

# Improving Uniformity of Potato Crops

Simon Edgar Hossack Smart



Girton College

University of Cambridge

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## Summary

### Improving Uniformity of Potato Crops

Simon Edgar Hossack Smart

Within potato crops some tubers are too small or too large to be marketable. There are economic and environmental incentives to improve uniformity, thereby increasing the fraction of yield that is marketable. The potato crop has a complex, three-tiered population structure consisting of plants, stems and tubers, each of which is a branch of the previous tier. Plant-to-plant variation in the number of stems, number of tubers and yield has long been noted to occur but the causes of this variability and how it impacts the uniformity of the crop are uncertain.

This thesis investigated how variability in seed tuber weight, within-row spacing and date of emergence affected the growth of individual plants in field-grown crops and how this affected the uniformity of the crops. Stem-to-stem variation in yield was described for the first time and shown to be considerably more variable than plant-to-plant variation. The causes of this stem-to-stem variation in yield and its influence on tuber size were investigated through detailed surveying of Desiree, King Edward, Maris Piper and Russet Burbank. Commercial crops grown from different seed tuber sizes and on contrasting soil types were surveyed to establish whether plant-to-plant variation was similar to that encountered in field experiments.

Within crops, plants with a higher average yield per stem were found to produce larger tubers and mean tuber size varied by *c.* 20 mm between plants. The number of tubers increased as the average yield per stem increased, but was insufficient to counter the influence of increased yield per stem on tuber size. These findings demonstrate that the same principles apply for explaining variation in mean tuber size between plants and between crops.

Although the average seed tuber weight correlates linearly with the average number of stems produced, for individual plants, seed tuber weight accounted for little of the variation in the number of stems per plant. In 2013 reducing variation in seed tuber weight did not reduce variation in stem number per plant nor yield per plant. In 2014 variation in the number of stems and yield per plant were decreased by reducing variation in seed tuber weight, but this did not affect uniformity. In Maris Piper, high levels of variability in within-row plant spacing did not affect uniformity in 2013, whilst in 2014 it caused a small but significant decrease of uniformity. In a separate experiment, variability in within-row plant spacing had a larger negative effect on uniformity in Markies and Marfona and possible reasons for the different responses are discussed. Variation in emergence was affected by differences in sprout development at planting, but only relatively small differences were created between treatments that had no detectable effect on uniformity.

In all four varieties where stem-to-stem variation was surveyed, there was a strong correlation between yield per stem and mean tuber weight. The number of tubers per stem was highly variable and did not increase with yield sufficiently to compensate for the effect of yield on mean tuber weight. The proportion of plant yield produced by each stem and the allocation of yield to tubers on the same stem were highly variable. Reducing variation in seed tuber weight reduced variation in plant yield, and during the initial phases of development plants growing from larger seed tubers grew at a faster rate. The implication for stems is that variation in the supply of seed tuber substrate is a substantial cause of stem-to-stem variation in yield.

Models were developed that provide a framework for analysing the contribution of variation at different scales to the overall tuber size distribution. The underlying mechanism governing uniformity is that decreasing variation in mean tuber weight between plants or stems improves uniformity. Differences in plant-to-plant variation do not have any effect on

uniformity if both variation in yield and number of tubers change by similar amounts. Models predicted that reducing variation in the yield per stem would improve uniformity, particularly in varieties where there is only a weak relationship between yield and number of tubers. The implications of these findings are discussed in relation to growers improving uniformity of present varieties and for breeders developing new varieties.

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Declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as specified in the text.

It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University of similar institution.

It does not exceed the prescribed word limit for the relevant Degree Committee.

Signed .....

Date: .....

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## Abbreviations

|                                     |                                       |
|-------------------------------------|---------------------------------------|
| AG – Above-ground stem              | n.s. – Not significant                |
| AMTW – Arithmetic mean tuber weight | P – Probability                       |
| ANOVA – Analysis of variance        | PSD – Proxy stem diameter             |
| BG – Below-ground stem              | SD – Stem diameter                    |
| COV – Coefficient of variation      | S.E. – Standard error                 |
| DAE – Days after 50 % emergence     | SG – Specific gravity                 |
| D.F. – Degrees of freedom           | SN – Number of stems                  |
| DM – Percentage dry matter          | SP – Space per plant                  |
| DW – Dry weight                     | ST – Seed tuber weight                |
| EC – Electrical conductivity        | t – Tonne                             |
| EM – Emergence                      | TN – Number of tubers                 |
| FW – Fresh weight                   | TNS – Number of tubers per stem       |
| GA – Gibberellic acid               | MTS – Mean tuber size                 |
| GC – Ground cover                   | MTW – Mean tuber weight†              |
| ha – Hectare                        | MXT – Maximum tuber weight            |
| kg – Kilogram                       | WL – Dry weight lost from seed tuber. |
| LA – Leaf area                      | YD – Yield                            |
| n.a. – Not applicable               | YDS – Yield per stem                  |
| n.d. – Not determined               |                                       |

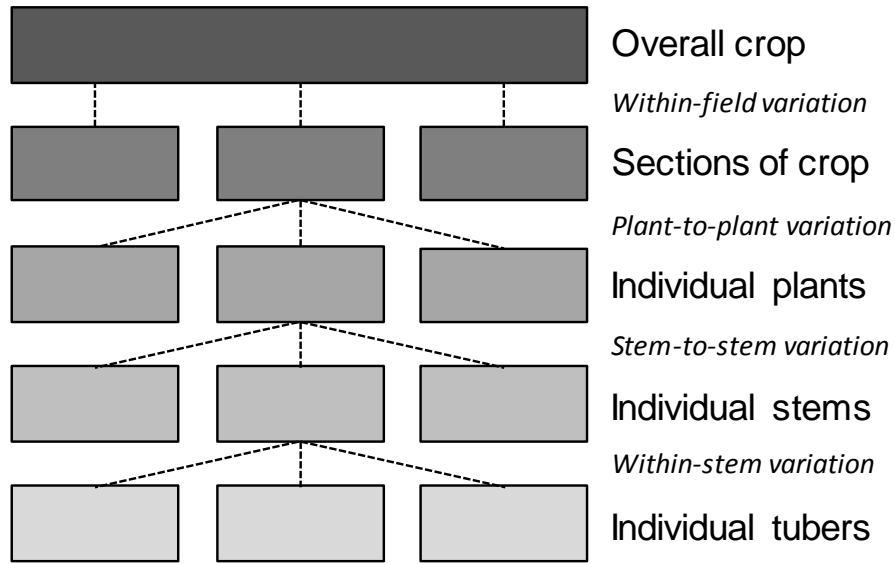
† This value is distinct from the arithmetic mean (yield divided by the number of tubers; see Section 3.1.3.2)

## 1. Introduction

Potato is the world's most important non-cereal crop of which the edible portion comprises the tuber - a swollen modified below-ground stem (Kiple & Coneè Ornelas 2000). Within a crop of potatoes there is substantial variation in the size of tubers, with the largest being 100-1000 times the weight of the smallest (MacKerron *et al.* 1988). Tubers which are too small or too large may not be marketable resulting in a fraction of the total yield being wasted or attracting a lower price. The primary aim of this work was to establish the agronomic causes of variation in tuber size, their relative importance, and means by which growers can increase the uniformity of their crops by reducing this variation. A secondary aim was to characterise the inherent variation in tuber size that occurs in crops to aid breeders in selecting traits that reduce variation in tuber size.

Variation in tuber size occurs at three distinct levels, each of which contributes to the overall variation within the crop (Figure 1). First, tubers growing on each stem vary in weight and size; second, the group of stems (referred to in this work as a singular plant) that grow from each seed tuber have different yields and numbers of tubers which results in variation in the mean tuber size of both stems and plants; and third, yield and the number of tubers vary at different locations (e.g. *c.* 100 m apart), causing variation in the mean tuber size. Improving uniformity requires the extent and causes of variation at each of these levels to be established and the relative importance of each level of variation to be evaluated.

**Figure 1. Different levels at which variation in tuber size occurs within a crop.**

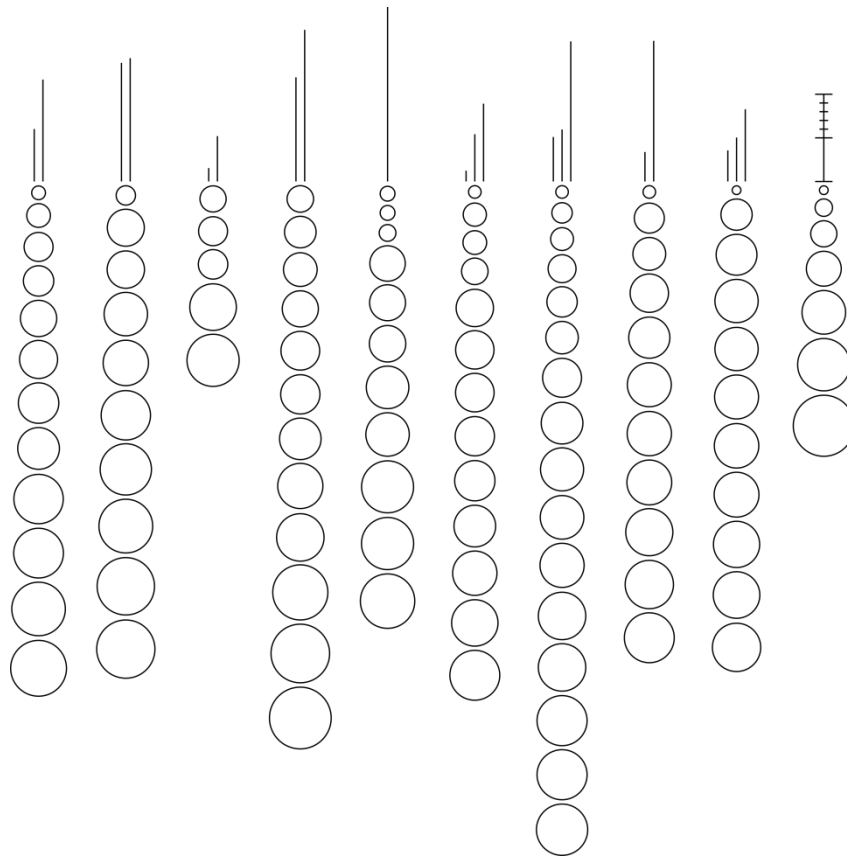


The growth of tubers is indeterminate so that they continue to grow, whilst leaves continue to photosynthesise and transport assimilates. The size of potatoes in a crop is an important quality attribute. Regardless of whether the crop is grown for seed, salads, baking or processing, tubers need to be within a specified size range to be marketable. Even in a relatively uniform ware crop, approximately 10 % of the yield occurs as tubers less than 45 mm in diameter, that are not marketable for general ware consumption (Wurr *et al.* 1993). Waste & Resources Action Programme have estimated that 28-48 % of the UK potato yield is wasted, of which grading losses accounted for 3-13 % (WRAP 2012). Quality control data from a UK potato packer show that common scab, blackspot bruising, mechanical damage and tuber greening are other substantial causes of waste (Coleman 2010).

