row spacing (Fowler 1988)—by decreasing row-width from 90 to 60 cm, whilst maintaining the same stem density, increased yield in plants grown from both very small, < 20 g, and larger, 40-60 g, seed tubers (Wiersema 1989). Though the increase in yield was greater in yield in the small than large tubers (24.5 and 19 %, respectively (Wiersema 1989)). It may be surmised that reductions in rectangularity enable more even increase in soil coverage, allowing earlier canopy closure and greater light interception, resulting in greater yields. Yet the benefits of reduced rectangularity diminish as tuber size increases (Wiersema 1989), presumably due to the more limited canopy production capacity of very small seed (Engels *et al.* 1993), whilst more indeterminate stem growth of the larger seed (97-105 g) can compensate for variation in row width resulting in limited overall difference in patterns of whole canopy growth (Ifenkwe & Allen 1978b). Hence, the positive effect of increasing stem density (at low stem densities) is expected to be greater when decreases in within-row spacing scale with decreases in row width, though this is impractical in an agricultural context where row width is typically constrained by machine capabilities, changing plant

spacing within a multiple-row bed system can increase light intercepted and yield as shown by Tarkalson *et al.* (2012).

In conclusion, stem density has a limited effect on IGC and this varies between cultivars due to the variable relationship between GCDur90 and stem density. Whilst increasing stem density can increase yield, mean tuber size decreases as a result of increased tuber number, likely reducing marketable yield and so increasing stem density is an agriculturally inappropriate strategy for increasing yield.

5.4.7 Links to determinacy

Canopy growth in response to increasing stem density was hypothesised to vary with determinacy and the responses of TiE25, GCDur90 and IGC to increasing stem density were all greater in Estima than in Maris Piper (Figures 74, 80 & 70, respectively), suggesting that determinate cultivars are more sensitive to variation in stem density than indeterminate ones, answering chapter aim four. This agrees with the findings of Tarkalson (2012), who reported that the indeterminate cultivar Russet Burbank was less sensitive to variation in plant distribution (due to varied row widths) than the more determinate cultivar Russet Norkotah, which intercepted an increasingly large proportion of PAR with increasingly even plant distribution. Additionally, Pavek and Thornton (2006) found that Russet Burbank was more able to compensation for lost yield in relation to missing plants than Russet Norkotah (71 and 60 % yield compensation, respectively). Likely, the greater foliage production capacity of indeterminate relative to determinate cultivars; with more mainstem leaves (Figure 85), sympodial branch leaves (Figure 90) and axillary branches (Figure 107b), enables indeterminate cultivars to continue canopy growth, achieving canopy closure at lower stem densities than determinate cultivars. Indeed, Tarkalson *et al.* (2012) attributed the ability of Russet Burbank to achieve maximal light interception irrespective of plant distribution to the 'large, vigorous and spreading' nature of the vine produced.

However, there were no clear differences in mean canopy variates between determinacy groups in the Seed Size experiments, with a wide range of values for each canopy variate within each determinacy group (Appendix 30). For example, the cultivar rankings with respect to IGC did not correlate well with the determinacy groups (Appendix 30, Table 270) they are currently placed in. This may indicate that the determinacy groupings are inaccurate or may be an artefact of early plot harvest truncating IGC and altering the ranking. The majority, 61.3 %, of plots in the Seed Size

experiments were harvested before 0 % GC was reached, so whilst IGC (as calculated here) encompasses the size and duration of the canopy throughout the growing season (providing a proxy for light interception and therefore a good link to yield) it does not accurately reflect the potential of each cultivar to produce and maintain foliage since they were harvested at different mean ground cover values. Variation in environmental conditions between years may have also masked differences in IGC between determinacy groups, although Khan *et al.* (2019) reported that a greater proportion of variation in IGC was explained by genotypic, as opposed to environmental, variation (51 compared to 31 %).

Unfortunately, the determinacy rankings of the cultivars within the Seed Size experiments were not well-established, with some cultivars likely misallocated (Appendix 30) and this may be the reason for the indistinct canopy growth responses to variation in stem density between determinacy groups in the Seed Size Experiments. There did not appear to be any link between canopy growth responses to stem density and determinacy group (Appendix 30, Figure 169), similar to the lack of relationship reported between length of tuber dormancy and maturity type (Muthoni *et al.* 2014). Yet, in both the Seed Size and Planting Date experiments, determinacy was linked with ability to achieve near-complete ground cover and the majority of plots which failed to produce ≥ 90 % GC were more determinate (in determinacy group two, Appendix 30, Table 269).

In summary, analysing the canopy growth responses of individual cultivars to changing stem density with respect to determinacy groupings can allow predictions about canopy growth responses to be made for cultivars which have limited or no stem density data. Hence, determinacy may provide a useful lens when investigating canopy growth responses, to changes in stem density and other agronomic variables, assuming that the determinacy levels are accurately assigned and expected patterns of cultivar growth are derived from a sufficient number of cultivars in each determinacy group. Yet variation within determinacy groups is to be expected due to the influence of environmental variables and between cultivar variation.

5.4.8 Modelling outlook

Including stem density in future canopy models will increase the accuracy of the models as stem density increases the initial rate of canopy expansion in a wide range of cultivars, extends the duration of near-complete ground cover and in consequence

increases integrated ground cover in some cultivars. However, these effects are cultivar specific and cultivars of the same determinacy group do not exhibit identical responses, requiring large amounts of data to be able to predict the nature of the response to changes in stem density in a model. The Seed Size experiments provide an indication of the range of responses in potato canopy growth to changes in stem density (caused by differences in seed weight) but was not conclusive due to limited data available for each cultivar (with number of plots per seed weight ranging from four to twelve) and the limited range in cultivar type (all processing). More work is required to give a more definitive description of cultivar canopy growth responses to changing stem density, yet this analysis still indicates which of the 20 cultivars considered are particularly sensitive to changes in stem density.

This understanding of cultivar stem density sensitivity could be incorporated into future models of canopy expansion. Seed mass and spacing would be input and combined with a cultivar-specific stem production score (since cultivars differ in mean number of stems and responsiveness of stem production with increasing seed weight) to predict stem density. The data to predict stem population from seed mass and spacing already exists for many cultivars and forms the basis of the AHDB seed rate guides (Potato Council 2009). A cultivar-specific stem density sensitivity score could be applied to anticipate the effect of the calculated stem density on canopy growth, with a general value (where initial canopy expansion is affected by stem density but that the influence of stem density is reduced as the growing season progresses) for when there is no cultivar-specific score due to lack of experimental data.

Future work on the effects of stem density on canopy growth should consider a wider range of cultivars, generating more data to parameterise the effects of stem density. There may also be more variation in response to increasing stem density in potato crops grown for different end markets; whilst the Seed Size experiments were useful in increasing the number of cultivars analysed, all of the cultivars were processing cultivars and so were selected for certain attributes and similar patterns of canopy growth may have been inadvertently been selected for in addition to fry quality, optimum tuber size grade, reduced bruising, disease resistance and tolerance to water-stress. Furthermore, the results here (5.4.4.3 & 5.4.6.1) and elsewhere (Allen & Scott 1980; Engels *et al*. 1993) suggest that the relationship between canopy growth and stem density is non-linear, with a threshold above which increases in stem density appear to have little effect on whole canopy growth. However, this threshold also appears to

vary between cultivars and so thresholds for determinacy groups must be identified, assuming the threshold varies with determinacy, to allow modelling of canopy growth responses to varied stem density.

In summary, incorporating stem density into a model of canopy growth will allow better prediction of canopy expansion and could predict if canopy growth later in the season is likely to be negatively affected by low stem density. Yet further data on the influence of stem density upon canopy growth of differing cultivars is required to determine if there is a common, generalizable growth response within determinacy groups.

6 DISCUSSION

Many different approaches have been used to improve understanding of variation in potato yield, typically focusing on the direct effects of agronomic treatments on tuber yield. Whilst much has been learnt from this approach, there is potential to increase understanding of the influence of crop management and the environment on potato growth by considering the mechanisms by which yield is generated, specifically radiation interception by the canopy, using the long-understood relationship between intercepted radiation and yield (Monteith 1977; Allen & Scott 1980). The method presented here was developed to help address the variability of potato yield, particularly in the UK, capturing the differences in canopy growth by mathematically describing the pattern of canopy growth throughout the season. Firstly, model functionality and the relationship between canopy variation and tuber yield are discussed, fulfilling aim one (6.1). This is followed by key findings from the Planting Date and Planting Density experiments (6.2), considering variation in canopy in response to planting date (6.2.1), planting density (6.2.2), applied nitrogen (6.2.3) and cultivar (6.2.4). The insight into canopy growth provided by differences in canopy components is then discussed (6.3). Lastly, future prospects, for model development (6.4.1), use in research (6.4.21.5.2) and use in agriculture (6.4.3), are reviewed and conclusions are drawn (6.5).

6.1 Model functionality

The canopy quantification (CQ) model was able to fit a curve to raw ground cover data from five experiments, over three years, describing the expansion, maintenance and senescence of the potato canopy with a high degree of accuracy, meeting thesis aim one (2) and enabling fulfilment of thesis aim two (4 & 5). This allowed both visual comparisons of canopy growth (4.3.3.1 & 5.3.3.1) and the calculation of descriptive variates which enable quantitative comparisons (4.3.3 & 5.3.3).

The CQ model is useful for comparing both commercial crops and experimental plots by growers and researchers, respectively. Whilst similar to an existing canopy description model (Khan 2012) in approach and goodness of fit (2.4), the CQ model output enables more fine-grained canopy growth analysis since canopy development can be partitioned to describe specific periods of growth (2.5). To retain model simplicity, canopy development was plotted against time, not thermal time, as in

Khan's model; increasing ease of interpretation, reducing calculations required, reducing potential for error by use of inappropriate base temperatures and allowing analysis of the effect of temperature on canopy development (4.1.1.1). Furthermore, leaf temperature can differ markedly from air temperature due to evaporative cooling (Smith 1978), uncoupling leaf temperature—and the rate of photosynthesis and other leaf processes—from air temperature and reducing the relevance of air temperature data for measuring crop growth against.

In summary, fitting ground cover values against thermal time did not improve model fit, confirming the rationale for fitting the CQ model against time and illustrating that a simple model can be used to quantify variation in canopy expansion, maintenance and senescence.

6.1.1 Integrated ground cover and yield

Despite success in describing canopy growth within each experimental plot, there were limitations to using whole-season canopy cover to analyse yield variability, resulting from an imperfect relationship between IGC and yield. In the Planting Date and Density experiments respectively, IGC alone explained 37.4 and 37.7 % of variation in dry weight tuber yield (DWyield). Yet this is not surprising, since radiation is not converted directly into tuber dry matter, and processes between radiation interception by the canopy and tuber dry matter production are variable, influenced by cultivar and the environment (Fahem & Haverkort 1988). For example, Allen and Scott (1980) reported that waterlogging and variation in planting date both reductions in tuber dry weight relative to total radiation intercepted.

Differences in radiation use efficiency (RUE) have been associated with differences in yield between cultivars (Burstall & Harris 1986; Fahem & Haverkort 1988), with lower RUE linked to lower yield capacity (Oliveira *et al*. 2016), and potentially explaining variation in yield between crops which intercepted a similar quantity of solar radiation (Burstall & Harris 1986). Biomass partitioning also varies between cultivars (Geremew *et al*. 2007) and a higher proportion of biomass is partitioned to tubers, relative to haulm, in determinate than indeterminate cultivars (Allison 2019), as illustrated by the consistent differences in HI between Estima and Maris Piper (Figure 61). Consequently, accounting for differences between cultivars resulted in a greater proportion of variation in tuber yield accounted for; 47.1 and 59.2 % in the Planting Date and Density experiments, respectively.

Furthermore, nitrogen application can reduce HI when harvest occurs prior to resource reallocation from haulm to tubers (4.3.7.4). Moreover, the response is cultivar dependent, with a greater reduction in HI under high nitrogen (Fowler 1992, 1993) and a more prolonged negative effect of additional nitrogen on HI (Figure 61) in indeterminate than determinate cultivars. Hence the relationship between IGC and yield can vary depending on point of harvest relative to the effect of applied nitrogen on cultivar biomass partitioning (4.4.5.3), therefore, these factors must be accounted for when predicting yield from canopy data. The effect of applied nitrogen on IGC and yield also depends upon existing soil fertility; applied nitrogen increases yield via increases in IGC when the crop is nitrogen limited, yet under nitrogen replete conditions, additional nitrogen increases LAI with minimal increases in IGC, increasing canopy light interception (4.4.5.3). Conversely, stem density does not appear to alter the relationship between IGC and yield, with increases in stem density, resulting in earlier canopy closure, increasing yield via greater light interception (5.4.6.3).

On the other hand, the relationship between IGC and dry weight tuber yield was stronger in the Planting Density than Planting Date experiments (59.2 and 47.1 %, respectively once differences between cultivars and year of experiment had been accounted for), suggesting that the absence of variation in radiation environment reduces also variation in the relationship between IGC and yield. Thus, accounting for differences in incident radiation, in addition to plant capacity to intercept radiation, could provide a better relationship between canopy size and total biomass or yield, contrary to the hypothesis of Monteith (1977). Yet it is unclear if the strong relationships between intercepted PAR and yield reported by Fahem and Haverkort (1988), and van der Zaag and Doornbos (1987), are universal, as Zhou *et al.* (2017) reported a limited relationship across multiple experiments, despite strong relationships within individual experiments. Accounting for intercepted radiation may improve the ability to explain yield variation between highly contrasting environments (e.g. the Netherlands, Italy and Israel (van der Zaag & Doornbos 1987)), yet smaller differences between similar radiation environments may be less useful e.g. in experiments within the same region (Zhou *et al.* 2017). Hence, different methods of quantifying canopy light interception should be directly compared on the same dataset consisting of data from contrasting radiation environments, both within the same season (due to varied planting date) and from differing locations, and crops whose

growth varies within the same environment due to other differences in agronomy. Potential metrics to quantifying canopy light interception were identified in the Planting Date introduction (4.1.2) and include; cumulative PAR intercepted, cumulative 'useable' PAR (capped daily at the light saturation point), seasonal ground cover (IGC) and duration of complete or near-complete ground cover (GCDur90) and must be compared to ascertain if additional metric complexity accounts for additional variation in tuber yield described.

In summary, canopy quantification allows the analysis of potato yields in terms of canopy cover throughout the season, specifically by utilising IGC. However, cultivar, nitrogen rate and season length all modify the relationship between IGC and yield (Figure 137) and must be accounted for when predicting yield from canopy data. This work highlights that larger, more persistent canopies do not necessarily result in greater yields, but that variation in this occurs in a predictable fashion resulting from the interaction between cultivar determinacy, nitrogen rate and season length. Consequently, further experiments, with more frequent harvests, a wider range of cultivars across the determinacy spectrum, and more rates of nitrogen, are required to accurately predict variation in the relationship between IGC and yield relative to cultivar, nitrogen rate and time of harvest.

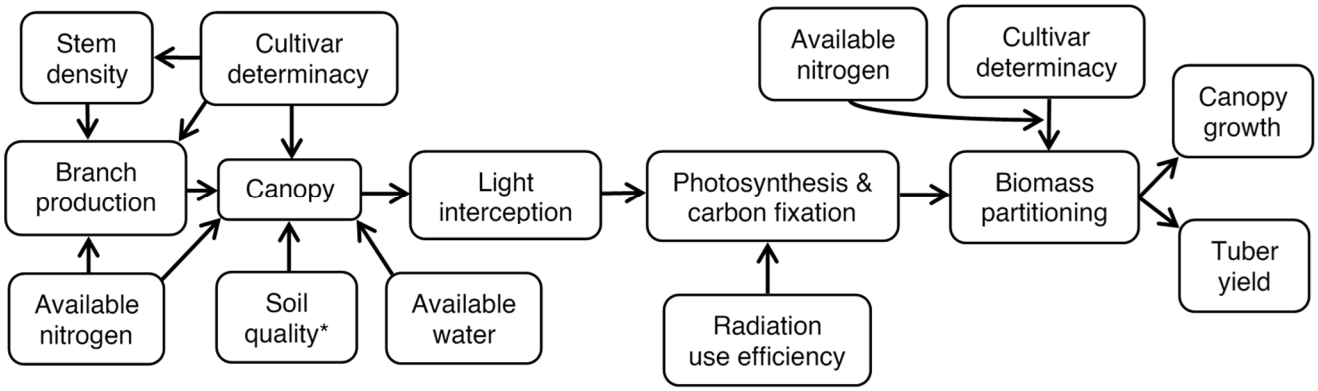

Figure 137. Illustration of the link between canopy and yield, with canopy size modifiers and yield modifiers. *Including degree of compaction, organic material, soil type and microbiology.

6.2 Agronomy-associated variation in canopy growth

6.2.1 Planting date

Varying planting date affects potato development in three main ways: altering temperature and daylength at each stage of canopy development and modifying potential growing season length.

In general, faster crop development can be expected at warmer temperatures, resulting in shorter crop cycles and lower yield potentials (Hatfield & Prueger 2015). This appears to be broadly true of potatoes with more rapid emergence and early growth at the later, warmer planting dates, though there was no relationship between mid-canopy expansion and air temperature (4.4.2.1). It is possible the contrasting responses of leaf appearance and leaf expansion to increased temperatures—greater under warmer (Kirk & Marshall 1992; Firman *et al.* 1995) and cooler (Fleisher & Timlin 2006) conditions, respectively—counteract each other, resulting in a minimal effect of temperature on whole canopy expansion. Reduced tuber yield has also been reported in response to small temperature increases, < 2 °C, under temperate conditions (Zhou *et al.* 2017), likely due to reduced HI (Kim & Lee 2019).

Secondly, the influence of small differences in daylength on canopy growth remains uncertain (4.4.1.1, 4.4.2.1 & 4.4.3.1.1). Although decreasing daylength may form part of an end of season signal, hastening the onset of senescence, differences between Estima and Maris Piper in senescence onset showed that decreasing daylength is not necessary initiate senescence (4.4.4.1). Hence, canopy growth responses to variation in the rate of change in daylength should be quantified in the UK, as describing photoperiod by the mean alone is likely to oversimply it's influence (Streck *et al.* 2007b).

Thirdly, delay in planting reduced the length of the growing season available, consequently reducing near-complete canopy duration, overall canopy size (as measured by IGC), total radiation intercepted and yield (4.4.5.2). Reductions in number of main axis leaves, sympodial branch length and sympodial branch leaves with delay in planting in Maris Piper, but not Estima, suggest that leaf production in indeterminate cultivars was more sensitive to changes in length of growing season than determinate cultivars (4.4.3.1.2). Differences in canopy growth between cultivars of differing determinacy will be explored further below (6.2.4). However, delaying planting by a week did not result in a seven-day reduction in GCDur90 (Figure 20), since rapid emergence under warmer conditions partially compensated for later planting (Figure 7), reducing the imperative to plant very early in February or March. Avoiding extremely early planting not only reduces the likelihood of frost damage, but also reduces the likelihood of damaging soil structure by cultivating under wet conditions and causing compaction which restricts canopy growth throughout the season (Stalham *et al.* 2007).

An additional consequence of delaying planting date is increased seed chronological age since seed for each subsequent planting date remained in stores, aging chronologically (Firman *et al.* 1991). This difference in seed age may confound some of the findings associated with later planting, since greater seed age is associated with a greater number of stems (Eshel & Teper-Bamnolker 2012). Seed stocks of the same cultivar, with the same mean tuber weight, can differ significantly in stem number (Figure 9) and this can affect subsequent canopy growth. Hence better tracking of the 'history' of potato seed, including mother tuber planting date, seed crop harvest date and details of storage conditions, would give growers more accurate expectations for crop performance and these details could also be included in a predictive yield model.

In summary, early planting results in a longer growing season in which canopy longevity and light interception can be maximised for greater yield, despite initially slow growth. Yet the trade-off between the benefits of a longer season and the risks of wet cultivation and frost damage varies between growers depending upon soil type, supply chain requirements and determinacy of cultivars being grown, and not all these factors are within grower control.

6.2.2 Planting density

Varying seed size and spacing results in a wide range of stem densities, additionally varying with seed chronological age (5.4.1). The relationship between seed mass, chronological age and number of stems produced also varies between cultivars (5.4.1.1) as illustrated by the Seed Size experiments (Figure 124) and the development of cultivar-specific seed rate guides (e.g. Maris Piper (Potato Council 2009)). This highlights the importance of seed age and mass when predicting crop stem density at planting.

The greatest influence of stem density and stem distribution occurred prior to canopy closure, with faster canopy expansion in greater, more evenly distributed stem populations (5.4.2). Consequently, it is beneficial for growers to attain their desired stem density using smaller, more closely spaced seed as this produces a more uniform canopy, with fewer gaps and more rapid expansion, than canopies resulting from widely spaced large seed. Narrower seed spacing is additionally beneficial as canopies are less likely to sustain large gaps should a seed be missed at planting or fail to emerge, as observed by Allen and Wurr (1992). However, the effect of stem density and distribution on whole-crop canopy production when plants are missing is

currently unknown (5.4.1.3) and further experiments are required to quantify how crop ability to produce a complete canopy when plants are missing varies with both stem density and distribution in determinate and indeterminate cultivars.

Whilst increasing stem density resulted in large structural changes within the canopy, with decreasing axillary branch production and greater stem length increases in canopy duration (5.4.4), IGC (5.4.6.1) and tuber yield (5.4.6.3) were slight and stem density had no effect upon the timing of senescence onset (5.4.5). Canopy growth appeared to be most sensitive to variation in stem density when stem density was lowest, appearing to plateau at *c.* 150 000 stems/ha. Differing results reported in the literature suggest that the response threshold differs between cultivars, likely with a lower threshold in indeterminate cultivars, due to greater foliage production capacity enabling 'gap-filling' at wider plant spacing (5.4.4.3). Consequently, future work should analyse the influence of stem density on each aspect of canopy growth using a non-linear approach similar to that of Engels *et al.* (1993), to identify the threshold below which decreasing stem density negatively affects canopy growth and persistence, and how this differs between cultivars.

In summary, stem density can be manipulated by varying seed size, spacing and chronological age and is determined at planting. Increasing stem density increases the rate of early canopy expansion, but the extent of increases in canopy variates following canopy closure with increasing stem density decreases. Thus, providing that canopy closure was not substantially delayed by low stem density, there is little effect of stem density on whole canopy size and functionality due to the flexibility of potato canopy production.

6.2.3 Applied nitrogen

Nitrogen is essential for plant growth and has a large influence upon canopy development by promoting leaf expansion, increasing canopy size, radiation interception and ultimately increasing final tuber yield (Allen & Scott 2001). Yet, despite differences in internal canopy structure, with more axillary branches and branch leaves, longer sympodial branches, with more sympodial branch leaves and greater LAI at the higher nitrogen rate (4.4.2.2), there was little overall difference in whole canopy growth between the nitrogen treatments in the Planting Date experiments (Figure 12). Whilst both canopy expansion and senescence were faster at the higher nitrogen rate, as found by both Khan *et al.* (2019a) and Ospina *et al.* (2014),

there was no difference in IGC, very little difference in duration of near-complete ground cover and a small increase in fresh weight yield. The limited effect of nitrogen on IGC reported here was unexpected since high applied nitrogen has previously been shown to increase the duration of complete canopy (MacKerron & Davies 1986; Firman 1987; Vos 2009; Ospina *et al.* 2014), increase IGC (Ospina *et al.* 2014) and enable greater radiation interception (Vos 2009), but may indicate that all treatments were supplied with sufficient nitrogen due to the relative abundance of plant available soil nitrogen (Table 5). Additionally, nitrogen is not the only limiting factor to potato growth and whilst low amounts of applied N (60 kg N/ha) have been shown to greatly increase intercepted PAR (Zhou *et al.* 2016), as the plant transitions from nitrogen deficiency (which can limit maximum canopy cover canopy growth (MacKerron & Davies 1986)) to nitrogen sufficient conditions, further increases in nitrogen can have limited effects as canopy growth is no longer nitrogen-limited and may adversely affect biomass partitioning to tubers (Fowler 1992).

In summary, when nitrogen-limited, applied nitrogen increases maximum canopy cover, extending duration of near-complete canopy cover and increases light interception, resulting in greater yield. However, in nitrogen-replete conditions, as in Expts 1 and 3, additional nitrogen can increase intercepted radiation by increasing LAI and increasing light interception within the canopy. Yet if applied greatly in excess, nitrogen can negatively affect biomass partitioning, particularly in indeterminate cultivars as discussed above (6.1.1).

6.2.4 Effect of cultivar and determinacy

Cultivar can have a large effect on growth as illustrated by the many differences in canopy variates between Estima and Maris Piper throughout Expts 1-5 (addressing thesis aim four). Differences between the two cultivars became more apparent as the season progressed with few differences in canopy expansion, followed by a consistently larger and more persistent canopy produced by Maris Piper relative to Estima (Figures 14 & 69), with greater GCDur90, IGC and total LAI. Mainstems and sympodial branches in Maris Piper were also longer than those of Estima (4.3.6.4), with more leaves on both (4.3.4.1 & 4.3.4.4), reflecting the capacity of indeterminate cultivars to continue leaf production for longer, partitioning a higher proportion of biomass to the canopy than determinate cultivars. These findings reflect those of Khan *et al.* (2019a) who reported that the duration of canopy expansion varied little with cultivar determinacy (described as maturity by Khan *et al.*), due to the strong influence of

environmental variables, particularly nitrogen rate, but that a high proportion of the variation in IGC was accounted for by genotypic variation. However, differences between cultivars of differing determinacy levels are not always clear, as observed in the Seed Size experiments and this likely resulted from poor determinacy classification. Consequently, better classification of determinacy is required, either by comparing IGC under a common nitrogen rate (Khan *et al.* 2013; Allison 2020), counting mainstem and main axis leaves (Allison 2020) or identifying QTLs associated with determinacy (Khan *et al.* 2019a). The rapid assessment of determinacy which these methods provide will enable more cultivars to be assigned accurately to determinacy groups, allowing more reliable predictions of expected patterns of canopy development to be made when there is little information about an individual cultivar available.

The differences in canopy production propensity between determinacy groups governs the interactions of cultivars with season length and available nitrogen (4.4.5.2). Since determinate cultivars produce fewer leaves (4.4.3.2.2), with smaller canopies (Figures 11 & 65) they require a shorter season length to complete their growth cycle, so are less sensitive to reductions in growing season length due to delayed planting than indeterminate cultivars (4.4.3.1.2 & 4.4.5.2). Whilst no interaction between planting date, applied nitrogen and cultivar was reported in Expts 1 and 3, the negative effect of a shorter season on indeterminate cultivar IGC and yield is typically greater as it is likely to result in harvest prior to senescence (Ospina *et al.* 2014), since both light interception and remobilisation of nitrogen from haulm to tubers were curtailed and this is exacerbated by applied nitrogen (Tiemens-Hulscher *et al.* 2014) (4.4.5.3). Further research, with more nitrogen treatments, comparing a wide range of cultivars, from all determinacy groups, is required to better quantify the interactions between determinacy, nitrogen application and season length, including the effects of varying season length on biomass partitioning by changing planting date and also varying the timing of harvest.

In summary, cultivar determinacy has a substantial effect on canopy production and determinate cultivars produce smaller, less persistent canopies than indeterminate cultivars, yet still achieve high yields due to greater biomass partitioning to tubers than haulm, relative to indeterminate cultivars (6.1.1). It is important for growers to be aware of cultivar determinacy to optimise crop agronomy, applying suitable quantities of nitrogen for the cultivar and available season length. Yet, in order to aid growers in this, determinacy levels must be accurately and more widely assigned. This ought to

become standard practice for breeders in cultivar development, since differing agronomy has a large influence on crop yield (Appendix 1, (Tompkins *et al.* 2019)) and poor, non-cultivar specific, agronomy will likely reduce yields.

6.3 Canopy architecture and whole canopy growth

6.3.1 Leaf appearance

Stem number per plant had a relatively large influence on the rate of mainstem leaf appearance, which decreased as stem number increased in each experiment (Figures 29 & 88), though scatter within the relationship suggests the importance of environmental influence (5.4.3.3). It is unclear from Expts 1-5 if the reduction in leaf appearance rate results from between-stem competition for tuber resources or light, hence further experiments which manipulate both tuber resources per stem and stem density are required.

Surprisingly, no significant effect of temperature on leaf appearance rate was found in the Planting Date experiments (Figure 28). It seems likely that the relationship reported by Kirk and Marshall (1992) and Firman *et al.* (1995) was obscured by variation in leaf appearance resulting from differing stem densities and nitrogen rates (4.4.2.1). The phyllochron data for Estima and Maris Piper additionally suggests that leaf appearance relative to thermal time is also quite variable (4.3.4.3). Many different factors including leaf position, daylength and carbon requirements of other plant organs (4.4.2.1) can influence phyllochron. Phyllochron may also be more variable in potato than in other species due to the variable number of meristems producing leaves simultaneously. This varies greatly with axillary branching in potato, unlike in grasses, which was the context in which the concept of the phyllochron was originally developed (Wilhelm & McMaster 1995). Further research also suggests that the relationship between temperature and leaf appearance is non-linear—both Fleisher *et al.* (2006a) and Streck *et al.* (2007) concluded that phyllochron based models for predicting leaf appearance were less accurate than non-linear temperature models; a modified β function (Fleisher *et al.* 2006a) and a non-linear multiplicative model (Streck *et al.* 2007a). Therefore, in order to accurately describe variation in leaf appearance rate, stem density, nitrogen rate and the non-linear relationship with air temperature and leaf appearance must be taken into account.

In both the Planting Date and Density experiments, rate of whole plant leaf appearance explained a limited proportion of the variation in canopy expansion as measured by

ground cover (4.4.2.3 & 5.4.3.2). Accounting for variation in leaf expansion would likely enable a more accurate relationship between variation at leaf-level in and whole canopy expansion to be established, since potato typically responds to environmental stress by altering leaf expansion rate, not leaf appearance (Vos & Biemond 1992; Jefferies 1993; Vos & van der Putten 1998; Fleisher *et al.* 2008). The spatial arrangement of leaves, including degree of overlap and how this varies with environmental conditions (Seijo-Rodríguez *et al.* 2017), would also need to be accounted for in order to accurately model whole canopy expansion, resulting in a highly mechanistic and complex model. However, this increased complexity is unnecessary since canopy expansion can be measured directly, by recording % GC, which is more closely related to canopy ability to intercept light. Hence rate of leaf appearance is of limited inherent agricultural importance, though of biological interest.

6.3.2 Branching

Axillary branch production in potato is highly indeterminate (Ifenkwe & Allen 1978b), enabling complete canopy cover to be achieved almost irrespective of plant spacing (5.4.4.1). Branch growth is likely heavily influenced by competition for radiation and under minimal shade branches are produced to maximise radiation interception by forming a complete canopy. Yet these large differences in branch production were not associated with differences in whole canopy growth, for example, earlier axillary branch production in Estima did not result in faster canopy expansion than in Maris Piper in Expt 1 (Table 26 & Figure 17). Similarly, increases in the number of axillary branches were not associated with increased canopy duration and had no significant effect on either onset of or rate of senescence (5.4.5). Additionally, the weak positive relationship between branch number and tuber yield identified by Minda *et al.* (2019), likely results from branch number acting as a proxy for canopy size and consequent light interception (Minda *et al.* 2019), not an inherent link between branch and tuber production. Furthermore, increased number of axillary branches has a limited effect on changes in whole canopy cover due to the self-regulatory nature of the potato canopy described below (6.3.3). Since increasing branch LAI results in decreased mainstem LAI, the proportion of components within the canopy is functionally unimportant as Fleisher (2006b) has reported that the ratio of mainstem to branch leaves within the canopy has little functional effect on whole canopy photosynthesis.

6.3.3 Leaf area index

Prior to canopy closure % GC increased with increasing LAI as expected (Khurana & McLaren 1982; Firman & Allen 1989a; Haverkort *et al.* 1991), although there was a high degree of scatter (4.3.5.4). Following canopy closure, LAI of individual canopy components varied substantially in response to changing agronomy, yet total LAI was less variable. The increased axillary branch LAI and concomitant decrease in mainstem LAI in response to both higher nitrogen rate and increased stem density suggest that canopy size is somewhat self-regulating, as shade cast by continued leaf production in the upper levels of the canopy reduces the lifespan of mainstem leaves, as previously discussed (4.4.3.2.3 & 5.4.4.3). However, this self-regulation appears to occur within limits set by cultivar and nitrogen availability (4.4.3.2.3).

Greater total LAI was weakly associated with both greater near-complete canopy cover duration and greater light interception at complete canopy cover in the Planting Date experiments (4.4.3.2.3), yet no linear relationship was found between total LAI and GCDur90 in the Planting Density experiments (5.4.4.3). Whilst this suggests that canopy duration is largely independent of canopy size, maximum LAI, as opposed to LAI at the onset of senescence (as recorded in Expts 1-5), may be a better predictor of canopy longevity although this remains uncertain (4.4.5.1). Further experiments could enable better quantification of the relationship between leaf area and canopy longevity by recording LAI weekly to identify maximum LAI and how it differs between agronomic treatments. Yet this may be unnecessary as changes both % GC and LAI similarly reflect increases in nitrogen and between-cultivar differences, and once LAI > 4 increases in LAI are of limited importance to canopy light interception (Khurana & McLaren 1982), which depends primarily on the uppermost leaves in the canopy (Fleisher *et al.* 2006b). In conclusion, variation in each of these canopy components alone explains a limited amount of variation in whole canopy development. Similar to the weak relationship between number of leaves on the main axis and near-complete canopy duration found across Expts 1-5, differences in canopy components can act as weak proxies for determinacy (4.4.5.1). These differences in canopy component growth can help explain differences in canopy growth retrospectively, but the strong influence of the environment and the high degree of plasticity in canopy production means that they are poor predictors of likely growth. Hence, well classified determinacy groups are better indicators of likely growth and should be an industry priority. Furthermore, whilst it may be possible to combine the

responses of individual canopy components to delayed planting, increased nitrogen or reduced stem density, in order to model growth within the canopy, this would generate a highly complex and mechanistic model, more useful to researchers than growers. Hence, it is more parsimonious to focus on variation in canopy cover and total light interception, not canopy composition when attempting to model yield in potato (Fleisher *et al.* 2006b),

6.4 Future prospects

This work has confirmed the utility of statistical models to describe differences in patterns of growth, identifying differences between and within cultivars in canopy expansion, whole season canopy cover (IGC) and the rate of senescence, meeting thesis aim one. Canopy growth responses to a wide range of UK agronomic conditions were recorded, identifying sources of variation in canopy size, light interception ability and ultimately variation in yield, addressing thesis aims two, three and four. However, limitations in relying solely upon the relationship between canopy capacity to intercept radiation and yield were also identified and so modifiers for the basic relationship are required (Figure 137) to account for differences in yield formation which occur after light interception. Further work to develop the function and use of the Canopy Quantification (CQ) model can be divided into three parts. Firstly, areas for improvement in model function are identified and explored. Secondly, future opportunities for applying the CQ model within research and agriculture are identified. Thirdly, ways in which data collected through canopy quantification can be applied in a predictive model, and the further steps required to develop a predictive model are discussed in the context of precision agriculture.

6.4.1 Further model developments

The CQ model is currently capable of describing the expansion, maintenance and senescence of potato canopies grown under a wide range of agronomic conditions. It is only unable to fit a curve to the data when canopy expansion is severely disrupted, characteristic of crops growing under extremely water or nitrogen limited conditions and which have difficulty producing complete ground cover, similar to the difficulties in model fit encountered by Khan *et al.* (2019a). Increasing the operating efficiency of the CQ model with greater automation is an important priority; automating the flow of data through the programmes required for canopy description in association with meteorological data. Within this work data were transferred between data processing

stages manually—from data sorting (Appendix 3, Programme 1), to curve fitting (Appendix 3, Programme 2) then calculation of linked meteorological values (Appendix 3, Programme 3). Combining the component programmes into a single programme will reduce user data-handling, increasing the speed of data processing and reducing the likelihood of user error.

The ability of the model to describe canopy data which deviates from the expected pattern of steady increase, maintenance and senescence of GC could also be improved. This may involve adapting the curve fitting programme to use a wider range of starting values to estimate the canopy expansion and senescence parameters (*B* and *D*, Figure 3 & Appendix 3, Programme 2). It may also include enabling the programme to pass over plot data which it cannot fit a curve to, returning missing values within the master output as well as returning the details of the plot data which has not been fitted separately to make the identification of poorly performing crops easier and faster.

Finally, the CQ programmes could be translated into a more widely used coding language to enable free access to the underlying code, allowing more researchers to utilise it without Genstat (VSN International 2014). Candidate languages include R and Python, as two widely used languages in research. Translation of the CQ model programme from Genstat to R or Python would require substantial testing to ensure that the curve fitting can be carried out with similar accuracy and that the new version has the same functionality and precision. Translation would also provide the opportunity to streamline the code and create a smoother data flow and clearer system for processing data to which a curve cannot be fitted, addressing the two challenges above. There is also the possibility of developing a more user-friendly interface which could allow users who are unfamiliar with programming to run the CQ model and to change the descriptive variates produced, potentially incorporating it into an existing canopy measurement app (such as Canopeo (Patrignani & Ochsner 2015)), to give growers information about whole canopy development and growth in addition to capturing % GC.

In summary, increasing automation of data flow through the canopy quantification process, improving the handling of atypical ground cover data and making the model more widely accessible could all improve model functionality.

6.4.2 Future model use

As a research tool, the CQ model can be applied to almost any experimental dataset where GC data has been collected at regular intervals throughout the growing season. This provides researchers with another perspective on variation in canopy growth and yield resulting from experimental treatments, granting deeper understanding of the developmental responses of the potato canopy to varying growing conditions. For instance, the CQ model could be used to investigate the influence of seed age (chronological and physiological) on canopy growth throughout the season. It would also be useful to extend the work herein and to quantify the variation in canopy development in a greater range of cultivars of differing determinacy in response to varying levels of available nitrogen, to determine how generalizable the differences reported between Maris Piper and Estima are. Additionally, output from the CQ model could also be analysed in a more nuanced fashion, using mixed effects modelling to quantify the effects of agronomic treatments whilst accounting for the multiple sources of variability present in agricultural experiments. For example a mixed-effects model may be more sensitive to the effects of differing components of planting date and allows analysis of temperature, daylength and season length variation in a single model, as illustrated by Zhou *et al.* (2017). Mixed-effects modelling may also be used to analyse non-experimental, crowd-sourced data, which is inherently more variable than experimental data but is essential to understanding variation in canopy and yield under commercial agricultural conditions.

Throughout this work, GC was measured within the field using a handheld grid as described by Burstall and Harris (1983), and whilst this method is suitable for tracking the canopy growth of experimental plots it is prohibitively expensive to scale up due to the labour required. In order to widen the scope of canopy analysis within research and make it an accessible tool for use within agriculture, photography can be used to allow more rapid GC data collection at different levels. At field level, digital photography (Campillo *et al.* 2008) and smart-phone based applications (Canopeo (Patrignani & Ochsner 2015) and CanopyCheck, no longer available (Allison *et al.* 2013)) have been used to measure green crop canopy cover in tomatoes (Campillo *et al.* 2008), grasslands (Xiong *et al.* 2019) and potatoes (Allison *et al.* 2013), with a high degree of accuracy when used correctly ($R^2 > 0.95$, 0.97 and 0.98 respectively). Since image processing software is incorporated within both apps the user is rapidly provided with % GC output, yet the scope of data collection is still limited by labour,

as plots are photographed individually and, as found by Allison *et al.* (2013), lack of user experience can reduce data collection accuracy. Nevertheless, smartphones provide a useful platform for GC data collection and automate collection of meta-data (e.g. date and location), improving data-flow within analysis. Moreover, if combined with the CQ model in a single app, have the potential to make a large difference to the farming practise of a grower—tracking crop development, enabling yield predictions and allowing end-of-season diagnosis of poor yield—without access to largescale and expensive crop monitoring systems.

Data collection on a larger scale is enabled by unmanned aerial vehicles (UAVs), which can be flown over larger areas, using a wide range of sensors to map spatial variability of crop growth (Maes & Steppe 2019). UAVs offer the potential to map spatial variability of crop development, in order to target agricultural inputs, e.g. irrigation, herbicides, fertilizers with greater precision, reducing farmer inputs and increasing yields (Maes & Steppe 2019). In potato, UAVs have been used to assess variation in plant emergence with a high degree of accuracy (Li *et al.* 2019) and over 20 companies offer their services to farmers to help monitor crop development (Postscapes 2019) though the accuracy of these services is typically unverified. Challenges to accurate GC data analysis with UAV derived data include expense, legal restrictions, physical restrictions upon flights (high wind or proximity of roads or powerlines) and inaccurate data processing. For instance, raw photographs from multiple flight passes must be 'stitched' together to provide an image of a single field, accounting for differences in UAV height and camera angle. The field must then be subdivided to identify variability within it, but divisions are not always suitably small; in one example crops were subdivided into 25 m^2 squares, some of which included field margins and headlands, resulting in erroneous readings and GC could also vary considerably within the large squares (Smart 2019). Hence, whilst UAVs offer growers opportunity for farm-wide canopy quantification, current image processing techniques are unrefined and substantial improvements are required, as noted by Smart (2019).

Another opportunity for wide-scale data collection arises from regular field operations such as crop spraying. Mounting cameras on crop sprayers, or other farm equipment which regularly traverses the crop, could increase the quantity of GC data it is possible to collect. This would enable growers to monitor whole crops without extensive investments in equipment or time and then compare crop development both within and between fields to identify potential areas of reduced yield. Equipping growers to

collect and interpret canopy data using the CQ model has the potential to change the focus of research as more growers are empowered to identify differences within the growth of their crops and investigate their causes through more farmer-centric research, as proposed by Sylvester-Bradley *et al.* (2019). Identifying differences in canopy growth early in the season may also help identify areas of a crop which are experiencing water shortage or are nitrogen deficient, allowing earlier intervention to reduce or prevent loss of yield. Yet, significant work in trialling and developing the technology to collect and analyse GC data from farm equipment is required first.

In summary, scaling up GC data collection using UAVs or sprayer-mounted cameras has the potential to quantify and then help address variability in canopy growth at the field, farm, regional and national scale. When linked to agronomic data, this large quantity of canopy data could help increase national yields as best practise is identified and adopted. Yet, the accuracy of data collection is not currently sufficient to be relied upon for identifying variation in crop canopy growth. On a smaller scale, the CQ model can describe canopy data within experiments and crops, increasing understanding of the variation in whole canopy growth, light interception and subsequent differences in yield.

6.4.3 Predictive model development

Lastly, the greater understanding of canopy development acquired during this work will enable the development of a predictive model which predicts expected canopy growth throughout the season based on initial agricultural conditions. Such a model could then be linked to an existing yield model, using the differences in canopy growth (caused by agricultural conditions) to generate agronomy-specific yield predictions for individual crops. Details of crop planting date, expected stem density, cultivar determinacy, applied nitrogen, likely water availability, and seed chronological and physiological age determine expected canopy growth and duration, setting the maximum potential light interception and expected yield, which can be further modified by factors affecting the post-light interception processes of yield formation (Figure 137). Yet, more data is required for accurate parameterisation of a predictive canopy growth model, particularly focusing on interactions between planting date, determinacy, and nitrogen rate. Experiments to better predict changes in canopy growth are discussed above, and include better quantification of the effect of applied nitrogen on biomass partitioning in determinate and indeterminate cultivars

throughout the season (6.2.4) and identification of the thresholds at which canopy growth becomes sensitivity to stem density in cultivars of differing determinacy (6.2.2).

Moreover, in yield models which use intercepted radiation to predict yield, accuracy of predictions is improved by using a model of canopy growth which reflects differences caused by growing conditions rather than a reference curve. This is due to the typically idealised patterns of canopy growth in reference curves, which may not be possible under the actual growing conditions. For example, it has been suggested that the yield prediction model within the Management Advisory Package for Potatoes (Marshall 2001) fell out of use as the reference canopy curve, from which light interception and yield were calculated, was based on the growth of Maris Piper, under ideal conditions and did not reflect the growth of other cultivars under more variable agricultural conditions (Allison 2019, personal communication).

More accurate yield models have the potential to increase the stability of the potato supply chain as growers will be able to state expected yields with greater certainty, allowing buyers further up the supply chain (for processing, wholesale and retail) to better plan how to meet market demands. A recent project analysing yield differences by the Waste and Resources Action Plan (WRAP) illustrates how forecasting could be useful, both in aiding decisions within the supply chain and reviewing the impact of farm management decisions (Tompkins *et al.* 2019). Additionally, the understanding of variability in crop canopy growth and yield that would result from widespread canopy quantification and modelling will help to improve yield predictions as variation in crop growth can be accounted for, as also noted by Al-Gaadi *et al.* (2016).

Additionally, expected canopy development, as predicted by a model, can act as a benchmark to measure crop development against throughout the season. This should enable growers to identify sub-optimal patterns of growth early in the season, allowing them to respond more effectively. For example, soil compaction slows canopy expansion (Stalham *et al.* 2007) and whilst soil compaction cannot be ameliorated within the growing season, irrigation can be reduced on heavy soil to avoid waterlogging and further reductions in growth and yield (Stalham *et al.* 2007).

The greater information about crop development which the CQ model offers is central to the ideals of precision farming which aims to apply the right management practices at the right to time to the right place with the right intensity (Maes & Steppe 2019). Whilst the CQ model may not provide immediate solutions, accurate records of canopy

growth from known agricultural conditions allow growers insight into the causes of a given farming outcome in order to improve and adapt practise in the following season.

6.5 Conclusions

Canopy quantification is a useful tool in research and agriculture, capturing variation in canopy growth as potato crops respond to a wide range of genotypic and environmental variables. Due to the strong link between radiation interception and dry matter production, insight into canopy growth can help to identify mechanisms underlying yield variation, although modifiers of radiation use efficiency and biomass partitioning must also be considered.

Agronomic variables such as planting date, nitrogen rate and stem density result in considerable variation in canopy branch and leaf production and in whole canopy growth dynamics. Yet understanding variation in within canopy growth is not essential to understanding and predicting variation in whole canopy growth, since these factors are typically varied in order to maintain whole canopy cover (6.3) and because the proportion of canopy components does not have a significant effect on canopy function (Fleisher *et al.* 2006b). Greater understanding of variation in canopy growth can increase the relevance of potato yield models to individual crops, helping improve supply chain security with more accurate yield forecasts and greater insights for growers into the impacts of crop management decisions. The simple input required to quantify potato growth using the CQ model also allows the analysis of archival data allowing the comparison of many cultivars grown in different years. For example, the CQ model identified limited variation between cultivars in duration of early canopy expansion but a wide range within cultivars as stem density increased in the Seed Size experiments. The analysis also showed that influence of stem density was stronger prior to canopy closure but varied considerably between cultivars and diminished as the season progressed. Comparison of Estima and Maris Piper illustrated differences in canopy growth in the second half of the season, including greater sensitivity to season length and greater biomass partitioning to the canopy in indeterminate than determinate cultivars, highlighting the importance of cultivar determinacy to crop agronomy.

Earlier planting has the potential to increase yield, both by increasing canopy duration (particularly in indeterminate cultivars) and resulting in a larger canopy earlier in the season, when incident radiation is typically greatest due to longer daylength. Yet

emergence relative to planting is delayed in the cooler soil conditions of earlier planting and planting a month earlier does not result in a month of additional canopy cover, so very early planting may not be worth the increased risk of soil compaction and frost damaging subsequent canopy growth.

The CQ model can be used in both research and agriculture since it does not require specialist equipment for data collection, although currently data analysis is restricted to Genstat users. A key future development of the model will be to convert the programme into a more widely used coding language—for use in research—and incorporate it into a canopy ground cover measuring app—for use in agriculture. Finally, this method of analysis can be applied to ground cover data from any source, providing that it is accurate and collected regularly, allowing the analysis of larger datasets and to begin to identify variation in canopy growth within and between farms, to identify best practise in potato agronomy and, ultimately, reduce variability in potato yields across the UK and further afield.

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8 APPENDICES

APPENDIX 1

Within-cultivar yield variability

A large survey of commercial crops was carried out over five years (2010-14) and illustrates the variation in yield between and within cultivars. The survey covered 363 crops, including seven cultivars (Arsenal, Hermes, Lady Claire, Lady Rosetta, Saturna, Shelford and VR808) with a minimum of 20 crops per cultivar. There was limited variation in mean fresh tuber yield between cultivars (6.9 t/ha, Figure 138). The mean yield of Arsenal and Hermes were significantly different from Lady Rosetta, but there were no significant differences between other pairs of cultivars (ANOVA, $P = 0.002$ and Tukey's HSD) and standard deviation in yield within each cultivar ranged from 9.02-11.3 t/ha (Table 88). This indicates a high degree of within-cultivar yield variability, likely due to differences in agronomy between individual crops surveyed, and limited yield differences between cultivars.

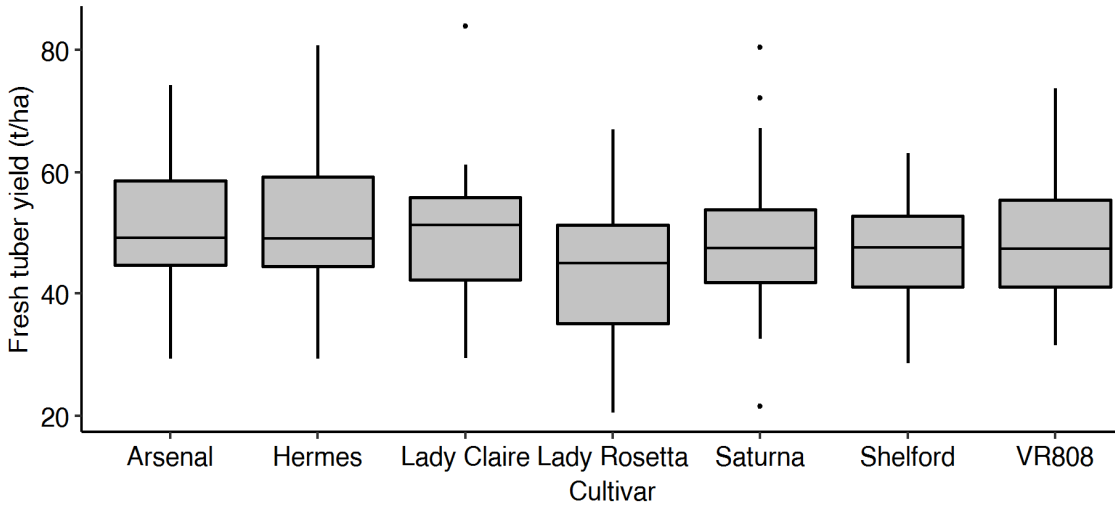

Figure 138. Boxplot of observed yield at a mid-season harvest for seven commercially grown cultivars. Treatment medians are shown as horizontal bars, box shows interquartile range (IQR, with hinges at the 25th and 75th percentiles), whiskers show the full range of the data and values more than 1.5 x IQR outside the IQR are plotted individually as outliers.

Table 88. Mean tuber yield and standard deviation for seven commercially grown potato cultivars.

Cultivar	Mean yield (t/ha)	Standard deviation (t/ha)
Arsenal	50.5	10.3
Hermes	50.9	11.3
Lady Claire	49.8	11.2
Lady Rosetta	44.0	11.2
Saturna	48.4	10.8
Shelford	46.7	9.02

APPENDIX 2

Exploratory Gompertz curve fitting

The Gompertz equation and adaptations of the equation have been used to describe the growth of crop canopies, including lettuce (Tei *et al.* 1996), sugar beet (Werker & Jaggard 1997) and potato (Bojacá *et al.* 2011). The ability of both models described by Werker and Jaggard (1997) and Bojacá *et al.* (2011) to fit curves to potato ground cover data throughout the whole season was explored in Excel. Raw data and the Gompertz curves were plotted in Excel, improving curve-fit with incremental changes to parameter values in order to identify initial values from which the optimum fit of individual potato crops or experimental plots could be iteratively estimated in Genstat using the 'RCYCLE' directive. Raw data, from a nitrogen and irrigation response experiment conducted in 2015 at NIAB CUF (Firman 2016), were used to illustrate curve fit to three canopies with contrasting canopy growth forms.

Simple Gompertz equation

Bojacá *et al.* (2011) were able to fit a simple Gompertz curve (Equation 8) to ground cover data during potato canopy expansion with reasonable success, using a non-linear mixed effects model to capture the variation between plots and locations. Relative ground cover is represented by y, with values between 1 and 0, at thermal time after planting, t. Maximum ground cover achieved is represented by the upper asymptote, a, c is the maximum relative growth rate, measured at the inflection point, and d is the thermal time at which the inflection point occurs. Figure 139 illustrates that whilst the simple Gompertz curve can describe canopy expansion with a degree of accuracy, it is unable to describe the latter half of canopy growth once senescence has begun as ground cover, y, tends to a positive maximum, a, as thermal time, t, tends to infinity, and there is no decay function within the equation. Consequently, the simple Gompertz curve is unsuitable for use without amendments when describing canopy growth throughout the whole season.

Equation 8. Gompertz equation, as used by Bojacá *et al.* (2011) to describe canopy expansion.

$$y = a \times e^{\left(-e^{c(d-t)}\right)}$$

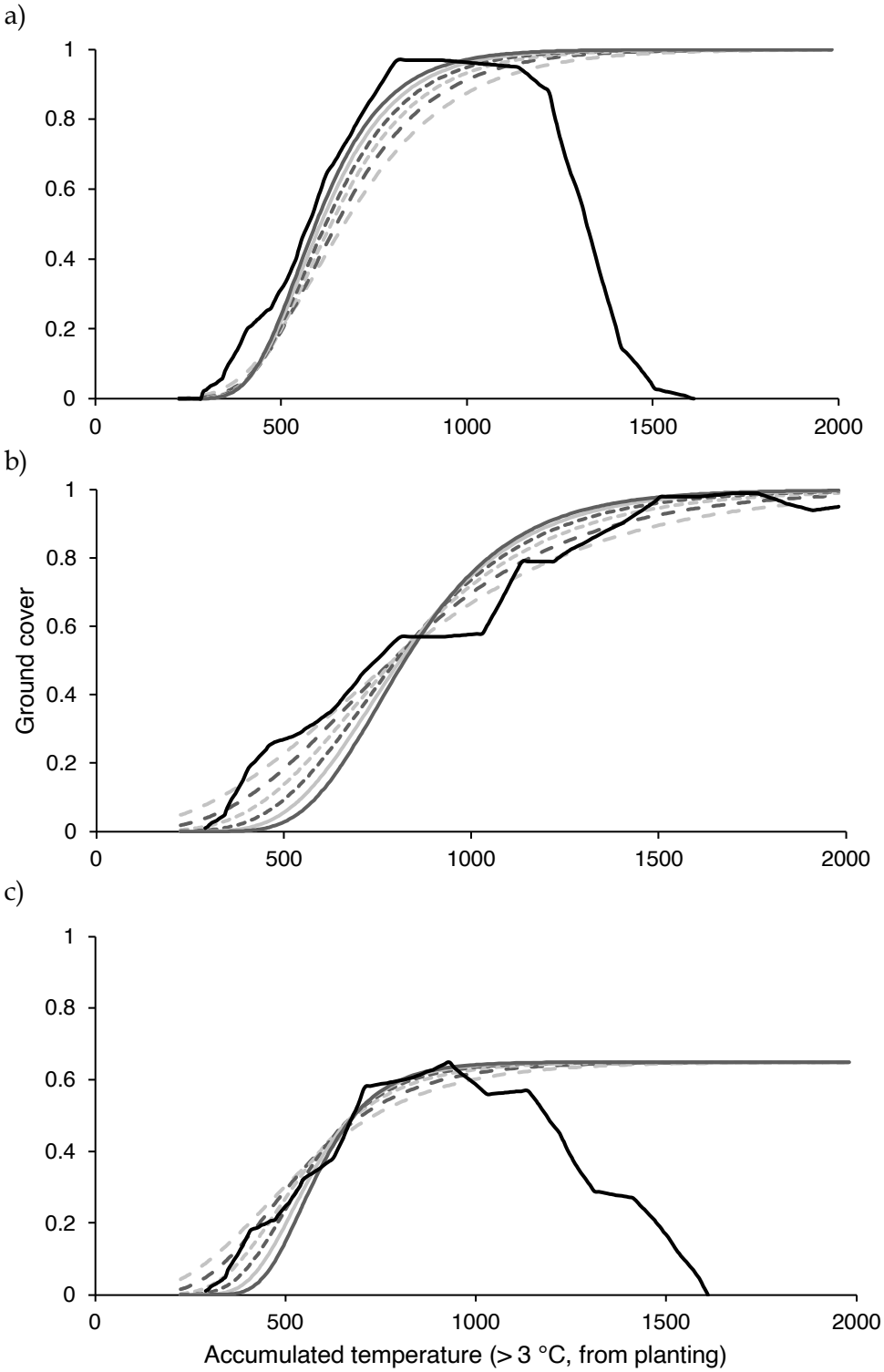

Figure 139. A simple Gompertz curve fitted to example ground cover data. Representative plots of (a) 'normal', (b) 'non-senescing' and (c) 'stunted' canopies grown at NIAB CUF in 2015 (Firman 2016) (Estima, unirrigated at 150 kg N/ha; Cara, unirrigated at 20 kg N/ha and Estima, irrigated 30 kg N/ha, respectively). Raw ground cover, ——; and examples 1, – –; 2, – –; 3, – –; 4, – –; 5, —— and 6, ——. Parameter values for each example curve are shown in Table 89.

Table 89. Parameters used to estimate example illustrative Gompertz curves as described by Equation 8.

		Example parameter values					
Curve	Parameter	1	2	3	4	5	6
(a) 'normal'	a	1.00	1.00	1.00	1.00	1.00	1.00
	c	0.0050	0.0058	0.0063	0.0068	0.0073	0.0078
	d	595	585	575	565	555	545
(b) 'non-senescing'	a	1.00	1.00	1.00	1.00	1.00	1.00
	c	0.0026	0.0031	0.0036	0.0041	0.0046	0.0051
	d	650	670	690	710	730	750
(c) 'stunted'	a	0.65	0.65	0.65	0.65	0.65	0.65
	c	0.0046	0.0056	0.0066	0.0076	0.0086	0.0096
	d	440	460	480	500	520	540

Gompertz-like function

Werker and Jaggard (1997) developed a Gompertz-like function (Equation 9) to represent the rising and falling growth of the sugar beet canopy. Relative ground cover is represented by y, with values between 0 and 1, μ_0 represents initial relative growth rate and y_0 is the initial size of y, at time t_0. The speed at which the initial growth rate, μ_0, approaches the final growth rate, $\mu_{\min}$, as t tends to infinity, is described by the rate constant, k. Figure 140 illustrates that the Gompertz-like function can describe initial canopy growth, with a relatively good fit in Figure 140a and c, which improved as parameter values were adjusted. However, Equation 9 was unable to describe a flat plateau in the curve generated by sustained complete ground cover and characteristic of a high yielding maincrop potato crop (Figure 140a). Nor was Werker and Jaggard's curve able to describe the rapid canopy senescence often exhibited by potato crops, as seen in the discrepancy between the raw data and estimated canopy curves in Figure 140a. Genstat was unable to fit a curve using the 'RCYCLE' directive, suggesting that the discrepancy between raw and fitted values was too great.

Equation 9. Gompertz-like function as described by Werker and Jaggard (1997).

$$y = y_0 e^{\left(\mu_{min}(t-t_0)+\frac{\mu_0-\mu_{min}}{k}\left(1-e^{(-k(t-t_0))}\right)\right)}$$

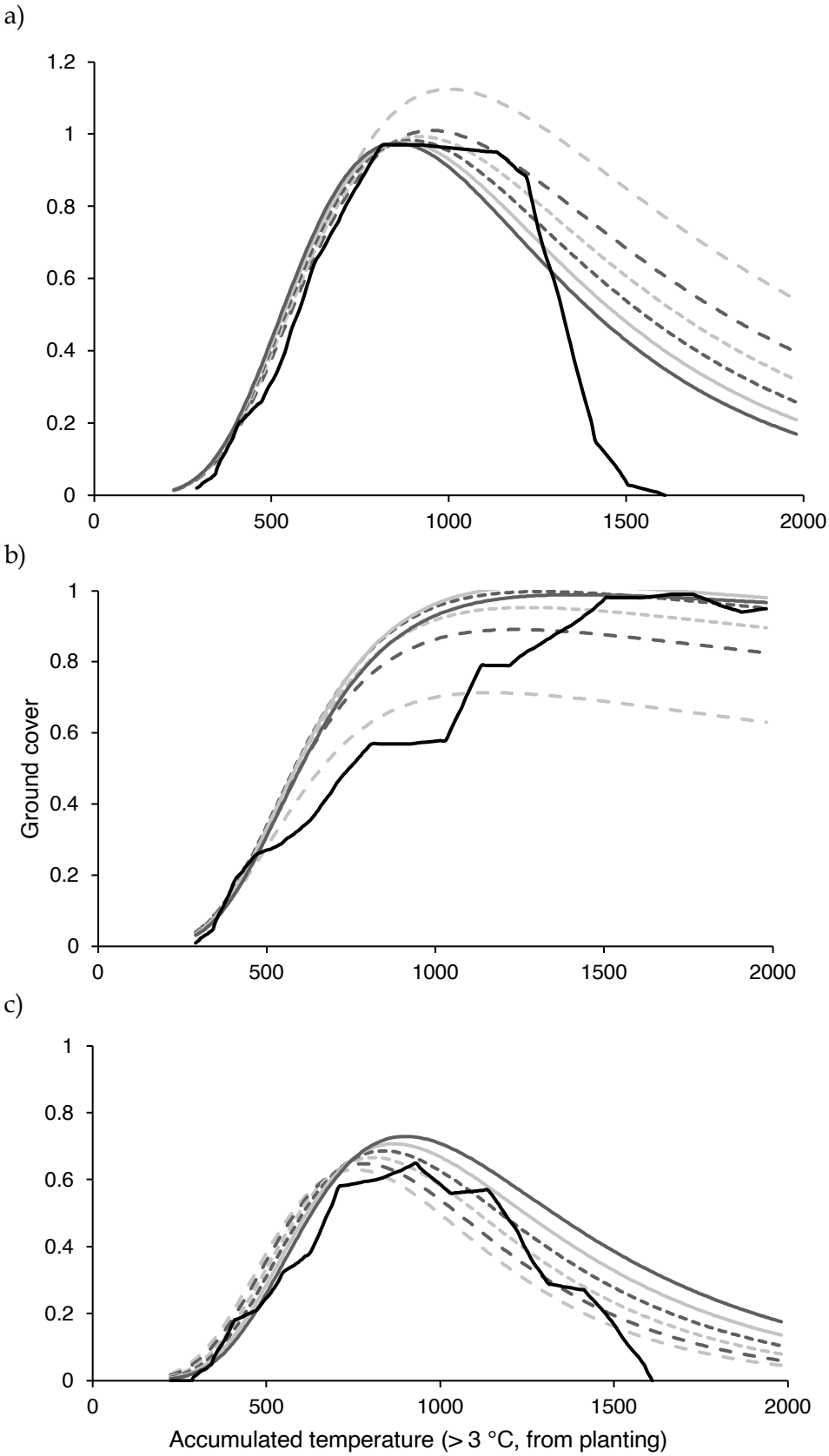

Figure 140. A Gompertz curve fitted to example ground cover data. Representative plots of (a) 'normal', (b) 'non-senescing' and (c) 'stunted' canopies grown at NIAB CUF in 2015 (Firman 2016) (Estima, unirrigated at 150 kg N/ha; Cara, unirrigated at 20 kg N/ha and Estima, irrigated 30 kg N/ha, respectively). Raw ground cover, ——; and examples 1, – –; 2, – –; 3, – –; 4, – – –; 5, —— and 6, ——. Parameter values for each estimate are shown in Table 90.

Table 90. Parameters used to estimate example Gompertz-like curves as described by Equation 9.

		Example parameter values					
Curve	Parameter	1	2	3	4	5	6
(a) 'normal'	μ_{min}	-0.0010	-0.0012	-0.0014	-0.0016	-0.0018	-0.0020
	μ_0	0.0300	0.0302	0.0304	0.0306	0.0308	0.0310
	k	0.00395	0.00398	0.00396	0.00394	0.00392	0.00390
	y_0	0.00135	0.00137	0.00139	0.00141	0.00143	0.00145
	t_0	132	132	132	132	133	134
(b) 'non-senescing'	μ_{min}	-0.00020	-0.00014	-0.00012	-0.00010	-0.00008	-0.00006
	μ_0	0.0350	0.0360	0.0370	0.0380	0.0390	0.0400
	k	0.00500	0.00501	0.00502	0.00503	0.00504	0.00505
	y_0	0.000800	0.000788	0.000688	0.000588	0.000488	0.000388
	t_0	130	130	130	130	130	130
(c) 'stunted'	μ_{min}	-0.0027	-0.0025	-0.0023	-0.0021	-0.0019	-0.0017
	μ_0	0.0290	0.0291	0.0292	0.0293	0.0294	0.0295
	k	0.00395	0.00397	0.00399	0.00401	0.00403	0.00405
	y_0	0.0022	0.0021	0.0020	0.0019	0.0018	0.0017
	t_0	132	142	152	162	172	182

Summary

In summary, both curves provided a good fit to the canopy expansion data and were able to describe the rate of canopy expansion, capable of describing crops where the canopy did not senesce, as in Figure 139b and Figure 140b, but neither curve was sufficient to describe growth throughout the season. It can be concluded from visual inspection that neither the Gompertz equation not the Gompertz-like function are able to describe the potato canopy in the latter half of the season, either not allowing for any canopy senescence or predicting a higher maximum canopy and the earlier but less rapid, senescence. Hence, neither equation explored here was suitable for describing potato canopy growth throughout the whole season and alternative equations must be considered.

APPENDIX 3

Examples of the Genstat programmes used to quantify canopy growth are below.

Programme 1 – data sorting

This programme sorts raw canopy data based on maximum and final ground cover values for each plot. Plots are separated into 'short' with maximum GC values < 75 % (short), 'non-senescing' with final GC values > 90 % (high-ending, HE) and 'normal' which achieve maximum GC > 75 % with final GC values < 90 % (low-ending, LE).

Read data in

```
SET [WORKINGDIRECTORY='f:/PhD/Reference Crop/CanopyQuantification/All
years/Analysis inc SMD/all data/CanVar']
"************************************************************************
 NoJD = number of dates with GC measurments, NoY = number of years,
 NoP = number of plots in a given year, NoPY = sum of number of plots from
each year
************************************************************************"
Open 'RefCrop_data93-94.txt'; Channel=2; File=In; Width=350 "GC raw data"
scalar [value=2]NoE
text plotname, variety, waterTreat, sstock, ssize
factor [levels=NoE; labels=!t('RefCrop1993', 'RefCrop1994')]exp "list must be
in the same order as data in files"
Read [Channel=2] exp, plotname, variety, waterTreat, pdate, emdate, nrate,
sstock, ssize, smass, sspace, stemden, year, haulmDW, tuberDW, gc[1...24];
Frepresentation=lab,lab,lab,lab,lev,lev,lev,lab,lab
Close channel=2

Open 'RefCropDates_93-17.txt'; Channel=2; File=In; Width=350 "no measurements
taken in each year"
factor [levels=NoE; labels=!t('RefCrop1993', 'RefCrop1994')]dexp
Read [Channel=2] dexp, dyear, jd[1...24]; Frepresentation=lab
Close channel=2

scalar [value=0]NoY
scalar [value=0]NoPY
scalar [value=24]NoVR "number of GC placeholder values in dataset"
```

For each experiment

```
For y=1...NoE "check number of experiments is correct at NoE"
    calc NoY=NoY+1
    Subset [dexp.eq.y] jd[1...NoVR]; jdY[y][1...NoVR]

    print jdY[y][1...NoVR]

    Variate [nvalues=NoVR] uJDs[y] "uncut lists of JDs"
    Equate jdY[y]; uJDs[y]
    Calc NoJD[y]=NoVR-nmv(uJDs[y]) "number of non-missing values for each
    year"

    Variate [nvalues=NoJD[y]] JDs[y]
    Equate uJDs[y]; JDs[y] "only non-missing JDs"

    Subset [exp.eq.y] gc[1...NoJD[y]]; gcY[y][1...NoJD[y]] "non-missing GCs &
    JDs"
    Calc NoP[y]=nvalues(gcY[y][1]) "Number of plots per year"
    Variate [values=1...NoP[y]] pmark[y] "marker to split plots for each year"
       calc NoPY=NoP[y]+NoPY

       subset [exp.eq.y] gc[1...NoVR]; gcYa[y][1...NoVR]
```

```
        "splitting experiment and variety lists by year"
        Subset [exp.eq.y] emdate,exp,variety; EMdateY[y],expY[y],varietyY[y]

        "structures for storing all tidied GC values"
```

For each plot identify the last GC value

```
    For n=1...NoP[y] "plots 1 to end"

          Subset [pmark[y].eq.n] gcY[y][1...NoJD[y]]; gcIP[1...NoJD[y]][n]
          "split up values for each plot"
          Append [PGC[n]] gcIP[1...NoJD[y]][n] "join values from each plot"
          "calculating max canopy extent for each crop from raw data"
          calc cropMax[n]=max(PGC[n])
          Variate [values=1...NoJD[y]] dmark

          Subset [pmark[y].eq.n] gcYa[y][1...NoVR]; gcI[1...NoVR][n] "split up
          values for each plot, inc missing values"

          for o=NoVR...1 "last measurement to first"
                   if gcI[o][n].gt.0
                            if o.eq.NoVR
                               calc GCfinal[n]=gcI[o][n]
                               calc JDfinal[n]=jdY[y][o]
                            else
                               calc q=o+1
                               calc nextValue[o][n]=gcI[q][n]
                               if nextValue[o][n].eq.0
                                  calc GCfinal[n]=0
                                  calc JDfinal[n]=jdY[y][q]
                               else
                                  calc GCfinal[n]=gcI[o][n]
                                  calc JDfinal[n]=jdY[y][o]
                               endif
                            endif
                            exit
                   elsif gcI[o][n].eq.0
                            calc p = o-1
                            calc prevValue[o][n] = gcI[p][n]
                            if prevValue[o][n].eq.0
                                     calc gcI[o][n] = 0/0
                            elsif prevValue[o][n].gt.40
                                     calc gcI[o][n] = 0/0
                            endif
                   endif
          endfor "o"
    endfor "n"

    For i=1...NoVR
          variate [nvalues=NoP[y]]  gcAY[i][y]
          Equate gcI[i];gcAY[i][y]
    Endfor "i"

    variate [nvalues=NoP[y]] nEMDate[y], nGCfinal[y], nJDfinal[y], ncMax[y]
    equate EMdateY[]; nEMDate[y]
    equate GCfinal, JDfinal; nGCfinal[y], nJDfinal[y]
    equate cropMax;ncMax[y]
    print expY[y], plotname, nGCfinal[y], nJDfinal[y], ncMax[y]

endfor "y"

For i=1...NoVR
   variate [nvalues=NoPY]  gcA[i]
   Equate gcAY[i];gcA[i]
Endfor "i"

variate [nvalues=NoPY]EMDates, PDates, EndGC, JDlast, cMax
equate nEMDate, pdate;EMDates, PDates
equate ncMax;cMax
```

```
equate nGCfinal, nJDfinal;EndGC, JDlast
text [nvalues=NoPY] Experiment, PlotName, Variety
Equate exp,plotname,variety;Experiment,PlotName,Variety
```

Sort data depending on final GC value and output in separate .csv files

```
"Plots harvested before passing 90% GC during senescence"
subset [condition = EndGC.ge.90] Experiment, PlotName, Variety, waterTreat,
PDates, EMDates, nrate, sstock, ssize, smass, sspace, stemden, year, haulmDW,
tuberDW, EndGC, JDlast, cMax, gcA[1...NoVR]; hExperiment, hPlotName, hVariety,
hWaterTreat, hPDates, hEMDates, hNRate, hSeedStock, hSeedSize, hSeedMass,
hSeedSpace, hStemDen, hYear, hHaulmDW, hTuberDW, hEndGC, hJDlast, hcMax,
hGC[1...NoVR]

TEXT OutFile; VALUE='19.5.15_RefCrop1993-2017_HE.csv'
Export [Outfile=OutFile; CSVOPTIONS=noquotes] hExperiment, hPlotName,
hVariety, hWaterTreat, hPDates, hEMDates, hNRate, hSeedStock, hSeedSize,
hSeedMass, hSeedSpace, hStemDen, hYear, hHaulmDW, hTuberDW, hEndGC, hJDlast,
hcMax, hGC[1...NoVR]

"Plots harvested after passing 90% GC during senesence"
subset [condition = EndGC.lt.90] Experiment, PlotName, Variety, waterTreat,
PDates, EMDates, nrate, sstock, ssize, smass, sspace, stemden, year, haulmDW,
tuberDW, EndGC, JDlast, cMax, gcA[1...NoVR];lExperiment, lPlotName, lVariety,
lWaterTreat, lPDates, lEMDates, lNRate, lSeedStock, lSeedSize, lSeedMass,
lSeedSpace, lStemDen, lYear, lHaulmDW, lTuberDW, lEndGC, lJDlast, lcMax,
lGC[1...NoVR]

"plots which don't reach 75% GC - shorties"
subset [condition = lcMax.le.75] lExperiment, lPlotName, lVariety,
lWaterTreat, lPDates, lEMDates, lNRate, lSeedStock, lSeedSize, lSeedMass,
lSeedSpace, lStemDen, lYear, lHaulmDW, lTuberDW, lEndGC, lJDlast, lcMax,
lGC[1...NoVR];slExperiment, slPlotName, slVariety, slWaterTreat, slPDates,
slEMDates, slNRate, slSeedStock, slSeedSize, slSeedMass, slSeedSpace,
slStemDen, slYear, slHaulmDW, slTuberDW, slEndGC, slJDlast, slcMax,
slGC[1...NoVR]

TEXT OutFile; VALUE='19.5.15_RefCrop1993-2017_shorties.csv'
Export [Outfile=OutFile; CSVOPTIONS=noquotes] slExperiment, slPlotName,
slVariety, slWaterTreat, slPDates, slEMDates, slNRate, slSeedStock,
slSeedSize, slSeedMass, slSeedSpace, slStemDen, slYear, slHaulmDW, slTuberDW,
slEndGC, slJDlast, slcMax, slGC[1...NoVR]

"plots which don't reach 75% GC - shorties"
subset [condition = lcMax.gt.75] lExperiment, lPlotName, lVariety,
lWaterTreat, lPDates, lEMDates, lNRate, lSeedStock, lSeedSize, lSeedMass,
lSeedSpace, lStemDen, lYear, lHaulmDW, lTuberDW, lEndGC, lJDlast, lcMax,
lGC[1...NoVR];flExperiment, flPflotName, flVariety, flWaterTreat, flPDates,
flEMDates, flNRate, flSeedStock, flSeedSize, flSeedMass, flSeedSpace,
flStemDen, flYear, flHaulmDW, flTuberDW, flEndGC, flJDlast, flcMax,
flGC[1...NoVR]

TEXT OutFile; VALUE='19.5.15_RefCrop1993-2017_LE.csv'
Export [Outfile=OutFile; CSVOPTIONS=noquotes] flExperiment, flPflotName,
flVariety, flWaterTreat, flPDates, flEMDates, flNRate, flSeedStock,
flSeedSize, flSeedMass, flSeedSpace, flStemDen, flYear, flHaulmDW, flTuberDW,
flEndGC, flJDlast, flcMax, flGC[1...NoVR]

stop
```

Programme 2 – ground cover curve fitting

This programme is one of three and iteratively fits the canopy quantification (CQ) curve to 'normal' raw GC data, then calculates descriptive variates from the curve for each plot. The other programmes are adapted to fit the CQ curve to 'short' and 'non-senescing' data.