Tuber size distributions have been of academic interest for almost a century (Salaman 1922; Bates 1935) and whilst considerable progress has been made in understanding the processes controlling mean tuber size, (e.g. Firman 2014) there remain opportunities to improve understanding to decrease wastage and increase returns for growers. Several authors have investigated whether agronomic factors such as nitrogen rate and irrigation affect variation in tuber size (Wurr *et al.* 1993; Firman & Shearman 2007) but the underlying biological

mechanisms that cause variation in tuber size remain poorly understood. Even within a single variety, the morphology of the potato crop is highly heterogeneous with the number of stems per plant, tubers per plant and yield per plant all varying considerably (Svensson 1966). The causes of this variation in morphology are undetermined and it is unclear how it influences variation in tuber size. In onions and carrots the relationship between variation in plant size and uniformity of the crop is simple since each plant produces one marketable unit (Bleasdale 1982). In cereal crops, seed number per plant is very plastic and responsive to growth rate around the time of flowering, so variation in seed size is low, and seed size varies relatively little across planting densities and yields (Sadras 2007). Potato is intermediate between these crops as seed tubers produce multiple stems, each producing multiple tubers, but the number of tubers is fixed relatively early in development before plants are able to determine the resources that will be available later in the season. Consequently mean tuber size is highly variable and dependent on variety, planting density and yield (Allen & Wurr 1992). Although the number of tubers per stem changes with density there is relatively little plasticity and the relationships between yield per plant and mean tuber size per plant have not been established. The stems that seed tubers produce are the true unit of population of the potato crop but despite their average size being vital to controlling mean tuber size (Allen & Wurr 1992) there are no existing descriptions of the variation in yield that occurs between stems or the extent of variation in tuber size between stems. The relationship between the size of stems and tuber size in potato is both more complex (Figure 2), and more difficult to determine than the relationship between plant size and marketable organ size in other crops because the stems grow close to each other and tubers are easily detached from stolons, hence making accurate destructive measurements difficult.

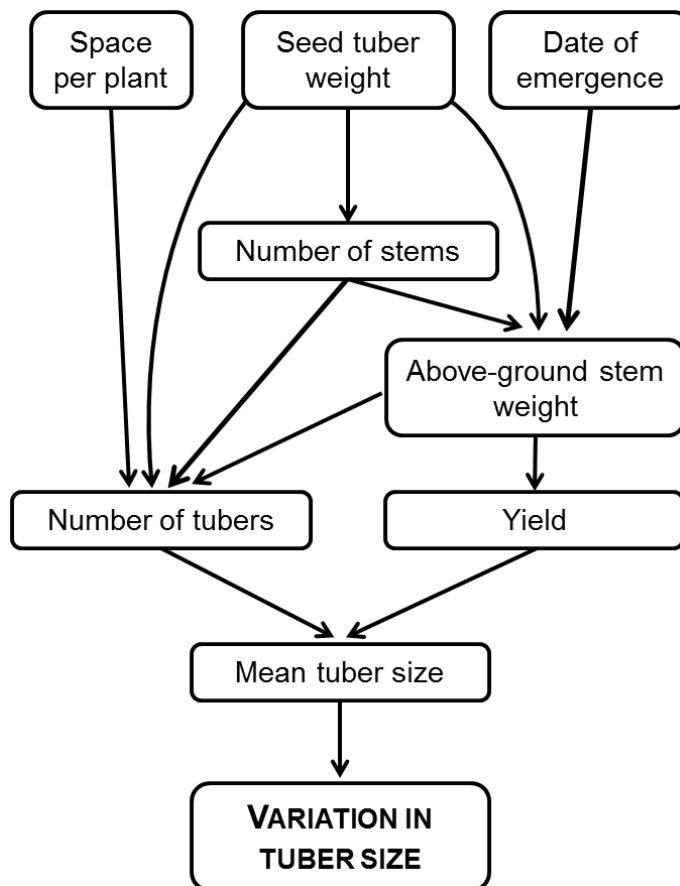
**Figure 2. Diagrammatic representation of a potato crop illustrating the number and size of above-ground stems (vertical lines) and the number and size of tubers per plant (circles). Scale bar (far right): large increments = 250 g FW, small increments = 50 g FW; tubers = 10-70 mm in diameter. Data are from the seventh harvest of Survey 2.**



Crop establishment is important in determining both the yield and uniformity of other vegetable crops (Bleasdale 1982) and early and complete emergence is beneficial to maximise potato yield (Hirst *et al.* 1973; Allen & Scott 1980). The importance of crop establishment in potato crops where almost all plants emerge is uncertain and there are no available detailed descriptions of plant development between emergence and tuber initiation (2-3 weeks after emergence). The main focus of this thesis was to examine variation between plants and stems and determine the effect on the uniformity of the crop. The three factors investigated were variation in seed tuber weight, variation in date of emergence of plants or stems and variation in space between plants. These factors were expected to influence the growth of individual plants and stems by altering the time that autotrophic growth began, the initial rate of growth or the number of stems produced and the final size of the plant. In turn these could result in

differences in the variation in yield per plant and depending on the effect on the number of tubers per plant, increase mean tuber size per plant which was hypothesised to affect the overall variation in tuber size (Figure 3).

**Figure 3. Potential interactions between the factors investigated in this work.**



### 1.1. Thesis structure

In the second chapter, literature has been reviewed to provide an overview of current understanding relating to the growth of the potato crop, the tuber size distribution and plant-to-plant variation. In the last section of the chapter, hypotheses tested in Expts 1-3 and knowledge gaps examined in Surveys 2 and 3 are identified. In the third chapter, materials and methods used in all of the experiments and surveys are discussed, first for all common methods and then for specific methods used in each experiment or survey. Results are presented in the fourth chapter in the chronological order in which the experiments and surveys were conducted as the findings from earlier experiments influenced the design of later



ones. A summary of the results from work conducted in 2013 and how this influenced the work conducted in 2014 is provided after the results of Survey 3. A modelling framework is presented in Chapter 5 that can be used to analyse the relative importance variation at different scales within the crop and make novel predictions. In the final chapter, the causes of variation in tuber size at each level it occurs are examined and the implications for industry and future research are discussed.

## 2. Literature review

### 2.1. Terminology and morphology

#### 2.1.1. Units of population

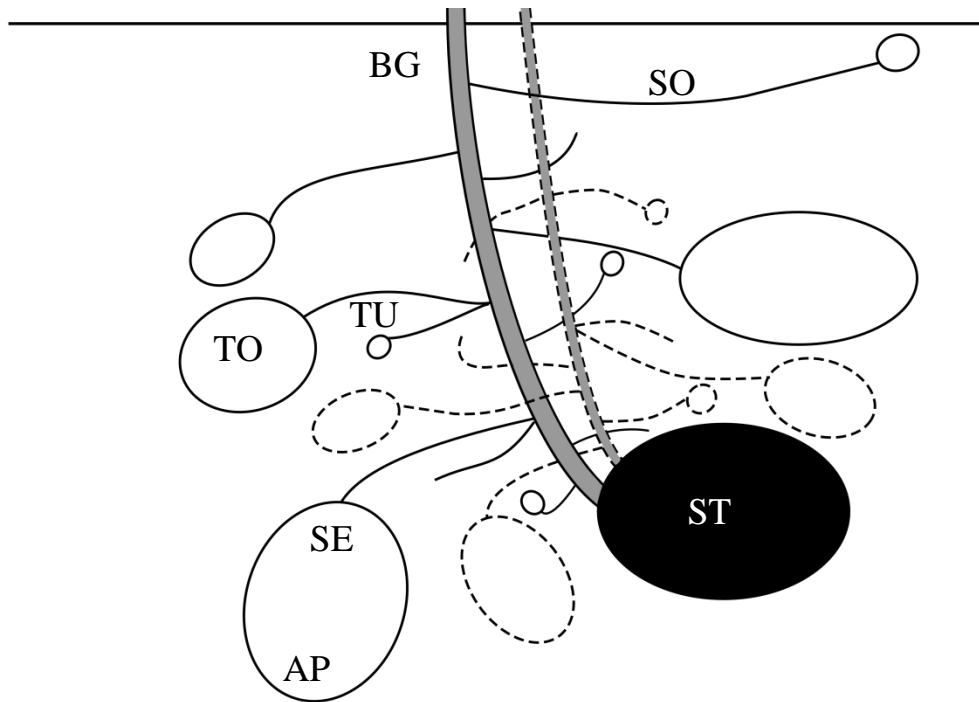
When discussing the potato crop it is important to distinguish between different units of population. The main stems are the effective unit of population of the potato crop, but multiple main stems tend to arise from each seed tuber (Bleasdale 1965; Allen & Wurr 1992; Figure 4). In the current work, the group of stems that grow from an individual seed tuber are referred to as a singular plant although other authors have referred to this group as a ‘hill’ (Bates 1935; Svensson 1966; Silva & Andrew 1985). The sprouts that grow from the seed tuber and emerge at the soil surface are main stems (Allen & Wurr 1992). Secondary stems grow as branches from main stems (Allen & Wurr 1992), but in this work, stem refers to a main stem unless secondary stem is clearly specified.

#### 2.1.2. Tubers

Early in their development, tubers are defined as swellings at the end of stolons with a diameter greater than twice that of the stolon (O’Brien *et al.* 1998). However, not all tubers that are initiated persist until harvest and to distinguish between tubers which are more likely to persist, tubers > 10 mm in diameter are treated separately from those < 10 mm in diameter

(O'Brien *et al.* 1998). In the current work, tuber refers to those > 10 mm in diameter unless specified otherwise.

**Figure 4. Simplified below-ground morphology of a potato plant with two stems. The first stem is drawn in solid lines and the second is drawn in dashed lines. Not to scale or morphologically accurate. Key: AP = apical end of tuber, BG = below-ground stem, SE = stolon end of tuber, SO = stolon, ST = seed tuber, TO = tuber > 10 mm in diameter, TU = tuber < 10 mm in diameter.**



### 2.1.3. Quantifying variation

Variation in a plant population can be summarised by the mean and standard deviation of the frequency distribution (Benjamin & Hardwick 1986). The standard deviation is the square root of the variance which itself is derived by squaring the difference from the mean of each value, and averaging these for the sample (Snedecor & Cochran 1980). For a population, *c.* 68 % of values lie within  $\pm$  one standard deviation of the mean and *c.* 95 % within two standard deviations (Snedecor & Cochran 1980). If the frequency is normally distributed, the mean and the standard deviation contain all the necessary information to describe the population (Benjamin & Hardwick 1986). The coefficient of variation (COV) is derived from these statistics as the ratio of the standard deviation to the mean and provides a consistent

description of the extent of variation that does not change as the mean changes (Benjamin & Hardwick 1986). In non-normal populations, the standard deviation and mean cannot adequately describe the population, and skewness and kurtosis are required to describe the shape of the distribution (Benjamin & Hardwick 1986). The COV can also be used to describe variation in non-normal populations, but care must be taken to ensure that the shape of the distributions do not differ substantially when comparing populations (Benjamin & Hardwick 1986).