Read data in

```
SET [WORKINGDIRECTORY='f:/PhD/Reference Crop/CanopyQuantification/All
years/Analysis inc SMD/all data/CanVar']
"************************************************************************"
"NoJD = number of dates with GC measurments, NoY = number of years,
 NoP = number of plots in a given year, NoPY = sum of number of plots from
each year"
scalar [value=24]NoVR "number of values read"
Open 'RefCrop_data93-94_LE.txt'; Channel=2; File=In; Width=350 "GC raw data"
text plotname, variety, waterTreat, sstock, ssize
scalar [value=2]NoE
factor [levels=NoE; labels=!t('RefCrop1993','RefCrop1994')]exp "experiment
reference to match details w/measurement dates"
Read [Channel=2] exp, plotname, variety, waterTreat, pdate, emdate, nrate,
sstock, ssize, smass, sspace, stemden, year, haulmDW, tuberDW, endGC, endJD,
caMax, gc[1...NoVR]; Frepresentation=lab,lab,lab,lab,lev,lev,lev,lab,lab
Close channel=2

Open 'RefCropDates_93-17.txt'; Channel=2; File=In; Width=350 "no measurements
taken in each year"
factor [levels=NoE; labels=!t('RefCrop1993','RefCrop1994')]dexp "experiment
reference to match details w/measurement dates"
Read [Channel=2] dexp, dyear, jd[1...NoVR];Frepresentation=lab
Close channel=2
```

Tidy data and split by experiment

```
scalar [value=0]NoY "number of years"
scalar [value=0]NoPY "number of plots in all of the years"

For e=1...NoE "check number of experiments in data, change NoE above"
   calc NoY=NoY+1
   Subset [dexp.eq.e] jd[1...NoVR]; jdY[e][1...NoVR]

   Variate [nvalues=NoVR] uJDs[e] "uncut lists of JDs"
   Equate jdY[e]; uJDs[e]
   Calc NoJD[e]=NoVR-nmv(uJDs[e]) "number of non-missing values by year"

   Variate [nvalues=NoJD[e]] JDs[e]
   Equate uJDs[e]; JDs[e] "only non-missing JDs"

   Subset [exp.eq.e] gc[1...NoVR]; gcY[e][1...NoVR] "non-missing GCs"

   Calc NoP[e]=nvalues(gcY[e][1]) "Number of plots per year"
   Variate [values=1...NoP[e]] pmark[e] "marker to split plots by year"
   calc NoPY=NoP[e]+NoPY
   "print NoP[e],pmark[e],NoPY, NoY,NoJD[e]"

   "splitting experiment and variety lists by year"
    Subset [exp.eq.e] pdate, emdate, exp, plotname, variety, endGC, endJD;
    PdateY[e], EMdateY[e], expY[e], plotnameY[e], varietyY[e], endGCY[e],
    endJDY[e]
```

Tidy data and split by plot

```
   For n=1...NoP[e] "plots 1 to end"
         Subset [pmark[e].eq.n] gcY[e][1...NoVR], endJDY[e];
         gcI[1...NoVR][n], endJDI[n] "split up values for each plot"
         Append [PGC[n]] gcI[1...NoVR][n] "join values from each plot"

         "calculating max canopy extent for each crop from raw data"
         calc cMax[n]=max(PGC[n])

         "fitting the length of date list to the length of non-missing values
         in GC"
         Calc NoGC[n]=NoVR-nmv(PGC[n]) "number of non-missing values for each
         plot"

         calc mv=0/0
```

```
calc NoVRs=NoVR-1 "one fewer than number of values read in to prevent
programme from trying to read values which aren't there"
calc NoJDp[n]=NoGC[n]

"ensures that if there are any missing values mid-season that they
are included in the total number of GC count"
for m=1...NoVRs
    if gcI[m][n].eq.mv
       calc q=m+1
       if gcI[q][n].gt.0
           calc NoJDp[n]=NoJDp[n]+1
       endif
    endif
endfor

Variate [nvalues=NoJDp[n]] JDs[n]
Equate uJDs[e]; JDs[n] "only JDs when there is a real GC value"

"recreating list of GC values, doesn't contain trailing missing
values"
Subset [pmark[e].eq.n] gcY[e][1...NoJDp[n]]; gcI[1...NoJDp[n]][n]
"split up values for each plot"
Append [PGCshort[n]] gcI[1...NoJDp[n]][n] "join values from each
plot"
```

Estimate starting values for the *N* parameter

```
For o=1...NoJDp[n]"for each GC reading"
   variate [values=1...NoJDp[n]]gcmark
   subset [gcmark.eq.o] PGCshort[n];iPGC[n]

   "listing the dates when GC is greater than 50%"
   if iPGC[n]<50
      calc V1[n][o]=0
   else
      calc V1[n][o]=1
   endif

   variate [nvalues=NoJDp[n]] V2
   equate old=V1[n]; new=V2
Endfor "o"

 "calculating approx >50% canopy duration as starting point for N in
Rcycle"
calc [zdz=zero] V3 = JDs[n]/V2
calc JDMin = Min(V3)
calc JDMax = Max(V3)
calc Nest = JDMax - JDMin

"curve equation"
Expression e1; Value=!e(F=(cMax[n]/(1+EXP(-B[n]*(JDs[n]-M[n])))))-
(cMax[n]/(1+EXP(-D[n]*(JDs[n]-M[n]-N[n])))))
Model PGCshort[n]; Fitted=F "might need to use PGCnmv here"
"separating emdates, experiment and variety to get individual values
for each plot"
subset [condition=pmark[e].eq.n]EMdateY[e], expY[e], varietyY[e],
endGCY[e], PdateY[e];\iEMDate[n], iExp[n], iVar[n], iendGC[n],
iPDate[n]

calc MS[n]=(iEMDate[n]+19) "Ms = start point for estimating value of
M"
print Nest,MS[n]
```

Fit the curve to data, iteratively estimating parameters

```
RCycle B[n], D[n], M[n], N[n]; Initial=0.22, 0.25, MS[n], Nest;
Fitnonlinear [Print=m,s,e,f; Selection=%variance, adjustedr2;
Fprob=yes;Calculation=e1]
 "details about the curve fit to store and print"
```

```
Rkeep [Statistics=Stat]PGCshort[n]; RESIDUALS=Res[n];
FITTEDVALUES=FittedVals[n]; Tdeviance=TSS[n]; Deviance=RSS[n]
Scalar adjR2[n]
Equate [Oldformat=!(-1,-1,1,-1,-1,-1,-1,-1,-1,-1,-1,-1)]
Oldstructure=Stat; Newstructure=adjR2[n]
Calc cFitMax[n]=max(F)
```

Plot fitted CQ curve and raw GC data

```
"labelling graph output with plot number and variety"
subset [condition = pmark[e].eq.n] expY[e], plotnameY[e],
varietyY[e]; LabC[n], LabP[n], LabV[n]
Concatenate [Newtext=Cropinfo] Oldtext=LabP[n],' ',LabV[n]
"drawing a  graph with a fixed axis"
XAXIS WINDOW=3; TITLE='Ordinal Date'; LOWER=120; upper=300
YAXIS WINDOW=3; TITLE='Ground cover (%)'; LOWER=0; upper=110
Pen 1; symbol=0;join=given; method=monotonic;
pen 2; symbol=13; colour=RGB(30; 144; 255)
pen 4; symbol=0; colour=RGB(255; 127; 80); join=given; method=line;
DGRAPH [Title=Cropinfo; WINDOW=3; KEYWINDOW=0] F;JDs[n]; pen = 1
"fitted curve"
dgraph [window=3; screen=keep]PGCshort[n];JDs[n]; pen=2 "original
data points"
dgraph [window=3; screen=keep]PGCshort[n];JDs[n]; pen=4 "joining
original data points"
```

Calculate descriptive canopy variates

```
"calculating point of canopy senescence (10% below canMax)"
calc cMax10[n] = cMax[n]*0.1
calc canSenesce[n] = cMax[n]-cMax10[n]
print canSenesce[n],cMax[n]

"equation for calculating time in JD when reached x% GC"
Expression [value=JD25[n]=((log((cMax[n]/25)-1))/(-B[n]))+M[n]]jd25
"date of 25% GC during expansion"
Expression [value=JD50[n]=((log((cMax[n]/50)-1))/(-B[n]))+M[n]]jd50
"date of 50% GC during expansion"
Expression [value=JD75[n]=((log((cMax[n]/75)-1))/(-B[n]))+M[n]]jd75
"date of 75% GC during expansion"
Expression [value=JD90[n]=((log((cMax[n]/90)-1))/(-B[n]))+M[n]]jd90
"date of 90% GC during expansion"

"calculating time in JD when reached x% GC"
RFUNCTION [;se=err25[n];calc=jd25] JD25[n]
RFUNCTION [;se=err50[n];calc=jd50] JD50[n]
RFUNCTION [;se=err75[n];calc=jd75] JD75[n]

"to skip calculating the date 90%GC reached when canopy doesn't reach
90%GC"
if cFitMax[n]>=90
    RFUNCTION [;se=err90[n];calc=jd90] JD90[n]
else
    calc JD90[n]=0/0
endif

"equation for calculating time in JD when reached x% GC during the
senescing period"
Expression [value=JD50s[n]=((log((cMax[n]/50)-1))/(D[n]))
+(M[n]+N[n])]jd50s "date of 50% during senescence"
Expression [value=JD75s[n]=((log((cMax[n]/75)-1))/(D[n]))
+(M[n]+N[n])]jd75s "date of 50% during senescence"
Expression [value=JD90s[n]=((log((cMax[n]/90)-1))/(D[n]))
+(M[n]+N[n])]jd90s "date of 50% during senescence"
Expression [value=JDsens[n]=((log((cMax[n]/canSenesce[n])-1))/
(D[n]))+(M[n]+N[n])]jdSENs "date of 50% during senescence"
Expression [value=JDlast[n]=((log((cMax[n]/iendGC[n])-1))/(D[n]))

+(M[n]+N[n])]jdlast "date of last measurement"
```

```
        "calculating time in JD when reached x% GC as the canopy senesces"
        RFUNCTION [;se=err50s[n];calc=jd50s] JD50s[n]
        RFUNCTION [;se=err75s[n];calc=jd75s] JD75s[n]
        if cFitMax[n]<90
            calc JD90s[n]=0/0
        elsif iendGC[n]>90 "produces a missing value if canopy didn't decline
        to 90%"
            calc JD90s[n]=0/0
        else
            RFUNCTION [;se=err90s[n];calc=jd90s] JD90s[n]
        endif
        RFUNCTION [;se=errlast[n];calc=jdSENs] JDsens[n]
        RFUNCTION [;se=errlast[n];calc=jdlast] JDlast[n]


        "ensuring a value for the date of the last GC measurement"
        if JDlast[n].eq.(0/0)
            calc lastethJD[n] = endJDI[n]
        else
            calc lastethJD[n] = round(JDlast[n])
        endif

        "calculating integrated ground cover - IGCfinal"
        scalar InitialAreaF;value= 0
        FOR JDI=(iPDate[n]...lastethJD[n])
             Calculate AS[n]=(cMax[n]/(1+EXP(-B[n]*(JDI-M[n]))))-
             (cMax[n]/(1+EXP(-D[n]*(JDI-M[n]-N[n]))))
        Calculate InitialAreaF=InitialAreaF+AS[n]
        ENDFOR "JDI"
        scalar TotalAreaF[n];value=InitialAreaF
        variate [nvalues=NoP[e]]igcf[e][n]
        equate TotalAreaF;igcf[e][n]

        "calc GCDur90=0 when 90% GC not achieved"
        if JD90[n].eq.(0/0)
           calc gcDur90[n] = 0
        else
           calc gcDur90[n] = JD90s[n]-JD90[n]
        endif

        calc Emdate[n]=MS[n]-19

       DELETE [redefine=yes] F,V1,V2,V3,LabC[n],LabV[n]

        "canopy durations"
        if JD90s[n].eq.0/0
           calc gcDur90[n]=lastethJD[n]-JD90[n]
        else
          Calc gcDur90[n]=JD90s[n]-JD90[n]
        endif

        "rates of canopy senescence"
        if JD90s[n].eq.0/0
           calc gcRate9050[n]=0/0
        else
          calc gcRate9050[n]=40/(JD90s[n]-JD50s[n])
        endif

endfor "n"
```

Testing output

```
"checking residuals against fitted values for curve to check fit
 throughout the season"
append [FitValues[e]] FittedVals[]
append [ResidualValues[e]] Res[]
model ResidualValues[e]
fit [fprob=yes; tprob=yes] FitValues[e]
rgraph
```

Returning plot details and canopy descriptive variates

```
  variate [nvalues=NoP[e]] nIGCf[e]
  equate igcf[][];nIGCf[e]

  variate [nvalues=NoP[e]] nGCdur90[e], nJDlast[e], nEMDate[e]
  equate gcDur90, lastethJD, Emdate;nGCdur90[e], nJDlast[e], nEMDate[e]

  variate [nvalues=NoP[e]] bpar[e], dpar[e], mpar[e], npar[e]
  equate B,D,M,N; bpar[e], dpar[e], mpar[e], npar[e]

  Variate [NValues=NoP[e]]JD25R[e], JD50R[e], JD75R[e], JD90R[e
  Equate JD25, JD50, JD75, JD90;JD25R[e], JD50R[e], JD75R[e], JD90R[e]

  Variate [NValues=NoP[e]] JD50Rs[e], JD75Rs[e], JD90Rs[e], JDsen[e
   Equate JD50s, JD75s, JD90s, JDsens;JD50Rs[e], JD75Rs[e], JD90Rs[e], JDsen[e]

  variate [nvalues=NoP[e]]nCMax[e], nCFMax[e], nAdjR2[e]
  equate cMax, cFitMax, adjR2;nCMax[e], nCFMax[e], nAdjR2[e]

endfor "e"

variate [values=1...NoPY] CropNo "though it is really plot number from all
years, keeping old name"

variate [nvalues=NoPY]IGCf
equate nIGCf;IGCf

variate [nvalues=NoPY]EMDates, PDates, CMax, CFMax, AdjR2
equate nEMDate, pdate, nCMax, nCFMax, nAdjR2; EMDates, PDates, CMax, CFMax,
AdjR2

variate [nvalues=NoPY] GCDur90
equate nGCdur90;GCDur90

Variate [nvalues=NoPY] NRate, SeedMass, SeedSpacing, StemDen, Year, HaulmDW,
TuberDW, EndGC "Crop details, collecting for printing"
equate nrate, smass, sspace, stemden, year, haulmDW, tuberDW, endGC; NRate,
SeedMass, SeedSpacing, StemDen, Year, HaulmDW, TuberDW, EndGC

Variate [nvalues=NoPY] Bpar, Dpar, Mpar, Npar
equate bpar, dpar, mpar, npar; Bpar, Dpar, Mpar, Npar

Variate [NValues=NoPY] JDemr, JD25r, JD50r, JD75r, JD90r
Equate JD25R, JD50R, JD75R, JD90R; JD25r, JD50r, JD75r, JD90r

Variate [NValues=NoPY] JD50rs, JD75rs, JD90rs, JDend, JDsenesces
Equate JD50Rs, JD75Rs, JD90Rs, nJDlast, JDsen; JD50rs, JD75rs, JD90rs, JDend,
JDsenesces

text [nvalues=NoPY] Experiment, PlotName, Variety, WaterTreat, SeedStock,
SeedSize
Equate exp, plotname, waterTreat, sstock, ssize; Experiment, PlotName,
WaterTreat, SeedStock, SeedSize
Equate variety; Variety

"rate of canopy expansion"
Calc GCRate2575=50/(JD75r-JD25r)

"rate of canopy senescence"
Calc GCRate9050=40/(JD90rs-JD50rs)

"time intervals"
calc TiE25=JD25r-EMDates"emergence-25%GC"
calc TiE50=JD50r-EMDates"emergence-25%GC"
calc TiE90 = JD90r - EMDates "emergence to 90%GC"
calc TiE90s = JD90rs - EMDates "emergence - 90% GC senesence point"
calc TiESc = JDsenesces - EMDates "canopy duration"
```

Export plot details and descriptive variates in .csv

```
TEXT OutFile; VALUE='19.5.17_CanVar_1993-2017RefCrop.csv'
Export [Outfile=OutFile; CSVOPTIONS=noquotes] CropNo, Experiment, PlotName,
WaterTreat, Variety, PDates, EMDates, SeedMass, SeedStock, SeedSize,
SeedSpacing, StemDen, NRate, Year, HaulmDW, TuberDW, CMax, CFMax, AdjR2, IGCf,
TiE25, TiE50, TiE90, TiE90s, TiESc, GCRate2575, GCRate9050, GCDur90, EndGC,
JDend, JD25r, JD50r, JD75r, JD90r, JD50rs, JD75rs, JD90rs, JDsenesces, CMax,
Bpar, Dpar, Mpar, Npar
stop
```

Programme 3 – linking to meteorological data

Calculation of meteorological values linked to each plot. This is example is for the 'normal' plot data.

Read in air and soil temperature, radiation and plot canopy variates

```
SET [WORKINGDIRECTORY='F:/PhD/Reference Crop/CanopyQuantification/All
years/Analysis inc SMD/all data/CanVar']

"Define number of sites (weather stations) and number of crops"
scalar [value=14]NoY
Scalar [value=193] NoP "total number of plots read in"

"Read in temp metdata"
Open 'CUF_93-17_temp.txt'; Channel=2; width=1400
Read [Channel=2] yearD,tday[60...334]; Frepresentation=Lab
Close channel=2

"Read in radiation metdata"
Open 'CUF_93-17_rad.txt'; Channel=2; width=1300
Read [Channel=2] yearD,rday[60...334]; Frepresentation=Lab
Close channel=2

"Read in soil temp metdata"
Open 'CUF_93-17_soiltemp.txt'; Channel=2; width=1500
Read [Channel=2] yearD,stday[32...212]; Frepresentation=Lab
Close channel=2

"Read in soil moisture deficit metdata"
Open 'CUF_93-06_SMD.txt'; Channel=2; width=2000
text smdPName
Read [Channel=2] yearSMD,PlotNumber,smdPName,smdday[91...290];
Frepresentation=Lev,lev,lab
Close channel=2

Open '1993-2006RefCrop_outLE.txt'; Channel=2; width=1000
factor Variety,WaterTreat
Text PlotName,Experiment,SeedStock,SeedSize
Read [Channel=2] CropNo, Experiment, PlotName, WaterTreat, Variety, PDates,
EMDates, SeedMass, SeedStock, SeedSize, SeedSpacing, StemDen, NRate, Year,
HaulmDW, TuberDW, CMax, CFMax, AdjR2, IGCf, TiE25, TiE50, TiE90, TiE90s,
TiESc, GCRate2575, GCRate9050, GCDur90, EndGC, JDend, JD25r, JD50r, JD75r,
JD90r, JD50rs, JD75rs, JD90rs, JDScs, CMax, Bpar, Dpar, Mpar, Npar;\
         Frepresentation=Lev,lab,lab,lab,lab,lev,lev,lev,lab,lab,lev",lab"
Close channel=2
```

For each plot, identify dates of interest to calculate mean temperature, and other variables, between

```
"Loop for each crop"
For n=1...NoP

         "Split up crop values into pointers"
```

```
Subset [condition=CropNo.eq.n] old=Year, PDates, EMDates, JDend,
JD25r, JD75r;new=YearE[n], plant[n], minC[n], maxC[n], JD25[n],
JD75[n]

Subset [condition=CropNo.eq.n] old = CMax, Bpar, Dpar, Mpar, Npar;
new = cMax[n], B[n], D[n], M[n], N[n]

"Values need to be scalars to use in the next step (they are
redefined on each loop) days are now integers"
Scalar plotyear, pdate, minday, maxday, d25, d75
calc plotyear=YearE[n]
calc pdate=plant[n]
Calc minday=minC[n]
Calc maxday=round(maxC[n])
calc d25, d75=round(JD25[n], JD75[n])
```

Calculate temperature variates for the whole season (emergence to complete senescence or harvest) in each plot

```
Subset [condition=yearD.eq.plotyear] old=tday[minday...maxday],
stday[pdate...minday];new=tdayplot[n][minday...maxday],
stdayPreEM[n][pdate...minday]
"Join the values for each day together - Append can deal with
different lengths, unlike equate - temp"
Append [new=tdayplots[n]] tdayplot[n][minday...maxday]
Append [new=stdayPreEMs[n]] stdayPreEM[n][pdate...minday]
"Calculate the mean"
Calc meantemp[n]=mean(tdayplots[n])
calc meantempPreEM[n] = mean(stdayPreEMs[n])

"Calculating growing degree days"
calc NoDays=nvalues(tdayplots[n])
calc NoDaysPreEM=nvalues(stdayPreEMs[n])
calc CulmBaseTemp=NoDays*4.4
calc CulmBaseTempPreEM=NoDaysPreEM*4.4
calc CulmTemp=sum(tdayplots[n])
calc CulmTempPreEM=sum(stdayPreEMs[n])
calc GDD[n]=CulmTemp-CulmBaseTemp
calc GDDPreEM[n]=CulmTempPreEM-CulmBaseTempPreEM

calc culmtemp[n]=sum(tdayplots[n])
calc culmtempPreEM[n]=sum(stdayPreEMs[n])
calc AveDailyIGCf=IGCf/NoDays
```

Calculate temperature variates for each plot

```
"use scalars to calc the temp over canopy expansion time interval"
subset [condition=yearD.eq.plotyear]old=tday[minday...d25],
tday[d25...d75];new=TiE25temp[n][minday...d25], midtemp[n][d25...d75]
append [new=TiE25temps[n]] TiE25temp[n][minday...d25]
append [new=midtemps[n]] midtemp[n][d25...d75]
calc meanTiE25temp[n], meanmidtemp[n]=mean(TiE25temps[n],
midtemps[n])
print meanTiE25temp[n],meanmidtemp[n]

"calc GDD for canopy expansion time periods - base temp 4.4"
calc noTiE25Days=nvalues(TiE25temps[n])
calc noMidDays=nvalues(midtemps[n])
calc totTiE25Btemp=noTiE25Days*4.4
calc totMidBtemp=noMidDays*4.4
calc totTiE25Temp=sum(TiE25temps[n])
calc totMidTemp=sum(midtemps[n])
calc TiE25GDD[n]=totTiE25Temp-totTiE25Btemp
calc midGDD[n]=totMidTemp-totMidBtemp

"calc accumulated heat for canopy expansion periods - base temp 0"
calc culmTiE25Temp=sum(TiE25temps[n])
calc culmMidTemp=sum(midtemps[n])
```

```
        calc totTiE25temp[n]=sum(TiE25temps[n])
        calc totMidtemp[n] =sum(midtemps[n])
```

Calculate radiation variates for the whole season (emergence to complete senescence or harvest) in each plot

```
        Subset [condition=yearD.eq.plotyear] old=rday[minday...maxday],
        rday[pdate...maxday]; new=rdayplot[n][minday...maxday],
        rdayAll[n][pdate...maxday]

        "Join the values for each day together - Append can deal with
        different lengths, unlike equate - radiation"
        Append [new=rdayplots[n]] rdayplot[n][minday...maxday]

        "Calculate the mean"
        Calc meanrad[n]=mean(rdayplots[n])
        "Calculating cumulative radiation"
        calc CulmRad[n]=sum(rdayplots[n])

        "use scalars to calc radiation over canopy expansion time interval"
        subset [condition=yearD.eq.plotyear]old=rday[minday...d25],
        rday[d25...d75];new=TiE25rad[n][minday...d25], midrad[n][d25...d75]
        append [new=TiE25rads[n]] TiE25rad[n][minday...d25]
        append [new=midrads[n]] midrad[n][d25...d75]
        calc meanTiE25rad[n], meanmidrad[n]=mean(TiE25rads[n], midrads[n])
        calc TiE25CulmRad[n], midCulmRad[n]=sum(TiE25rads[n], midrads[n])
        print TiE25CulmRad[n], midCulmRad[n]
Endfor
```

Output calculated meteorological values with other plot data

```
Variate [nvalues=NoP] cMaxp,Bp,Dp,Mp,Np
Equate cMax,B,D,M,N;cMaxp,Bp,Dp,Mp,Np
Variate [nvalues=NoP] meantemps, allGDD, CulmTemps, meantempPreEMs, GDDPreEMs,
CulmTempPreEMs, GDDTiE25, CulmTempsTiE25, GDD2575, CulmMidTemps, meanrads,
culmrads, tempE25, temp2575, radE25, rad2575, CulmRadTiE25, CulmRad2575

Equate old=meantemp, GDD, culmtemp, meantempPreEM, GDDPreEM, culmtempPreEM,
TiE25GDD, totTiE25temp, midGDD, totMidtemp, meanrad, CulmRad, meanTiE25temp,
meanmidtemp, meanTiE25rad, meanmidrad, TiE25CulmRad, midCulmRad;\
new=meantemps, allGDD, CulmTemps, meantempPreEMs, GDDPreEMs, CulmTempPreEMs,
GDDTiE25, CulmTempsTiE25, GDD2575, CulmMidTemps, meanrads, culmrads, tempE25,
temp2575, radE25, rad2575, CulmRadTiE25, CulmRad2575

calc EmDAP=EMDates-PDates
```

Export plot details, canopy variates and meteorological values in .csv

```
TEXT OutFile; VALUE='19.5.21_CVmetlink_1993-2006_SMD.csv'

Export [Outfile=OutFile; CSVOPTIONS=noquotes] CropNo, Experiment, PlotName,
WaterTreat, Variety, PDates, EMDates, EmDAP, SeedStock, SeedSize, SeedMass,
SeedSpacing, StemDen,NRate, Year, HaulmDW, TuberDW, CMax, CFMax, AdjR2, IGCf,
TiE25, GCRate2575, GCRate9050, GCDur90, EndGC, JDend, JD25r, JD75r, JD90r,
JD50rs, JD90rs, TiE90s, TiESc, meantemps, allGDD, CulmTemps, meantempPreEMs,
GDDPreEMs, CulmTempPreEMs, GDDTiE25, CulmTempsTiE25, GDD2575, CulmMidTemps,
meanrads, culmrads, tempE25, temp2575, radE25, rad2575, CulmRadTiE25,
CulmRad2575, cMaxp, Bp, Dp, Mp, Np

stop
```

APPENDIX 4

Emergence and number of stems

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on pre-emergence growth and early season stem counts in Expts 1 and 3. Mean values for each variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 91. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the delay between emergence and planting (EmDAP) and the number of stems per plant (stems) in Expts 1 and 3. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Expt 1		Expt 3	
Treatments and interactions	EmDAP	stems	EmDAP	stems
Planting date	< 0.001	0.007	< 0.001	0.796
Cultivar	0.430	< 0.001	0.989	0.072
Nitrogen rate	1.000	0.900	0.305	0.922
Planting date * Cultivar	0.534	0.270	0.948	0.027
Planting date * Nitrogen rate	1.000	0.077	0.298	0.500
Cultivar * Nitrogen rate	0.430	0.802	0.167	0.288
Planting date * Cultivar * Nitrogen rate	0.534	0.698	0.587	0.626

Emergence

Table 92. Duration between planting and emergence (EmDAP, days) for each treatment combination in Expt 1 (13.98 D.F.) and Expt 3 (22.43 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		38.0	38.0	38.0	38.0	1.03
	May		28.0	28.0	28.0	28.0	
	June		23.0	24.0	23.0	22.0	
3	March		51.3	52.6	48.3	56.4	2.93
	April		38.5	36.0	35.9	39.1	
	May		25.8	25.3	25.1	24.5	

Number of stems

Table 93. Number of stems per plant (stems) for each treatment combination in Expt 1 (32.87 D.F.) and Expt 3 (31.38 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		2.38	3.00	5.88	6.63	0.538
	May		3.50	3.38	7.75	8.50	
	June		3.88	3.00	8.87	7.50	
3	March		2.75	2.88	2.25	2.50	0.371
	April		2.13	2.63	3.13	2.88	
	May		2.00	2.00	3.38	2.63	

APPENDIX 5

Canopy Ground Cover Development

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on each of the ground cover canopy variates in Expt 1 and 3. Mean values for each canopy variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 94. Table of *P* values showing the significance of treatments and interactions, ANOVA, on integrated ground cover (IGC), early canopy expansion (TiE25), rate of mid-canopy expansion (GCRate2575), duration of near-complete canopy cover (GCDur90), duration of canopy growing season (GrowDur) and rate of canopy senescence (GCRate9050) in Expt 1. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	IGC	TiE25	GCRate 2575	GCDur 90	Grow Dur	GCRate 9050
Planting date	< 0.001	< 0.001	0.002	0.014	< 0.001	0.272
Cultivar	< 0.001	0.261	0.101	< 0.001	< 0.001	< 0.001
Nitrogen rate	0.687	0.788	< 0.001	0.088	0.208	< 0.001
Planting date * Cultivar	< 0.001	0.172	0.655	0.488	0.231	0.461
Planting date * Nitrogen rate	0.069	0.243	0.011	0.302	0.851	0.453
Cultivar * Nitrogen rate	0.068	0.145	0.982	< 0.001	< 0.001	0.026
Planting date * Cultivar * Nitrogen rate	0.716	0.606	0.95	0.284	0.457	0.826

Table 95. Table of *P* values showing the significance of treatments and interactions, ANOVA, on integrated ground cover (IGC), early canopy expansion (TiE25), rate of mid-canopy expansion (GCRate2575), duration of near-complete canopy cover (GCDur90), duration of canopy growing season (GrowDur) and rate of canopy senescence (GCRate9050) in Expt 3. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	IGC	TiE25	GCRate 2575	GCDur 90	Grow Dur	GCRate 9050
Planting date	0.033	< 0.001	0.015	0.029	0.004	0.160
Cultivar	< 0.001	0.813	0.007	< 0.001	< 0.001	< 0.001
Nitrogen rate	0.570	0.069	< 0.001	< 0.001	0.252	< 0.001
Planting date * Cultivar	0.174	0.187	< 0.001	0.320	0.030	0.047
Planting date * Nitrogen rate	0.032	0.799	0.008	0.002	0.091	0.005
Cultivar * Nitrogen rate	0.594	0.513	0.903	0.938	0.905	< 0.001
Planting date * Cultivar * Nitrogen rate	0.713	0.658	0.016	0.520	0.131	0.534

Integrated ground cover

Table 96. Integrated ground cover (IGC, % days) for each treatment combination in Expt 1 (29.03 D.F.) and Expt 3 (23.68 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima 0	Estima 250	Maris Piper 0	Maris Piper 250	S.E.
1	April		7660	7310	11 070	10 440	216
	May		6930	7500	9930	10 210	
	June		6600	6910	7870	10 010	
3	March		8070	8230	10 630	10 440	291
	April		8800	8350	10 490	10 210	
	May		7000	7790	9530	10 010	

Early canopy expansion

Table 97. Interval between emergence and 25 % GC (TiE25, days) for each treatment combination in Expt 1 (31.14 D.F.) and Expt 3 (27.72 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		16.31	16.65	17.28	16.02	0.562
	May		9.90	10.00	10.46	9.37	
	June		10.88	11.62	9.69	10.34	
3	March		18.86	16.38	18.32	17.86	0.958
	April		17.14	16.37	18.19	17.53	
	May		13.26	12.56	12.10	11.32	

Mid-canopy expansion

Table 98. Rate of canopy expansion between 25 and 75 % GC (GCRate2575, %/day) for each treatment combination in Expt 1 (32.67 D.F.) and Expt 3 (9.55 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		4.01	4.91	4.08	4.95	0.197
	May		4.03	5.93	4.32	6.14	
	June		4.20	5.60	4.47	5.97	
3	March		2.51	2.78	2.30	3.30	0.292
	April		3.71	4.61	3.59	4.35	
	May		2.84	4.51	3.97	5.01	

Duration of near-complete ground cover

Table 99. Duration of 90 % GC (GCDur90, days) for each treatment combination in Expt 1 (31.35 D.F.) and Expt 3 (26.53 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		51.5	55.6	85.8	84.2	2.90
	May		43.6	58.7	81.4	79.5	
	June		42.0	51.5	77.2	69.5	
3	March		41.8	53.7	64.2	75.0	4.87
	April		58.5	63.3	76.1	74.8	
	May		35.7	58.3	43.9	74.9	

Duration of canopy growth

Table 100. Duration of canopy growing season (from emergence to onset of senescence (defined as 90 % of maximum canopy cover), GrowDur, days) for each treatment combination in Expt 1 (32.19 D.F.) and Expt 3 (27.79 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		86.7	87.6	121.5	115.4	2.81
	May		75.0	81.4	109.3	101.3	
	June		71.1	76.5	103.8	92.5	
3	March		92.9	97.5	116.0	115.8	3.44
	April		96.4	96.1	115.4	109.7	
	May		86.1	87.7	88.5	101.5	

Canopy senescence

Table 101. Rate of canopy senescence (GCRate9050, %/day) for each treatment combination in Expt 1 (29.86 D.F.) and Expt 3 (29.33 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		-3.27	-5.61	-3.19	-3.60	0.562
	May		-2.98	-5.47	-2.06	-3.57	
	June		-3.23	-5.01	-1.98	-2.26	
3	March		-2.19	-3.99	-2.09	-2.82	0.282
	April		-2.48	-4.37	-2.60	-2.56	
	May		-1.76	-4.80	-0.98	-2.45	

APPENDIX 6

Planting date mean treatment interaction CQ curves

The effect of interactions between cultivar, planting date and nitrogen rate upon canopy development throughout the growing season is presented below for experiments 1 and 3 (Figures 141 & 142, respectively). The goodness of fit of each curve to the treatment mean of the raw data was described using both Willmott's index of agreement (*d*, Table 102) and the root mean square error (RMSE, % GC, Table 103).

Experiment 1

The difference in canopy expansion between rates of applied nitrogen was small in both cultivars, though at 250 kg N/ha complete canopy cover was reached earlier than without additional applied nitrogen (Figure 141). The difference in canopy expansion between nitrogen rates was greatest in the May planting in both cultivars, and May planted Estima did not reach 100 % GC (Figure 141a) unlike the May planted Maris Piper (Figure 141b). Duration of complete or near-complete canopy cover shortened with the delay in planting in both cultivars, though the difference was greater in Maris Piper than Estima (Figure 141). In Estima, senescence between nitrogen rates varied more than the rate of canopy expansion and the difference was greatest in the May planting (Figure 141a). Senescence in Maris Piper began later but was faster at the higher nitrogen rate than without additional nitrogen in each planting date (Figure 141b).

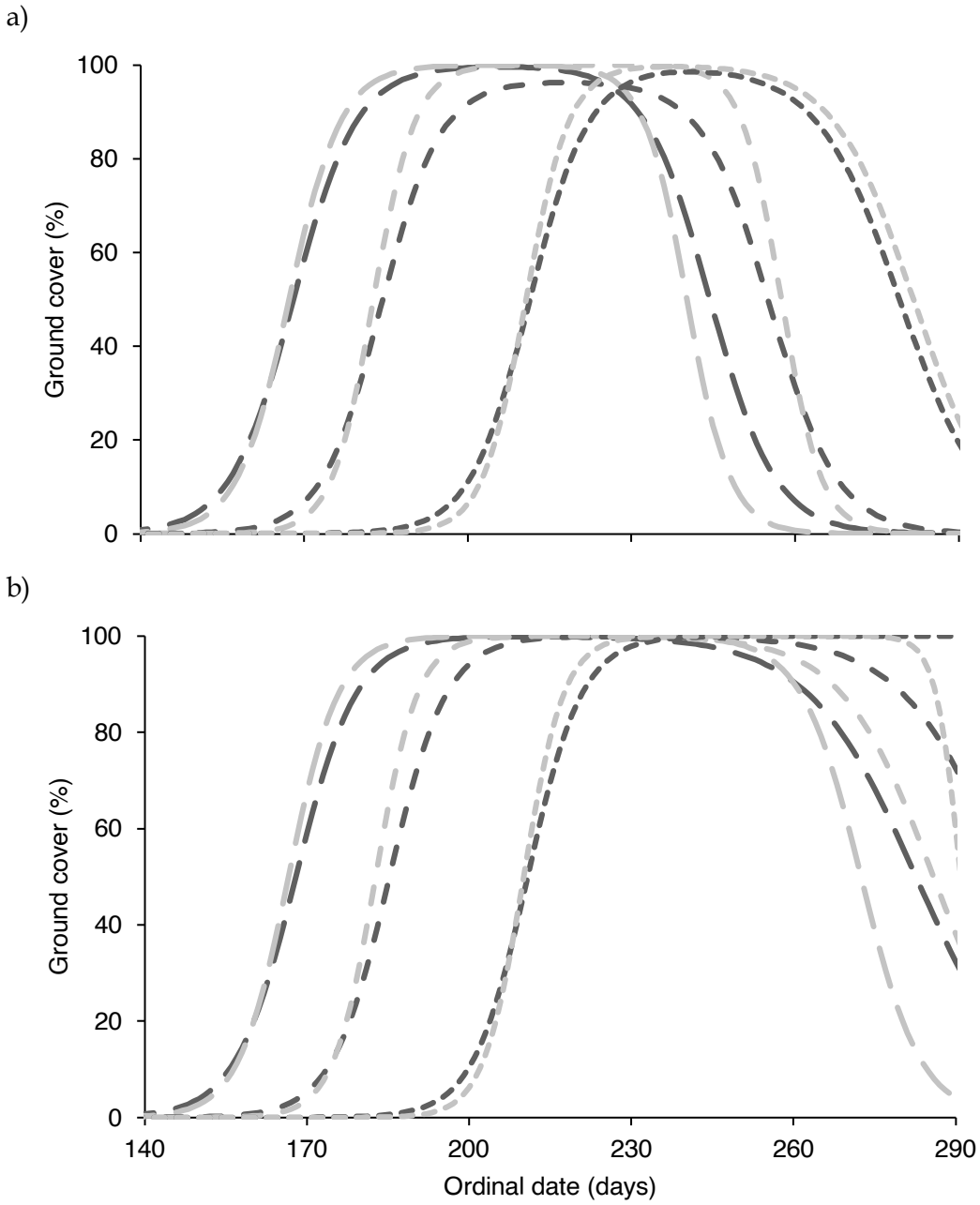

Figure 141. Average ground cover curve for all combinations of treatments (planting date * cultivar * nitrogen rate), plotted against days after emergence, (a) Estima and (b) Maris Piper in Expt 1. 0 kg N/ha, — ; 250 kg N/ha, — ; April planting, — — ; May planting, – – –; June planting, – – – – .

Experiment 3

In Expt 3, canopy expansion was slower in both cultivars in March planted plots than in the later plantings (Figure 142). There was little overall difference between 0 and 250 kg N/ha in relation to canopy expansion, however there were exceptions. The rate of March planted Maris Piper canopy expansion was slower at 0 than 250 kg N/ha and plots without additional N achieved maximum GC *c.* 10 days after the 250 kg N/ha treatments. May planted Estima and Maris Piper at 0 kg N/ha also produced smaller

canopies, only reaching a maximum of *c.* 80 and 95 % GC, respectively (Figure 142). Rates of senescence were similar across most treatments, though senescence was slowest in May planted Maris Piper at 250 kg N/ha (Figure 142b). There was a greater degree of overlap in complete canopy cover between planting dates in Expt 3 than Expt 1 (Figures 142 & 141, respectively).