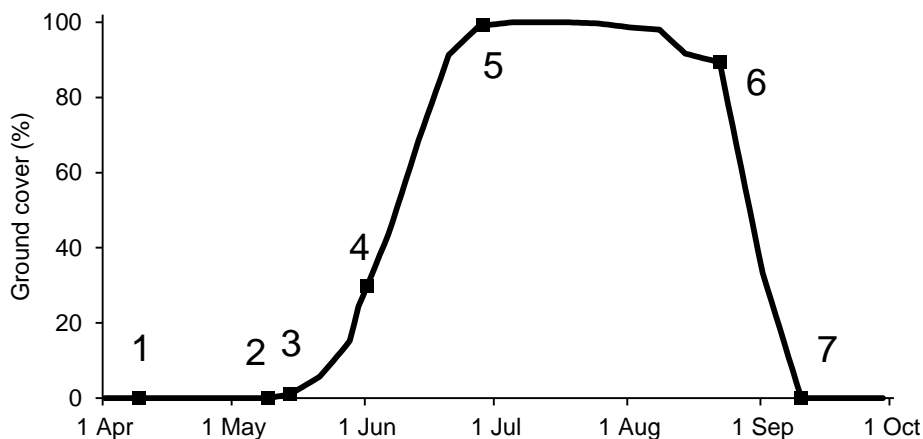
## 2.2. Growth of the potato crop

Before considering the growth of individual plants, stems and tubers within the crop, it is pertinent to provide an overview of the growth of the potato crop as a whole. It should be stressed that this overview is a generalisation of the processes that occur during the growing season for a typical ware crop and that there are many possible exceptions, but these are outside the scope of the current work.

### 2.2.1. Stages of crop development

In temperate climates such as in the United Kingdom, the potato crop is propagated vegetatively from seed tubers produced the previous year. Seed tubers are planted in the spring (March-May) and the sprouts emerge at the surface of the soil 2-6 weeks later (Allen *et al.* 2001). The canopy expands rapidly and tubers are initiated 2-3 weeks after emergence (O'Brien *et al.* 1998). The canopy continues to expand and completely covers the ground 5-7 weeks after emergence. Tuber growth is most rapid once a full canopy has developed (i.e. 100 % ground cover), slows as the canopy begins to senesce (10-18 weeks after emergence) and declines rapidly once it falls below *c.* 80 % ground cover. A typical ground cover curve with the relevant stages of development marked is shown in Figure 5.

**Figure 5. A typical ground cover curve for a ware crop grown in the UK with stages in the crop's development marked. 1 = planting date, 2 = start of emergence, 3 = 50 % emergence, 4 = start of tuber initiation, 5 = complete canopy formation, 6 = beginning of rapid senescence, 7 = complete senescence. Data are for a crop of Desiree, as discussed in Survey 4.**



### 2.2.2. Dry matter production and yield formation

Dry matter production in potato crops is a function of the quantity of solar radiation the canopy intercepts and the efficiency at which it is converted to dry matter (Monteith 1977; Allen & Scott 1980). In disease-free, irrigated crops, radiation use efficiency is similar and therefore total dry weight can be predicted from ground cover curves (such as that shown in Figure 5) combined with meteorological data on solar radiation levels (Allen & Scott 1980). With knowledge of the partitioning of dry matter between the canopy and the tubers, and the dry matter percentage of the tubers, the yield can be modelled and predicted (Allison 2011). Knowledge of these mechanisms has been crucial to improving our understanding of the effects of different agronomic practices on yield (Allen *et al.* 2001). Given the robustness of this principle in relation to the growth of potato crops under a range of environmental conditions in the United Kingdom and similar principles also being used to model the growth of individual plants within monocultures (e.g. Benjamin & Park 2007), it is assumed in this work that the same principles apply to individual plants and stems. Applying mechanistic models to the growth of crops or to the growth of individual plants within the population falls outside the scope of the current work.

## 2.3. Number and size of tubers at the field scale

### 2.3.1. Number of tubers

Understanding variation in tuber size within a crop, requires an understanding of the factors that determine the average number and size of tubers in a crop. Many different factors can influence the tuber size distribution of a crop and they often interact with each other making it difficult to predict and manipulate (Struik *et al.* 1990). The mean tuber size of a crop is a function of the tuber population and the yield. Haverkort *et al.* (1990) described the tuber population with the following equation:

$$\text{tuber population} = \text{seed tuber population} \times (\text{sprouts/seed tuber}) \times (\text{stems/sprout}) \times (\text{stolons/stem}) \times (\text{tubers/stolon})$$

Which can be simplified to the following:

$$\text{tuber population} = \text{seed tuber population} \times (\text{stems/seed tuber}) \times (\text{tubers/stem})$$

For a given variety, the tuber population is most strongly influenced by the stem density which is in turn influenced by the seed tuber population (Allen & Wurr 1992). Once the relationships between seed tuber population, stem density and the number of tubers per stem have been elucidated, the number of tubers can be predicted and manipulated by varying the seed tuber size and seed tuber spacing (Allen & Wurr 1992). Larger seed tubers usually produce a greater number of stems than smaller seed tubers and by increasing or decreasing the spacing between plants, the stem density can be altered (Allen & Wurr 1992). Since the total yield is relatively stable at different stem densities, altering the stem density causes the average yield per stem to change (Moorby 1978).

A complicating factor is that the age of the seed tubers affects the number of stems produced. Aging of seed tubers can be classified into two distinct types; physiological aging and chronological aging, although these have often not been distinguished in the literature (Firman, pers. comm.; e.g. Coleman (2000); Struik *et al.* (2006)). Physiological aging is

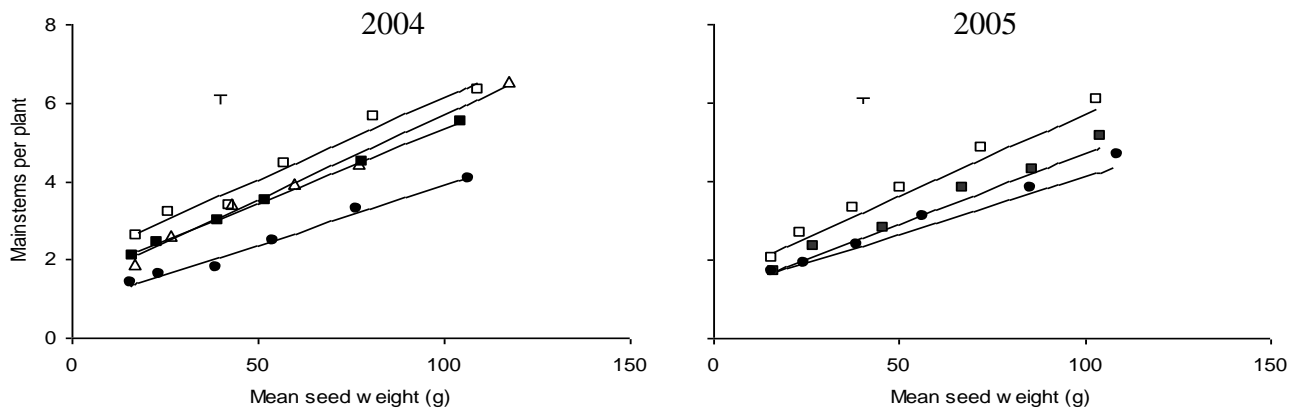
temperature dependent and manifests as sprout growth prior to planting (O'Brien *et al.* 1983); it decreases the number of stems produced and also hastens crop development but shortens canopy longevity (O'Brien *et al.* 1983). Chronological aging occurs independently of temperature and does not cause any visual changes in the seed tuber but increases the number of stems produced (Firman 1997b; Firman 2014).

Chronological age is defined as the interval from emergence of the seed crop (a proxy for the date of tuber initiation) until the planting of the seed tubers and can therefore be accurately determined (Firman 2014). Initially apical dominance inhibits the growth of more than one stem, but over time this effect is reduced and multiple sprouts are able to develop. As a result, chronologically older seed tubers produce more stems than chronologically younger seed tubers (Allen *et al.* 1992; Firman & Daniels 2011; Figure 6).

Measuring the accumulated degree days is the simplest method by which the physiological age of seed tubers can be quantified (e.g. O'Brien *et al.* 1983). Struik *et al.* (2006) found that tubers responded differently to temperature depending on their chronological age.

Consequently, Struik *et al.* (2006) suggested that there is no reliable method by which the physiological age of tubers can be determined prior to planting and hence there is always some uncertainty about how many stems a stock of seed tubers will produce. However, if seed tubers are held at 2 °C prior to planting (preventing physiological aging) then the number of stems produced is relatively predictable. This information can then inform the optimum seed rate (t/ha of seed tubers planted) required to achieve the target mean tuber size can be calculated (Firman 2014).

**Figure 6. Relationships between the number of stems per plant and seed weight for Maris Piper in 2004 and 2005 using seed tuber stocks of different chronological ages. Seed tuber stocks: Welsh P1, □; Northumberland, △; Welsh P2, ●; Wiltshire, ■. Bar indicates S.E. Reproduced with permission from Firman & Shearman (2006a)**



The number of tubers per stem is predominantly determined by the number of tubers that are initiated. The majority of tubers that grow to over 10 mm in diameter persist until the crop is harvested, although some are resorbed (O'Brien *et al.* 1998). It is unclear what factors influence tuber resorption and how these affect the final number of tubers (O'Brien *et al.* 1998). Without frequent sampling, it can be unclear whether a crop with fewer tubers at the final harvest initiated fewer tubers, or resorbed more.

The number of tubers that are initiated is influenced by the amount of solar radiation intercepted during tuber initiation 2-3 weeks after emergence (O'Brien *et al.* 1998). Evidence for this is provided by experiments in which crops were shaded at tuber initiation resulting in reductions in the number of tubers (Gray & Holmes 1970; Sale 1976; O'Brien *et al.* 1998; Allison 2007). Firman & Daniels (2011) reported a correlation between the solar radiation intercepted per stem during tuber initiation and the number of tubers per stem for Maris Peer and Estima. The relationships varied between years and depending on planting date.