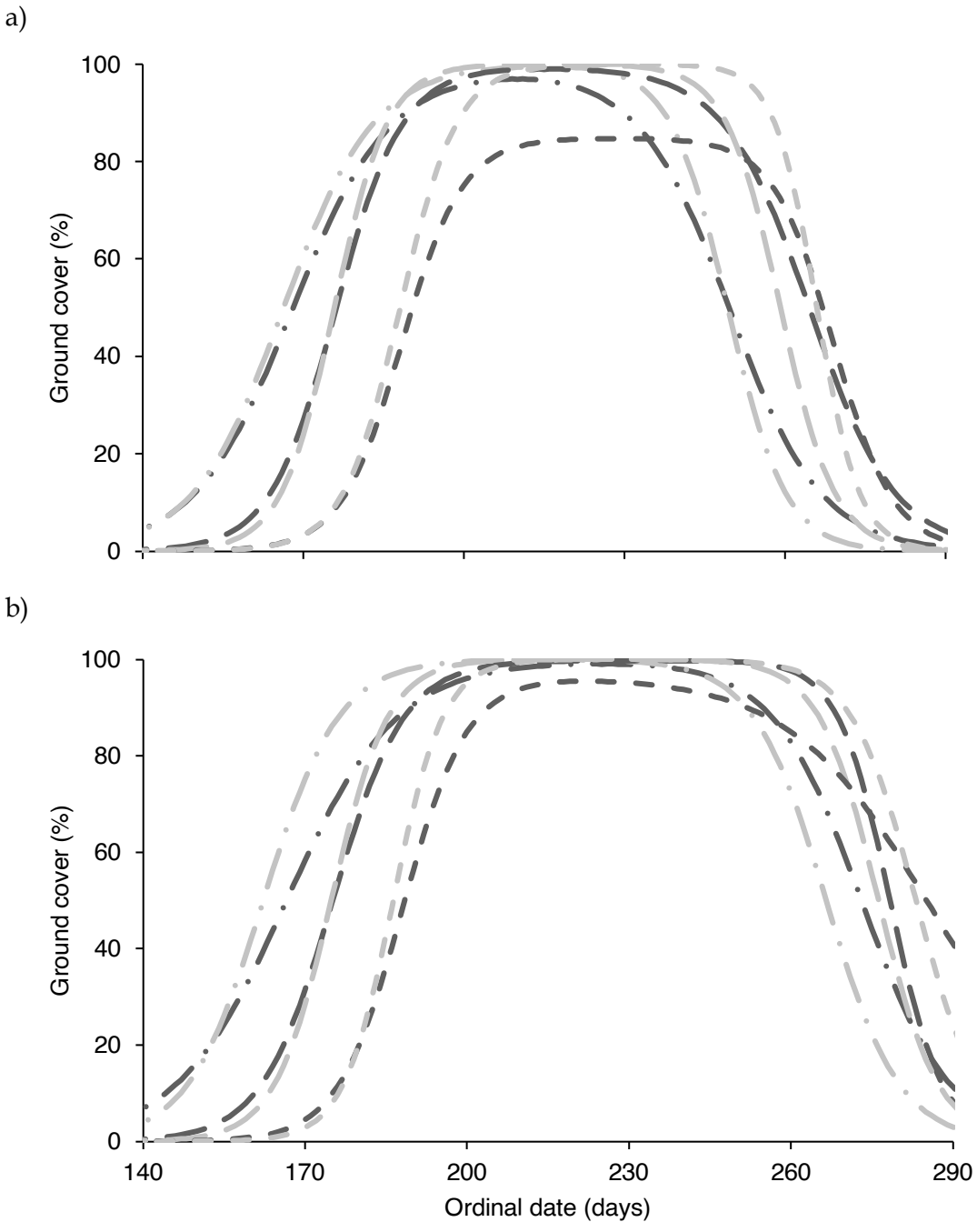

Figure 142. Average ground cover curve for all combinations of treatments (planting date * cultivar * nitrogen rate), plotted against days after emergence, (a) Estima and (b) Maris Piper in Expt 3. 0 kg N/ha, — ; 250 kg N/ha, — ; March planting, — · — ; April planting, — — ; May planting, – – –.

Goodness of fit

Willmott's index of agreement shows a good fit of the CQ curve to each treatment mean ($d \geq 0.993$) and the numerical differences in goodness of fit between treatments were minimal, though the range in goodness of fit was greater in Maris Piper than Estima (Table 102).

Table 102. Goodness of fit scores for treatment means of each all treatment combinations in Expts 1 and 3. Goodness of fit measured using Willmott's index of agreement (*d*).

		Nitrogen rate	Estima		Maris Piper	
Expt	Planting date	(kg N/ha)	0	250	0	250
1	April		0.999	0.998	0.998	0.998
	May		0.999	0.999	0.999	0.999
	June		0.999	0.998	1.000	0.999
3	March		0.999	0.999	0.996	0.999
	April		0.999	0.999	0.996	0.998
	May		0.997	0.999	0.993	0.997

Low root mean square error values also show a good fit of each curve to the treatment means (Table 103), though there was greater variation in RMSE than *d* values, allowing greater discrimination between treatment curve-fit. RMSE ranged from 1.23 % GC (June planted Maris Piper at 0 kg N/ha, Expt 1) to 4.19 % GC (May planted Maris Piper at 0 kg N/ha, Expt 3) and curve-fit was numerically worse in Expt 3 than Expt 1 (3.00 and 2.38 % GC, respectively, Table 103). There were no consistent differences in RMSE between cultivars, planting dates or nitrogen rates (Table 103).

Table 103. Goodness of fit scores for treatment means of each all treatment combinations in Expts 1 and 3. Goodness of fit measured using root mean square error (RMSE, % GC).

		Nitrogen rate	Estima		Maris Piper	
Expt	Planting date	(kg N/ha)	0	250	0	250
1	April		2.81	3.48	2.71	3.24
	May		2.09	1.91	1.62	2.04
	June		2.30	3.29	1.23	1.86
3	March		2.50	2.42	4.03	2.71
	April		2.50	1.91	3.82	3.12
	May		3.02	2.82	4.19	2.99

APPENDIX 7

Daylength variation throughout the growing season

There were significant variations in daylength at each stage of canopy development between treatments and their interactions, yet they were typically small, differing by less than one hour. These differences are reported here in interaction tables, indicating which treatments and interactions of treatments had a significant effect on daylength at different points, relative to canopy development, throughout the season, in Expt 1 and 3. Mean values for each variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 104. Table of *P* values showing the significance of treatments and interactions, ANOVA, on daylength at emergence (dLengthEM) and the onset of senescence (dLengthSen), and mean daylength during mid-canopy expansion (dLength2575) and near-complete canopy cover (dLength90) in Expt 1. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	dLength EM	dLength 2575	dLength 90	dLength Sen
Planting date	< 0.001	< 0.001	< 0.001	< 0.001
Cultivar	< 0.001	0.462	< 0.001	< 0.001
Nitrogen rate	< 0.001	0.046	0.008	0.264
Planting date * Cultivar	< 0.001	0.170	0.818	0.472
Planting date * Nitrogen rate	< 0.001	0.105	0.806	0.900
Cultivar * Nitrogen rate	< 0.001	0.996	0.002	0.001
Planting date * Cultivar * Nitrogen rate	< 0.001	0.974	0.418	0.380

Table 105. Table of *P* values showing the significance of treatments and interactions, ANOVA, on daylength at emergence (dLengthEM) and the onset of senescence (dLengthSen), and mean daylength during mid-canopy expansion (dLength2575) and near-complete canopy cover (dLength90) in Expt 3. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	dLength EM	dLength 2575	dLength 90	dLength Sen
Planting date	< 0.001	< 0.001	0.002	0.002
Cultivar	< 0.001	0.054	< 0.001	< 0.001
Nitrogen rate	0.264	0.020	0.547	0.180
Planting date * Cultivar	0.004	0.002	0.071	0.121
Planting date * Nitrogen rate	0.144	< 0.001	0.006	0.154
Cultivar * Nitrogen rate	0.422	0.249	0.878	0.989
Planting date * Cultivar * Nitrogen rate	0.562	0.282	0.038	0.113

Daylength

Table 106. Daylength at emergence (dLengthEM, hours) for each treatment combination in Expt 1 (25.40 D.F.) and Expt 3 (9.9 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		16.02	16.02	15.98	16.02	0.002
	May		16.72	16.72	16.73	16.74	
	June		16.48	16.48	16.45	16.45	
3	March		15.93	15.95	15.85	15.81	0.040
	April		16.46	16.51	16.38	16.43	
	May		16.77	16.77	16.77	16.77	

Table 107. Mean daylength during mid-canopy expansion emergence (dLength2575, hours) for each treatment combination in Expt 1 (32.18 D.F.) and Expt 3 (24.70 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		16.71	16.70	16.70	16.69	0.019
	May		16.69	16.72	16.68	16.72	
	June		15.78	15.83	15.82	15.86	
3	March		16.72	16.70	16.70	16.68	0.025
	April		16.74	16.75	16.74	16.75	
	May		16.37	16.53	16.51	16.58	

Table 108. Mean daylength during near-complete canopy cover (dLength90, hours) for each treatment combination in Expt 1 (32.87 D.F.) and Expt 3 (18.59 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		15.91	15.93	14.97	15.19	0.096
	May		15.30	15.22	14.18	14.58	
	June		13.81	13.76	12.76	13.24	
3	March		15.57	15.52	14.95	15.21	0.126
	April		15.07	15.09	14.55	14.75	
	May		14.64	14.53	14.71	14.17	

Table 109. Daylength at onset of senescence (dLengthSen, hours) for each treatment combination in Expt 1 (32.47 D.F.) and Expt 3 (29.39 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		14.62	14.57	12.42	12.75	0.189
	May		13.90	13.50	11.58	12.10	
	June		12.45	12.07	10.22	10.96	
3	March		14.33	14.03	12.97	13.03	0.223
	April		13.29	13.20	12.17	12.47	
	May		12.80	12.68	12.64	11.77	

The final date of 90 % GC (final90GC) explained 86.0 % of the variation in daylength during near-complete canopy cover (dLength90), once variation between experimental blocks was accounted for (multiple linear regression; dLength90 ~ final90GC + block/main plot, $P < 0.001$). Intercepts differed significantly with block and main plot structure (ANOVA, $P = 0.004$), but, to maintain clarity, regression coefficients which do not account for the differences between blocks were reported below (Figure 143 & Table 110). Hence, the variation in mean daylength during near-complete canopy cover is, at least in part, an artefact of the final date of near-complete canopy cover.

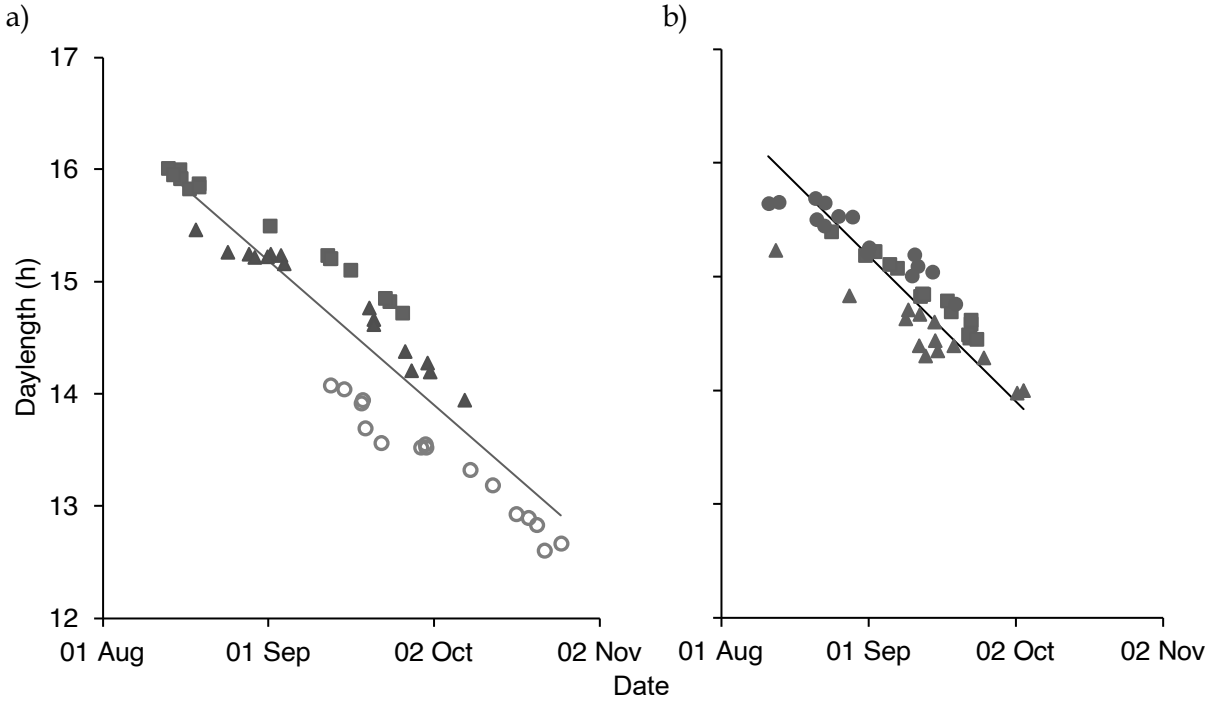

Figure 143. Relationship between mean daylength during near-complete canopy cover (dLength90) and the final date of 90 % GC (final90GC) in (a) Expt 1 and (b) Expt 3. March, ●; April, ■; May, ▲; June, O. $R^2 = 0.838$. See Table 110 for details of multiple linear regression.

Table 110. Relationship between mean daylength during near-complete canopy cover (dLength90) and the final date of 90 % GC (final90GC). dLength90 = β0 + β1*final90GC.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	25.34	0.483	< 0.001
1	final90GC	-0.0414	0.00188	< 0.001

APPENDIX 8

Mean temperature during near-complete ground cover

Mean air temperature during near-complete ground cover (Temp90) varied with planting date, cultivar, and nitrogen rate, though the differences were typically small, < 2 °C. In Expt 1, Temp90 was similar in Estima and Maris Piper in the April and May planting days, but was *c.* 2 °C in Maris Piper than in Estima in the June planting (P < 0.001, Table 111). Mean air temperature was greatest in May planting, but was < 1 °C greater than Temp90 in the June planting, which experienced the coolest mean temperature (P < 0.001, Table 111). Mean air temperature during near-complete cover was greater at 0 than 250 kg N/ha in Estima (18.2 compared to 18.0 °C, respectively) whereas Temp90 in Maris Piper was greater at 250 than 0 kg N/ha (17.6 and 17.1 °C, respectively, P < 0.001). In both experiments, Temp90 was slightly lower in Maris Piper than in Estima; a difference of 0.7 and 0.4 °C in Expts 1 and 3, respectively, both P < 0.001, Table 111). In Expt 3, there was little difference in Temp90 between nitrogen rates in the March and April plantings, but in the May planting Temp90 was lower at 250 than at 0 kg N/ha (P < 0.001, Table 112). Temp90 declined from the March to the May plantings, but again the difference was < 1 °C (P = 0.003, Table 111).

Table 111. Mean air temperature during the period of near-complete ground cover (GCDur90) for Estima and Maris Piper in Expt 1 (25.03 D.F.) and Expt 3 (13.00 D.F.). Data presented are a mean of nitrogen rates.

		Cultivar		
Expt	Planting date	Estima	Maris Piper	S.E.
1	April	17.7	17.9	0.097
	May	18.4	18.0	
	June	18.1	16.2	
3	March	16.9	16.7	0.104
	April	16.8	16.2	
	May	16.3	16.0	

Table 112. Mean air temperature during the period of near-complete ground cover (GCDur90) at 0 and 250 kg N/ha in Expt 1 (25.03 D.F.) and Expt 3 (13.00 D.F.). Data presented are a mean of cultivars.

		Applied nitrogen (kg N/ha)		
Expt	Planting date	0	250	S.E.
1	April	17.8	17.8	0.097
	May	18.2	18.2	
	June	17.0	17.3	
3	March	16.8	16.9	0.104
	April	16.3	16.6	
	May	16.4	15.9	

APPENDIX 9

Leaf Appearance

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on leaf appearance measurements in Expts 1 and 3. Mean values for each canopy variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 113. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of mainstem leaves (msL), rate of leaf appearance on the mainstem (msLA), phyllochron (Phyllo), rate of whole plant leaf appearance (pLA), number of leaves on the main axis (maL) and rate of leaf appearance on the sympodial branch (sbLA) in Expt 1. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	msL	msLA	Phyllo	pLA	maL	sbLA
Planting date	0.750	0.054	0.129	0.007	< 0.001	0.002
Cultivar	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.944
Nitrogen rate	0.874	0.760	0.515	0.480	< 0.001	< 0.001
Planting date * Cultivar	0.054	0.516	0.858	0.780	0.005	0.802
Planting date * Nitrogen rate	0.354	0.085	0.164	0.549	0.242	0.401
Cultivar * Nitrogen rate	0.117	0.024	0.152	0.030	0.219	0.107
Planting date * Cultivar * Nitrogen rate	0.653	0.087	0.301	0.406	0.472	0.107

Table 114. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of mainstem leaves (msL), rate of leaf appearance on the mainstem (msLA), phyllochron (Phyllo), rate of whole plant leaf appearance (pLA), number of leaves on the main axis (maL) and rate of leaf appearance on the sympodial branch (sbLA) in Expt 3. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	msL	msLA	Phyllo	pLA	maL	sbLA
Planting date	0.750	0.325	0.769	0.630	0.198	0.600
Cultivar	< 0.001	0.003	0.094	0.353	< 0.001	0.006
Nitrogen rate	0.874	0.230	0.085	0.412	< 0.001	< 0.001
Planting date * Cultivar	0.054	0.001	< 0.001	0.178	0.005	0.596
Planting date * Nitrogen rate	0.354	0.071	0.146	0.476	0.524	0.108
Cultivar * Nitrogen rate	0.117	0.063	0.046	0.793	0.065	0.077
Planting date * Cultivar * Nitrogen rate	0.653	0.921	0.735	0.625	0.572	0.931

Mainstem leaves

Table 115. Number of mainstem leaves (msL) for each treatment combination in Expt 1 (25.87 D.F.) and Expt 3 (32.47 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		12.75	12.38	15.62	17.25	0.707
	May		12.25	11.38	18.19	17.62	
	June		12.62	11.88	16.29	16.88	
3	March		12.00	12.12	15.88	15.88	0.413
	April		12.88	13.00	18.75	17.88	
	May		13.50	13.25	20.12	19.62	

Mainstem leaf appearance

Table 116. Rate of leaf appearance on the mainstem (msLA) for each treatment combination in Expt 1 (32.8 D.F.) and Expt 3 (16.46 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		0.781	0.588	0.464	0.489	0.0473
	May		0.572	0.646	0.434	0.459	
	June		0.773	0.714	0.411	0.590	
3	March		0.557	0.495	0.578	0.565	0.0385
	April		0.640	0.654	0.495	0.576	
	May		0.659	0.669	0.520	0.613	

Phyllochron

Table 117. Mainstem phyllochron (Phyllo) for each treatment combination in Expt 1 (33.00 D.F.) and Expt 3 (16.74 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		20.0	26.1	34.3	38.1	3.98
	May		30.5	27.5	41.3	37.2	
	June		27.1	29.9	49.1	34.0	
3	March		35.0	36.5	31.3	31.1	1.92
	April		30.2	30.8	37.1	33.1	
	May		30.5	29.2	37.0	31.2	

Whole plant leaf appearance rate

Table 118. Rate of whole plant leaf appearance (pLA) for each treatment combination in Expt 1 (32.97 D.F.) and Expt 3 (21.05 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		1.81	1.72	2.68	3.16	0.331
	May		2.03	2.18	3.26	3.90	
	June		3.06	2.07	3.66	4.36	
3	March		1.47	1.41	1.25	1.39	0.193
	April		1.34	1.71	1.54	1.65	
	May		1.32	1.32	1.69	1.60	

Main axis leaves

Table 119. Number of leaves on the main axis (maL) for each treatment combination in Expt 1 (32.4 D.F.) and Expt 3 (17.05 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		20.75	23.50	29.12	31.88	1.090
	May		18.75	22.38	20.88	25.62	
	June		20.12	23.75	21.88	29.50	
3	March		19.75	23.62	27.12	32.38	0.926
	April		21.50	23.88	25.62	30.75	
	May		20.00	23.12	24.25	28.00	

Sympodial branch leaf appearance

Table 120. Rate of leaf appearance on the sympodial branch (sbLA) for each treatment combination in Expt 1 (30.73 D.F.) and Expt 3 (18.36 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		0.301	0.320	0.275	0.327	0.0184
	May		0.196	0.280	0.215	0.278	
	June		0.291	0.290	0.238	0.339	
3	March		0.210	0.266	0.211	0.299	0.0242
	April		0.215	0.241	0.232	0.298	
	May		0.207	0.287	0.225	0.357	

APPENDIX 10

Leaf Area Index

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on both total and canopy component leaf area index (LAI) at each harvest, for Expts 1 and 3. Mean values for LAI with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Mainstem leaf area index

Table 121. Table of *P* values showing the significance of treatments and interactions, ANOVA, on mainstem leaf area index in Expt 1 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	0.010	0.436	0.168	n/a
Cultivar	0.577	0.005	< 0.001	n/a
Nitrogen rate	0.010	< 0.001	< 0.001	n/a
Planting date * Cultivar	0.531	0.675	0.320	n/a
Planting date * Nitrogen rate	0.287	0.975	0.026	n/a
Cultivar * Nitrogen rate	0.824	0.195	0.038	n/a
Planting date * Cultivar * Nitrogen rate	0.490	0.407	0.095	n/a

Table 122. Table of *P* values showing the significance of treatments and interactions, ANOVA, on mainstem leaf area index in Expt 3 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	0.062	0.120	0.062
Cultivar	n/a	0.038	0.056	0.051
Nitrogen rate	n/a	< 0.001	< 0.001	< 0.001
Planting date * Cultivar	n/a	0.007	< 0.001	0.139
Planting date * Nitrogen rate	n/a	0.661	0.151	0.357
Cultivar * Nitrogen rate	n/a	0.609	0.005	0.461
Planting date * Cultivar * Nitrogen rate	n/a	0.293	0.297	0.340

Table 123. Mainstem leaf area index at harvest 1 for each treatment combination in Expt 1 (28.99 D.F.) and Expt 3.

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		1.71	1.98	1.61	1.51	0.137
	May		1.37	1.68	1.28	1.76	
	June		1.79	2.20	1.67	2.45	
3	March		n/a	n/a	n/a	n/a	n/a
	April		n/a	n/a	n/a	n/a	
	May		n/a	n/a	n/a	n/a	

Table 124. Mainstem leaf area index at harvest 2 for each treatment combination in Expt 1 (20.6 D.F.) and Expt 3 (20.98 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		2.28	3.37	2.43	3.85	0.204
	May		2.44	3.08	2.49	4.20	
	June		2.27	3.56	2.97	4.21	
3	March		2.22	2.89	2.12	2.31	0.302
	April		2.77	3.27	3.04	3.82	
	May		2.41	2.84	2.97	4.05	

Table 125. Mainstem leaf area index at harvest 3 for each treatment combination in Expt 1 (15.48 D.F.) and Expt 3 (32.66 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		2.45	1.93	2.91	2.22	0.199
	May		2.23	1.55	3.17	2.33	
	June		1.91	1.13	3.54	1.18	
3	March		3.15	2.68	2.51	1.21	0.250
	April		2.89	2.83	2.99	1.35	
	May		2.31	2.30	3.33	2.93	

Table 126. Mainstem leaf area index at harvest 4 for each treatment combination in Expt 1 and Expt 3 (26.53 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		1.58	1.00	1.32	0.29	0.275
	April		2.24	0.73	1.48	0.37	
	May		1.94	1.35	2.38	1.17	

Axillary branch leaf area index

Table 127. Table of *P* values showing the significance of treatments and interactions, ANOVA, on axillary branch leaf area index in Expt 1 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest			
	1	2	3	4
Planting date	n/a	n/a	0.145	n/a
Cultivar	n/a	n/a	< 0.001	n/a
Nitrogen rate	n/a	n/a	< 0.001	n/a
Planting date * Cultivar	n/a	n/a	0.069	n/a
Planting date * Nitrogen rate	n/a	n/a	0.680	n/a
Cultivar * Nitrogen rate	n/a	n/a	0.002	n/a
Planting date * Cultivar * Nitrogen rate	n/a	n/a	0.204	n/a

Table 128. Table of *P* values showing the significance of treatments and interactions, ANOVA, on axillary branch leaf area index in Expt 3 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	0.018	0.007	0.534
Cultivar	n/a	0.094	< 0.001	0.004
Nitrogen rate	n/a	< 0.001	< 0.001	< 0.001
Planting date * Cultivar	n/a	0.210	< 0.001	0.115
Planting date * Nitrogen rate	n/a	0.227	0.042	0.810
Cultivar * Nitrogen rate	n/a	0.011	< 0.001	0.065
Planting date * Cultivar * Nitrogen rate	n/a	0.470	0.070	0.106

There were too many missing values to reliably run an ANOVA test, including all treatments, on axillary branch leaf area index at Harvest 1 and 2 in Expt 1, treatment means not shown.

Table 129. Axillary branch leaf area index at harvest 2 for each treatment combination in Expt 1 and Expt 3 (32.24 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		0.19	0.42	0.18	1.37	0.181
	April		0.56	1.11	0.40	1.58	
	May		0.20	1.26	0.04	1.36	

Table 130. Axillary branch leaf area index at harvest 3 for each treatment combination in Expt 1 (16.51 D.F.) and Expt 3 (23.85 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		0.23	1.11	0.98	2.06	0.135
	May		0.44	0.76	0.24	1.68	
	June		0.22	0.91	0.74	2.25	
3	March		0.27	1.08	0.96	3.22	0.193
	April		0.49	1.72	1.18	3.96	
	May		0.36	1.51	0.13	1.77	

Table 131. Axillary branch leaf area index at harvest 4 for each treatment combination in Expt 1 and Expt 3 (21.58 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		0.12	1.15	0.57	1.28	0.268
	April		0.38	0.91	0.69	2.23	
	May		0.40	1.05	0.13	1.63	

Sympodial branch leaf area index

Table 132. Table of *P* values showing the significance of treatments and interactions, ANOVA, on sympodial branch leaf area index in Expt 1 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest			
	1	2	3	4
Planting date	n/a	n/a	0.017	n/a
Cultivar	n/a	n/a	< 0.001	n/a
Nitrogen rate	n/a	n/a	< 0.001	n/a
Planting date * Cultivar	n/a	n/a	0.066	n/a
Planting date * Nitrogen rate	n/a	n/a	0.231	n/a
Cultivar * Nitrogen rate	n/a	n/a	0.003	n/a
Planting date * Cultivar * Nitrogen rate	n/a	n/a	0.488	n/a

Table 133. Table of *P* values showing the significance of treatments and interactions, ANOVA, on sympodial branch leaf area index in Expt 3 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest			
	1	2	3	4
Planting date	n/a	0.776	< 0.001	0.140
Cultivar	n/a	< 0.001	0.508	0.056
Nitrogen rate	n/a	< 0.001	< 0.001	< 0.001
Planting date * Cultivar	n/a	0.188	0.042	0.581
Planting date * Nitrogen rate	n/a	0.060	0.034	0.481
Cultivar * Nitrogen rate	n/a	0.006	0.315	0.554
Planting date * Cultivar * Nitrogen rate	n/a	0.171	0.240	0.765

Symopdial branches were only produced in the June planting. There were too many missing values to reliably run an ANOVA test on sympodial branch leaf area index at Harvest 1 in Expt 1, treatment means not shown.

Table 134. Sympodial branch leaf area index at harvest 2 for each treatment combination in Expt 1 (11.61 D.F.) and Expt 3 (22.76 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		0.250	0.657	0.095	0.481	0.0642
	April		0.289	0.667	0.147	0.279	
	May		0.182	0.782	0.028	0.316	

Table 135. Sympodial branch leaf area index at harvest 3 for each treatment combination in Expt 1 (16.01 D.F.) and Expt 3 (32.85 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		0.409	0.963	1.130	1.934	0.0963
	May		0.209	0.849	0.289	1.606	
	June		0.431	1.081	0.883	2.049	
3	March		0.47	1.49	0.48	1.90	0.142
	April		0.37	1.26	0.41	1.69	
	May		0.22	1.00	0.08	0.61	

Table 136. Sympodial branch leaf area index at harvest 4 for each treatment combination in Expt 1 and Expt 3 (29.97 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		0.25	0.60	0.50	0.86	0.129
	April		0.30	0.88	0.36	0.94	
	May		0.17	0.54	0.18	0.81	

Total leaf area index

Table 137. Table of *P* values showing the significance of treatments and interactions, ANOVA, on total leaf area index in Expt 1 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

Treatments and interactions	Harvest			
	1	2	3	4
Planting date	0.015	0.384	0.006	n/a
Cultivar	0.490	0.627	< 0.001	n/a
Nitrogen rate	0.009	< 0.001	< 0.001	n/a
Planting date * Cultivar	0.659	0.745	0.680	n/a
Planting date * Nitrogen rate	0.347	0.823	0.301	n/a
Cultivar * Nitrogen rate	0.672	0.958	0.118	n/a
Planting date * Cultivar * Nitrogen rate	0.560	0.312	0.466	n/a

Table 138. Table of *P* values showing the significance of treatments and interactions, ANOVA, on total leaf area index in Expt 3 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	0.042	0.040	0.365
Cultivar	n/a	0.127	0.003	0.113
Nitrogen rate	n/a	< 0.001	< 0.001	0.009
Planting date * Cultivar	n/a	0.376	0.657	0.648
Planting date * Nitrogen rate	n/a	0.124	0.722	0.653
Cultivar * Nitrogen rate	n/a	0.103	0.376	0.254
Planting date * Cultivar * Nitrogen rate	n/a	0.969	0.581	0.040

Table 139. Total leaf area index at harvest 1 for each treatment combination in Expt 1 (32.98 D.F.) and Expt 3 (22.76 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		1.73	1.99	1.61	1.60	0.210
	May		1.41	1.68	1.28	1.76	
	June		1.85	2.25	1.67	2.45	
3	March		n/a	n/a	n/a	n/a	n/a
	April		n/a	n/a	n/a	n/a	
	May		n/a	n/a	n/a	n/a	

Table 140. Total leaf area index at harvest 2 for each treatment combination in Expt 1 (31.44 D.F.) and Expt 3 (19.71 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		2.63	4.05	2.55	4.03	0.362
	May		2.56	3.48	2.48	4.20	
	June		2.54	4.57	2.97	4.21	
3	March		2.66	3.97	2.39	4.16	0.360
	April		3.62	5.05	3.58	5.67	
	May		2.79	4.88	3.04	5.73	

Table 141. Total leaf area index at harvest 3 for each treatment combination in Expt 1 (33 D.F.) and Expt 3 (28.02 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		3.10	4.00	5.02	6.21	0.284
	May		2.41	3.16	3.70	5.61	
	June		2.56	3.12	4.70	5.47	
3	March		3.88	5.26	3.95	6.33	0.413
	April		3.75	5.82	4.58	7.00	
	May		2.89	4.81	3.53	5.31	

Table 142. Total leaf area index at harvest 4 for each treatment combination in Expt 1 and Expt 3 (16.5 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		1.96	2.75	2.39	2.44	0.369
	April		2.91	2.51	2.53	3.54	
	May		2.51	2.94	2.69	3.60	

Specific leaf area

Table 143. Table of *P* values showing the significance of treatments and interactions, ANOVA, on specific leaf area by canopy component in Expt 1 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Specific leaf area			
	Mainstem	Axillary branch	Sympodial branch	Weighted average
Planting date	0.008	0.387	< 0.001	0.002
Cultivar	< 0.001	0.925	< 0.001	< 0.001
Nitrogen rate	0.004	0.278	0.190	0.040
Planting date * Cultivar	0.822	0.289	0.913	0.970
Planting date * Nitrogen rate	0.207	0.374	0.508	0.409
Cultivar * Nitrogen rate	0.896	0.346	0.281	0.480
Planting date * Cultivar * Nitrogen rate	0.505	0.258	0.509	0.965

Table 144. Table of *P* values showing the significance of treatments and interactions, ANOVA, on specific leaf area by canopy component in Expt 3 at harvests throughout the season. n/a where missing values prevented the comparison of each treatment within the ANOVA. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Specific leaf area			
	Mainstem	Axillary branch	Sympodial branch	Weighted average
Planting date	0.169	0.048	0.938	0.277
Cultivar	< 0.001	< 0.001	0.617	0.006
Nitrogen rate	< 0.001	0.343	0.001	0.001
Planting date * Cultivar	0.406	0.125	0.869	0.666
Planting date * Nitrogen rate	0.536	0.140	0.770	0.659
Cultivar * Nitrogen rate	0.134	0.158	0.031	0.171
Planting date * Cultivar * Nitrogen rate	0.194	0.190	0.532	0.941

Table 145. Mainstem specific leaf area at harvest 3 for each treatment combination in Expt 1 (30.65 D.F.) and Expt 3 (28.15 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		282	325	343	350	21.3
	May		279	335	327	409	
	June		370	379	409	439	
3	March		241	291	265	363	18.5
	April		269	277	295	388	
	May		253	306	293	324	

Table 146. Axillary branch specific leaf area at harvest 3 for each treatment combination in Expt 1 (28.26 D.F.) and Expt 3 (32.97 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		558	293	323	331	72.7
	May		276	309	348	328	
	June		382	358	415	408	
3	March		225	286	286	289	14.9
	April		277	273	307	324	
	May		258	266	354	321	

Table 147. Sympodial branch specific leaf area at harvest 3 for each treatment combination in Expt 1 (30.95 D.F.) and Expt 3 (26.29 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		254	264	297	317	16.9
	May		265	278	337	321	
	June		324	375	397	400	
3	March		213	308	253	286	26.8
	April		216	318	265	263	
	May		239	291	267	293	

Table 148. Average specific leaf area for whole canopy, weighted by proportion of canopy components at harvest 3 for each treatment combination in Expt 1 (29.09 D.F.) and Expt 3 (28.38 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		278	302	329	333	16.3
	May		277	317	328	360	
	June		359	372	408	410	
3	March		236	287	266	289	14.3
	April		262	294	294	302	
	May		253	289	293	315	

APPENDIX 11

Leaf area index: interaction between cultivar and nitrogen rate

There were few significant differences in total LAI and LAI distribution at the early harvests (H1 and H2) although in Expt 3, Maris Piper produced significantly more axillary branch LAI in response to additional nitrogen than Estima at H2 (Figure 144b) and the degree of increase in LAI in response to additional nitrogen was also greater in Maris Piper than Estima, although Estima produced a numerically greater sympodial branch LAI (Figure 144b). At H3, in both experiments, the reduction in mainstem LAI in response to additional nitrogen was greater in Maris Piper than Estima (by 0.64 and 0.94 LAI in Expts 1 and 3, respectively), the increase in axillary branches was also greater in Maris Piper than Estima (by 0.72 and 1.16 LAI in Expts 1 and 3, respectively) and in Expt 1 the increase in sympodial branch LAI was greater (by 0.48 LAI). Overall, Maris Piper showed a greater increase in branch leaf production to additional nitrogen.

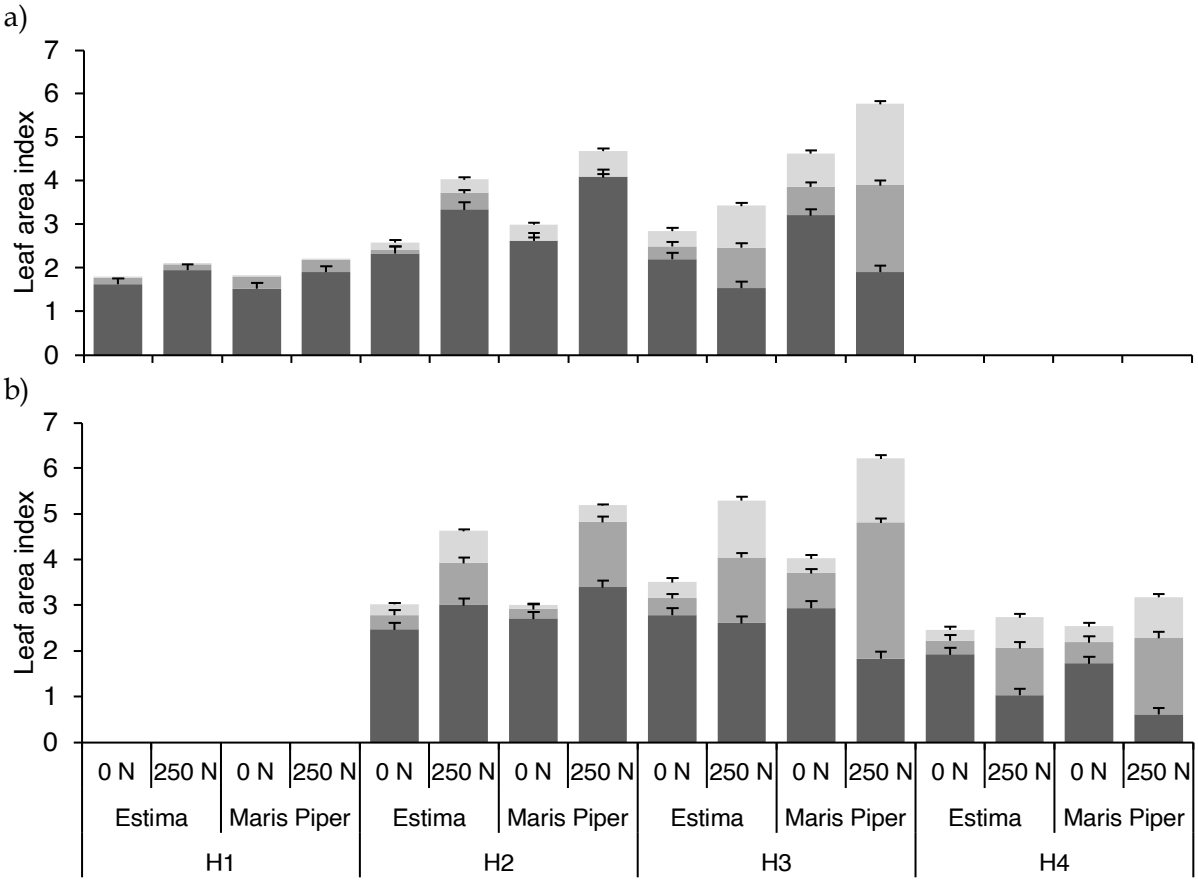

Figure 144. Effect of cultivar and nitrogen rate on total LAI throughout the season in (a) Expt 1 and (b) Expt 3)). Mainstem LAI, ■; axillary branch LAI, ■; sympodial branch LAI, ■. H1, mid canopy expansion (GC~50 %); H2, early canopy closure (GC~100 %); H3, beginning of senescence (GC~90 %), H4, mid-senescence (GC~50 %). Bars represent S.E. (Expt 1; mainstem LAI 27 D.F., axillary branch LAI H2 9 D.F., H3 23 D.F., sympodial branch LAI H2 8 D.F. and H3 25 D.F. and Expt 3; 27 D.F. for all bars but the mainstem in H4, which had 24 D.F.). Data presented are a mean of planting date treatments.

APPENDIX 12

Branch Production

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on different aspects of branch production, for Expts 1 and 3. Mean values for LAI with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Axillary branches

Table 149. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of axillary branches per stem in Expt 1 at harvests throughout the season. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	0.028	0.004	< 0.001	n/a
Cultivar	< 0.001	< 0.001	0.034	n/a
Nitrogen rate	0.086	< 0.001	0.001	n/a
Planting date * Cultivar	< 0.001	0.008	0.911	n/a
Planting date * Nitrogen rate	0.364	0.013	0.079	n/a
Cultivar * Nitrogen rate	0.180	0.022	0.151	n/a
Planting date * Cultivar * Nitrogen rate	0.284	0.640	0.198	n/a

Table 150. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of axillary branches per stem in Expt 3 at harvests throughout the season. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	0.030	0.139	0.107
Cultivar	n/a	0.004	< 0.001	< 0.001
Nitrogen rate	n/a	< 0.001	< 0.001	< 0.001
Planting date * Cultivar	n/a	0.601	0.089	0.097
Planting date * Nitrogen rate	n/a	0.012	0.093	0.020
Cultivar * Nitrogen rate	n/a	0.003	0.203	0.318
Planting date * Cultivar * Nitrogen rate	n/a	0.416	0.342	0.213

Table 151. Number of axillary branches per stem at harvest 1 for each treatment combination in Expt 1 (30.74 D.F.) and Expt 3.

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		0.33	0.83	0.00	0.33	0.484
	May		0.00	0.08	0.00	0.00	
	June		1.67	3.67	0.00	0.00	
3	March		n/a	n/a	n/a	n/a	n/a
	April		n/a	n/a	n/a	n/a	
	May		n/a	n/a	n/a	n/a	

Table 152. Number of axillary branches per stem at harvest 2 for each treatment combination in Expt 1 (25.61 D.F.) and Expt 3 (32.92 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima 0	Estima 250	Maris Piper 0	Maris Piper 250	S.E.
1	April		1.75	3.25	0.75	1.17	0.614
	May		0.50	3.17	0.00	0.25	
	June		3.92	7.83	0.58	3.33	
3	March		1.50	3.00	3.17	6.42	0.982
	April		3.92	5.17	3.58	9.25	
	May		2.92	7.00	1.25	10.83	

Table 153. Number of axillary branches per stem at harvest 3 for each treatment combination in Expt 1 (30.33 D.F.) and Expt 3 (32.57 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima 0	Estima 250	Maris Piper 0	Maris Piper 250	S.E.
1	April		3.75	4.92	2.67	3.75	0.745
	May		5.08	6.42	1.83	7.08	
	June		2.50	3.00	1.50	2.42	
3	March		1.33	2.67	6.00	7.67	0.998
	April		3.17	4.92	5.50	7.50	
	May		3.92	6.42	3.58	10.08	

Table 154. Number of axillary branches per stem at harvest 4 for each treatment combination in Expt 1 and Expt 3 (32.98 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima 0	Estima 250	Maris Piper 0	Maris Piper 250	S.E.
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		1.42	2.83	5.00	5.17	0.775
	April		2.83	3.00	4.58	6.00	
	May		3.42	5.75	2.50	7.67	

Axillary branch leaves

Table 155. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the mean number of leaves per axillary branch in Expt 1 at harvests throughout the season. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

Treatments and interactions	Harvest 1	Harvest 2	Harvest 3	Harvest 4
Planting date	n/a	0.142	0.010	n/a
Cultivar	n/a	0.002	< 0.001	n/a
Nitrogen rate	n/a	< 0.001	< 0.001	n/a
Planting date * Cultivar	n/a	0.800	0.101	n/a
Planting date * Nitrogen rate	n/a	0.024	0.061	n/a
Cultivar * Nitrogen rate	n/a	0.180	0.638	n/a
Planting date * Cultivar * Nitrogen rate	n/a	0.089	0.088	n/a

Table 156. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the mean number of leaves per axillary branch in Expt 3 at harvests throughout the season. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	0.016	0.035	0.011
Cultivar	n/a	0.871	0.002	< 0.001
Nitrogen rate	n/a	< 0.001	< 0.001	< 0.001
Planting date * Cultivar	n/a	0.075	0.008	0.004
Planting date * Nitrogen rate	n/a	0.616	0.321	0.178
Cultivar * Nitrogen rate	n/a	0.563	0.212	0.001
Planting date * Cultivar * Nitrogen rate	n/a	0.854	0.673	0.583

Data from H1 could not be analysed as only 18 % of stems had produced axillary branches.

Table 157. Mean number of leaves per axillary branch at harvest 2 for each treatment combination in Expt 1 (18.9 D.F.) and Expt 3 (32.68 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		4.07	5.92	4.08	3.33	0.770
	May		2.18	5.78	1.09	3.62	
	June		2.79	3.44	1.46	2.72	
3	March		3.55	5.50	4.21	7.03	0.365
	April		4.73	6.08	4.01	5.76	
	May		3.38	5.40	2.67	4.62	

Table 158. Mean number of leaves per axillary branch at harvest 3 for each treatment combination in Expt 1 (32.42 D.F.) and Expt 3 (33 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		3.48	5.64	7.62	9.32	0.923
	May		2.20	5.50	4.15	5.53	
	June		4.21	7.21	5.08	12.01	
3	March		3.74	5.76	5.45	7.52	0.568
	April		4.61	5.68	6.19	8.83	
	May		4.15	5.50	3.14	5.31	

Table 159. Mean number of leaves per axillary branch at harvest 4 for each treatment combination in Expt 1 and Expt 3 (32.75 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		3.94	6.51	5.56	11.67	0.786
	April		3.91	6.78	4.81	12.10	
	May		4.11	6.01	2.68	6.63	

Sympodial branch position

Table 160. Table of *P* values showing the significance of treatments and interactions, ANOVA, on sympodial branch position in Expt 1 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	0.532	0.599	n/a
Cultivar	n/a	< 0.001	< 0.001	n/a
Nitrogen rate	n/a	< 0.001	< 0.001	n/a
Planting date * Cultivar	n/a	0.589	0.127	n/a
Planting date * Nitrogen rate	n/a	0.020	0.048	n/a
Cultivar * Nitrogen rate	n/a	0.004	< 0.001	n/a
Planting date * Cultivar * Nitrogen rate	n/a	0.431	0.826	n/a

Table 161. Table of *P* values showing the significance of treatments and interactions, ANOVA, on sympodial branch position in Expt 3 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	< 0.001	< 0.001	< 0.001
Cultivar	n/a	< 0.001	< 0.001	< 0.001
Nitrogen rate	n/a	0.334	< 0.001	0.001
Planting date * Cultivar	n/a	< 0.001	< 0.001	< 0.001
Planting date * Nitrogen rate	n/a	0.238	0.227	0.248
Cultivar * Nitrogen rate	n/a	0.144	0.108	0.340
Planting date * Cultivar * Nitrogen rate	n/a	0.402	0.043	0.835

Data for H1, Expt 1, are not shown as only 12 % of stems measured had sympodial branches.

Table 162. Sympodial branch position at harvest 2 for each treatment combination in Expt 1 (19.02 D.F.) and Expt 3 (32.17 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		498	493	560	621	30.9
	May		430	520	450	637	
	June		478	494	522	661	
3	March		386	380	470	456	18.0
	April		459	472	580	636	
	May		425	402	704	739	

Table 163. Sympodial branch position at harvest 3 for each treatment combination in Expt 1 (22.9 D.F.) and Expt 3 (30.93 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		513	513	602	691	17.8
	May		501	534	603	745	
	June		496	487	633	709	
3	March		386	423	481	499	17.4
	April		461	477	593	621	
	May		450	459	694	807	

Table 164. Sympodial branch position at harvest 4 for each treatment combination in Expt 1 and Expt 3 (32.71 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		397	412	476	502	22.0
	April		478	512	626	678	
	May		441	492	718	816	

Total stem length

The data collection methodology for analysis of branch production was developed throughout the early harvests of Expt 1 and total stem length was not recorded until H2 of the June planting date. Hence, there is no total stem length data for harvest 1 in any planting dates nor for harvest 2 in the April and May planting dates. The interaction between cultivar and nitrogen rate in the June planting date is shown below, calculated using the 'RESTRICT' command in the ANOVA.

Table 165. Table of *P* values showing the significance of treatments and interactions, ANOVA, on total stem length in Expt 1 at harvests throughout the season. The effect of planting date could not be analysed at harvest 2, n/a, due to missing data (see above). Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest			
	1	2	3	4
Planting date	n/a	n/a	0.691	n/a
Cultivar	n/a	0.405	< 0.001	n/a
Nitrogen rate	n/a	< 0.001	< 0.001	n/a
Planting date * Cultivar	n/a	n/a	0.681	n/a
Planting date * Nitrogen rate	n/a	n/a	0.049	n/a
Cultivar * Nitrogen rate	n/a	0.548	0.038	n/a
Planting date * Cultivar * Nitrogen rate	n/a	n/a	0.111	n/a

Table 166. Table of *P* values showing the significance of treatments and interactions, ANOVA, on total stem length in Expt 3 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest			
	1	2	3	4
Planting date	n/a	< 0.001	0.311	< 0.001
Cultivar	n/a	< 0.001	< 0.001	< 0.001
Nitrogen rate	n/a	< 0.001	< 0.001	0.534
Planting date * Cultivar	n/a	0.143	0.231	< 0.001
Planting date * Nitrogen rate	n/a	0.042	0.063	0.421
Cultivar * Nitrogen rate	n/a	0.491	0.001	0.185
Planting date * Cultivar * Nitrogen rate	n/a	0.598	0.237	0.164

Table 167. Total stem length at harvest 2 for each treatment combination in Expt 1 (9 D.F.) and Expt 3 (32.99 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	13.1
	May		n/a	n/a	n/a	n/a	
	June		635	762	601	756	
3	March		580	710	642	795	20.6
	April		729	829	755	901	
	May		642	850	760	953	

Table 168. Total stem length at harvest 3 for each treatment combination in Expt 1 (31.6 D.F.) and Expt 3 (23.13 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		697	867	887	1059	38.6
	May		669	848	751	1159	
	June		731	875	854	1057	
3	March		610	936	769	1183	35.5
	April		698	884	850	1251	
	May		664	890	811	1116	

Table 169. Total stem length at harvest 4 for each treatment combination in Expt 1 and Expt 3 (33 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		628	840	813	1332	35
	April		730	993	931	1341	
	May		667	883	888	1267	

Sympodial branch leaves

Table 170. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of sympodial branch leaves present in Expt 1 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest			
	1	2	3	4
Planting date	n/a	0.275	0.034	n/a
Cultivar	n/a	< 0.001	< 0.001	n/a
Nitrogen rate	n/a	< 0.001	< 0.001	n/a
Planting date * Cultivar	n/a	< 0.001	0.008	n/a
Planting date * Nitrogen rate	n/a	0.053	0.020	n/a
Cultivar * Nitrogen rate	n/a	0.149	0.770	n/a
Planting date * Cultivar * Nitrogen rate	n/a	0.619	0.638	n/a

Table 171. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of sympodial branch leaves present in Expt 3 at harvests throughout the season. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

	Harvest			
Treatments and interactions	1	2	3	4
Planting date	n/a	0.144	< 0.001	0.003
Cultivar	n/a	0.004	< 0.001	< 0.001
Nitrogen rate	n/a	< 0.001	< 0.001	< 0.001
Planting date * Cultivar	n/a	< 0.001	< 0.001	< 0.001
Planting date * Nitrogen rate	n/a	0.012	0.084	0.450
Cultivar * Nitrogen rate	n/a	0.414	0.101	< 0.001
Planting date * Cultivar * Nitrogen rate	n/a	0.050	0.283	0.826

Very few plants had produced sympodial branches at harvest 1, so number of sympodial branch leaves could not be analysed.

Table 172. Number of sympodial branch leaves present at harvest 2 for each treatment combination in Expt 1 (26.89 D.F.) and Expt 3 (21.22 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		5.67	6.33	3.62	3.58	0.676
	May		3.67	6.67	4.78	6.65	
	June		5.00	8.33	1.75	3.42	
3	March		5.42	8.67	5.75	10.04	0.520
	April		6.00	8.42	5.00	7.25	
	May		4.75	10.08	3.63	6.83	

Table 173. Number of sympodial branch leaves present at harvest 3 for each treatment combination in Expt 1 (32.8 D.F.) and Expt 3 (30.93 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		6.7	11.1	17.5	21.3	1.91
	May		4.3	13.3	5.5	18.3	
	June		7.2	19.5	9.5	20.7	
3	March		5.50	10.58	8.83	16.58	0.627
	April		6.00	9.50	7.50	12.83	
	May		5.08	9.75	4.09	8.33	

Table 174. Number of sympodial branch leaves present at harvest 4 for each treatment combination in Expt 1 and Expt 3 (31.46 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		5.33	9.13	9.17	16.75	0.755
	April		5.83	8.75	6.75	13.00	
	May		4.79	8.00	4.21	9.92	

APPENDIX 13

Mid-season and final tuber harvests

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect for each of the tuber variates describing the mid-season harvest for Expts 1 and 3. Mean values for each tuber variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Number of tubers

Table 175. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare in Expt 1 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest				
Treatments and interactions	1	2	3	4	Final
Planting date	0.029	0.199	< 0.001	n/a	0.017
Cultivar	0.013	0.002	< 0.001	n/a	< 0.001
Nitrogen rate	0.141	0.312	0.250	n/a	0.908
Planting date * Cultivar	0.069	0.146	0.002	n/a	< 0.001
Planting date * Nitrogen rate	0.045	0.831	0.166	n/a	0.847
Cultivar * Nitrogen rate	0.647	0.803	0.784	n/a	0.075
Planting date * Cultivar * Nitrogen rate	0.857	0.442	0.670	n/a	0.976

Table 176. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare in Expt 3 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest				
Treatments and interactions	1	2	3	4	Final
Planting date	n/a	0.418	< 0.001	0.119	0.439
Cultivar	n/a	0.559	0.153	0.201	< 0.001
Nitrogen rate	n/a	0.787	0.099	0.033	0.626
Planting date * Cultivar	n/a	0.009	0.017	0.001	0.001
Planting date * Nitrogen rate	n/a	0.079	0.842	0.941	0.586
Cultivar * Nitrogen rate	n/a	0.473	0.238	0.277	0.260
Planting date * Cultivar * Nitrogen rate	n/a	0.913	0.948	0.704	0.429

Table 177. Number of tubers per hectare at harvest 1 for each treatment combination in Expt 1 (23.93 D.F.) and Expt 3.

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		804	731	1031	869	122.1
	May		635	413	669	326	
	June		652	750	974	1111	
3	March		n/a	n/a	n/a	n/a	n/a
	April		n/a	n/a	n/a	n/a	
	May		n/a	n/a	n/a	n/a	

Table 178. Number of tubers per hectare at harvest 2 for each treatment combination in Expt 1 (19.27 D.F.) and Expt 3 (25.99 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		703	655	778	848	137.2
	May		794	856	1178	1289	
	June		674	907	935	904	
3	March		489	556	439	444	51.8
	April		420	513	365	407	
	May		465	387	581	496	

Table 179. Number of tubers per hectare at harvest 3 for each treatment combination in Expt 1 (28.75 D.F.) and Expt 3 (30.39 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		537	526	991	926	57.7
	May		635	609	1207	1293	
	June		600	739	848	993	
3	March		502	576	528	531	40.1
	April		419	467	411	420	
	May		419	522	607	633	

Table 180. Number of tubers per hectare at harvest 4 for each treatment combination in Expt 1 and Expt 3 (20.97 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		483	567	491	496	38.0
	April		409	457	380	426	
	May		382	435	537	548	

Table 181. Number of tubers per hectare (tubers/ha) at final harvest for each treatment combination in Expt 1 (24.30 D.F.) and Expt 3 (21.37 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		485	428	919	970	49.7
	May		586	533	1193	1222	
	June		602	580	876	944	
3	March		511	467	474	483	38.6
	April		406	385	437	515	
	May		341	369	532	537	

Fresh tuber yield

Table 182. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the fresh weight tuber yield per hectare in Expt 1 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest				
Treatments and interactions	1	2	3	4	Final
Planting date	0.013	0.003	< 0.001	n/a	< 0.001
Cultivar	0.419	< 0.001	< 0.001	n/a	0.343
Nitrogen rate	0.094	0.439	0.136	n/a	0.007
Planting date * Cultivar	0.653	0.333	0.633	n/a	0.217
Planting date * Nitrogen rate	0.207	0.488	0.706	n/a	0.090
Cultivar * Nitrogen rate	0.325	0.173	0.041	n/a	0.071
Planting date * Cultivar * Nitrogen rate	0.399	0.949	0.293	n/a	0.436

Table 183. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the fresh weight tuber yield per hectare in Expt 3 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest				
Treatments and interactions	1	2	3	4	Final
Planting date	n/a	0.129	0.024	0.392	0.409
Cultivar	n/a	< 0.001	< 0.001	< 0.001	< 0.001
Nitrogen rate	n/a	0.016	0.027	< 0.001	0.006
Planting date * Cultivar	n/a	0.437	0.200	0.001	0.021
Planting date * Nitrogen rate	n/a	0.232	0.197	0.600	0.330
Cultivar * Nitrogen rate	n/a	0.765	0.331	0.048	0.695
Planting date * Cultivar * Nitrogen rate	n/a	0.982	0.892	0.007	0.116

Table 184. Fresh yield per hectare at harvest 1 for each treatment combination in Expt 1 (31.30 D.F.) and Expt 3.

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		3.58	3.15	2.01	1.41	1.361
	May		0.42	0.2	0.19	0.05	
	June		5.17	4.12	7.39	1.77	
3	March		n/a	n/a	n/a	n/a	n/a
	April		n/a	n/a	n/a	n/a	
	May		n/a	n/a	n/a	n/a	

Table 185. Fresh yield per hectare at harvest 2 for each treatment combination in Expt 1 (28.65 D.F.) and Expt 3 (15.39 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		12.63	13.38	11.34	10.51	1.091
	May		11.83	12.85	8.08	7.34	
	June		13.50	13.04	11.99	8.91	
3	March		22.65	22.75	15.64	14.79	1.985
	April		23.17	19.36	14.99	10.79	
	May		26.15	24.1	20.51	18.28	

Table 186. Fresh yield per hectare at harvest 3 for each treatment combination in Expt 1 (29.13 D.F.) and Expt 3 (26.40 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		59.26	67.31	45.89	45.77	2.865
	May		51.73	55.51	38.27	41.67	
	June		45.03	52.81	35.09	28.58	
3	March		53.94	56.92	41.2	41.61	3.089
	April		48.95	57.92	39.04	46.27	
	May		40.52	44.87	36.55	35.53	

Table 187. Fresh yield per hectare at harvest 4 for each treatment combination in Expt 1 and Expt 3 (14.67 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		59.65	79.45	54.28	57.38	2.887
	April		64.47	72.54	52.28	61.19	
	May		54.83	64.68	51.93	62.78	

Table 188. Fresh yield per hectare at final harvest for each treatment combination in Expt 1 (30.31 D.F.) and Expt 3 (16.97 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		70.01	68.49	66.93	77.42	3.469
	May		57.62	69.06	54.25	65.94	
	June		51.52	47.54	41.42	47.06	
3	March		66.88	75.53	59.16	58.21	4.091
	April		67.37	66.51	54.23	61.31	
	May		55.43	61.74	52.73	65.00	

Tuber percent dry matter

Table 189. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the tuber percent dry matter in Expt 1 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest				
	1	2	3	4	Final
Planting date	0.439	< 0.001	0.001	n/a	0.004
Cultivar	0.564	0.979	< 0.001	n/a	< 0.001
Nitrogen rate	0.864	< 0.001	< 0.001	n/a	0.004
Planting date * Cultivar	0.312	0.450	< 0.001	n/a	0.021
Planting date * Nitrogen rate	0.184	0.152	0.260	n/a	0.664
Cultivar * Nitrogen rate	0.233	0.939	0.324	n/a	0.496
Planting date * Cultivar * Nitrogen rate	0.620	0.998	1.000	n/a	0.802

Table 190. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the tuber percent dry matter in Expt 3 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Harvest				
Treatments and interactions	1	2	3	4	Final
Planting date	n/a	0.043	0.003	0.656	0.372
Cultivar	n/a	< 0.001	< 0.001	< 0.001	< 0.001
Nitrogen rate	n/a	< 0.001	< 0.001	0.030	< 0.001
Planting date * Cultivar	n/a	0.691	0.506	0.996	0.171
Planting date * Nitrogen rate	n/a	0.884	0.818	0.312	0.225
Cultivar * Nitrogen rate	n/a	0.123	0.591	0.110	< 0.001
Planting date * Cultivar * Nitrogen rate	n/a	0.144	0.823	0.687	< 0.001

Table 191. Tuber percent dry matter at harvest 1 for each treatment combination in Expt 1 (30.87 D.F.) and Expt 3.

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		16.16	14.70	17.81	14.59	2.435
	May		14.80	13.55	16.02	13.64	
	June		15.43	22.45	15.18	15.03	
3	March		n/a	n/a	n/a	n/a	n/a
	April		n/a	n/a	n/a	n/a	
	May		n/a	n/a	n/a	n/a	

Table 192. Tuber percent dry matter at harvest 2 for each treatment combination in Expt 1 (32.37 D.F.) and Expt 3 (22.16 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		14.63	13.66	14.96	13.94	0.382
	May		15.59	14.22	15.71	14.29	
	June		17.07	16.76	16.69	16.38	
3	March		16.55	16.08	17.87	16.72	0.347
	April		17.20	16.30	18.05	17.52	
	May		15.96	15.70	17.32	15.73	

Table 193. Tuber percent dry matter at harvest 3 for each treatment combination in Expt 1 (13.84 D.F.) and Expt 3 (27.15 D.F.).

		Nitrogen rate	Estima		Maris Piper		
Expt	Planting date	(kg N/ha)	0	250	0	250	S.E.
1	April		22.61	22.01	25.74	24.79	0.411
	May		21.34	20.22	23.66	22.21	
	June		20.59	19.33	21.95	20.37	
3	March		20.13	19.17	22.03	21.46	0.273
	April		21.05	20.35	23.00	22.23	
	May		20.02	19.00	21.62	20.75	

Table 194. Tuber percent dry matter at harvest 4 for each treatment combination in Expt 1 and Expt 3 (32.04 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		20.89	20.94	24.17	23.96	0.456
	April		21.35	20.95	25.12	23.35	
	May		21.30	21.14	24.92	23.78	

Table 195. Tuber percent dry matter at final harvest for each treatment combination in Expt 1 (32.58 D.F.) and Expt 3 (26.24 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		21.97	20.98	26.37	25.33	0.401
	May		20.98	20.38	24.54	23.77	
	June		21.00	20.88	24.03	23.15	
3	March		19.29	20.67	25.44	23.49	0.315
	April		20.84	20.16	24.70	23.92	
	May		20.47	19.70	24.51	23.27	

Harvest index

Table 196. Table of *P* values showing the significance of treatments and interactions, ANOVA, on dry matter harvest index in Expt 1 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest				
	1	2	3	4	Final
Planting date	< 0.001	0.019	< 0.001	n/a	< 0.001
Cultivar	0.002	< 0.001	< 0.001	n/a	< 0.001
Nitrogen rate	< 0.001	< 0.001	< 0.001	n/a	0.762
Planting date * Cultivar	0.247	0.181	0.001	n/a	0.691
Planting date * Nitrogen rate	0.116	0.362	0.121	n/a	0.811
Cultivar * Nitrogen rate	0.097	0.216	< 0.001	n/a	0.787
Planting date * Cultivar * Nitrogen rate	0.083	0.766	0.219	n/a	0.933

Table 197. Table of *P* values showing the significance of treatments and interactions, ANOVA, on dry matter harvest index (%) in Expt 3 at harvests throughout the season. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Harvest				
	1	2	3	4	Final
Planting date	n/a	0.046	0.206	0.186	0.037
Cultivar	n/a	< 0.001	< 0.001	< 0.001	< 0.001
Nitrogen rate	n/a	< 0.001	< 0.001	0.125	0.444
Planting date * Cultivar	n/a	0.462	0.297	0.663	0.354
Planting date * Nitrogen rate	n/a	0.200	0.664	0.918	0.437
Cultivar * Nitrogen rate	n/a	0.049	0.098	0.232	0.066
Planting date * Cultivar * Nitrogen rate	n/a	0.821	0.367	0.564	0.576

Table 198. Dry matter harvest index (%) at harvest 1 for each treatment combination in Expt 1 (27.18 D.F.) and Expt 3.

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		31.6	24.9	23.3	15.0	3.95
	May		5.9	2.5	3.0	0.6	
	June		37.5	34.0	37.3	12.7	
3	March		n/a	n/a	n/a	n/a	n/a
	April		n/a	n/a	n/a	n/a	
	May		n/a	n/a	n/a	n/a	

Table 199. Dry matter harvest index (%) at harvest 2 for each treatment combination in Expt 1 (30.29 D.F.) and Expt 3 (16.09 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		51.1	42.5	45.8	34.8	2.46
	May		51.9	44.5	41.9	27.4	
	June		58.7	44.7	48.0	31.8	
3	March		65.1	57.4	56.4	44.1	2.74
	April		60.3	48.8	49.3	30.9	
	May		67.6	55.0	57.6	41.8	

Table 200. Dry matter harvest index (%) at harvest 3 for each treatment combination in Expt 1 (31.43 D.F.) and Expt 3 (28.86 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		86.3	84.7	75.4	69.2	1.25
	May		84.8	84.3	77.3	67.7	
	June		85.6	83.4	71.8	58.2	
3	March		81.6	77.5	73.7	64.0	1.55
	April		79.7	76.0	69.1	62.1	
	May		81.6	74.4	72.6	65.6	

Table 201. Dry matter harvest index (%) at harvest 4 for each treatment combination in Expt 1 and Expt 3 (28.40 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		n/a	n/a	n/a	n/a	n/a
	May		n/a	n/a	n/a	n/a	
	June		n/a	n/a	n/a	n/a	
3	March		90.2	88.7	86.5	84.6	1.44
	April		87.0	88.0	84.5	81.2	
	May		87.1	86.7	84.8	83.4	

Table 202. Dry matter harvest index (%) at final harvest for each treatment combination in Expt 1 (31.83 D.F.) and Expt 3 (24.06 D.F.).

Expt	Planting date	Nitrogen rate (kg N/ha)	Estima		Maris Piper		S.E.
			0	250	0	250	
1	April		90.1	90.1	84.8	86.0	2.25
	May		89.6	89.2	82.6	81.5	
	June		82.7	83.3	74.6	76.9	
3	March		92.2	93.6	86.6	86.3	1.18
	April		91.0	90.2	83.6	81.6	
	May		89.9	91.3	83.5	80.8	

APPENDIX 14

Climate graphs

Figure 145 shows the differences in weather patterns across the three years of field experiments. Expts 3 and 4 received the greatest volume of rainfall (393, 522 and 337 mm of rainfall between March and October in 2016, 2017 and 2018, respectively, Figure 145b), whilst Expt 5 experienced the hottest conditions, with very limited rain during June and July (Figure 145c). Whilst irrigation was scheduled in response to the evapotranspirative demand of each experiment (Stalham & Allen 2004), irrigation applications were occasionally delayed and during drier and hotter periods plots may have become water-stressed.

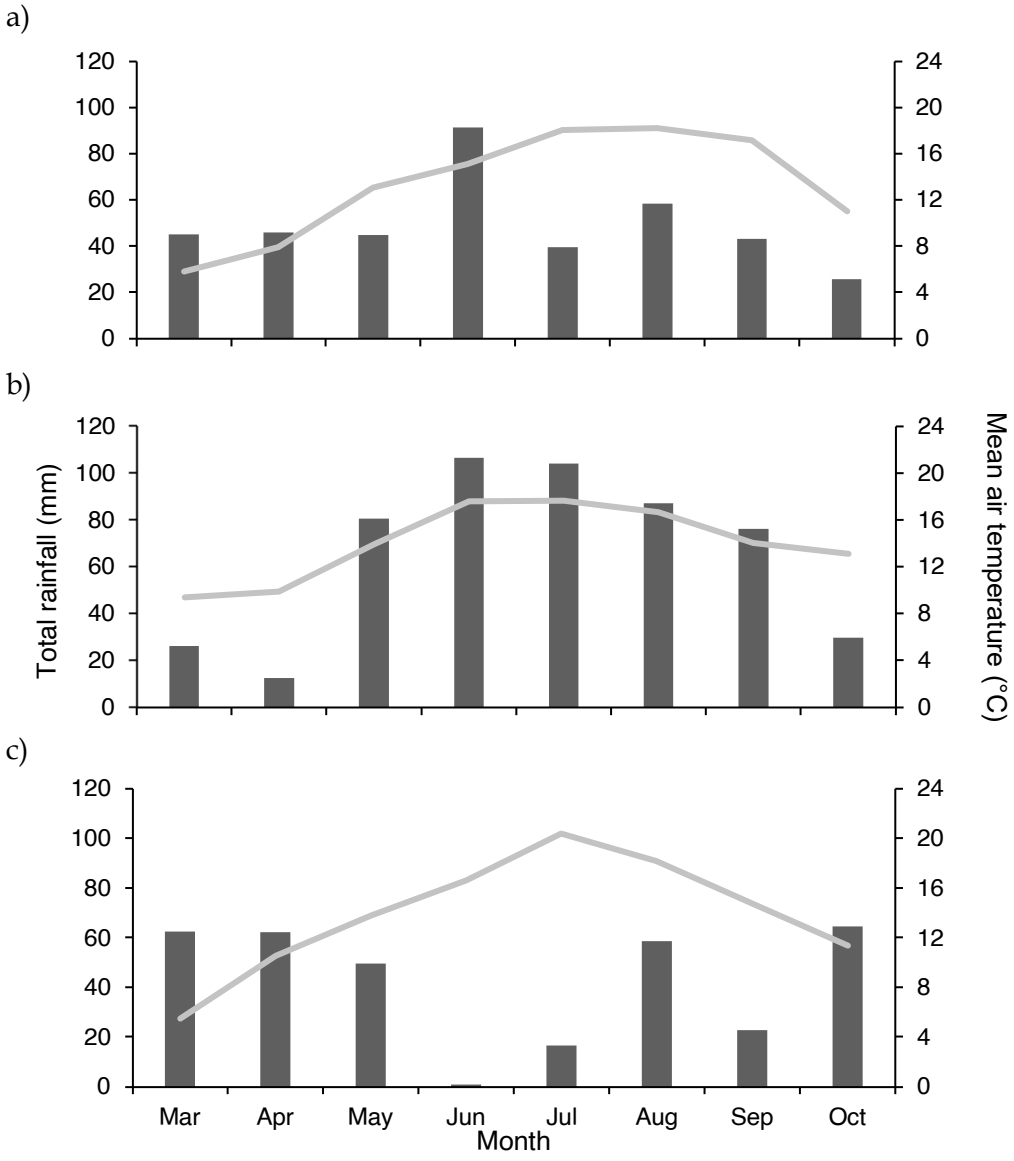

Figure 145. Climate graphs for each year of experiments, (a) 2016; Expts 1 and 2, (b) 2017; Expts 3 and 4, (c) 2018; Expt 5. Monthly total rainfall (mm), ■; mean monthly air temperature (°C), —.

Despite relatively small differences in mean monthly temperature, particularly during the summer months of 2016 and 2018, mean daily temperature was highly variable (Figure 146).

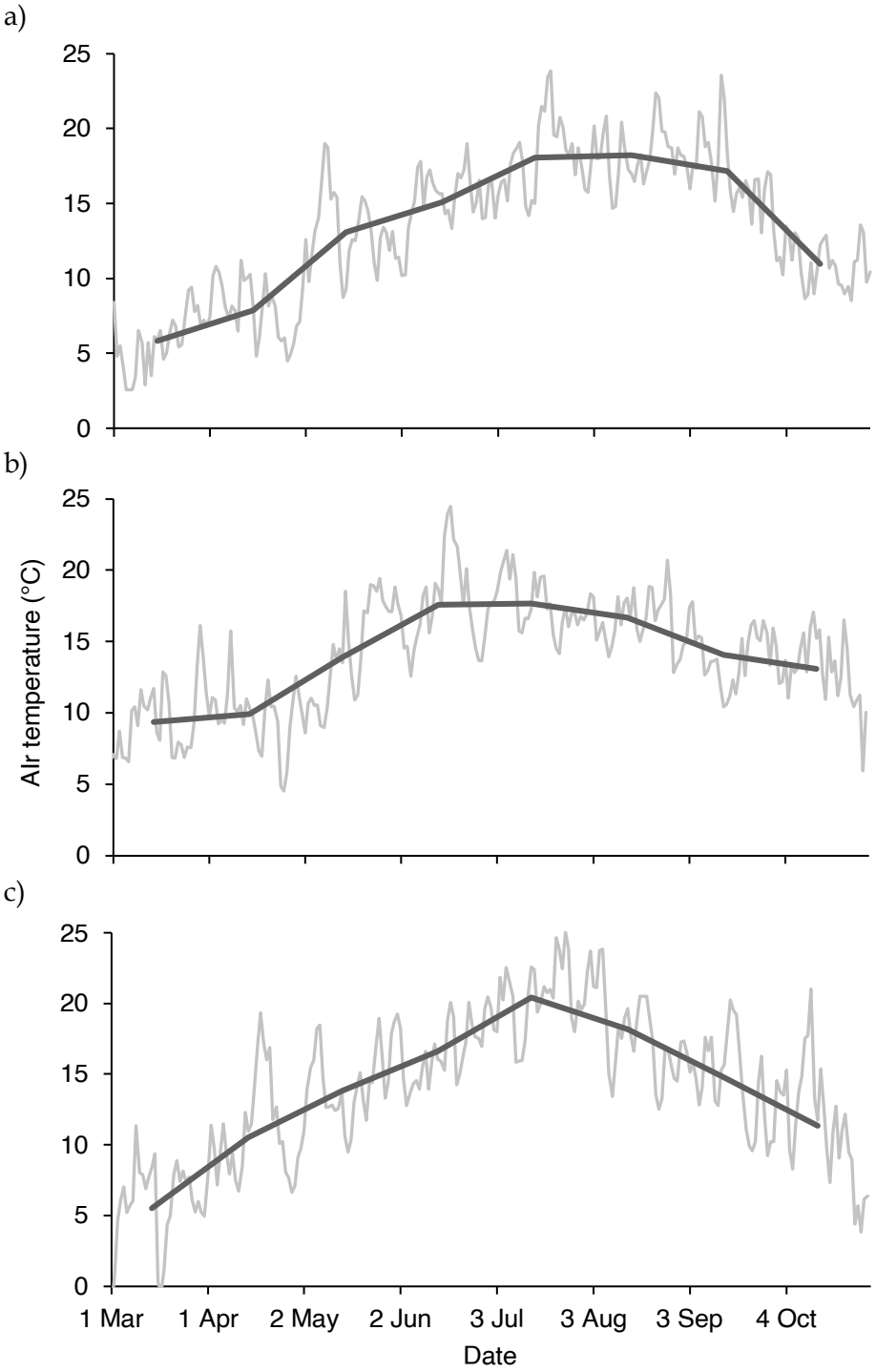

Figure 146. Mean monthly and daily air temperature for each experimental growing season, (a) 2016; Expts 1 and 2, (b) 2017; Expts 3 and 4, (c) 2018; Expt 5. Mean monthly air temperature (°C), —; mean daily temperature (°C), —.

APPENDIX 15

Climatic conditions before senescence

Mean temperature and radiation were calculated for each plot in the 3 weeks preceding the senescence of that plot and treatment means were calculated for the planting dates and varieties. This indicates in which treatments the climatic conditions were becoming cooler and less bright closer to the onset of senescence.

Planting date

There was no decrease in temperature before senescence in April plantings in Expt 1 so it is unlikely that temperature was a significant factor in triggering the onset of senescence. Temperature may have influenced the onset of senescence in May and June plantings as the last week prior to senescence was significantly cooler than the ones which preceded it (Figure 147a). Mean temperature decreased in each of the 3 weeks preceding senescence in Expt 3, but the difference was not significant in the March planting (Figure 147b). It is plausible that absolute temperature was not as important as changes of temperature between the weeks since the average temperature was 2 °C warmer in Expt 1 than Expt 3 in the last week before senescence began.

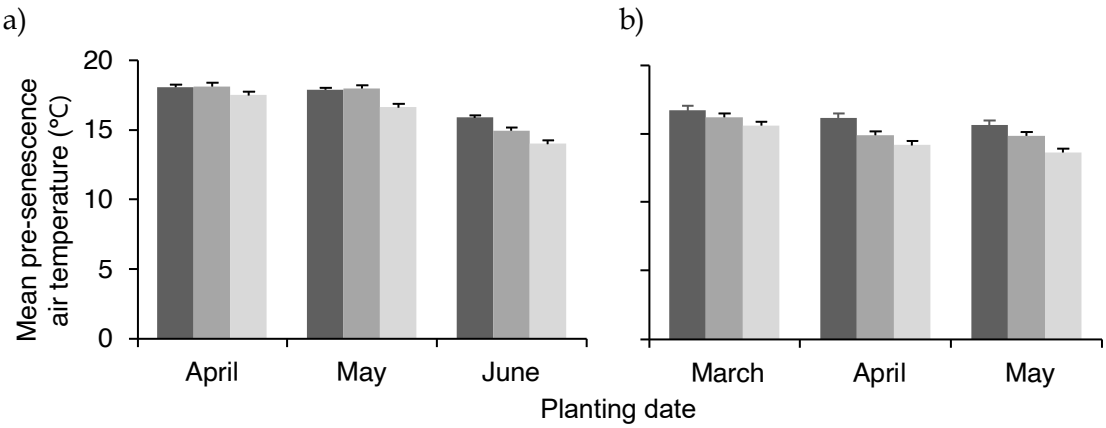

Figure 147. Mean temperature during each of the last three weeks of canopy cover prior to senescence, by planting date. 3 weeks before senescence, ■; 2 weeks before senescence, ■; 1 week before senescence, ■. (a) Expt 1 and (b) Expt 3.