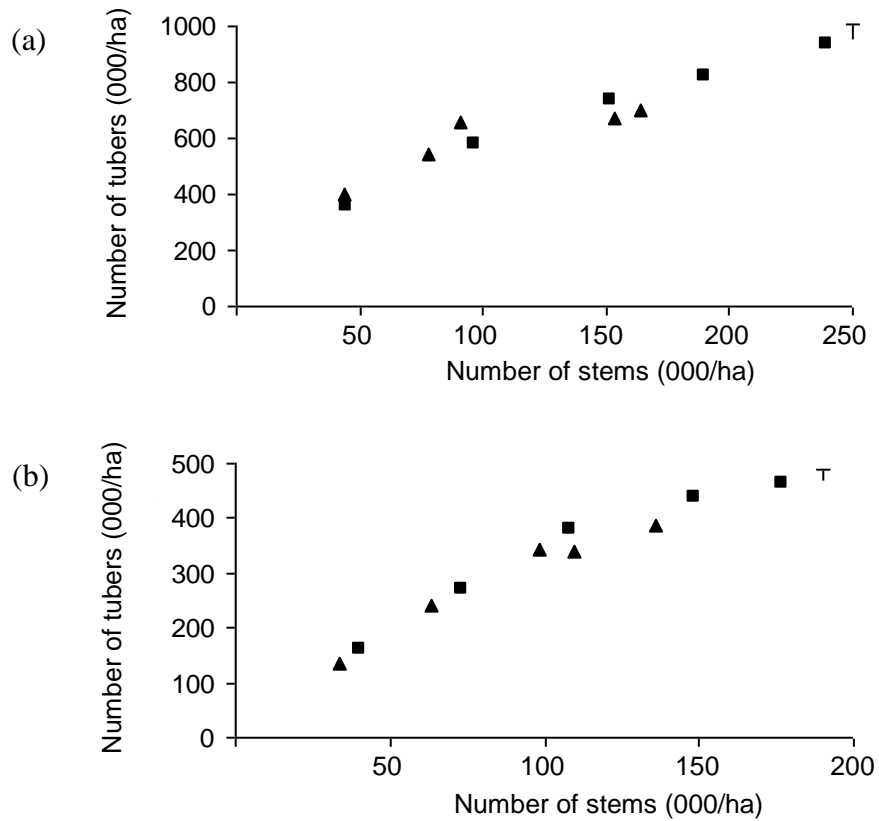
It could therefore be expected that the number of tubers initiated per stem is proportional to the solar radiation that its leaves intercept during tuber initiation, which is largely determined by its leaf area. Tuber initiation occurs over a relatively short period, between two and four

weeks after emergence (O'Brien *et al.* 1998) and therefore weather conditions during this period could affect the total number of tubers at the final harvest.

As the number of stems increases, the number of tubers per stem decreases (Allen & Wurr 1992). During the 1970s, variation in the number of tubers per stem was ascribed to variations in the availability of water (Allen & Wurr 1992). Later work however showed that much of the variation in number of tubers was due to variation in the number of tubers < 10 mm which may not develop into harvestable tubers (Burstall *et al.* 1987). Since the 1990s, greater attention has been made to distinguish between tubers > 10 mm and < 10 mm and counting only tubers >10 mm results in less variable numbers of tubers (Allen & Wurr 1992). There is considerable variation in the number of tubers per stem that develop on different varieties, and how the number of tubers responds to changes in stem density (Firman 2014). For example, Firman & Daniels (2011) found that at a stem density of 50,000 stems/ha, King Edward produced approximately eight tubers per stem, whereas Russet Burbank produced approximately three tubers per stem. As the stem density increased, King Edward produced fewer tubers per stem, but at a density of 200,000 stems/ha, still produced four tubers per stem. In contrast, Russet Burbank showed relatively little response to increased stem density and it produced approximately three tubers per stem between 50,000 and 150,000 stems/ha (Figure 7).

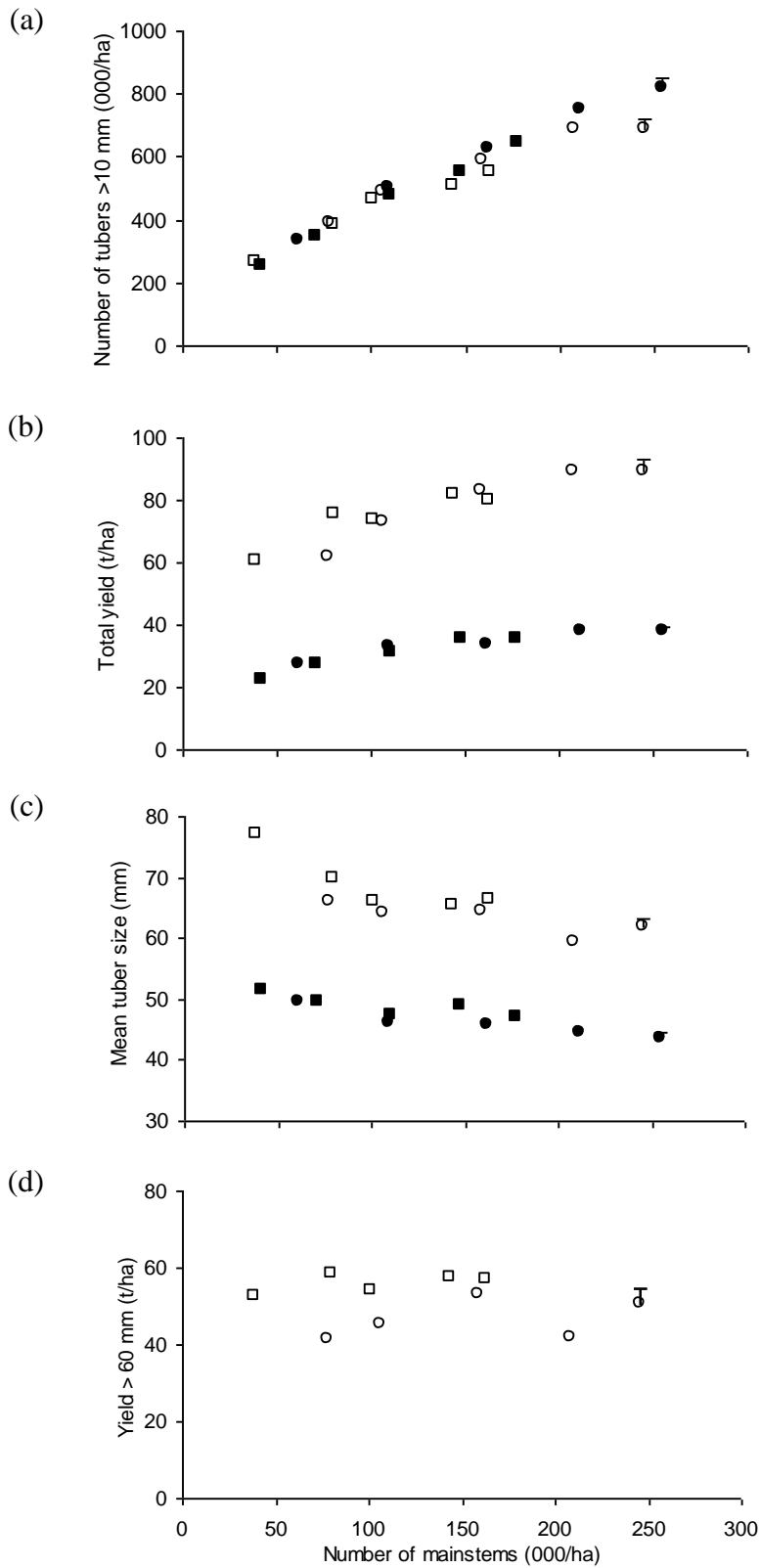


**Figure 7. Relationship between number of stems and number of tubers in (a) King Edward and (b) Russet Burbank. Seed tuber stocks: Welsh late, ■; Wiltshire, ▲. Reproduced with permission from Firman & Daniels (2011).**



Firman & Shearman (2006a) and Firman & Daniels (2011) examined the effect of stem density on the number of tubers in Maris Piper. They found the number of tubers exhibited an intermediate degree of plasticity to changes in stem density in comparison to King Edward and Russet Burbank. At 50,000 stems/ha approximately 5 tubers per stem were produced and this reduced to approximately 3 tubers per stem at 200,000/ha.

**Figure 8. The relationship between (a) number of tubers > 10 mm, (b) tuber yield, (c) mean tuber size ( $\mu$ ), and (d) yield of tubers > 60 mm and number of stems/ha at two harvest dates of Maris Piper. Stocks: Welsh P1 first harvest, ●; Welsh P2 first harvest, ■; Welsh P1 second harvest, ○; Welsh P2 second harvest, □. Bars indicate S.E.s. Reproduced with permission from Firman & Shearman (2006a)**



It is unclear how variable the number of tubers on individual stems within a crop is. The relative stability of the total tuber number between crops of King Edward could translate into plasticity in individual stems, i.e. with higher yielding stems (equivalent to those grown at low densities) producing more tubers and lower yielding stems producing fewer tubers. In contrast, Russet Burbank may have less variable numbers of tubers per stem within a crop than King Edward. Plasticity in the number of tubers per stem could be a beneficial varietal trait since it could decrease variation in the mean tuber weight of stems with different yields and consequently if the variation in stem yields remained equal, variation in tuber size would be reduced.

### 2.3.2. Mean tuber size

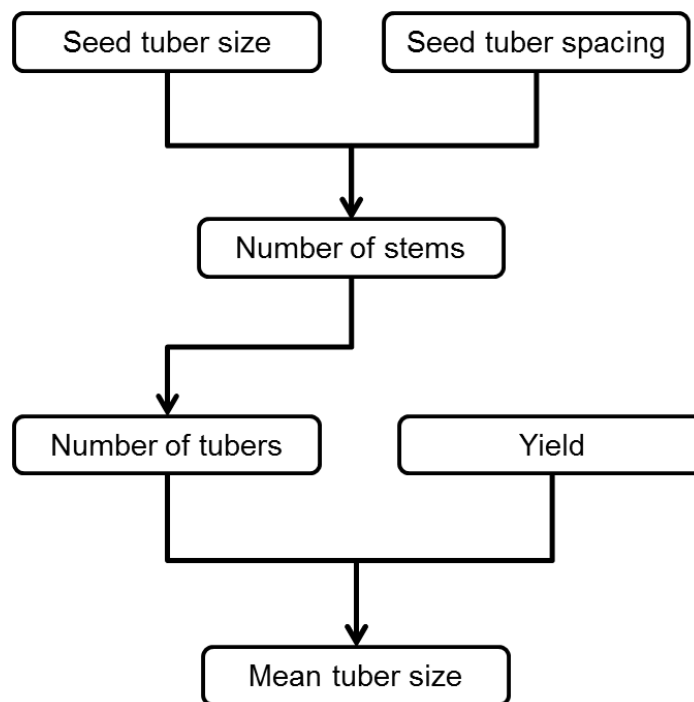
The mean tuber size of a crop is the size of tuber at which 50 % of the yield is composed of smaller tubers and 50 % of the yield is composed of larger tubers (Travis 1987).

Simplistically, the mean tuber size is determined by the number of tubers and the yield of the crop (Travis 1987). Mean tuber size increases over the growing season as the yield increases (e.g. Figure 8c).

The relationships between seed tuber weight and the number of stems, and between the number of stems and the number of tubers can be used to predict tuber populations that a particular seed rate will produce. For a given yield, the mean tuber size can then be predicted prior to planting to maximise returns for the grower (Figure 9; Firman 2014). While the concept of determining optimum seed rates is well-established (e.g. Wurr *et al.* 1992a) previous methods required a large number of experiments, planting different sized seed tubers at different densities and were principally concerned with how the seed rate should be altered depending on the relative cost of seed tubers and the ware crop in order to achieve the stem density to give the optimum economic return, determined by the relationship between seed

rate and yield. The model developed by Firman (2014) allowed optimum seed rates to be determined for new varieties using relatively few experiments and taking into account that different size grades of tubers attract different prices which can affect the optimum return for growers. Planting a range of seed tuber sizes and chronological ages at the same spacing produced sufficient information to model the effect of different seed rates on the mean tuber size. The characters that are used in the model were the following: the number of tubers per stem, the change in the number of tubers per stem as the stem density changes, the number of stems per seed tuber of a particular age and weight, the change in the number of stems per seed tuber with a change in seed tuber weight, the percentage change in stems per seed tuber as the chronological age of the seed increased and a tuber shape constant.