Mean radiation decreased with each week closer to senescence in the June planting, Expt 1, and in all three plantings of Expt 3 (Figure 148). Mean radiation also decreased in the week prior to senescence in the May planting but did not vary in the April planting in Expt 1 (Figure 148a). Figure 148 suggests that mean radiation tends to decrease on a weekly basis in the later part of the season whether at the end of August (March planting, Expt 3) or beginning of September (June planting, Expt 1). This is

probably due to the reduction in daylength which occurs steadily after the longest day of the year, on 21 June. It is unclear if weekly reduction in mean daily radiation is a signal for canopy senescence.

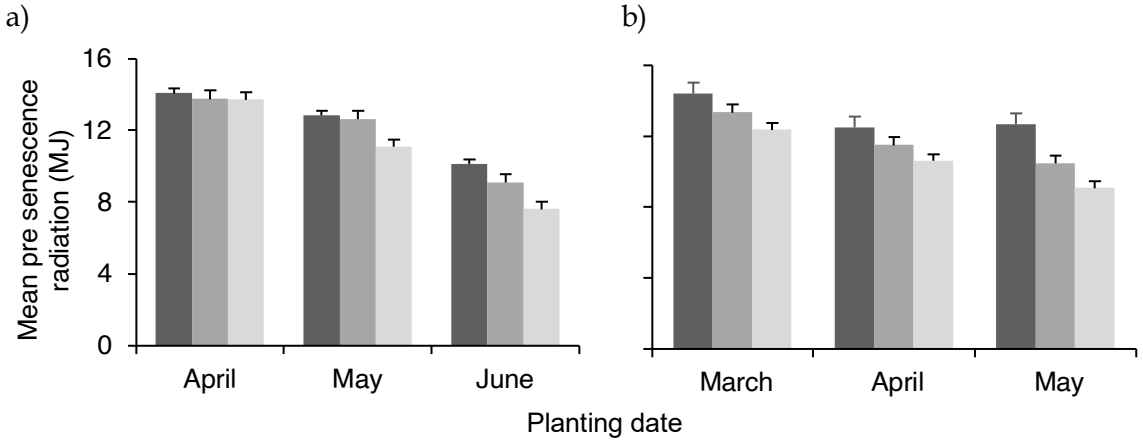

Figure 148. Mean radiation during each of the last three weeks of canopy cover prior to senescence, by planting date. 3 weeks before senescence, ■; 2 weeks before senescence, ■; 1 week before senescence, ■. (a) Expt 1 and (b) Expt 3.

Cultivar

In both experiments, mean temperature tended to decrease each week prior to senescence in Maris Piper. There was a less distinct trend in Estima and mean temperature either varied little (Expt 1, Figure 149a) or only decreased in the immediately preceding senescence (Expt 3, Figure 149b). This may mean that decreasing weekly temperature was a signal to Maris Piper to initiate senescence, but not in Estima, probably due to the difference in timing of senescence between the varieties; Estima senesced earlier in the season (when there was no monthly decrease in temperature between the months) and Maris Piper senesced later in the season.

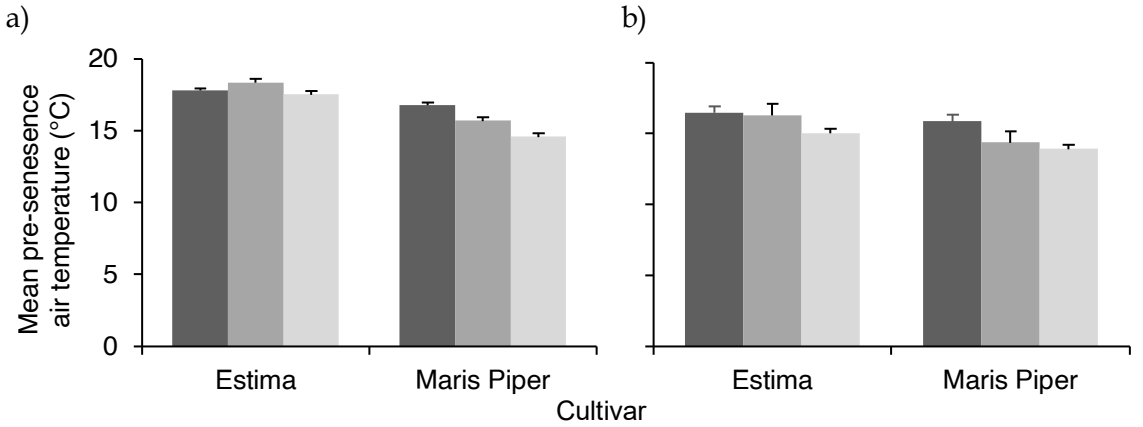

Figure 149. Mean temperature during each of the last three weeks of canopy cover prior to senescence, by cultivar. 3 weeks before senescence, ■; 2 weeks before senescence, ■; 1 week before senescence, ■. Expt 1 (a) and Expt 3 (b).

Mean radiation decreased each week prior to senescence in Maris Piper, in both experiments, and in Estima, in Expt 3 (Figure 150), however the implications of this for decreasing radiation as a signal for senescence are unclear.

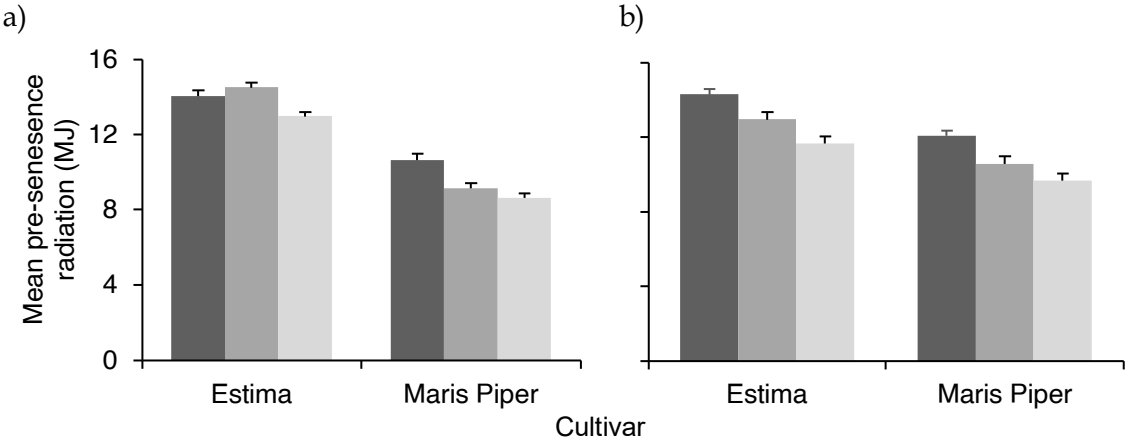

Figure 150. Mean radiation during each of the last three weeks of canopy cover prior to senescence, by cultivar. 3 weeks before senescence, ■; 2 weeks before senescence, ■; 1 week before senescence, ■. (a) Expt 1 and (b) Expt 3.

APPENDIX 16

Specific leaf area variation with nitrogen and cultivar

Specific leaf area was greater at higher than low nitrogen by 19.2 and 28.5 cm^2/g in Expts 1 and 3, respectively (Figure 151). Maris Piper SLA was greater than that of Estima by 43.8 and 23.3 cm^2/g in Expts 1 and 3, respectively (Figure 151). High SLA may be related to faster rates of senescence, since senescence is faster at high nitrogen, but other factors, such as number of leaves, are also involved as indicated by the slower rate of senescence in Maris Piper than Estima, despite higher SLA.

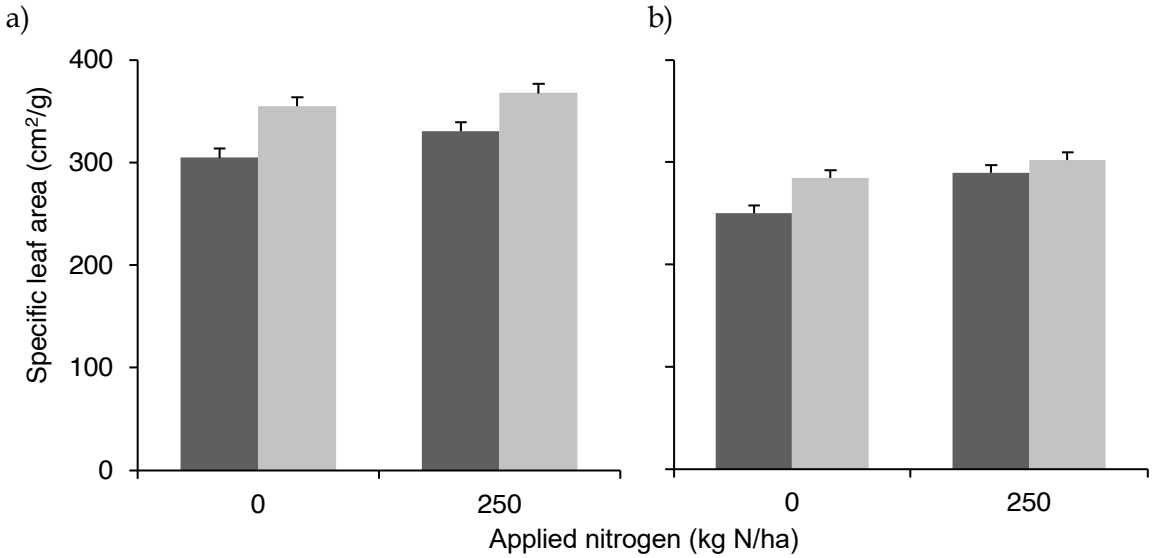

Figure 151. Effect of cultivar and nitrogen rate on specific leaf area in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (27 D.F. (a), 25 D.F. (b)). Data presented are a mean of planting dates.

Whilst there was no overall relationship between SLA and GCRate9050 (multiple linear regressions; GCRate9050 ~ SLA + block/main plot, $P = 0.857$), when differences between cultivar were considered 25.4 % of the variation in GCRate9050 was explained by SLA (multiple linear regressions; GCRate9050 ~ SLA + cultivar + block/main plot, $P < 0.001$, Figure 152, Table 203) and there was a slight increase in the rate of senescence with decreasing leaf thickness, as indicated by greater SLA values (Figure 152), yet there remained a high degree of variability in the rate of senescence.

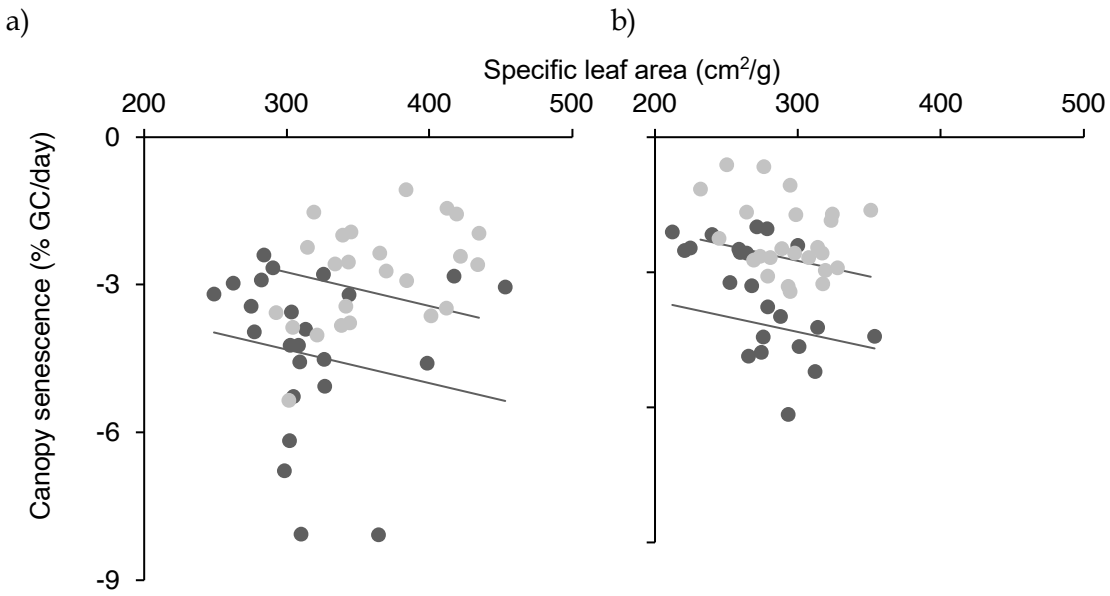

Figure 152. Relationship between specific leaf area (SLA) and rate of canopy senescence (GCDRate9050) in (a) Expt 1 and (b) Expt 3. Estima, ●; Maris Piper, ■. R^2 = 0.254, see Table 203 for details of multiple linear regression.

Table 203. Relationship between specific leaf area (SLA), rate of canopy senescence (GCDRate9050) and cultivar (MP). GCRate9050 = β0 + β1*SLA + β2*MP.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	-2.26	0.937	0.018
1	SLA	-0.0068	0.00275	0.015
2	MP	1.58	0.267	< 0.001

APPENDIX 17

Canopy efficiency

Tuber production can be considered in terms of efficiency in conversion of canopy size and light interception potential in relation to fresh or dry weight yield, calculated by dividing the IGC of a plot by fresh or dry weight yield. The canopy required (CanReq) to produce one tonne of dry weight yield is inversely related to the canopy efficiency. Canopy required to produce a tonne of tuber dry matter increased with lateness of planting date in Expt 1 (Figure 153a), but did not vary significantly in Expt 3 (Figure 153b).

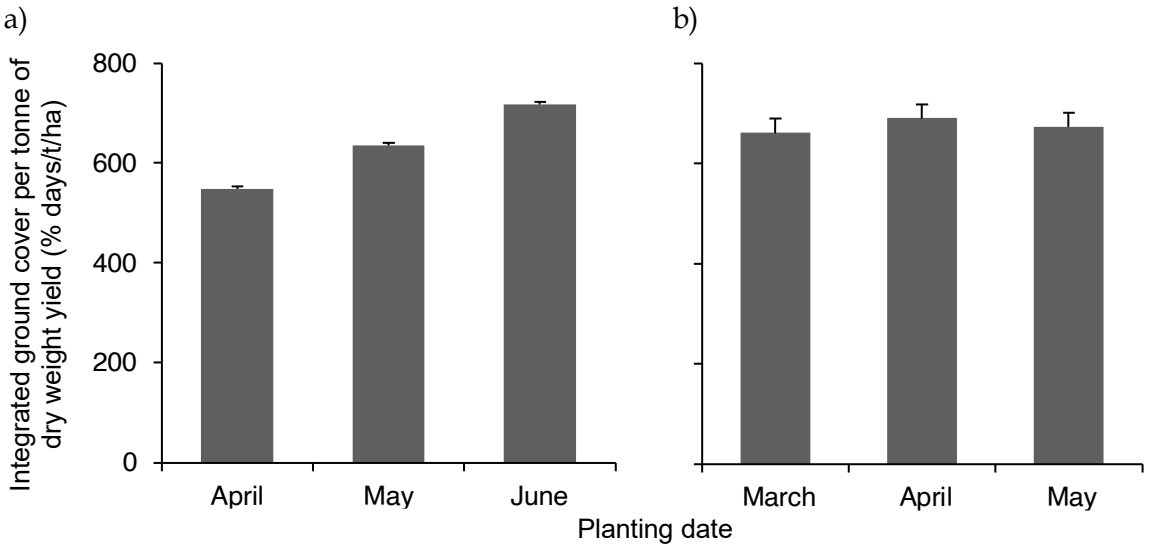

Figure 153. Effect of planting date on canopy required (integrated ground cover per tonne of dry weight tuber yield) in (a) Expt 1 and (b) Expt 3. Bars represent S.E. (6 D.F.). Data presented are means of cultivars and nitrogen rates.

Maris Piper required greater canopy area and duration for dry matter tuber production, indicating that its canopy was less efficient than that of Estima (Figure 154). The difference between the two cultivars was similar in both experiments and Maris Piper CanReq was 97 and 115 % days/t/ha greater than Estima in Expts 1 and 3, respectively. In Expt 1 additional nitrogen increased CanReq for tuber production in Estima, but decreased CanReq by Maris Piper (Figure 154a), whilst in Expt 3 additional nitrogen resulted in slight (and non-significant) decreases in the ratio of IGC to dry matter yield (Figure 154b). This suggests that nitrogen can affect cultivars differently; in Estima increasing canopy size relative to yield and in Maris Piper enabling greater yield production relative to canopy size, increasing canopy efficiency. However, these results are inconclusive as they were only observed in one year.

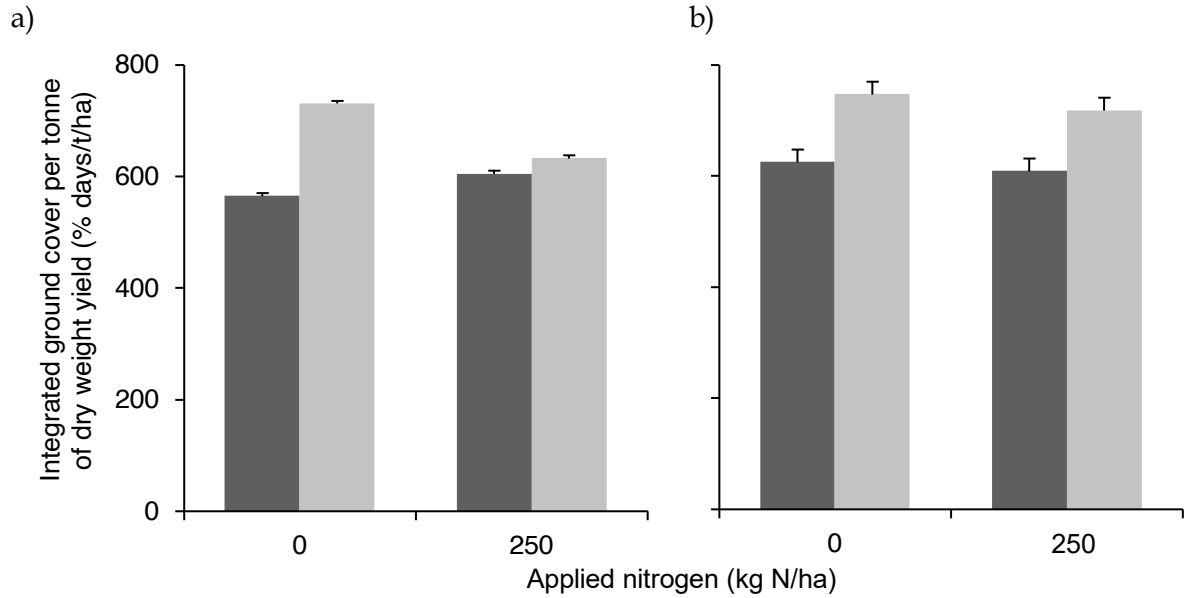

Figure 154. Effect of cultivar on canopy required (integrated ground cover per tonne of dry weight tuber yield) in (a) Expt 1 and (b) Expt 3. Estima, ■; Maris Piper, ■. Bars represent S.E. (26 D.F.). Data presented are means of planting date treatments.

Small seed tended to have less efficient canopies with a larger CanReq than large seed, although this difference was only significant in Expt 4 (Figure 155b).

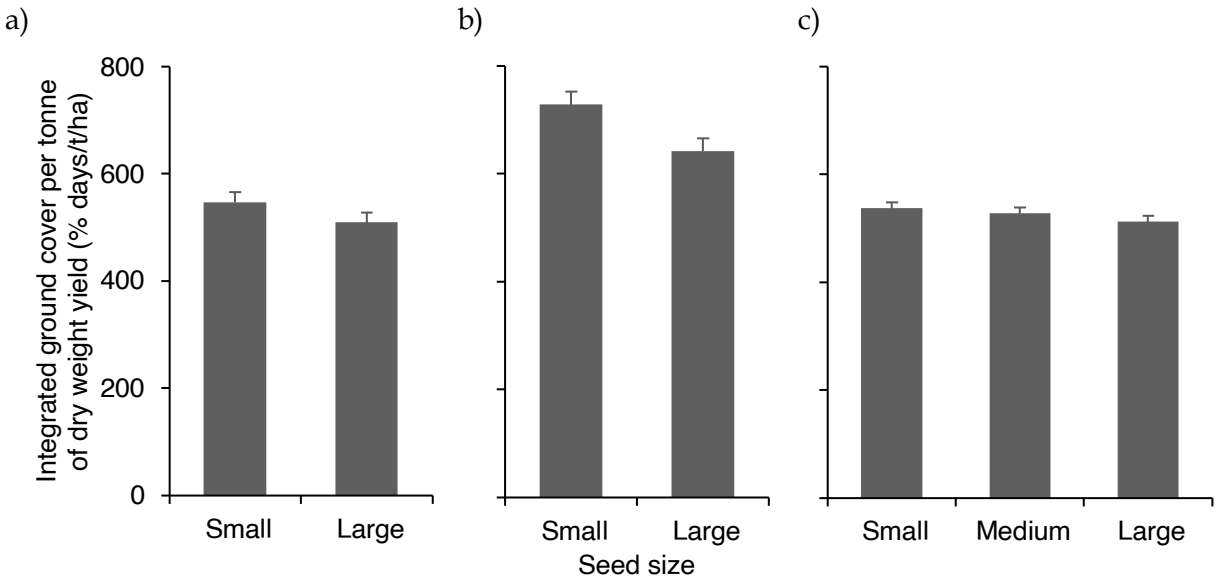

Figure 155. Effect of seed size on canopy required (integrated ground cover per tonne of dry weight tuber yield) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of cultivar and seed spacing treatments.

Estima consistently had a lower CanReq than Maris Piper, although the extent of the difference varied between experiments and was greatest in Expt 4, followed by Expts 5 and 2 (216, 102 and 64 % days/t/ha, respectively, Figure 156).

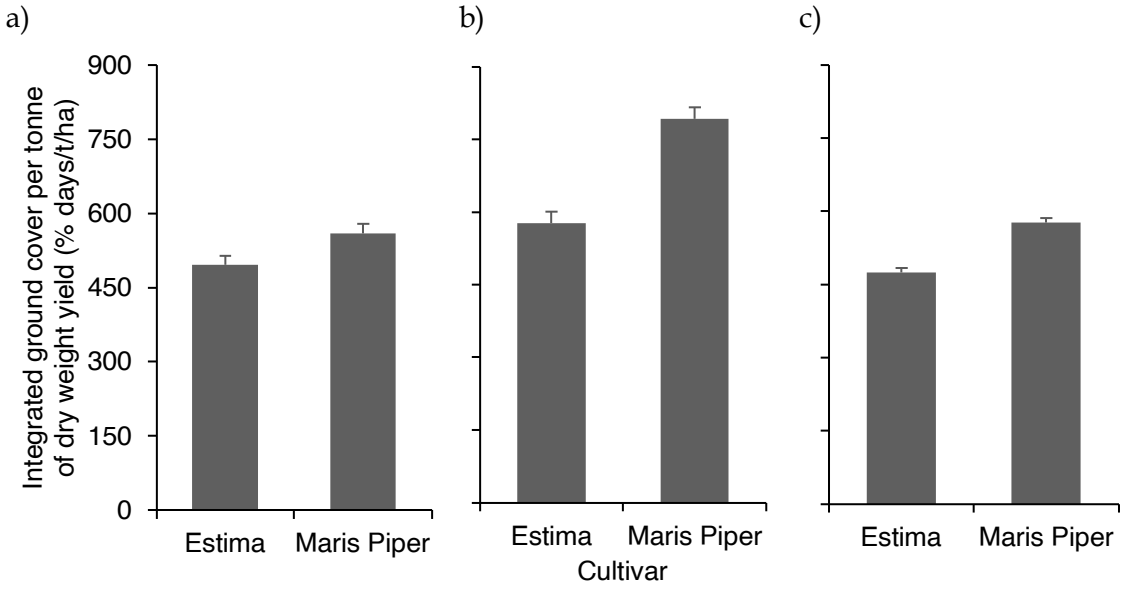

Figure 156. Effect of cultivar on canopy required (integrated ground cover per tonne of dry weight tuber yield) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of seed spacing and seed size treatments.

There was little variation in CanReq with seed spacing (Figure 157), only varying significantly in Expt 5 when plots at 40 cm spacing were least efficient at converting canopy mass into dry weight yield (Figure 157c).

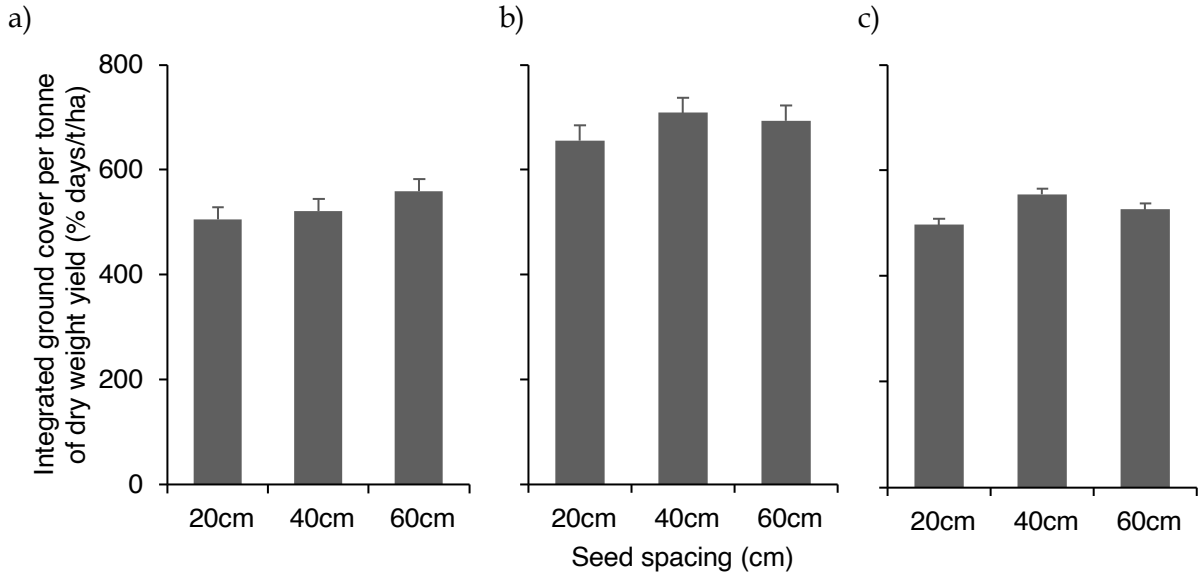

Figure 157. Effect of seed spacing on canopy required (integrated ground cover per tonne of dry weight tuber yield) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 22 D.F. and (c) 34 D.F.). Data presented are means of cultivar and seed size treatments.

APPENDIX 18

Emergence and number of stems

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on pre-emergence growth and stem counts in Expts 2, 4 and 5. Mean values for each variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 204. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the delay between emergence and planting (EmDAP) and the number of stems per plant (stems) in Expts 2, 4 and 5. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	Expt 2		Expt 4		Expt 5	
Treatments and interactions	EmDAP	stems	EmDAP	stems	EmDAP	stems
Seed spacing	0.098	0.735	0.015	0.310	0.072	0.499
Cultivar	0.363	< 0.001	0.003	0.909	< 0.001	< 0.001
Seed size	1.000	< 0.001	0.009	< 0.001	0.008	< 0.001
Seed spacing * Cultivar	0.436	0.150	0.015	0.310	0.589	0.346
Seed spacing * Seed size	1.000	0.538	0.166	0.361	0.553	0.684
Cultivar * Seed size	1.000	0.045	0.009	0.732	0.926	0.003
Seed spacing * Cultivar * Seed size	0.098	0.783	0.166	0.602	0.316	0.298

Emergence

Table 205. Duration between planting and emergence (EmDAP, days) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		35.0	37.0	35.0	35.0	35.0	36.0	0.622
	Large		35.0	36.0	36.0	35.0	36.0	35.0	
4	Small		50.0	50.0	50.0	50.0	48.3	51.0	0.767
	Large		50.0	50.0	50.0	45.0	46.7	50.0	
5	Small		30.0	30.0	31.0	29.7	29.7	29.7	0.283
	Medium		29.7	30.0	30.0	29.0	29.0	29.7	
	Large		29.7	30.0	30.0	29.0	29.3	29.0	

Number of stems

Table 206. Number of stems per plant (stems) for each treatment combination in Expt 2 (58 D.F.), Expt 4 (22 D.F.) and Expt 5 (83 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		1.50	2.17	2.17	4.17	3.50	2.83	0.540
	Large		3.00	3.83	4.00	6.33	6.67	6.33	
4	Small		2.00	2.00	1.67	2.00	1.67	1.67	0.420
	Large		3.67	3.67	4.00	4.50	3.00	4.00	
5	Small		1.97	1.83	1.43	2.23	2.17	2.33	0.440
	Medium		3.17	2.17	2.17	2.83	2.83	3.83	
	Large		2.50	3.00	3.33	5.17	4.67	5.33	

APPENDIX 19

Ground Cover Growth Patterns

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect for each of the ground cover canopy variates for Expts 2, 4 and 5. Mean values for each canopy variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 207. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the delay between emergence and planting (EmDAP), integrated ground cover (IGC), early canopy expansion (TiE25), rate of early canopy expansion per plant (TiE25Rate), rate of mid-canopy expansion (GCRate2575), duration of near-complete canopy cover (GCDur90), duration of canopy growing season (GrowDur) and rate of canopy senescence (GCRate9050) in Expt 2. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	IGC	TiE25	TiE25 Rate	GCRate 2575	GCDur 90	Grow Dur	GCRate 9050
Seed spacing	0.009	< 0.001	< 0.001	0.562	0.113	0.702	0.915
Cultivar	< 0.001	0.014	0.042	0.207	< 0.001	< 0.001	< 0.001
Seed size	< 0.001	< 0.001	< 0.001	0.003	0.001	0.282	0.871
Seed spacing * Cultivar	0.744	0.281	0.366	0.035	0.236	0.335	0.333
Seed spacing * Seed size	0.307	0.736	0.688	0.013	0.381	0.709	0.699
Cultivar * Seed size	0.025	0.031	0.057	0.617	0.045	0.144	0.685
Seed spacing * Cultivar * Seed size	0.345	0.079	0.078	0.618	0.224	0.350	0.324

Table 208. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the delay between emergence and planting (EmDAP), integrated ground cover (IGC), early canopy expansion (TiE25), rate of early canopy expansion per plant (TiE25Rate), rate of mid-canopy expansion (GCRate2575), duration of near-complete canopy cover (GCDur90), duration of canopy growing season (GrowDur) and rate of canopy senescence (GCRate9050) in Expt 4. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	IGC	TiE25	TiE25 Rate	GCRate 2575	GCDur 90	Grow Dur	GCRate 9050
Seed spacing	< 0.001	< 0.001	< 0.001	0.101	0.003	0.741	0.011
Cultivar	< 0.001	0.009	0.020	0.439	< 0.001	< 0.001	< 0.001
Seed size	< 0.001	< 0.001	< 0.001	0.912	< 0.001	0.750	0.288
Seed spacing * Cultivar	0.340	0.845	0.534	0.543	0.357	0.389	0.268
Seed spacing * Seed size	0.484	0.740	0.726	0.113	0.330	0.870	0.702
Cultivar * Seed size	0.265	0.570	0.100	0.705	0.534	0.469	0.636
Seed spacing * Cultivar * Seed size	0.145	0.115	0.137	0.892	0.339	0.712	0.778

Table 209. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the delay between emergence and planting (EmDAP), integrated ground cover (IGC), early canopy expansion (TiE25), rate of early canopy expansion per plant (TiE25Rate), rate of mid-canopy expansion (GCRate2575), duration of near-complete canopy cover (GCDur90), duration of canopy growing season (GrowDur) and rate of canopy senescence (GCRate9050) in Expt 5. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	IGC	TiE25	TiE25 Rate	GCRate 2575	GCDur 90	Grow Dur	GCRate 9050
Seed spacing	< 0.001	< 0.001	< 0.001	0.598	0.002	0.007	0.445
Cultivar	< 0.001	0.028	0.074	0.408	< 0.001	< 0.001	< 0.001
Seed size	< 0.001	< 0.001	< 0.001	0.003	< 0.001	0.391	0.499
Seed spacing * Cultivar	0.682	0.480	0.439	0.896	0.217	0.594	0.002
Seed spacing * Seed size	0.297	0.504	0.509	0.422	0.413	0.264	0.922
Cultivar * Seed size	0.680	0.251	0.639	0.105	0.130	0.867	0.003
Seed spacing * Cultivar * Seed size	0.295	0.017	0.067	0.035	0.166	0.880	0.534

Integrated ground cover

Table 210. Integrated ground cover (IGC, % days) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		7130	6790	6020	10 090	9960	9780	263
	Large		7960	7290	7540	10 570	9980	9920	
4	Small		8710	7950	7870	10 470	10 100	9170	255
	Large		9780	9160	8640	10 630	1074	10 450	
5	Small		5470	4620	4070	8760	8710	7830	242
	Medium		5190	5280	5120	8950	8860	8180	
	Large		5700	5810	5190	9570	9240	8770	

Early canopy expansion

Table 211. Interval between emergence and 25 % GC (TiE25, days) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		16.77	18.96	24.03	14.32	18.96	19.95	0.759
	Large		12.24	16.10	18.63	11.38	15.81	19.33	
4	Small		19.6	23.1	27.5	18.7	25.5	31.8	1.43
	Large		8.0	13.8	18.5	12.9	15.5	20.3	
5	Small		13.97	18.85	22.04	13.80	17.39	20.72	0.446
	Medium		12.14	14.33	18.57	10.67	15.80	17.76	
	Large		9.80	13.01	16.49	9.28	12.64	16.82	

Per plant early canopy expansion rate

Table 212. Rate of early canopy expansion between emergence and 25 % GC calculated per plant (TiE25Rate, %/day/plant) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		0.500	0.660	1.041	0.587	0.660	1.254	0.0416
	Large		0.686	0.786	1.347	0.735	0.792	1.303	
4	Small		0.43	0.54	0.91	0.46	0.49	0.79	0.103
	Large		1.17	0.93	1.37	0.65	0.82	1.25	
5	Small		0.597	0.664	1.135	0.606	0.719	1.209	0.0314
	Medium		0.689	0.874	1.348	0.782	0.792	1.409	
	Large		0.863	0.962	1.518	0.900	0.992	1.487	

Mid-canopy expansion

Table 213. Rate of canopy expansion between 25 and 75 % GC (GCRate2575, %/day) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		5.57	4.50	4.47	5.11	6.01	4.66	0.396
	Large		5.26	5.49	6.42	5.21	6.37	6.14	
4	Small		3.75	3.81	3.92	3.69	3.61	3.53	0.325
	Large		3.32	3.35	4.53	3.44	3.49	4.04	
5	Small		4.27	2.87	2.70	3.71	3.91	4.41	0.418
	Medium		4.01	3.71	4.77	4.34	3.62	3.57	
	Large		4.13	4.78	4.60	4.60	4.71	4.45	

Duration of near-complete ground cover

Table 214. Duration of 90 % GC (GCDur90, days) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (31 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		55.5	47.6	39.9	75.8	76.3	74.7	3.42
	Large		62.2	55.3	60.5	79.6	80.0	76.9	
4	Small		63.2	52.9	52.3	76.8	70.7	59.0	3.77
	Large		73.2	63.8	62.4	76.7	77.6	75.0	
5	Small		32.8	12.2	13.1	66.1	68.2	59.0	3.94
	Medium		29.5	25.7	26.5	67.1	66.9	57.4	
	Large		35.3	38.1	30.1	74.6	73.8	66.7	

Duration of canopy growth

Table 215. Duration of canopy growing season (from emergence until the onset of senescence (defined as 90 % of maximum canopy extent), GrowDur, days) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		85.8	84.5	80.8	104.8	107.9	111.1	3.03
	Large		88.7	85.2	90.9	105.5	107.6	108.5	
4	Small		103.6	95.9	100.0	115.9	117.6	113.9	4.05
	Large		103.7	100.5	98.1	111.4	114.6	113.9	
5	Small		67.1	68.3	65.5	100.3	105.1	98.1	2.19
	Medium		61.9	67.0	66.1	95.19	103.8	100.2	
	Large		63.5	67.4	66.6	100.7	102.4	101.0	

Canopy senescence

Table 216. Rate of canopy senescence (GCRate9050, %/day) for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (31 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		-6.06	-5.00	-4.65	-2.72	-2.81	-3.44	0.605
	Large		-5.49	-5.00	-5.82	-2.56	-3.35	-2.81	
4	Small		-3.77	-2.97	-3.05	-2.54	-2.21	-2.23	0.320
	Large		-4.30	-3.15	-3.21	-2.70	-2.59	-2.04	
5	Small		-4.10	-2.54	-3.30	-5.06	-6.84	-5.59	0.512
	Medium		-4.18	-3.40	-3.34	-3.87	-5.32	-5.26	
	Large		-4.34	-4.26	-4.03	-3.91	-5.26	-4.36	

APPENDIX 20

Planting density mean treatment interaction CQ curves

The effect of interactions between cultivar, seed size and seed spacing upon canopy development throughout the growing season is presented below for Expts 2, 4 and 5 (Figures 158, 159 & 160, respectively). The goodness of fit of each curve to the treatment mean of the raw data was described using both Willmott's index of agreement (*d*, Table 217) and the root mean square error (RMSE, % GC, Table 218).

Experiment 2

Canopy expansion was fastest when seed were most tightly spaced, slowing as seed spacing increased (Figure 158). Expansion was typically slower in small seed than large, though there was overlap between the most widely spaced large seed and most closely spaced small seed in both cultivars (Figure 158). Small Estima seed at 20 and 40 cm spacing 'struggled' to close gaps within the canopy, achieving complete ground cover *c.* 15 days later than the other treatments (Figure 158a), whilst the wide spaced small Maris Piper seed also expanded more slowly than other combinations of seed size and spacing (Figure 158b), the difference was less extreme than in Estima. All treatment combinations achieved complete canopy cover, though there was more variation in duration of complete canopy cover in Estima than Maris Piper (Figure 158). Onset and rate of senescence also varied more between seed size and spacing treatments in Estima than in Maris Piper (Figure 158).

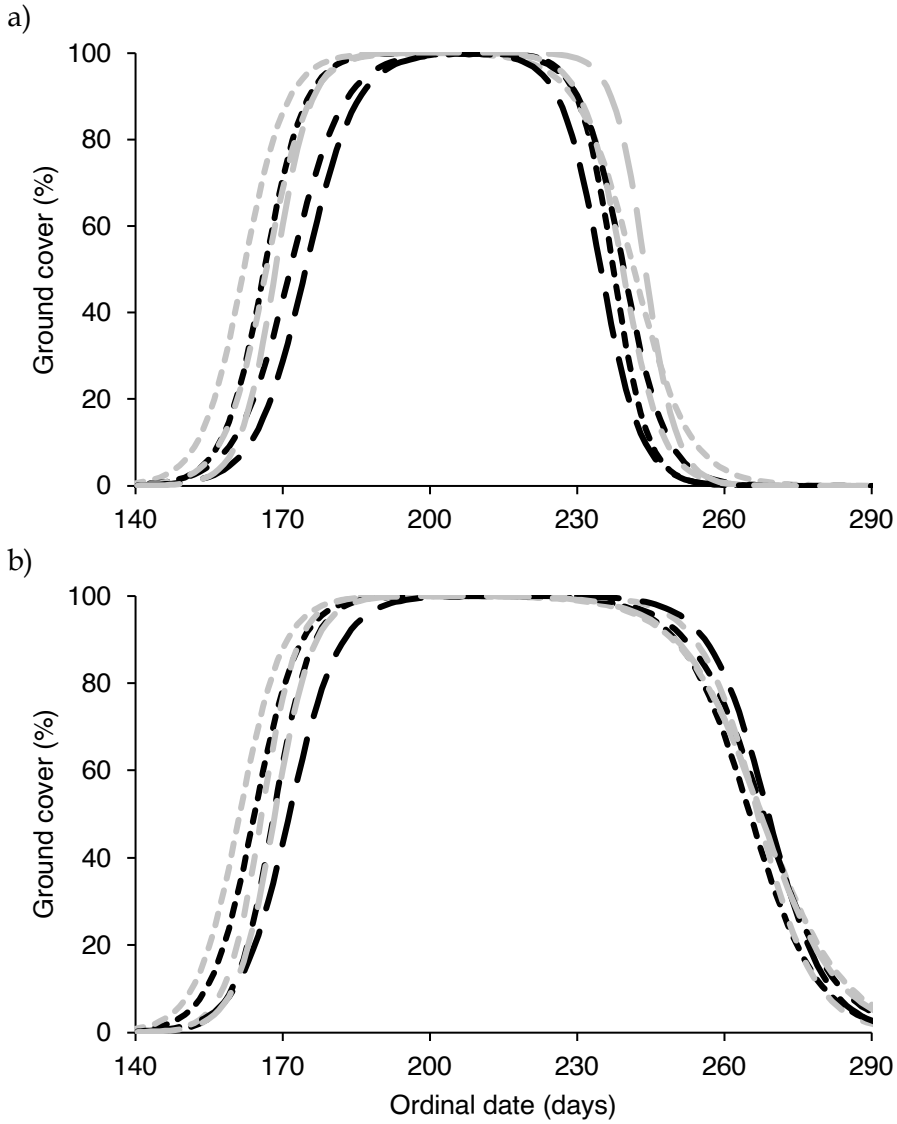

Figure 158. Average ground cover curve for all combinations of treatments (seed spacing * cultivar * seed size), plotted against days after emergence, (a) Estima and (b) Maris Piper in Expt 2. Small seed, ——; large seed, ——; 20 cm, – – – –; 40 cm, — — —, 60 cm, —— —— .

Experiment 4

Again, canopy expansion was more rapid when seed larger and was most closely spaced (Figure 159). There was no overlap in expansion between seed sizes in Estima (Figure 159a), but in Maris Piper, widely spaced large seed and closely spaced small seed were almost indistinguishable during canopy expansion (Figure 159b). All treatments achieved complete ground cover, though the date at which 100 % GC was reached varied considerably between seed size and spacing treatments, there was little variation in the onset or rate of senescence in Estima (Figure 159a). There was greater variation in the timing of Maris Piper canopy senescence between seed size and spacing treatments than in Estima, with large seed at 20 cm spacing senescing earlier

than the small seed at 60 cm, reflecting, though not perfectly replicating, the order of treatments reaching 100 % GC (Figure 159b).

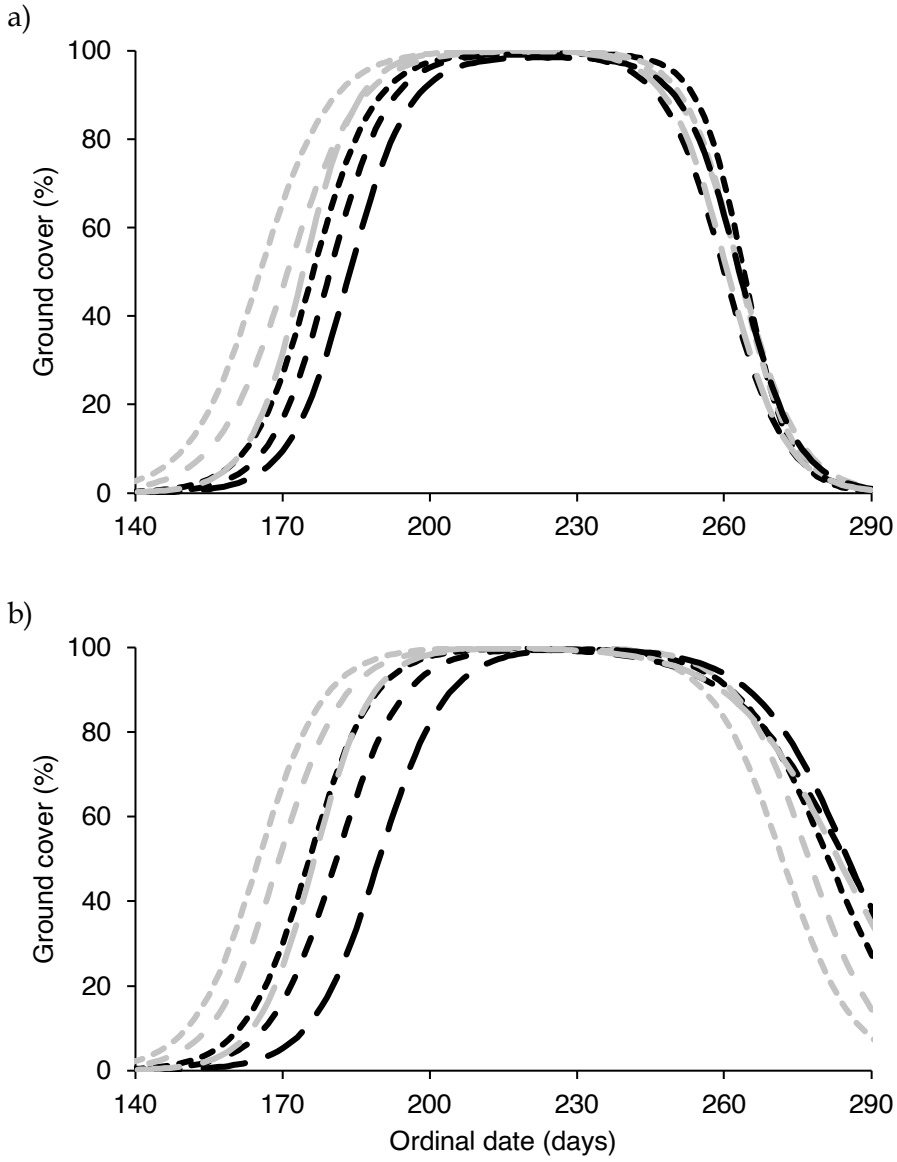

Figure 159. Average ground cover curve for all combinations of treatments (seed spacing * cultivar * seed size), plotted against days after emergence, (a) Estima and (b) Maris Piper in Expt 4. Small seed, ——; large seed, ——; 20 cm, - - - -; 40 cm, – – –, 60 cm, — — .

Experiment 5

As expected, more closely spaced seed produced canopies which expanded more rapidly than those spaced further apart in both cultivars (Figure 160). There was greater variation between seed size and spacing treatments in the rate of canopy expansion than in the rate of canopy senescence in both Estima and Maris Piper (Figures 160a & b, respectively). Estima did not achieve 100 % GC in any combination of seed sizes and spacings, though small seed at wider spacings performed the worst with 40 and 60 cm spaced seed achieving *c.* 84 and 81 % GC, respectively (Figure 160a).

All Maris Piper treatment combinations achieved 100 % GC, though maximal ground cover was maintained for a shorter duration at wider than closer seed spacing due to the delay in reaching complete canopy cover and the limited variation in timing of senescence (Figure 160b).

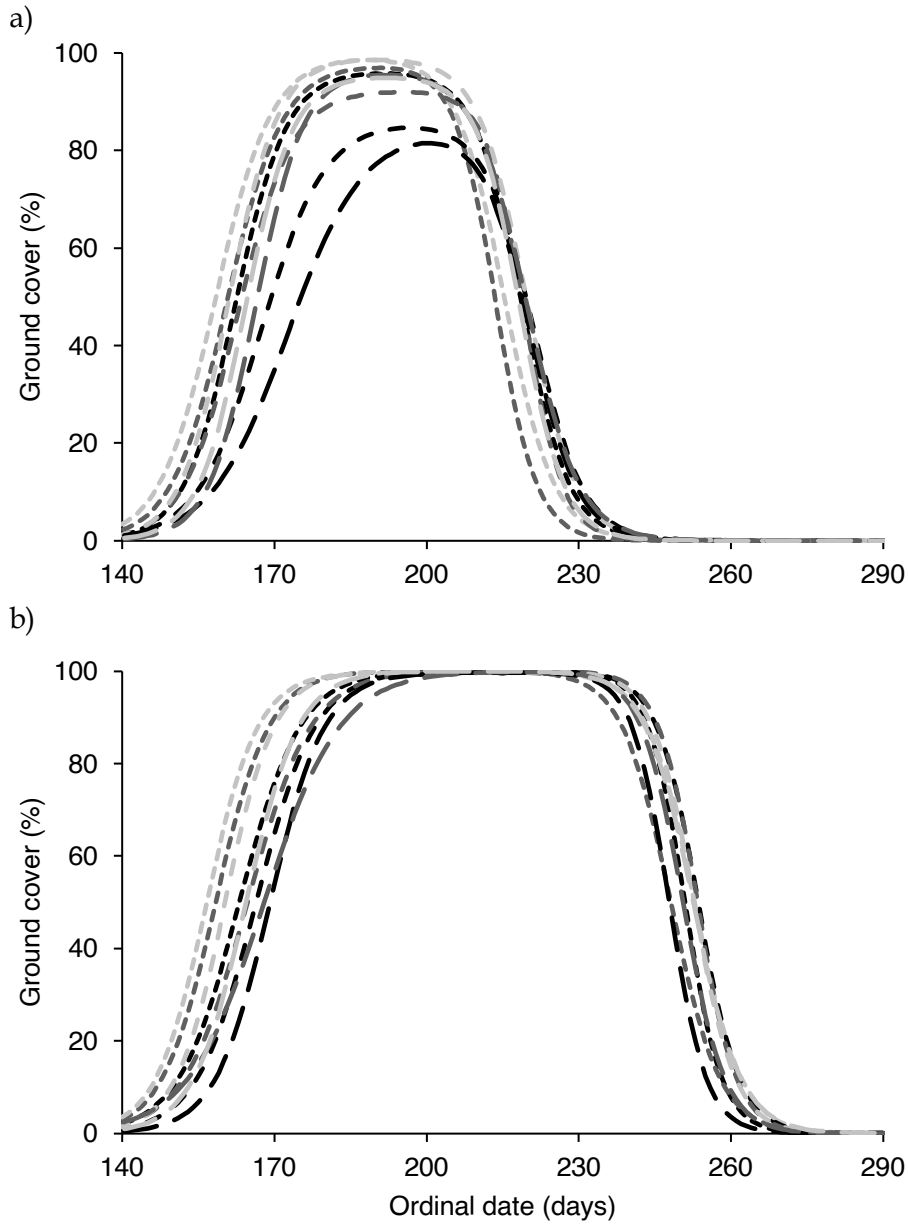

Figure 160. Average ground cover curve for all combinations of treatments (seed spacing * cultivar * seed size), plotted against days after emergence, (a) Estima and (b) Maris Piper in Expt 5. Small seed, ——; medium seed, ——; large seed, ——; 20 cm, – – – –; 40 cm, – – –, 60 cm, — — .

Goodness of fit

Willmott's index of agreement shows a good fit of the CQ curve to each treatment mean ($d \geq 0.996$) and the numerical differences in goodness of fit between treatments were minimal (Table 217).

Table 217. Goodness of fit scores for treatment means of each all treatment combinations in Expts 2, 4 and 5. Goodness of fit measured using Willmott's index of agreement (*d*).

		Seed spacing	Estima			Maris Piper		
Expt	Seed size	(cm)	20	40	60	20	40	60
2	Small		0.998	0.998	0.998	0.998	0.999	0.999
	Large		0.999	0.997	0.999	0.998	0.999	0.998
4	Small		0.999	0.998	0.999	0.999	0.999	0.999
	Large		0.998	0.999	0.999	0.996	0.998	0.999
5	Small		0.997	0.996	0.996	0.999	0.999	0.998
	Medium		0.998	0.997	0.997	0.999	0.998	0.998
	Large		0.996	0.999	0.998	0.998	0.999	0.999

Goodness of fit as described by root mean square error was more variable than when described using *d*, and ranged from 1.79 % (40 cm spaced, large seeded Maris Piper, Expt 5) to 5.09 % (20 cm spaced, large seeded Estima, Expt 5, Table 218). Curve fit was numerically better for Maris Piper than Estima (2.85 and 3.45 %, respectively), with no consistent difference in goodness of fit between seed sizes or spacings (Table 218).

Table 218. Goodness of fit scores for treatment means of each all treatment combinations in Expts 2, 4 and 5. Goodness of fit measured using root mean square error (RMSE, % GC).

		Seed spacing	Estima			Maris Piper		
Expt	Seed size	(cm)	20	40	60	20	40	60
2	Small		3.32	3.84	3.59	2.96	2.52	2.24
	Large		2.56	4.39	3.29	3.12	2.19	2.91
4	Small		2.77	3.24	2.95	2.38	2.14	2.72
	Large		3.43	2.41	2.84	4.32	3.06	2.73
5	Small		4.20	4.23	3.84	2.98	2.73	3.36
	Medium		3.87	3.75	3.87	2.95	3.33	3.48
	Large		5.09	2.59	3.72	3.50	1.79	2.75

APPENDIX 21

Leaf appearance

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on different leaf appearance measurements for Expts 2, 4 and 5. Mean values for each canopy variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 219. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of mainstem leaves (msL), rate of leaf appearance on the mainstem (msLA), rate of whole plant leaf appearance (pLA), number of leaves on the main axis (maL) and rate of leaf appearance on the sympodial branch (sbLA) in Expt 2. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	msL	msLA	pLA	maL	sbLA
Seed spacing	0.822	0.004	0.110	0.005	0.002
Cultivar	< 0.001	< 0.001	< 0.001	< 0.001	0.051
Seed size	0.695	0.003	< 0.001	0.004	0.200
Seed spacing * Cultivar	0.734	0.575	0.208	0.061	0.954
Seed spacing * Seed size	0.365	0.840	0.403	0.362	0.596
Cultivar * Seed size	0.376	0.533	0.140	0.527	0.407
Seed spacing * Cultivar * Seed size	0.705	0.106	0.913	0.260	0.344

Table 220. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of mainstem leaves (msL), rate of leaf appearance on the mainstem (msLA), rate of whole plant leaf appearance (pLA), number of leaves on the main axis (maL) and rate of leaf appearance on the sympodial branch (sbLA) in Expt 4. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	msL	msLA	pLA	maL	sbLA
Seed spacing	0.078	0.036	0.510	0.004	0.003
Cultivar	< 0.001	0.571	0.847	< 0.001	< 0.001
Seed size	0.427	0.034	< 0.001	0.050	0.017
Seed spacing * Cultivar	0.155	0.714	0.185	0.755	0.660
Seed spacing * Seed size	0.994	0.382	0.122	0.646	0.075
Cultivar * Seed size	0.525	0.610	0.563	0.899	0.374
Seed spacing * Cultivar * Seed size	0.994	0.386	0.545	0.772	0.736

Table 221. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of mainstem leaves (msL), rate of leaf appearance on the mainstem (msLA), rate of whole plant leaf appearance (pLA), number of leaves on the main axis (maL) and rate of leaf appearance on the sympodial branch (sbLA) in Expt 5. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	msL	msLA	pLA	maL	sbLA
Seed spacing	0.751	< 0.001	0.012	< 0.001	< 0.001
Cultivar	< 0.001	< 0.001	< 0.001	< 0.001	0.008
Seed size	0.500	< 0.001	< 0.001	< 0.001	0.008
Seed spacing * Cultivar	0.106	0.490	0.328	0.042	0.224
Seed spacing * Seed size	0.886	0.109	0.055	0.082	0.208
Cultivar * Seed size	0.193	0.369	0.003	0.128	0.100
Seed spacing * Cultivar * Seed size	0.738	0.352	0.617	0.160	0.373

Mainstem leaves

Table 222. Number of mainstem leaves (msL) for each treatment combination in Expt 2 (58 D.F.), Expt 4 (58 D.F.) and Expt 5 (85 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		12.67	11.83	11.33	15.33	15.33	15.00	0.579
	Large		11.67	11.50	12.17	15.50	15.79	15.67	
4	Small		13.50	12.83	12.67	19.00	17.67	19.17	0.602
	Large		13.33	12.83	12.67	18.50	17.17	18.67	
5	Small		11.00	11.67	11.50	15.83	15.67	15.83	0.592
	Medium		12.42	12.83	12.00	15.67	15.17	15.83	
	Large		11.72	12.33	11.67	15.33	14.83	16.67	

Mainstem leaf appearance

Table 223. Rate of leaf appearance on the mainstem (msLA) for each treatment combination in Expt 2 (58 D.F.), Expt 4 (58 D.F.) and Expt 5 (88 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		0.695	0.720	0.703	0.491	0.621	0.647	0.0354
	Large		0.564	0.655	0.672	0.510	0.526	0.573	
4	Small		0.578	0.585	0.633	0.549	0.624	0.549	0.0391
	Large		0.476	0.564	0.574	0.476	0.546	0.588	
5	Small		0.688	0.692	0.722	0.542	0.565	0.648	0.0446
	Medium		0.497	0.584	0.789	0.500	0.514	0.603	
	Large		0.452	0.596	0.620	0.448	0.544	0.548	

Whole plant leaf appearance rate

Table 224. Rate of whole plant leaf appearance (pLA) for each treatment combination in Expt 2 (58 D.F.), Expt 4 (58 D.F.) and Expt 5 (83 D.F.).

		Seed spacing	Estima			Maris Piper			
2	Small	(cm)	1.02	1.47	1.51	2.05	2.13	1.75	0.304
	Large		1.63	2.51	2.67	3.25	3.48	3.57	
4	Small		1.09	1.17	1.00	1.11	0.96	0.91	0.213
	Large		1.69	2.05	2.23	2.13	1.62	2.36	
5	Small		1.32	1.26	1.00	1.23	1.18	1.47	0.226
	Medium		1.58	1.21	1.74	1.41	1.39	2.24	
	Large		1.15	1.78	1.93	2.28	2.55	2.84	
2	Small		1.02	1.47	1.51	2.05	2.13	1.75	0.304

Main axis leaves

Table 225. Number of leaves on the main axis (maL) for each treatment combination in Expt 2 (58 D.F.), Expt 4 (58 D.F.) and Expt 5 (88 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		23.7	23.5	23.0	28.0	32.5	32.1	0.98
	Large		21.0	22.2	23.0	27.2	28.5	30.8	
4	Small		22.7	24.2	24.8	29.8	31.2	31.7	1.13
	Large		21.0	22.3	24.7	27.3	30.5	30.7	
5	Small		20.5	22.2	23.7	29.7	33.0	31.5	1.07
	Medium		19.2	20.0	23.7	24.3	32.0	31.5	
	Large		20.2	21.2	21.0	26.0	27.8	28.8	

Sympodial branch leaf appearance

Table 226. Rate of leaf appearance on the sympodial branch (sbLA) for each treatment combination in Expt 2 (58 D.F.), Expt 4 (58 D.F.) and Expt 5 (85 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		0.239	0.264	0.275	0.265	0.331	0.306	0.0254
	Large		0.190	0.294	0.273	0.234	0.276	0.297	
4	Small		0.225	0.255	0.263	0.319	0.321	0.326	0.0249
	Large		0.166	0.246	0.264	0.222	0.267	0.333	
5	Small		0.266	0.296	0.354	0.279	0.284	0.330	0.0257
	Medium		0.240	0.251	0.321	0.193	0.271	0.282	
	Large		0.333	0.245	0.309	0.202	0.222	0.254	

APPENDIX 22

Planting density whole plant mainstem leaf appearance

In Expt 5 there was an interaction between seed size and cultivar and the difference in pLA between small and large seed of Maris Piper was three times greater than in Estima (1.27 and 0.50 leaves/plant/day difference respectively, Figure 161c). In Expts 2 and 4 the difference in pLA between small and large seed was similar in both cultivars and there was no interaction (Figure 161a & b).

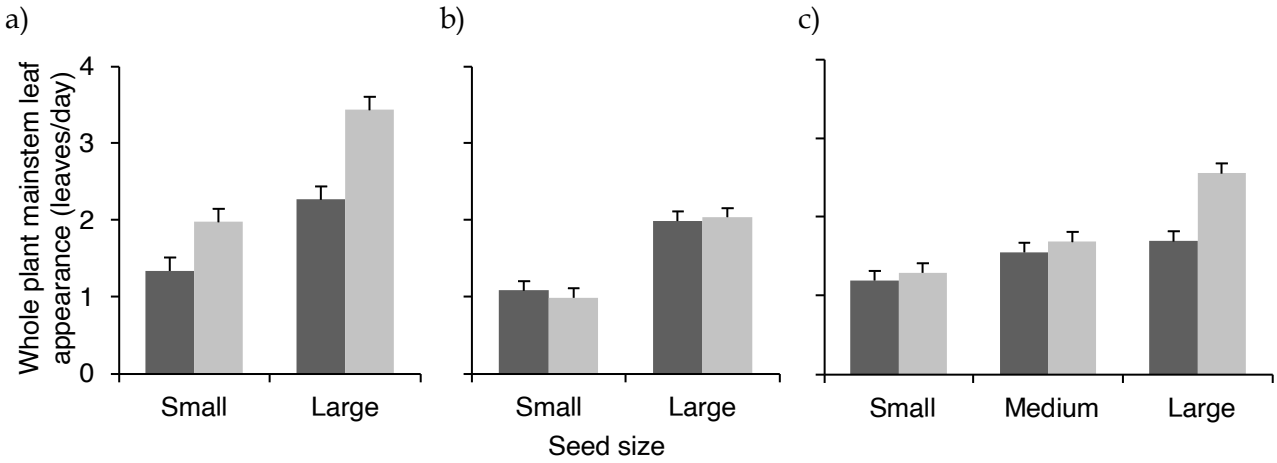

Figure 161. Effect of seed size and cultivar on rate of whole plant mainstem leaf appearance (pLA) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Bars represent S.E. ((a) & (b) 58 D.F. and (c) 83 D.F.). Data presented are means of seed spacing treatments.

APPENDIX 23

Leaf area index

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect for both total LAI and canopy component LAI for Expts 2, 4 and 5. Mean LAI values for each canopy variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 227. Table of *P* values showing the significance of treatments and interactions, ANOVA, on mainstem leaf area index (msLAI), axillary branch leaf area index (abLAI), sympodial branch leaf area index (sbLAI), total leaf area index (TotLAI) in Expt 2 at harvest prior to senescence. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

Treatments and interactions	msLAI	abLAI	sbLAI	TotLAI
Seed spacing	0.019	0.151	0.097	0.147
Seed size	0.170	0.553	0.471	0.431
Seed spacing * Seed size	0.059	0.538	0.789	0.115

Table 228. Table of *P* values showing the significance of treatments and interactions, ANOVA, on mainstem leaf area index (msLAI), axillary branch leaf area index (abLAI), sympodial branch leaf area index (sbLAI), total leaf area index (TotLAI) in Expt 4 at harvest prior to senescence. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

Treatments and interactions	msLAI	abLAI	sbLAI	TotLAI
Seed spacing	0.073	0.006	< 0.001	0.399
Cultivar	0.004	< 0.001	0.932	< 0.001
Seed size	0.034	0.292	< 0.001	0.015
Seed spacing * Cultivar	0.548	0.608	0.965	0.197
Seed spacing * Seed size	0.516	0.122	0.293	0.020
Cultivar * Seed size	0.014	0.790	0.130	0.393
Seed spacing * Cultivar * Seed size	0.276	0.749	0.904	0.156

Table 229. Table of *P* values showing the significance of treatments and interactions, ANOVA, on mainstem leaf area index (msLAI), axillary branch leaf area index (abLAI), sympodial branch leaf area index (sbLAI), total leaf area index (TotLAI) in Expt 5 at harvest prior to senescence. Significant at 95 % confidence level ($P \leq 0.05$) ; significant at 99.9 % confidence level ($P < 0.001$) .

Treatments and interactions	msLAI	abLAI	sbLAI	TotLAI
Seed spacing	0.006	0.002	< 0.001	0.840
Seed size	0.153	0.006	0.005	0.054
Seed spacing * Seed size	0.473	0.862	0.077	0.928

Mainstem leaf area index

Table 230. Mainstem leaf area index at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

			Estima			Maris Piper			
Expt	Seed size	Seed spacing (cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	2.58	1.17	0.17	0.404
	Large		n/a	n/a	n/a	0.81	1.19	0.45	
4	Small		1.26	0.83	0.82	1.31	0.72	0.61	0.200
	Large		2.08	2.02	1.21	0.80	0.76	0.89	
5	Small		n/a	n/a	n/a	1.16	0.38	0.17	0.282
	Medium		n/a	n/a	n/a	0.76	0.71	0.32	
	Large		n/a	n/a	n/a	1.28	1.20	0.37	

Axillary branch leaf area index

Table 231. Axillary branch leaf area index at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

			Estima			Maris Piper			
Expt	Seed size	Seed spacing (cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	1.42	1.57	1.71	0.280
	Large		n/a	n/a	n/a	1.06	1.27	1.94	
4	Small		1.70	1.54	2.09	2.93	3.19	3.56	0.502
	Large		0.68	1.34	2.13	1.76	2.84	4.39	
5	Small		n/a	n/a	n/a	2.38	3.55	4.54	0.468
	Medium		n/a	n/a	n/a	1.43	2.56	2.96	
	Large		n/a	n/a	n/a	1.56	2.14	2.80	

Sympodial branch leaf area index

Table 232. Sympodial branch leaf area index at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

			Estima			Maris Piper			
Expt	Seed size	Seed spacing (cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	1.47	1.53	0.75	0.296
	Large		n/a	n/a	n/a	1.44	1.73	1.13	
4	Small		1.23	0.71	0.61	1.06	0.51	0.47	0.178
	Large		1.60	1.22	0.82	1.81	1.42	0.87	
5	Small		n/a	n/a	n/a	1.12	0.79	0.46	0.102
	Medium		n/a	n/a	n/a	1.52	0.84	0.56	
	Large		n/a	n/a	n/a	1.37	0.96	1.00	

Total leaf area index

Table 233. Total leaf area index at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	5.47	4.27	2.63	0.668
	Large		n/a	n/a	n/a	3.32	4.20	3.52	
4	Small		4.19	3.07	3.53	5.29	4.42	4.64	0.382
	Large		4.37	4.58	4.17	4.37	5.01	6.15	
5	Small		n/a	n/a	n/a	4.67	4.72	5.16	0.450
	Medium		n/a	n/a	n/a	3.70	4.12	3.84	
	Large		n/a	n/a	n/a	4.22	4.30	4.17	

Specific leaf area

Table 233. Table of *P* values showing the significance of treatments and interactions, ANOVA, on specific leaf area by canopy component in Expt 2 at harvest prior to senescence. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Specific leaf area			
	Mainstem	Axillary branch	Sympodial branch	Weighted average
Seed spacing	0.127	0.014	0.022	0.012
Seed size	0.972	0.059	0.114	0.011
Seed spacing * Seed size	0.213	0.962	0.810	0.988

Table 234. Table of *P* values showing the significance of treatments and interactions, ANOVA, on specific leaf area by canopy component in Expt 4 at harvest prior to senescence. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Specific leaf area			
	Mainstem	Axillary branch	Sympodial branch	Weighted average
Seed spacing	0.319	0.319	0.193	0.276
Cultivar	0.528	0.528	0.080	0.048
Seed size	0.927	0.927	0.130	0.676
Seed spacing * Cultivar	0.086	0.086	0.625	0.411
Seed spacing * Seed size	0.606	0.606	0.501	0.727
Cultivar * Seed size	0.155	0.155	0.402	0.876
Seed spacing * Cultivar * Seed size	0.295	0.295	0.739	0.854

Table 235. Table of *P* values showing the significance of treatments and interactions, ANOVA, on specific leaf area by canopy component in Expt 5 at harvest prior to senescence. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	Specific leaf area			
	Mainstem	Axillary branch	Sympodial branch	Weighted average
Seed spacing	0.506	0.856	0.966	0.714
Seed size	0.210	0.574	0.354	0.387
Seed spacing * Seed size	0.148	0.352	0.890	0.700

Table 236. Mainstem specific leaf area at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	298	307	291	38.3
	Large		n/a	n/a	n/a	346	346	208	
4	Small		358	338	310	348	307	319	16.1
	Large		350	322	280	322	338	374	
5	Small		n/a	n/a	n/a	313	386	301	44.8
	Medium		n/a	n/a	n/a	339	272	185	
	Large		n/a	n/a	n/a	267	287	335	

Table 237. Axillary branch specific leaf area at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	318	252	272	17.8
	Large		n/a	n/a	n/a	347	288	299	
4	Small		317	296	287	333	346	321	13.7
	Large		304	302	311	335	329	327	
5	Small		n/a	n/a	n/a	351	303	293	21.8
	Medium		n/a	n/a	n/a	308	322	336	
	Large		n/a	n/a	n/a	298	300	312	

Table 238. Sympodial branch specific leaf area at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	310	241	235	20.5
	Large		n/a	n/a	n/a	323	275	274	
4	Small		336	310	290	326	348	295	14.1
	Large		291	286	276	315	318	312	
5	Small		n/a	n/a	n/a	284	297	296	14.9
	Medium		n/a	n/a	n/a	319	309	303	
	Large		n/a	n/a	n/a	302	297	298	

Table 239. Mean weighted specific leaf area at harvest prior to senescence for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	305	264	261	12.7
	Large		n/a	n/a	n/a	336	298	293	
4	Small		332	310	295	332	339	317	11.1
	Large		321	306	293	324	326	331	
5	Small		n/a	n/a	n/a	323	303	294	18.0
	Medium		n/a	n/a	n/a	319	308	327	
	Large		n/a	n/a	n/a	290	290	311	

APPENDIX 24

Branch Production

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect for each descriptor of branch production in Expts 2, 4 and 5. Mean values for each canopy variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 240. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of axillary branches per stem (NoB), mean number of leaves per axillary branch (aveBLeaves), total stem length (TotLength), sympodial branch insertion point (SBInsert) and the number of sympodial branch leaves (SBLeaves) in Expt 2 at harvest prior to senescence in Maris Piper. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	NoB	aveBLeaves	TotLength	SBInsert	SBLeaves
Seed spacing	< 0.001	0.062	0.708	< 0.001	0.105
Seed size	0.031	0.663	0.016	< 0.001	0.487
Seed spacing * Seed size	0.577	0.507	0.167	0.824	0.283

Table 241. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of axillary branches per stem (NoB), mean number of leaves per axillary branch (aveBLeaves), total stem length (TotLength), sympodial branch insertion point (SBInsert) and the number of sympodial branch leaves (SBLeaves) in Expt 4 at harvest prior to senescence. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	NoB	aveBLeaves	TotLength	SBInsert	SBLeaves
Seed spacing	< 0.001	0.481	0.028	< 0.001	0.672
Cultivar	< 0.001	0.002	< 0.001	< 0.001	< 0.001
Seed size	< 0.001	0.511	< 0.001	< 0.001	0.026
Seed spacing * Cultivar	0.009	0.384	0.315	0.908	0.960
Seed spacing * Seed size	0.490	0.282	0.658	0.247	0.859
Cultivar * Seed size	< 0.001	0.003	0.052	0.910	0.008
Seed spacing * Cultivar * Seed size	0.046	0.234	0.393	0.205	0.448

Table 242. Table of *P* values showing the significance of treatments and interactions, ANOVA, on number of axillary branches per stem (NoB), mean number of leaves per axillary branch (aveBLeaves), total stem length (TotLength), sympodial branch insertion point (SBInsert) and the number of sympodial branch leaves (SBLeaves) in Expt 5 at harvest prior to senescence in Maris Piper. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	NoB	aveBLeaves	TotLength	SBInsert	SBLeaves
Seed spacing	< 0.001	< 0.001	0.154	< 0.001	0.022
Seed size	< 0.001	< 0.001	0.016	< 0.001	0.003
Seed spacing * Seed size	0.901	0.351	0.328	0.069	0.436

Axillary branches

Table 243. Number of axillary branches per stem (NoB) at harvest prior to senescence for each treatment combination in Expt 2 (28 D.F.), Expt 4 (94 D.F.) and Expt 5 (70 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	2.8	5.0	11.3	1.44
	Large		n/a	n/a	n/a	1.5	2.7	7.0	
4	Small		3.78	6.11	7.33	6.89	13.11	17.22	0.970
	Large		1.33	2.44	6.44	2.22	7.00	8.00	
5	Small		n/a	n/a	n/a	8.2	11.9	13.2	1.12
	Medium		n/a	n/a	n/a	4.2	10.1	10.2	
	Large		n/a	n/a	n/a	3.6	8.0	9.2	

Axillary branch leaves

Table 244. Mean number of leaves per axillary branch (aveBLeaves) at harvest prior to senescence for each treatment combination in Expt 2 (28 D.F.), Expt 4 (94 D.F.) and Expt 5 (70 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	8.1	12.5	15.9	2.84
	Large		n/a	n/a	n/a	9.1	16.8	13.6	
4	Small		11.4	11.5	10.1	9.5	12.1	11.8	1.57
	Large		6.2	8.2	8.4	13.7	10.6	15.8	
5	Small		n/a	n/a	n/a	9.9	19.3	25.7	2.05
	Medium		n/a	n/a	n/a	8.6	13.2	19.1	
	Large		n/a	n/a	n/a	8.0	10.3	16.2	

Sympodial branch position

Table 245. Sympodial branch insertion point (SBInsert) at harvest prior to senescence for each treatment combination in Expt 2 (28 D.F.), Expt 4 (94 D.F.) and Expt 5 (70 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	626	520	430	19.6
	Large		n/a	n/a	n/a	739	643	567	
4	Small		360	290	329	556	466	471	21.8
	Large		530	387	395	664	565	587	
5	Small		n/a	n/a	n/a	528	456	461	26.0
	Medium		n/a	n/a	n/a	690	535	503	
	Large		n/a	n/a	n/a	745	659	562	

Total stem length

Table 246. Total stem length (TotLength) at harvest prior to senescence for each treatment combination in Expt 2 (28 D.F.), Expt 4 (94 D.F.) and Expt 5 (70 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	937	882	888	45.6
	Large		n/a	n/a	n/a	932	1006	1054	
4	Small		789	764	828	1112	965	993	43.8
	Large		933	838	866	1260	1204	1161	
5	Small		n/a	n/a	n/a	1021	1068	1142	61.1
	Medium		n/a	n/a	n/a	1220	1029	1152	
	Large		n/a	n/a	n/a	1196	1190	1286	

Sympodial branch leaves

Table 247. Number of sympodial branch leaves (SBLeaves) at harvest prior to senescence for each treatment combination in Expt 2 (28 D.F.), Expt 4 (94 D.F.) and Expt 5 (70 D.F.).

		Seed spacing	Estima			Maris Piper			
Expt	Seed size	(cm)	20	40	60	20	40	60	S.E.
2	Small		n/a	n/a	n/a	25.3	28.0	37.0	5.41
	Large		n/a	n/a	n/a	18.0	35.0	28.0	
4	Small		13.9	14.8	12.8	16.8	17.0	17.6	1.81
	Large		11.9	13.6	14.7	21.9	23.7	21.3	
5	Small		n/a	n/a	n/a	24.0	34.7	32.4	3.37
	Medium		n/a	n/a	n/a	20.3	24.0	24.3	
	Large		n/a	n/a	n/a	17.0	18.7	27.3	

APPENDIX 25

Mid-season tuber harvest

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect on each of the tuber variates describing the mid-season harvest for Expts 2, 4 and 5. Mean values for each tuber variate with every treatment combination are tabulated below enabling the calculation of significant treatment means. In Expts 2 and 5, senescence was greatly advanced in Estima at the mid-season harvest and neither haulm nor tubers were harvested. In Expt 2, stems per plant were not recorded at the mid-season harvest.