**Figure 9. The main factors that determine the mean tuber size of a crop.**



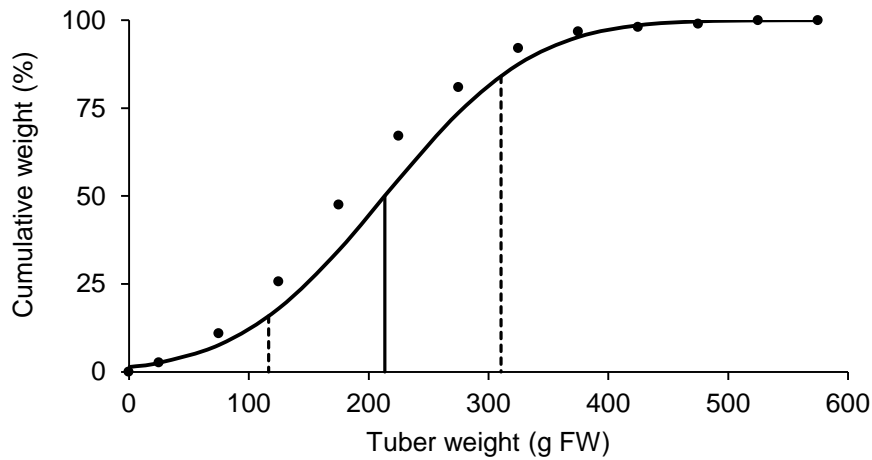
## 2.4. Variation in tuber size

### 2.4.1. Quantifying variation in tuber size

The yield of tubers within specific size grades has been of interest since at least the time of Salaman (1923), but until the 1980s (e.g. Bates 1935; Davies 1954; Pascal *et al.* 1977) the yield of tubers in each grade were treated in analyses as though they were independent variates, which could lead to spurious significant effects on the yield within a single grade (Hall and Glasbey 1993). Several different analytical techniques have been developed to describe the continuous distribution of tuber sizes within a crop and from this, the uniformity of the crop. These have modelled tuber weight (Sands & Regel 1983; Marshall 2000), tuber size (Travis 1987) or the number of tubers (Hide & Welham 1992). Various distributions have been fitted including normal distributions (Sands & Regel 1983; Travis 1987), gamma distributions (Marshall 2000; Firman 2008) and Weibull distributions (Nemecek *et al.* 1996; Bussan *et al.* 2007). Despite the advantages of these approaches, many authors continue to report the yields within specific grades and analyse the yield in each individually (e.g. Pavek & Thornton 2006; Blauer *et al.* 2013b) limiting the insights that can be drawn from results.

Sands & Regel (1983) graded tubers by weight, plotted the cumulative weight and fitted a cumulative probability distribution function to the data. From this they could predict the proportion of yield above and below any specific value. The mean tuber weight was calculated by establishing the point at which 50 % of the total yield is reached. The spread in yield was estimated from the same function (Figure 10). Marshall (1986) developed the method of Sands & Regel (1983) further by calculating the ‘relative variability’ of tuber weight by dividing the spread in yield by the mean tuber weight, which is analogous to the COV.

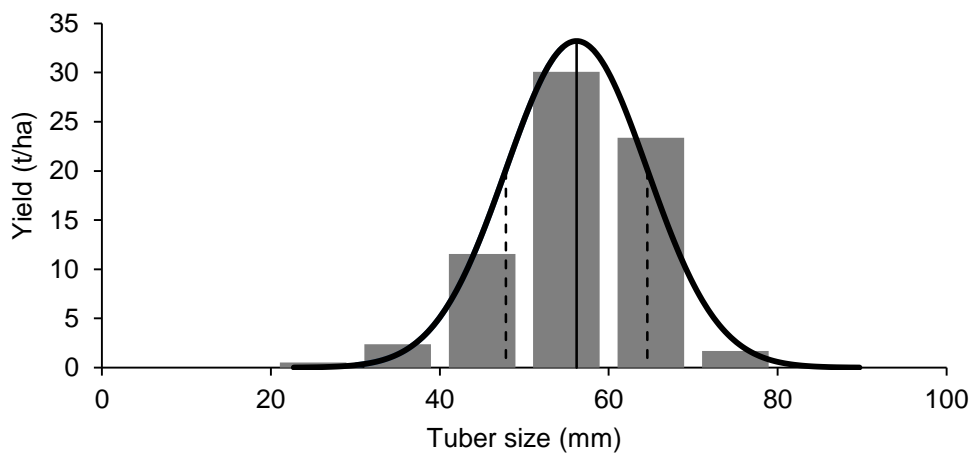
**Figure 10.** An example of a cumulative probability distribution as Sands and Regel (1983) used to describe the tuber size distribution. Observed values, ●; fitted distribution, mean tuber weight = 214.5 g, spread of yield = 96.6 g. Relative variability (after Marshall 1986) = 45.4 %. — = mean tuber weight; - - - = mean tuber weight ± spread of yield.



Travis (1987) introduced a method of modelling the tuber size distribution of a crop by fitting a normal distribution to the percentage of yield in discrete size grades (Figure 11).  $\mu$  described the mean tuber size and represented the size of tuber in the centre of the distribution of yield, such that 50 % of the yield was composed of tubers smaller and larger than  $\mu$ .  $\sigma$  was the standard deviation of the distribution and described the spread of the distribution, with c. 68 % of the yield found within  $\pm \sigma$  of  $\mu$ .  $\sigma$  increases as  $\mu$  increases and so to establish a standardised description of variation, Wurr *et al.* (1993) calculated the ratio of  $\sigma$  to  $\mu$  to give the COV of tuber size. Small changes in the COV of tuber size can make a substantial difference to the income of growers. For example in a ware crop where only tubers 40-80 mm are marketable, if the mean tuber size was 60 mm and the COV of tuber size was 20 %, 90.4 % of the crop would be marketable, but if the COV of tuber size was 18 %, 93.6 % of the crop would be marketable (Wurr *et al.* 1993). In current markets, there are often differences in value between different marketable size grades. For example a market report published by the Potato Council in November 2014 quoted free-buy prices for the salad variety Maris Peer of up to £250/t for 35-45 mm, but only £50-90/t for tubers > 45 mm (Anon, 2014). Similarly, a premium price of £100-140/t was paid for Estima baking potatoes

(65-85 mm) compared to £55-90/t for ungraded Estima (Anon, 2014). Knowledge of the value of different sized tubers allows the crop value to be predicted as the mean tuber size changes during the season (Allison & Firman 2014). With premiums paid for narrow size grades, the COV of tuber size is now more important in determining the value of a crop than in the past.

**Figure 11.** An example of a normal curve fitted to the yield of tubers within 10 mm size grades as used by Travis (1987). Data are from Survey 1. Yield = 69.7 t/ha, mean tuber size = 56.2 mm, COV = 14.9%. ----- = mean tuber size; - - - - = mean tuber size  $\pm$  spread of yield.



It is important to note that both Sands & Regel (1983) and Travis (1987) modelled the distribution of yield in different weight (or size) classes, rather than the individual tuber sizes or weights more typical when describing variation in plant populations (e.g. Benjamin & Hardwick 1986). Such an approach reduces the influence of small tubers in the crop on the overall distribution, giving a more economically relevant description of the distribution.

Hide & Welham (1992) developed a model to describe tuber size distributions using the number of tubers rather than weight. They observed that the size distribution began as one normal distribution at the beginning of the season, but that by July this had diverged into two separate populations, before reverting back to one normal distribution by September. They argued that studying the distribution of the number of tubers rather than weight should reveal the mechanisms of tuber growth with more precision than the method of Travis (1987) which

gave more influence to the large tubers in the crop. Such weighting is crucial to optimising marketable yields however since it is the proportion of yield that can be sold rather than the number of tubers. It was suggested that using their approach it would be possible to attempt to manipulate the population of small tubers separately from the large tubers although there was no evidence that this was physiologically possible.

Hall & Glasbey (1993) modelled the weight and size of tubers as a bivariate normal distribution. The method was considerably more complex than that developed by Travis (1987) and yet did not appear to offer any substantive advantages.

#### 2.4.2. Factors affecting variation in tuber size

##### 2.4.2.1. Agronomic factors

Wurr *et al.* (1993) reviewed the results from a wide range of experiments conducted at Cambridge University Farm to examine agronomic factors that could potentially affect the COV of tuber size, calculated using the method of Travis (1987). The factors investigated were nitrogen, phosphorus, potassium, seed tuber planting density, seed tuber weight, seed tuber physiological age, date of harvest, irrigation, variety and site of production. They concluded that nitrogen, harvest date, site of production and variety could influence the COV of tuber size but that the other factors did not. There was large variation in the COV of tuber size that occurred in experiments, even when significant effects were found. The  $R^2$  value for the regression of nitrogen fertilisation rates against the COV of tuber size was 0.39 indicating that much of the variation in tuber size resulted from other factors. More recent experiments have found that nitrogen rate had no effect on the COV of tuber size (e.g. Allison *et al.* 2012). The site of production was found to have the largest effect on the COV of tuber size but the reasons for this were not investigated. The COV of tuber size varied widely between experiments reported by Wurr *et al.* (1993) from *c.* 12-26 %. Travis (1987) reanalysed the results of various experiments but only reported  $\mu$  and  $\sigma$  rather than the COV of tuber size.



Analysis of the values reported by Travis (1987) showed that the COV of tuber size ranged from c. 14-23 % and that there were no consistent effects of irrigation on the COV of tuber size.

MacKerron *et al.* (1988) compared the variation in tuber size in droughted and irrigated crops using the relative variability measure of Marshall (1986). Drought did not affect the variation in tuber size but they reported a negative correlation between the number of tubers and variability in tuber weight.

Firman & Shearman (2006b; 2007) examined the effects of scheduled and variable irrigation (where high soil moisture deficits were allowed to accumulate and then the crop was over-watered), normal and high nitrogen (165 and 330 kg/ha) and seed tuber chronological age (early and late) on the COV of tuber size in Maris Piper. The combination of variable irrigation and high nitrogen increased the COV of tuber size relative to scheduled irrigation and normal nitrogen in both years, but the effects of these treatments when not combined were relatively small and not significantly different to the treatments with scheduled irrigation and normal nitrogen. There were no consistent effects of seed tuber chronological age on the COV of tuber size and, although the distribution of number of stems per plant did differ slightly between the stocks, the variations were not quantified. Although there were no significant effects of the treatments, the COV of tuber size varied substantially between years, with the average COV of tuber size being 20.9 % in Firman & Shearman (2006b) and 16.8 % in Firman & Shearman (2007).