Table 248. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare (nº Tubers), fresh weight tuber yield per hectare (FWyield), dry weight tuber yield (DWyield), number of stems per hectare (nº Stems) and percent tuber dry matter (% DM) in Expt 2. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	nº Tubers	FWyield	DWyield	nº Stems	% DM
Seed spacing	0.102	0.023	0.007	n/a	0.001
Seed size	0.958	0.662	0.648	n/a	0.768
Spacing * Size	0.348	0.047	0.050	n/a	0.370

Table 249. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare (nº Tubers), fresh weight tuber yield per hectare (FWyield), dry weight tuber yield (DWyield), number of stems per hectare (nº Stems) and percent tuber dry matter (% DM) in Expt 2. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	nº Tubers	FWyield	DWyield	nº Stems	% DM
Seed spacing	< 0.001	0.018	0.002	< 0.001	0.007
Cultivar	0.691	< 0.001	< 0.001	0.604	< 0.001
Seed size	< 0.001	< 0.001	< 0.001	< 0.001	0.801
Seed spacing * Cultivar	0.227	0.975	0.669	0.560	0.036
Seed spacing * Seed size	< 0.001	0.335	0.374	0.388	0.805
Cultivar * Seed size	0.902	0.787	0.796	0.905	0.042
Seed spacing * Cultivar * Seed size	0.191	0.334	0.071	0.310	0.010

Table 250. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare (nº Tubers), fresh weight tuber yield per hectare (FWyield), dry weight tuber yield (DWyield), number of stems per hectare (nº Stems) and percent tuber dry matter (% DM) in Expt 2. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

	nº Tubers	FWyield	DWyield	nº Stems	% DM
Seed spacing	< 0.001	0.075	0.015	< 0.001	0.004
Seed size	< 0.001	0.071	0.037	< 0.001	0.396
Spacing * Size	0.552	0.646	0.510	0.120	0.446

Number of tubers

Table 251. Number of tubers per hectare (000 tubers/ha) at mid-season harvest for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	1000	1356	474	311.6
	Large		n/a	n/a	n/a	1444	856	570	
4	Small		411	274	285	443	350	196	38.4
	Large		802	520	393	870	487	393	
5	Small		n/a	n/a	n/a	867	579	550	87.6
	Medium		n/a	n/a	n/a	1120	811	533	
	Large		n/a	n/a	n/a	1291	1037	820	

Fresh tuber yield

Table 252. Fresh weight tuber yield (t/ha) at mid-season harvest for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	107.3	68.5	55.2	8.96
	Large		n/a	n/a	n/a	74.1	81.1	66.0	
4	Small		61.2	55.5	54.1	44.3	38.1	30.2	3.32
	Large		70.8	71.0	64.4	51.2	50.0	49.8	
5	Small		n/a	n/a	n/a	58.5	51.3	49.7	3.53
	Medium		n/a	n/a	n/a	59.0	50.1	51.9	
	Large		n/a	n/a	n/a	60.9	62.0	56.1	

Dry weight tuber yield

Table 253. Dry weight tuber yield (t/ha) at mid-season harvest for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	27.4	16.1	12.3	2.30
	Large		n/a	n/a	n/a	18.9	18.8	15.3	
4	Small		12.57	11.78	10.61	10.90	8.86	6.92	0.784
	Large		15.75	15.33	12.57	11.45	11.61	11.58	
5	Small		n/a	n/a	n/a	12.59	10.80	10.15	0.714
	Medium		n/a	n/a	n/a	12.63	10.28	10.80	
	Large		n/a	n/a	n/a	13.09	13.06	11.79	

Mid-season harvest stem count

Table 254. Number of stems per hectare (000/ha) at mid-season harvest for each treatment combination in Expt 2, Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	n/a	n/a	n/a	n/a
	Large		n/a	n/a	n/a	n/a	n/a	n/a	
4	Small		122	67	43	126	52	44	13.2
	Large		215	122	87	183	128	98	
5	Small		n/a	n/a	n/a	163	62	56	14.5
	Medium		n/a	n/a	n/a	219	111	70	
	Large		n/a	n/a	n/a	306	165	115	

Tuber percent dry matter

Table 255. Percentage tuber dry matter (%) at mid-season harvest for each treatment combination in Expt 2 (10 D.F.), Expt 4 (22 D.F.) and Expt 5 (16 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		n/a	n/a	n/a	25.6	23.5	22.1	0.54
	Large		n/a	n/a	n/a	25.2	23.2	23.2	
4	Small		20.5	21.2	19.6	24.5	23.0	22.9	0.48
	Large		22.3	21.6	19.5	22.5	23.2	23.3	
5	Small		n/a	n/a	n/a	21.5	21.0	20.5	0.23
	Medium		n/a	n/a	n/a	21.4	20.6	20.8	
	Large		n/a	n/a	n/a	21.5	21.1	21.0	

APPENDIX 26

Final, end of season tuber harvest

Tables of interactions, indicating which treatments and interactions of treatments had a significant effect for each of the tuber variates describing the final harvest for Expts 2, 4 and 5. Mean values for each tuber variate with every treatment combination are tabulated below enabling the calculation of significant treatment means.

Table 256. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare (no Tubers), fresh weight tuber yield per hectare (FWyield), dry weight tuber yield (DWyield), number of stems per hectare (no Stems) and percent tuber dry matter (% DM) in Expt 2. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	nº Tubers	FWyield	DWyield	nº Stems	% DM
Seed spacing	< 0.001	0.077	0.010	< 0.001	0.008
Cultivar	< 0.001	0.332	< 0.001	< 0.001	< 0.001
Seed size	< 0.001	0.002	0.010	< 0.001	0.508
Seed spacing * Cultivar	0.001	0.091	0.046	< 0.001	0.547
Seed spacing * Seed size	0.656	0.406	0.568	0.031	0.760
Cultivar * Seed size	0.713	0.351	0.378	0.172	0.315
Seed spacing * Cultivar * Seed size	0.492	0.597	0.674	0.083	0.777

Table 257. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare (nº Tubers), fresh weight tuber yield per hectare (FWyield), dry weight tuber yield (DWyield), number of stems per hectare (nº Stems) and percent tuber dry matter (% DM) in Expt 4. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	nº Tubers	FWyield	DWyield	nº Stems	% DM
Seed spacing	< 0.001	0.009	0.012	< 0.001	0.057
Cultivar	0.131	< 0.001	0.005	0.740	< 0.001
Seed size	< 0.001	< 0.001	< 0.001	< 0.001	0.535
Seed spacing * Cultivar	0.325	0.188	0.260	0.067	0.674
Seed spacing * Seed size	0.003	0.222	0.408	< 0.001	0.330
Cultivar * Seed size	0.879	0.301	0.590	0.098	0.020
Seed spacing * Cultivar * Seed size	0.406	0.078	0.166	0.270	0.727

Table 258. Table of *P* values showing the significance of treatments and interactions, ANOVA, on the number of tubers per hectare (nº Tubers), fresh weight tuber yield per hectare (FWyield), dry weight tuber yield (DWyield), number of stems per hectare (nº Stems) and percent tuber dry matter (% DM) in Expt 5. Significant at 95 % confidence level (*P* ≤ 0.05) ; significant at 99.9 % confidence level (*P* < 0.001) .

Treatments and interactions	nº Tubers	FWyield	DWyield	nº Stems	% DM
Seed spacing	< 0.001	< 0.001	< 0.001	< 0.001	0.190
Cultivar	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Seed size	< 0.001	< 0.001	< 0.001	< 0.001	0.269
Seed spacing * Cultivar	0.053	0.484	0.144	< 0.001	0.538
Seed spacing * Seed size	0.457	0.805	0.844	< 0.001	0.609
Cultivar * Seed size	0.007	0.224	0.341	< 0.001	0.075
Seed spacing * Cultivar * Seed size	0.512	0.171	0.054	0.009	0.310

Number of tubers

Table 259. The number of tubers per hectare (nº Tubers) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 3 (34 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		380	287	241	933	520	528	58.8
	Large		572	424	420	1165	776	626	
4	Small		463	272	200	465	267	313	36.6
	Large		777	513	380	841	506	413	
5	Small		524	435	272	794	619	489	54.3
	Medium		596	522	372	1094	794	631	
	Large		796	604	439	1283	931	931	

Fresh tuber yield

Table 260. Fresh weight tuber yield per hectare (FWyield) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		67.0	64.8	67.0	84.3	69.1	63.0	5.22
	Large		77.6	86.4	75.2	85.9	79.6	74.1	
4	Small		79.9	64.9	58.1	50.7	45.6	46.2	3.72
	Large		78.0	80.9	75.2	67.7	56.9	62.7	
5	Small		56.3	48.7	47.3	63.0	57.4	51.5	2.95
	Medium		53.1	52.5	51.2	72.2	60.9	60.9	
	Large		67.2	60.4	52.2	76.3	65.8	68.8	

Dry weight tuber yield

Table 261. Dry weight tuber yield (DWyield, t/ha) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		13.8	13.1	12.9	21.3	16.9	14.8	1.31
	Large		15.8	17.5	14.8	21.4	18.7	17.2	
4	Small		16.8	13.8	11.6	12.7	11.5	11.2	1.05
	Large		16.7	17.3	15.6	16.6	13.5	14.9	
5	Small		11.31	9.63	9.47	15.28	13.98	12.69	0.661
	Medium		10.68	10.71	10.43	18.06	14.41	14.29	
	Large		13.86	12.07	10.42	18.26	15.20	16.14	

Final harvest stem count

Table 262. The number of stems per hectare (n° Stems) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		127.8	64.8	48.1	264.8	114.8	92.6	21.59
	Large		194.4	131.5	92.6	450.0	172.2	133.3	
4	Small		122.2	88.9	38.9	113.0	59.3	42.6	14.60
	Large		220.1	144.4	81.5	279.6	124.1	94.4	
5	Small		105.6	53.7	37.0	161.1	87.0	48.1	7.39
	Medium		151.9	88.9	88.9	268.5	118.5	68.5	
	Large		233.3	101.9	101.9	325.9	183.3	107.4	

Tuber percent dry matter

Table 263. Percent tuber dry matter (% DM) for each treatment combination in Expt 2 (22 D.F.), Expt 4 (22 D.F.) and Expt 5 (34 D.F.).

Expt	Seed size	Seed spacing (cm)	Estima			Maris Piper			S.E.
			20	40	60	20	40	60	
2	Small		20.55	20.13	19.21	25.24	24.58	23.50	0.553
	Large		20.32	20.26	19.66	24.92	23.51	23.26	
4	Small		21.01	21.16	19.90	24.92	25.22	24.18	0.471
	Large		21.45	21.40	20.75	24.44	23.51	23.81	
5	Small		20.08	19.87	20.02	24.25	24.39	24.72	0.431
	Medium		20.13	20.41	20.37	25.02	23.57	23.45	
	Large		20.59	19.99	19.98	23.93	23.09	23.45	

APPENDIX 27

Variation in tuber yield with stem density

As expected, number of tubers produced increased with increasing stem density in both Estima and Maris Piper, accounting for differences in mean tuber number between experiments and experimental blocks (multiple linear regression, $P < 0.001$, Figure 162). Maris Piper tended to produce a greater number of tubers than Estima.

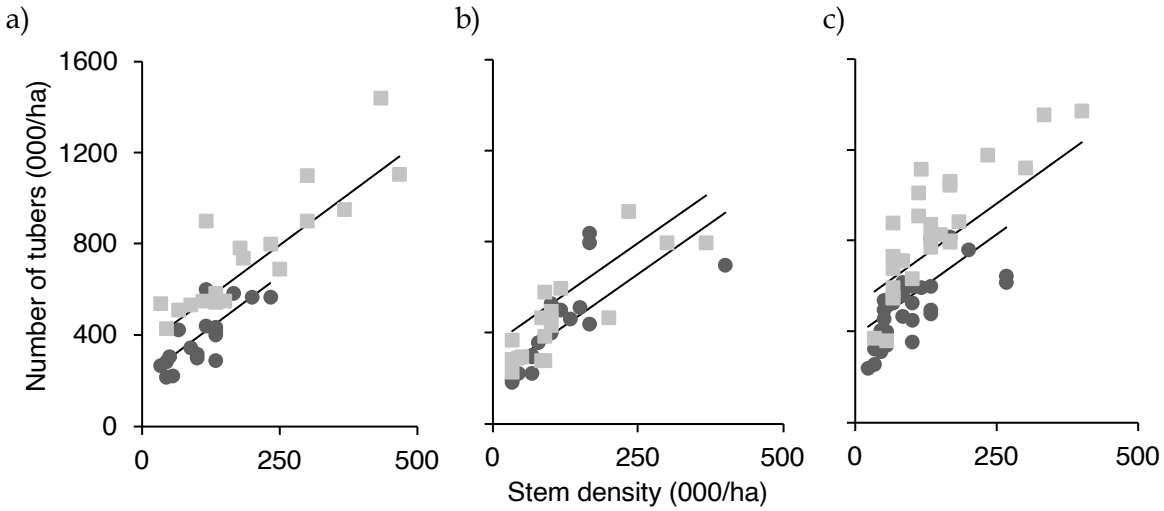

Figure 162. Relationship between number of tubers (TuberN°, 000/ha) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper (MP), ■. $R^2 = 0.764$. See Table 264 for details of multiple linear regression.

Table 264. Relationship between number of tubers (TuberN°) and stem density (S), cultivar (MP) and experiment (Expts 2, 4 or 5). TuberN° = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5 + β5*(S*MP).

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	211	39.7	< 0.001
1	S	1.79	0.247	< 0.001
2	MP	137	42.6	0.002
3	Expt 4	-45	31.5	0.156
4	Expt 5	171	28.5	< 0.001
5	S * MP	0.29	0.294	0.328

Fresh yield tuber increased with increasing stem density in both cultivars, accounting for differences in mean yields between experiments and experimental blocks (multiple linear regression, $P < 0.001$, Figure 163).

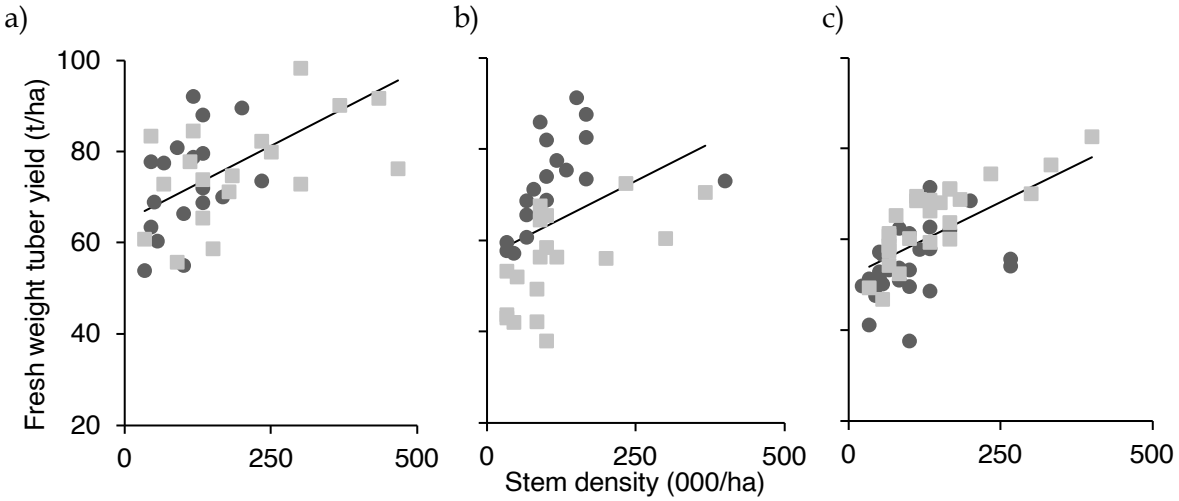

Figure 163. Relationship between fresh tuber yield (FWyield, t/ha) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.4351. See Table 265 for details of multiple linear regression.

Table 265. Relationship between fresh tuber yield (FWyield, t/ha) and stem density (S), cultivar (MP) and experiment (Expts 2, 4 or 5). FWyield = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	64.8	2.53	< 0.001
1	S	0.0658	0.00987	< 0.001
2	MP	-2.9	1.77	0.100
3	Expt 4	-8.2	2.30	< 0.001
4	Expt 5	-13.0	2.10	< 0.001

There was a slight increase in tuber percent dry matter with increasing stem density in both cultivars, accounting for differences in mean % DM between experiments and blocks (multiple linear regression, $P < 0.001$, Figure 164).

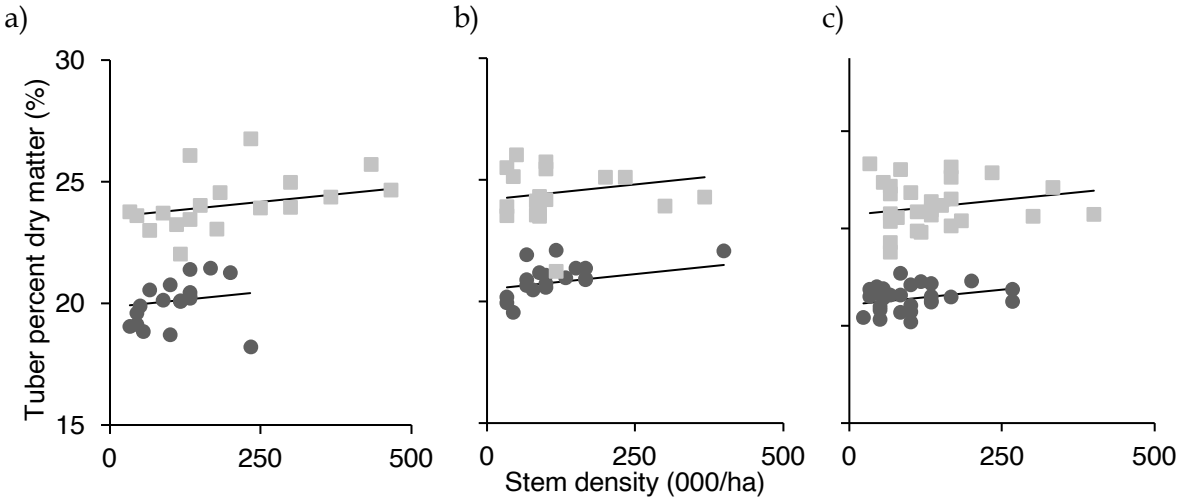

Figure 164. Relationship between tuber percent dry matter at final harvest (% DM) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. R^2 = 0.833. See Table 266 for details of multiple linear regression.

Table 266. Relationship between tuber percent dry matter at final harvest (%DM) and stem density (S), cultivar (MP) and experiment (Expts 2, 4 or 5). %DM = β0 + β1*S + β2*MP + β3*Expt 4 + β4*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	19.86	0.228	< 0.001
1	S	0.00250	0.000890	0.006
2	MP	3.69	0.160	< 0.001
3	Expt 4	0.64	0.207	0.002
4	Expt 5	0.06	0.189	0.737

APPENDIX 28

Relationship between stem density duration of complete canopy expansion

Duration of complete canopy expansion (from emergence to 90 % GC, TiE90) cover was typically shorter at higher stem densities in both Maris Piper and Estima (Figure 165). Stem density explained 48.3 % of the variation in TiE90 once differences between experimental blocks and years were accounted for (multiple linear regression; TiE90 ~ stem density + year + block, $P < 0.001$, Table 267), although the relationship may be better described by a non-linear function. Complete canopy expansion was slower in Expt 4 than in Expts 2 and 5, likely the result of the poor-quality seed bed impeding root growth and slowing subsequent canopy development.

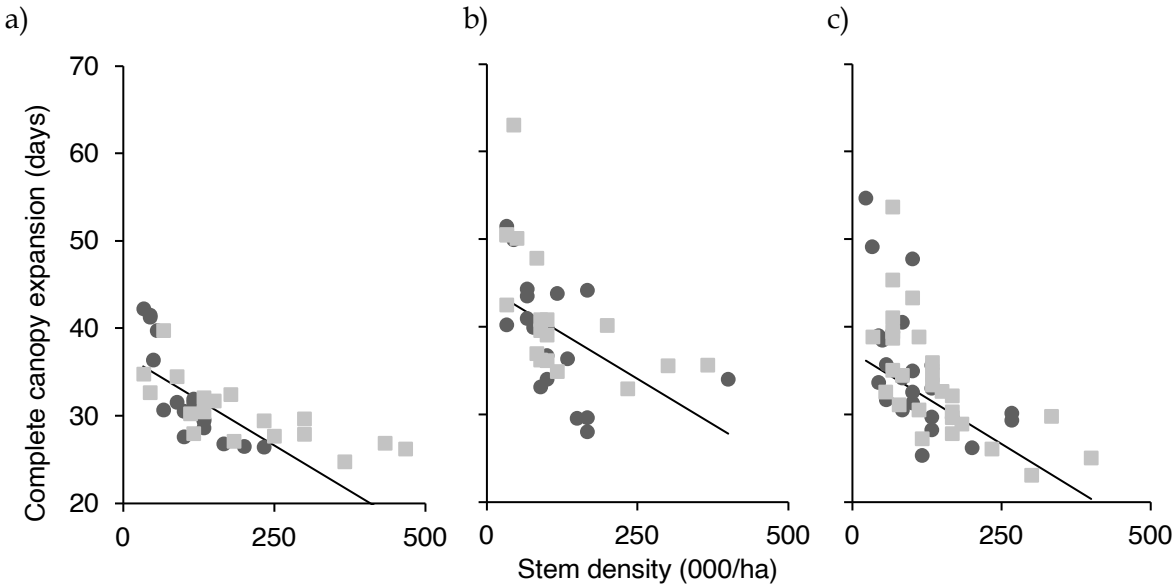

Figure 165. Relationship between duration of complete canopy expansion (from emergence to 90 % GC, TiE90) and stem density in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■. For Maris Piper, $R^2 = 0.483$. See Table 267 for details of multiple linear regression.

Table 267. Relationship between duration of complete canopy expansion (from emergence to 90 % GC, TiE90), stem density (S) and experiment (Expts 2, 4 or 5). TiE90 = β0 + β1*S + β2*Expt 4 + β3*Expt 5.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	37.1	1.37	< 0.001
1	S	-0.0418	0.00528	< 0.001
2	Expt 4	7.4	1.26	< 0.001
3	Expt 5	1.8	1.16	0.119

APPENDIX 29

Relationship between early and mid-canopy expansion

There was no overall relationship between duration of early canopy expansion (TiE25) and that rate of mid-canopy expansion (GCRate2575) in Expts 2, 4 and 5 (multiple linear regression; GCRate2575 ~ TiE25 + block, $P = 0.666$, Figure 166). Incorporating between-year variation explained 44.7 % of the variation in GCRate2575, but TiE25 remained an non-significant predictor in the model (multiple linear regression; GCRate2575 ~ TiE25 + year + block, $P < 0.001$, TiE25, ANOVA; $P = 0.553$) and GCRate2575 only differed significantly between experimental years.

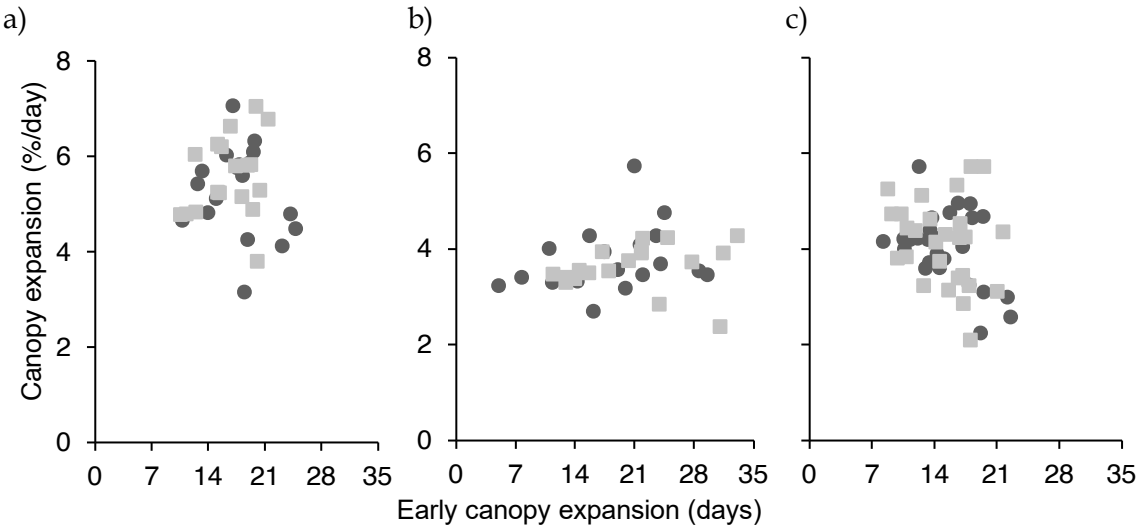

Figure 166. Relationship between early canopy expansion (TiE25) and mid-season canopy expansion rate (GCRate2575) in (a) Expt 2, (b) Expt 4 and (c) Expt 5. Estima, ●; Maris Piper, ■.

A slower rate of mid-canopy expansion was associated with a longer duration of early canopy expansion, though the relationship across the 20 cultivars in the Seed Size experiments was weak and TiE25 only accounted for 10.1 % of the variation in GCRate2575 (linear regression; GCRate2575 ~ TiE25, $P < 0.001$, Figure 167). Further variation is explained when the differences in mean GCRate2575 between cultivars were accounted for (multiple linear regression; GCRate2575 ~ TiE25 + cultivar, $P < 0.001$, $R^2 = 0.374$, data not shown).

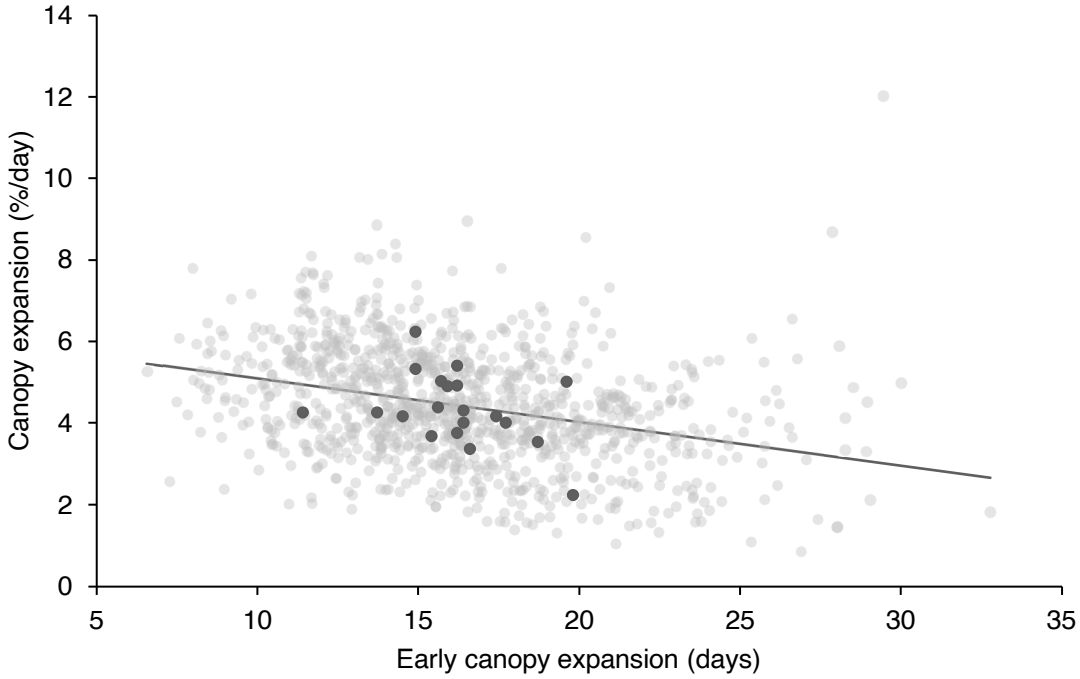

Figure 167. Relationship between early (TiE25) and mid-canopy expansion (GCRate2575) in Seed Size experiments. Individual plots, ●; cultivar means, ●. R^2 = 0.101. See Table 268 for details of linear regression.

Table 268. Relationship between early (TiE25) and mid-canopy expansion (GCRate2575). GCRate2575 = β0 + β1*TiE25.

β	Coefficient	Estimate	S.E.	*P* value
0	(intercept)	6.16	0.164	< 0.001
1	TiE25	-0.1067	0.00977	< 0.001

APPENDIX 30

Seed Size Experiments Determinacy Groups

Provisional determinacy groups for cultivars in the Seed Size experiments were provided by Marc Allison (2019, personal communication) and were derived as described below.

The cultivars within the Seed Size experiments were assigned provisional determinacy groupings by comparing the nitrogen response of each cultivar (data from commercial crops) to the nitrogen responses of cultivars with known determinacy groups. When limited commercial data for a given cultivar was available, the mid-season harvest index data from an earlier experiment stage of cultivar evaluation was compared to the harvest indices of cultivars with known determinacy groups. However, as the groupings were not assigned on the basis of determinacy experiments and the quantity of data was small for many of the cultivars due to limited data availability there is a low degree of confidence in many of the assigned determinacy groups (Table 269). Some cultivars varied little in their growth pattern between the years and so there can be greater confidence that determinacy group has been accurately assigned (indicated with a star in (Table 269). The growth behaviour of several cultivars (*cv.* 1, 2, 9 and 10) varied between years resulting in the assignment of different determinacy groupings between years; this is represented as a mean of determinacy groups which were assigned to each cultivar over the years.

Table 269. Provisional determinacy groups for Seed Size experiment cultivars, with data source indicated. Cultivars with the most consistent growth patterns and determinacy groupings are indicated by a star. Cultivars recorded as different determinacy groups in different years are in group 2-3.

	Cultivar determinacy groups			
	2	2-3	3	4
Nitrogen grouping data	6 8 16 * 19 * 20 *		5 * 18 *	11 *
Mid-season harvest index data	4 12 13 14 15 17	1 2 9 10	3 7	

The link between integrated ground cover and determinacy was weak and, contrary to expectation, the most determinate cultivars did not have the smallest IGC (Table 270).

Table 270. Comparison between the determinacy grouping rank and rank of integrated ground cover (IGC). Determinacy groups and IGC included for reference.

Cultivar	Determinacy Rank	IGC Rank	Determinacy group (mean)	IGC (% days)
1	15	15	2.7	8068
2	13	12	2.5	7830
3	17.5	20	3	10204
4	6	19	2	8814
5	17.5	14	3	7978
6	6	11	2	7819
7	17.5	8	3	7464
8	6	6	2	7097
9	13	2	2.5	6461
10	13	4	2.5	6855
11	20	17	4	8416
12	6	5	2	7078
13	6	18	2	8642
14	6	3	2	6615
15	6	10	2	7663
16	6	13	2	7849
17	6	9	2	7512
18	17.5	1	3	5205
19	6	7	2	7160
20	6	16	2	8291

The majority of plots in the Seed Size experiments achieved ≥ 90 % ground cover (98 % of plots), yet those which failed to reach 90 % GC tended to be more determinate cultivars (Table 271).

Table 271. Percentage of plots in each cultivar which did not achieve 90 % ground cover, linked with determinacy group.

Cultivar	Determinacy group	% plots with C_{max} < 90 % GC
1	2.7	0
2	2.5	0
3	3	0
4	2	0
5	3	0
6	2	0
7	3	1.4
8	2	0
9	2.5	6.9
10	2.5	0
11	4	0
12	2	2.8
13	2	0
14	2	4.2
15	2	0
16	2	4.2
17	2	18.75
18	3	0
19	2	0
20	2	0

Within each determinacy group, there was a large range of canopy growth responses within each canopy growth variate (Figure 168).

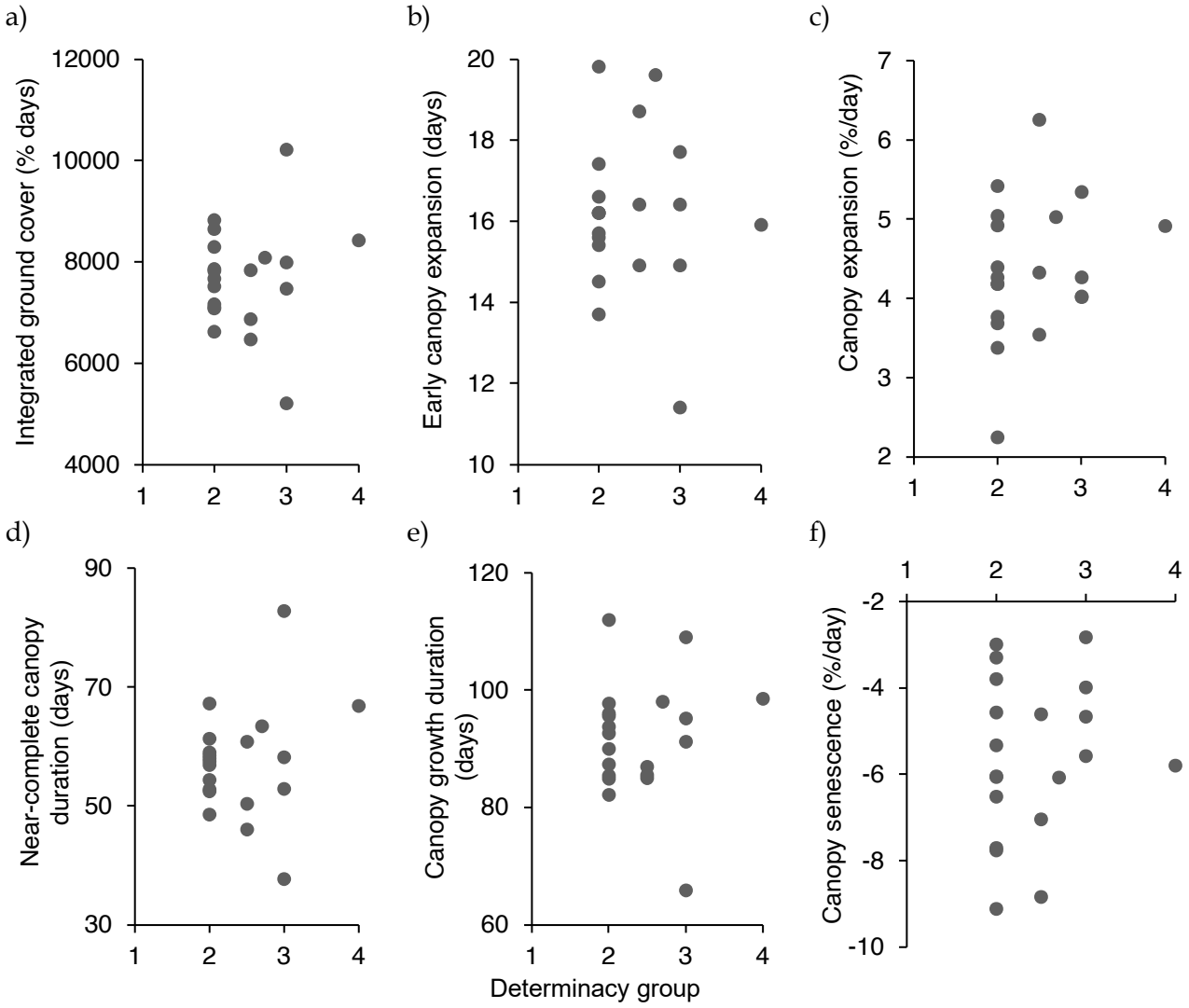

Figure 168. Relationship between cultivar determinacy group and canopy growth variates in Seed Size experiments. (a) Integrated ground cover. (b) Duration of early canopy expansion. (c) Mid-season canopy expansion rate. (d) Duration of near-complete ground cover. (e) Duration of canopy growth. (f) Rate of canopy senescence.

The responses, as measured by the canopy growth variates, of individual cultivars to increasing stem density did not cluster according to determinacy group (Figure 169).

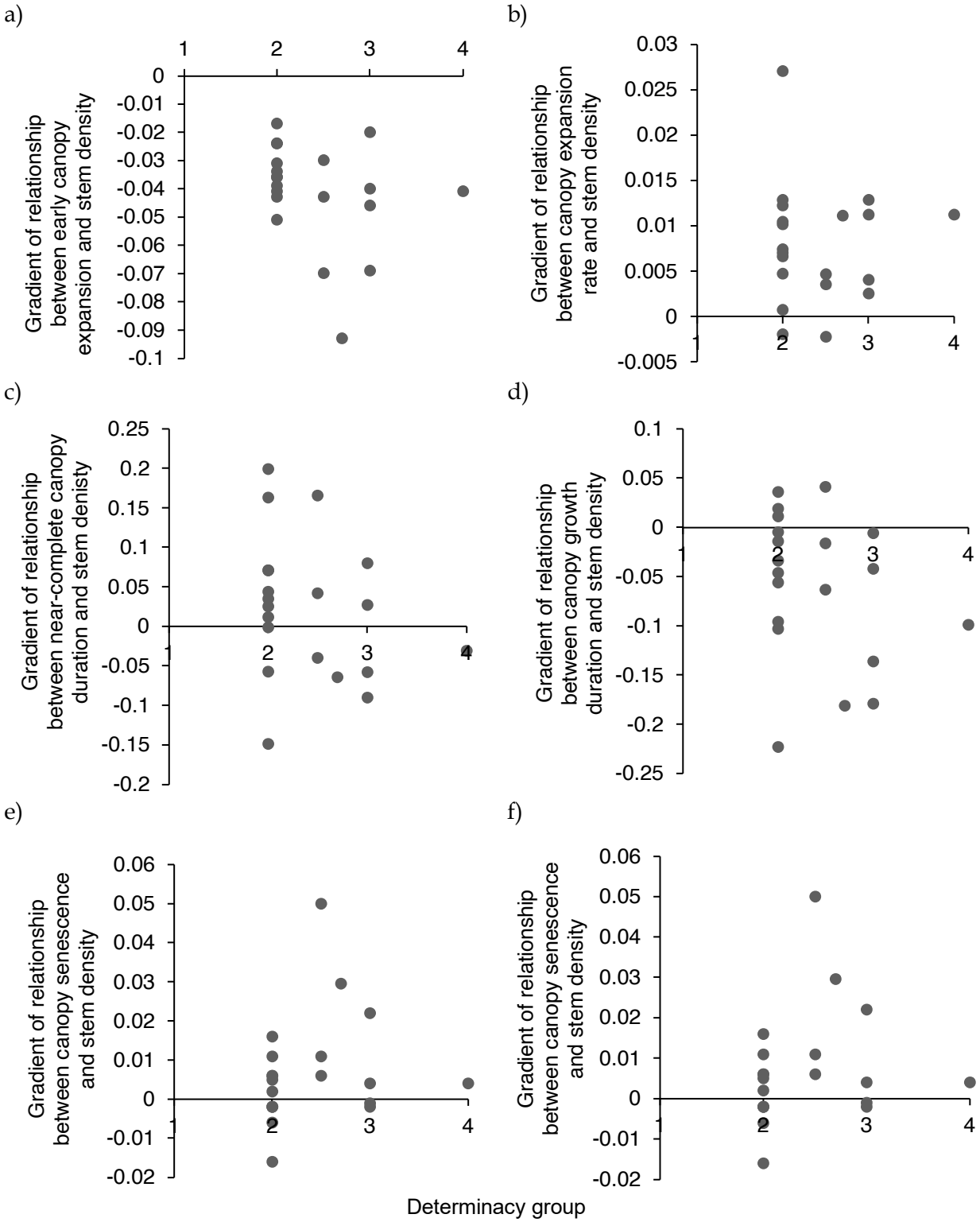

Figure 169. Relationship between cultivar determinacy group and the gradient of the relationship between individual canopy variates and stem density in the Seed Size experiments. (a) Integrated ground cover. (b) Duration of early canopy expansion. (c) Mid-season canopy expansion rate. (d) Duration of near-complete ground cover. (e) Duration of canopy growth. (f) Rate of canopy senescence. See section 1.8 of Planting Density Results for original gradient data.