#### 2.4.2.2. Pathology

Several pathogenic micro-organisms that infect potato plants can affect the tuber size distribution of the crop. Firman (2004) examined the effect of contamination of seed tubers with *Erwinia carotovara* subspecies *atroseptica* on the incidence of blackleg, using

artificially inoculated and naturally contaminated seed tubers with different levels of inoculum. Yield, the number of tubers and the mean tuber size were not significantly affected by the level of contamination. The COV of tuber size increased progressively with the level of contamination for the stocks that were artificially contaminated (from 17.6 – 20.2 %  $\pm$  0.74) but was lower in the naturally contaminated stock (16.5 – 17.4 %)

The fungus *Rhizoctonia solani* can increase the proportion of small tubers in a crop by infecting stolons and increasing branching (Hide *et al.* 1985a, 1985b). Firman & Shearman (2006b, 2007) compared seed tuber stocks of Maris Peer infected with *R. solani* with a healthy seed tuber stock and also examined the effect of treating each stock with one or both of the fungicides azoxystrobin (a broad-spectrum strobilurin) and penicuron (specific to *R. solani*). In the first year, the heavily infested and untreated seed tuber stock had a COV of tuber size of 21.1 % compared to 16.6 % in the untreated healthy seed tuber stock.

Applications of both fungicides largely negated the effect of disease reducing the COV of tuber size to 16.2 %. In the second year, across all the treatments, the COV of tuber size was significantly higher for the diseased seed tuber stock (20.9 %) than for the healthy seed tuber stock (18.5 %). There was no significant effect of either fungicide on the COV of tuber size, although the diseased, untreated stock had the numerically highest COV of tuber size (22.7 %). Differences in the distribution of number of stems per plant may have contributed to the increased COV of tuber size in the diseased stock. The healthy stock had fewer stems per plant ( $2.43 \pm 0.056$ ) than the diseased stock (3.39) and there was a greater range in the number of stems per plant in the diseased stock (1-7 vs 1-4), but the COV was not reported.

#### 2.4.2.3. Variety

Marshall (1986; 2000) examined the relative variability of tuber weight (from size-graded data) for a range of varieties. Marshall (1986) concluded that variability of tuber size within a variety was constant and identified Morene as a variety with an unusually low level of

variation in tuber weight. Marshall (2000) reported that variation in tuber size within a variety was relatively constant and that there were significant differences in the variation between varieties. Marfona was found to have a particularly high degree of variability whereas Pentland Dell was more uniform. The findings of Firman & Shearman (2006b) clearly contradict the claim made by Marshall (1986) that uniformity within a variety is constant. While it would be of interest to determine whether varieties do indeed display differing amounts of variation in tuber size, it is uncertain whether the findings of Marshall (2000) are reproducible. Given the other variables which could affect variation in tuber size it is unclear whether the differences observed were solely due to genetic differences rather than physiological or pathological differences resulting from interaction between genotype and environment.

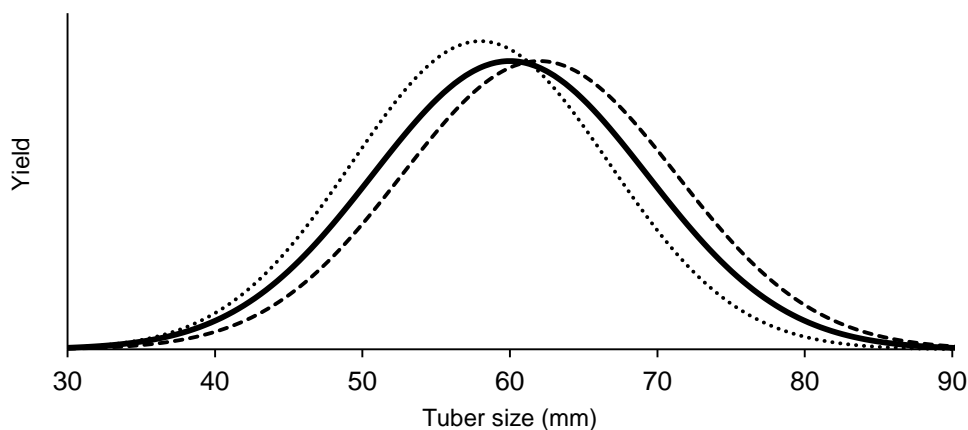
No specific attempts to improve uniformity through breeding have been reported in the literature and this is probably because agronomic traits such as pest and disease resistance and consumer traits such as a bright skin finish are considered in higher demand. However, varieties do need to be relatively uniform to be commercialised and there are some reports of it being assessed in the course of breeding programs based on visual assessments. Love *et al.* (1997) assessed the progeny of ten crosses and concluded that uniformity of tuber size was too variable between generations to be selected for in early generations and it had one of the lowest heritabilities of all the traits examined (0.44). A scale of 1-5 was used by da Silva *et al.* (2006) to assess 600 clones and they found uniformity of tuber size was the only trait that did not differ significantly between clones and the heritability was very low (0.06). Darsow (2014) scored clones on a scale of 1-9 where 9 was very uniform and found clones ranged from 3-8 but did not quantify what constituted “very uniform” nor the extent to which it was heritable. The International Potato Centre score clones based on a visual assessment on a scale of 1-9 ranging from samples where “all tuber sizes are present (from very small to

large)” to where “only one tuber size [is present]” (De Haan *et al.* 2014). Scoring varieties on a visual scale is likely to be highly dependent on the assessor and the chance of identifying uniform varieties would be greatly improved by a quantitative assessment. Given the difficulty in selecting uniform varieties, identifying component traits which contribute to uniformity may also aid breeders in making selections (Yin *et al.* 2004).

## 2.5. Within-field variation

Agricultural fields are heterogeneous, with soil texture, soil structure and soil nutrient concentrations displaying spatial variation (Earl *et al.* 2003). Each of these factors has been shown experimentally to influence the number of tubers and yield and it would therefore be expected that mean tuber size will vary at different locations within a field. If one location produces relatively small tubers and another relatively large tubers then when the two are combined at harvest, the overall COV will be larger than at either individual location (Figure 12).

**Figure 12. A theoretical example of how variation in the mean tuber size (MTS) within crops could affect the COV of tuber size. Site 1, ..... MTS = 58.0 mm, COV = 15.00 %; Site 2, - - - - MTS = 62.0 mm, COV = 15.00 %; Combined, — MTS = 60.3 mm, COV = 15.14 %.**



At the field scale, the processes that control mean tuber size are relatively well understood, but it is unclear to what extent the mean tuber size varies within crops. If this variation could

be quantified and consistently predicted, it would be possible to alter stem populations by varying seed tuber spacing, to counteract the effect of other factors.

One variable that can be measured easily and affordably over a whole field is the electrical conductivity (EC) of the soil. EC acts as a proxy for the relative particle size of the soil because sandy soils hold less water and therefore conduct less electricity than clay soils (Hedley *et al.* 2004, James *et al.* 2003). The particle size of the soil determines how it behaves during cultivation as sandy soils dry out faster and are easier to work. This in turn affects the mean ped size (aggregated units of soil structure) of the soil, which can affect the number of tubers per stem independently of the stem density (Firman & Daniels 2011).

No studies have specifically examined within-field variation in UK potato crops, but studies elsewhere give an indication of the extent of variation that may occur. Redulla *et al.* (2002) studied within-field variation in yield, number of tubers and the grading of tubers by weight over four years in Washington, USA. The sites were centre-pivot-irrigated, uniformly fertilised and were in crop rotations typical for the region. Each year, *c.* 80 samples each consisting of a 3 m length of row were dug in each field and the crop traits were related to variations in elevation, soil nutrients and soil texture. There were few significant correlations observed and no consistent trends over the four years. Generally, soil texture affected yield more strongly than soil nutrient concentrations.

Cambouris *et al.* (2006, 2007) and Allaire *et al.* (2014) investigated within-field variations in yield and examined whether the EC of soil could be used to establish management zones to reduce the variability. The crops were unirrigated and under continuous potato cultivation, making the findings less relevant to British production. Cambouris *et al.* (2006) measured the yield from a two-row harvester and found similar levels of variation at the same site over three years with a COV of 25-28 %. The soil was predominantly (mean of 87 %) composed of sand particles and there was a negative correlation between the proportion of sand and the

EC of the soil. Significant correlations were reported between yield and the EC of the soil in two years but variations in EC explained < 50 % of the variation in yield and the proportion of sand did not significantly correlate with yield. Yield in the same locations was significantly correlated in each of the years even though different varieties were grown, although the yield in one year accounted for < 50 % of the variation in yield in the next, suggesting that factors other than soil texture influenced yield. The concentrations of nitrogen and phosphorus both correlated significantly with the EC of the soil and yield. Soil organic matter correlated weakly, but significantly with yield in two years. The authors concluded that the primary cause of the variation in yield was variation in water availability, which was in turn caused by differences in soil texture that could be accurately determined by measuring the EC of the soil. At the study site, the EC was related to the depth from the soil surface to the clayey substratum and this finding was used to establish two distinct management zones within the site.

Cambouris *et al.* (2007) examined whether the distinct management zones identified by Cambouris *et al.* (2006) could be used to modify nitrogen inputs and reduce variation in yield with the field. Experiments were established in the two zones in three years and 21 treatments combining differing amounts (0-240 kg/ha) and timings of nitrogen fertilisation (from planting to ridging) were used. Yields increased with increasing nitrogen at both sites and applying all nitrogen at planting or all at ridging decreased yields slightly. There were no consistent differences in the response to nitrogen between the sites and the authors concluded that there would be no benefit to the grower of applying different N rates in each of the zones. The average number of tubers was higher in the zone with higher EC in every year, although from the data reported it is not possible to establish whether these differences were significant. Nonetheless, this trend is the opposite of what would be expected from the findings of Firman & Daniels (2011) where the number of tubers was higher in sandy soils (with a low EC) than in clayey soils (with a high EC). As a consequence of the lower number

of tubers, in one year Cambouris *et al.* (2007) found that the proportion of yield as large tubers increased more rapidly as the nitrogen rate increased in the low EC zone than in the high EC zone even though the total yield was lower. However, the proportion of yield as medium sized tubers did not differ between the zones in any year. The differences in the number of tubers and yield reported are of interest however as they demonstrate that areas of a crop with lower yields do not necessarily produce smaller tubers as the number of tubers can also decrease and compensate so that the mean tuber size is less affected.

Allaire *et al.* (2014) measured soil properties, nitrogen uptake and yield at 108 locations within two different sites and performed correlation analysis to establish which variables were related to each other. Variation in yield was similar to that reported by Cambouris *et al.* (2006) although in this study, the samples were dug by hand and were relatively small (1.5 m of row). The only consistent, significant correlation with yield found at both sites, was the soil temperature at 15 cm, measured one month after planting, which accounted for 34 % of the large scale variation at one site and 57 % at the other. Temperature is known to be the major controlling influence on the growth of potato crops at the start of the growing season (Firman *et al.* 1992; Yuan & Bland 2005). Emergence and ground cover data were not reported by Allaire *et al.* (2014) and so it is not possible to establish whether the differences in yield can be explained solely by differences in emergence, or whether there was also an influence of soil type or soil temperature on the rate of ground cover expansion or canopy longevity. Firman & Daniels (2011) experimentally manipulated soil temperature in the field during tuber initiation and found that it had no effect on the number of stems, number of tubers, yield or mean tuber size in either Hermes or Estima. However, the average difference between the treatments was relatively small (2.5 °C) in comparison to those that occurred within the crops studied by Allaire *et al.* (2014) where the COV was 11 % at both sites and the range in values was as much  $\pm 5$  °C from the mean.

Stalham & Allison (2014) performed pairs of destoning depth (soil cultivation) experiments on contrasting soil types within three crops. At Hales Hospital, emergence was delayed by *c.* 1 week and the yield and number of tubers reduced on the heavier soil compared to the lighter soil. Across the sites, yield and the number of tubers tended to be lower on the heavier soils and the maximum extent of the differences between the soil types was *c.* 15 %. In another similar experiment, Stalham (2015) found that the yield did not vary between soil types, but the number of tubers was *c.* 10 % lower on the heavier soil type.

## 2.6. Plant-to-plant variation

The potato crop is heterogeneous with the yield, number of stems and number of tubers per plant varying widely (Svensson 1966). Relatively little attention has been paid to quantifying this variation and determining the factors that affect it. Stewart (1921) was one of the first authors to note these variations, commenting: “Whatever the cause, the failure to secure more nearly equal yields from plants under supposedly parallel conditions is noteworthy. It shows that there are factors having a very important bearing on the yield of potatoes which are either unknown or not estimated at their proper value.” Although our knowledge of the growth of potato crops has advanced greatly since the time of Stewart (1921), the causes of this variation remain relatively unexplored. The work of Svensson (1966) was a notable exception as many different variables of individual plants were measured for several varieties at three planting densities. The variables measured were seed tuber weight, number of eyes per tuber, number of stems per plant, weight of seed tuber per stem, interval from planting to emergence, yield, number of tubers per plant and average tuber weight. The mean, standard deviation and COV were reported for each, and relationships between some of the variables were examined using linear regression. The mean COV values, the range of COVs and the COV of the COVs for each of these variables are listed in Table 1.



**Table 1. Summary of the results from Svensson (1966) listing the mean COV, the COV of COVs and the range of COVs reported for the variables measured.**

| Variable                        | Mean COV (%)               | COV of COV (%) | Range in COV (%) |       |
|---------------------------------|----------------------------|----------------|------------------|-------|
| Seed tuber weight               | 24                         | 10             | 20-30            |       |
| Eyes per tuber                  | 19                         | 12             | 16-24            |       |
| Days to emergence               | 10                         | 43             | 6-21             |       |
| Number of main stems per plant  | 34                         | 12             | 28-42            |       |
| Seed tuber weight per main stem | 42                         | 15             | 32-52            |       |
| 15 cm spacing                   | Yield                      | 39             | 12               | 33-52 |
|                                 | Number of tubers per plant | 34             | 10               | 29-41 |
|                                 | Mean tuber weight          | 35             | 11               | 29-41 |
| 30 cm spacing                   | Yield                      | 30             | 16               | 22-41 |
|                                 | Number of tubers per plant | 31             | 16               | 22-41 |
|                                 | Mean tuber weight          | 31             | 13               | 26-39 |
| 45 cm spacing                   | Yield                      | 31             | 13               | 19-34 |
|                                 | Number of tubers per plant | 25             | 18               | 23-42 |
|                                 | Mean tuber weight          | 30             | 15               | 23-40 |

Significant relationships were often found between the variables over multiple years, but with the exception of relationships between the number of stems and the number of tubers, typically the models explained little of the observed plant-to-plant variation and the amount of variation that could be explained varied greatly between experiments. The correlation coefficients reported by Svensson (1966) are summarised in Table 2.

**Table 2. Summary of the correlation coefficients between variables of individual plants within crops reported by Svensson (1966).**

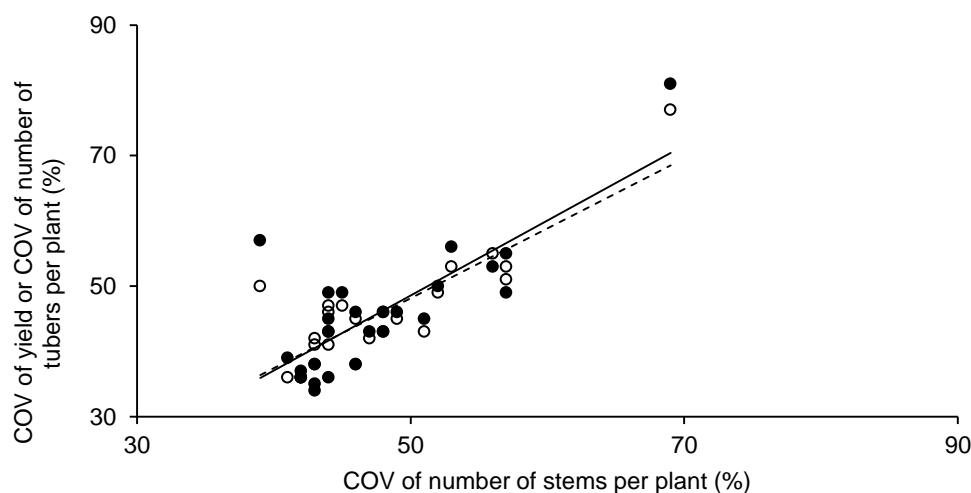
| Explanatory variable | Response variable | Mean $R^2$ value (%) | COV of $R^2$ (%) | % of regressions where $p < 0.01$ |     |
|----------------------|-------------------|----------------------|------------------|-----------------------------------|-----|
| Seed tuber weight    | Days to emergence | 1.8                  | 109              | 43                                |     |
| Seed tuber weight    | Number of stems   | 15.0                 | 48               | 100                               |     |
| 15 cm spacing        | Seed tuber weight | Yield                | 7.7              | 73                                | 95  |
|                      | Seed tuber weight | Number of tubers     | 8.3              | 66                                | 100 |
|                      | Number of stems   | Yield                | 2.8              | 101                               | 55  |
|                      | Number of stems   | Number of tubers     | 12.4             | 53                                | 100 |
| 30 cm spacing        | Seed tuber weight | Yield                | 10.6             | 70                                | 85  |
|                      | Seed tuber weight | Number of tubers     | 12.6             | 80                                | 90  |
|                      | Number of stems   | Yield                | 10.3             | 86                                | 75  |
|                      | Number of stems   | Number of tubers     | 26.4             | 32                                | 100 |
| 45 cm spacing        | Seed tuber weight | Yield                | 14.6             | 46                                | 95  |
|                      | Seed tuber weight | Number of tubers     | 14.3             | 61                                | 90  |
|                      | Number of stems   | Yield                | 11.0             | 73                                | 65  |
|                      | Number of stems   | Number of tubers     | 28.7             | 45                                | 100 |

No attempt was made to explain the variation in mean tuber weight from the other variables and neither did Svensson (1966) establish whether the variation in one variable affected the variation of others. Only individual plants were sampled rather than individual stems, and in most experiments only one sample was taken per year so it was not possible to determine

whether the variability changed over time. Although not noted by Svensson (1966), the weak relationships between the number of stems and yield indicate that the average yield per stem varied considerably between plants.

As well as examining plant-to-plant variation in an experimental setting, Svensson (1966) surveyed 25 commercial crops, sampling 300 plants in each and recording the number of stems, number of tubers and yield per plant. The variation was typically higher in the commercial crops than in the experiments. Significant relationships were found in all the crops between the number of stems and the number of tubers and also between the number of stems and yield. A reanalysis of the data reported found that there were strong and significant relationships between the variation in the number of stems per plant and the variation in the number of tubers and yield per plant (Figure 13).

**Figure 13. Relationships between the COV of number of stems per plant (SNCOV) and the COV of yield per plant (YDCOV) and COV of number of tubers per plant (TNCOV) for 25 crops. Data from Table 48 of Svensson (1966). COV of yield, ●; COV of number of tubers, ○. Fitted lines: YDCOV (—) =  $1.15 (\pm 0.196) \times \text{SNCOV} - 8.9 (\pm 9.46)$ ,  $R^2 = 0.58$ . TNCOV (- - -) =  $1.07 (\pm 0.141) \times \text{SNCOV} + 5.4 (\pm 6.81)$ ,  $R^2 = 0.70$ .**



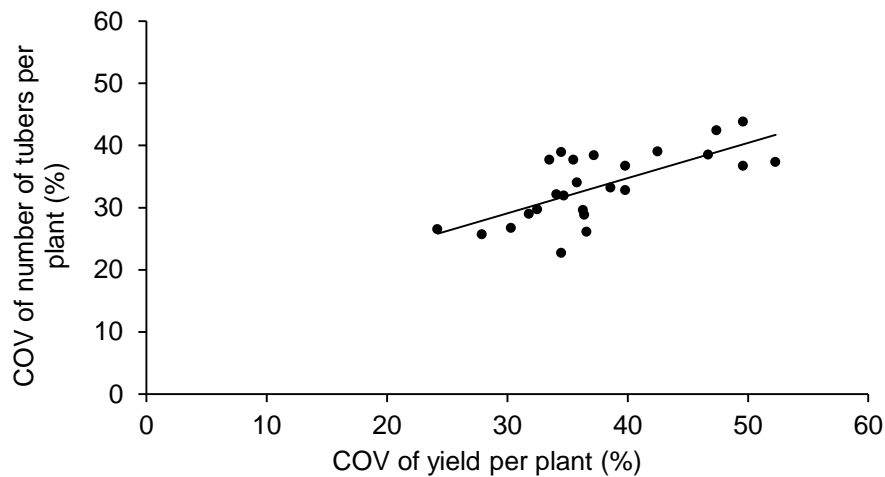
Silva & Andrew (1985) surveyed 29 fields in Alberta, Canada containing different varieties over 4 years. They examined variations in the number of stems, number of tubers and yield between plants. The extent of variation was similar to that reported by Svensson (1966) at the same spacing (30 cm) despite the varieties differing and the plants being propagated from cut as opposed to whole seed tubers (Table 3). Most of the variation occurred within, rather than

between rows, suggesting that local variations in soil conditions were not a substantial cause of the differences observed. Unlike the survey conducted by Svensson (1966) the COV of the number of stems per plant did not correlate strongly ( $R^2 < 0.10$ ) with either the COV of yield per plant or the number of tubers per plant, but as the COV of yield per plant increased, the COV of the number of tubers per plant also increased (Figure 14).

**Table 3. Mean COV, COV of COVs and the range of COVs for 29 crops as reported by Silva and Andrew (1985).**

| Variable                   | Mean COV (%) | COV of COVs (%) | Range of COVs (%) |
|----------------------------|--------------|-----------------|-------------------|
| Number of stems per plant  | 42           | 14              | 30-55             |
| Number of tubers per plant | 33           | 17              | 23-44             |
| Yield per plant            | 39           | 19              | 24-52             |

**Figure 14. Relationships between the COV of yield per plant (YDCOV) and COV of number of tubers per plant (TNCOV) for 25 crops. Data from Tables 1-3 of Silva & Andrew (1985). Fitted lines:  $TNCOV = 0.57 (\pm 0.121) \times YDCOV + 12.1 (\pm 4.63)$ ,  $R^2 = 0.47$ .**



The reasons for the variation in yield per plant, number of tubers per plant and mean tuber weight per plant that Svensson (1966) observed are still unclear. Benjamin & Hardwick (1986) reviewed the causes of variation in yield per plant in even-aged stands of plants, with a particular focus on field vegetables (carrots, onions, beets and lettuce), providing a framework which can be used to form hypotheses as to the causes of variation in the yield per plant in potato crops. Sources of variation were split into those that occurred pre- and post-emergence. Pre-emergence factors included, seed size, seed dormancy, planting depth and soil moisture content. Post emergence factors included the weight of the plant at the start

of photosynthetic growth, the duration of growth, differences in the relative growth rate and the space per plant. They excluded variation caused by pathogens, which may affect plant-to-plant variation in potato crops.

Considering the sources of variation noted by Benjamin & Hardwick (1986), potential influences on plant-to-plant variation in potato crops include seed tuber weight (independently, the fresh weight, dry weight and the percentage dry matter), the date of emergence, the number of stems per plant, the space per plant, neighbouring plants and disease. Since the crop is composed of individual plants and stems, it is anticipated that if the factors that affect the variation between individual plants can be elucidated, then these can be managed to reduce variation and improve the uniformity of the crop as a whole.

#### 2.6.1. Seed tuber weight

The implications of seed tuber weights varying between plants are currently unclear. Numerous experiments have shown that above *c.* 10 g, the mean weight of seed tubers has little effect on the final yield of the crop (Allen *et al.* 1991). Small seed tubers have advantages over large seed tubers as they produce more stems per unit weight and thus the transport and storage costs are lower for establishing crops from small seed tubers in comparison to large seed tubers (Allen *et al.* 1991). Despite the economic advantages of using small seed tubers, some growers continue to plant large seed tubers due to perceived differences in ‘seed vigour’. The seed tuber contains reserves of carbohydrates and mineral nutrients that are mobilised during the initial phases of growth (Pursglove & Sanders 1981; Ross & Davies 1985; Knowles 1987) and it could be expected that plants growing from larger seed tubers would initially grow faster than plants growing from smaller seed tubers. Assuming all other variables (e.g. emergence and the percentage dry matter of the seed tuber) were equal, plants growing from larger seed tubers would have a larger leaf area, higher net photosynthesis and a higher absolute growth rate, allowing them to out-compete neighbouring

plants growing from smaller seed tubers. Since the growth of the canopy is exponential, larger seed tubers would be expected to maintain their competitive advantage until canopy closure and consequently, produce a higher yield than those plants growing from smaller seed tubers.

Variation in seed weight has been studied in other crops and has generally been found to have only a weak influence on variation in yield per plant by the time of harvest (Benjamin & Hardwick 1986). The relevance of studies conducted with true seeds to the growth of potato is uncertain since the growth habit of a potato sprout is substantially different to that of a seedling and the average seed weight can be orders of magnitude greater in potato (for example, the carrot seeds examined by Benjamin (1982) were *c.* 1 mm in diameter equating to *c.* 10 mg whereas 55 mm seed tubers can exceed 150 g, equivalent to 30-38 g DW (MacKerron *et al.* 1988)).

Planting greater quantities of seed tubers per hectare can produce higher yields, but this is attributed to be a result of higher stem populations (Sharpe & Dent 1968; Allen & Wurr 1992). The relationship between stem population and yield is asymptotic and generally above *c.* 100,000 stems/ha there is little increase in total yield (Firman & Daniels 2011).

Distinguishing between the effects of different seed rates and different stem populations is difficult and few experiments have compared the effect of large differences in seed rate while controlling for stem density. Allen & Scott (1980) noted that the mean seed tuber substrate per stem varied relatively little between different seed tuber sizes of the same variety and discounted it as a factor affecting yield as the differences were equivalent to only 2-3 days net photosynthesis. However, this is distinct from the seed tuber substrate having no influence on the growth of the crop and there are several lines of evidence that indicate that it does indeed have some effect.

Denny (1929) examined the role of the mother tuber in the growth of crops by amputating seed tubers from plants at various stages of the crop's growth. Removing the seed tubers at emergence or when the plants were 5 cm tall significantly reduced yield, but no attempt was made to distinguish between the effect of removing the seed tuber and damage to the root system caused by removing the seed tuber. Bohl *et al.* (2001) amputated seed tubers at different dates after emergence and examined the effect on yield. To eliminate the confounding factor of damaging the root system, a positive control was used where the ridge was excavated until the seed tuber was visible but then the soil was replaced. Removing seed tubers when 90 % of plants had emerged substantially reduced the final yield to 22 t/ha compared to 43 t/ha in the control. The positive control also decreased yield to 38 t/ha, indicating that damage to the root system accounted for some of the decrease in yield observed. Removing the seed tuber when the plants were either 20 cm tall or when they began to flower also decreased yield compared to the control, but the differences were not significantly different to the positive control.

Headford (1962) measured the growth of sprouts that developed from seed tuber pieces of varying fresh weights (1, 4, 16 and 64 g) and found that their dry weight was directly proportional to the seed tuber weight. When King Edward was grown for 20 days in a nutrient solution it was found that 33 % of the dry weight was lost from the seed tuber, and 90 % of the weight lost had been translocated to the stem. 93 % of the total weight of the stem was derived from the seed tuber, with photosynthesis only accounting for the remaining 7 %.

Svensson (1977) measured the dry weight of seed tubers six dates at intervals of 8-10 days from planting. The date of emergence was not reported which makes it difficult to interpret what role the seed tuber substrate played in the growth of the crop, but the dry weight of the seed tubers decreased rapidly between the first and third sampling dates in each year and by the final harvest, the seed tubers were only 3-4 % dry matter. Moorby (1978) stated that

stems continue to be supplied with substrate from the seed tuber until 200-400 cm<sup>2</sup> of leaves have grown, but did not explain how this value was established. Moorby (1968) found <sup>14</sup>C supplied as <sup>14</sup>CO<sub>2</sub> was transported from the leaves into the seed tuber even after its dry weight had decreased to the point where it remained constant. Oparka & Davies (1985) showed that <sup>14</sup>C supplied as <sup>14</sup>CO<sub>2</sub> was transferred between stems via the seed tuber, but under normal conditions the movement was minimal and only substantial if an above-ground stem was removed, while others remained intact.

Haverkort *et al.* (1991) compared the performance of seed crops grown from microtubers (< 0.5 g) and conventional sized seed tubers (28-35 or 35-45 mm). Crops grown from microtubers developed ground-cover considerably more slowly than those grown from conventional tubers and consequently produced yields only *c.* 30-50 % of those grown from conventional seed tubers.

Hide *et al.* (1997) planted mixtures of small, medium and large seed tubers (mean weights 50, 104 and 153 g in 1989, and 41, 80 and 124 g in 1990) of Desiree and examined the effects on the number of stems per plant, number of tubers per plant, yield per plant and tuber size. Small seed tubers produced lower yields in both years, with larger seed tubers having yields on average *c.* 50 % higher than small seed tubers. Overall, variation in seed tuber weight accounted for 41 % of the variation in yield per plant in 1989 and 22 % in 1990. Competitive effects between plants were observed, with the highest yielding plants being those grown from large seed tubers with two small seed tubers as neighbours, but there were no effects of neighbouring plants on the number of tubers. It was suggested that similarly sized seed tubers would produce higher yields than mixtures although they did not explain the mechanism by which this could occur. Silva & Andrew (1985) weighed seed pieces and whole seed tubers of Russet Burbank and Norland with ranges of *c.* 30-100 g and found that only *c.* 10 % of the variation in yield per plant could be explained by variation in seed tuber weight.

Few experiments have investigated how variation in seed tuber weight affects variation in tuber size. Svensson (1966) compared seed tuber stocks with COVs of weight of 4 % and 24 % in 1964 and of 7 % and 21 % in 1965. In both experiments reducing variation in seed tuber weight reduced the variation in the yield per plant, number of stems per plant, number of tubers per plant and mean tuber weight per plant. However, the crops were not graded by size and no comparative statistics were reported so it is unclear whether the differences had any effects on variation in tuber size. Palmer (1976) grew Majestic and King Edward seed tubers of different size ranges (but equal mean weights) at various densities. The results are difficult to interpret as the analytical techniques developed by Travis (1987) were not used. In one year it was found that Majestic seed tubers graded 41-48 mm had a 4 % higher marketable yield (44-82 mm) than seed tubers graded 35-54 mm. In other years however there were no differences between treatments.

#### 2.6.2. Dry matter content of the seed tuber

As well as the fresh weight of seed tubers varying, the percentage dry matter of seed tubers varies (Svensson 1966; Wurr 1980). This could affect the growth of the plant directly due to the remobilisation of dry matter from the seed tuber during the early phases of growth and indirectly if the physiology of tubers differs according to their percentage dry matter and this were to affect either the number of stems produced or the growth rate of sprouts or stems.

Silva & Andrew (1983) measured the growth of sprouts on seed tubers of Russet Burbank with different specific gravities (which corresponds to different percentage dry matter contents (Schippers 1976)). They found a negative correlation between the specific gravity of a seed tuber and the weight of the sprouts growing from it after a period of storage. This was in agreement with the findings of an earlier study by Brown & Smith (1968). Wurr (1980) measured the total length and number of sprouts growing from tubers of different specific gravities in several varieties. The results were inconsistent as for large seed tubers



(> 50 mm), sprout length increased with increasing specific gravity in Desiree and Pentland Crown, but decreased slightly in Maris Piper, and had no effect in other varieties. In Desiree and Pentland Crown, the number of sprouts also increased with specific gravity, but no differences were found in other varieties. In a further experiment with Desiree using small seed tubers (20-29 g) that grew from different nodes of the mother plants, Wurr (1980) found specific gravity to be significantly lower as the distance from the mother tuber increased. When left to sprout, tubers from higher nodes had significantly longer total sprout lengths and more sprouts in January, but this effect diminished by April.

The findings that tubers with lower specific gravity can have larger sprouts are unexpected, given the evidence that seed tuber reserves limit sprout growth and thus it would be expected that tubers with a higher specific gravity would have produced heavier sprouts. A possible explanation for this is that the tubers of a lower specific gravity were physiologically older than those with a higher specific gravity due to them having respired a greater proportion of their dry weight during storage. Those with lower specific gravities would thus be expected to break dormancy and sprout earlier and this could explain the reported correlation. Blauer *et al.* (2013a) found that the rate of respiration of seed tubers during storage at 4 °C increased if the seed tubers were exposed to higher temperatures before being placed in storage. They suggested that tuber respiration acted as a marker of the physiological age of the seed tuber because those stored at the same temperature but, in a lower oxygen atmosphere, respired more slowly and produced fewer stems and tubers. There are apparently no reported studies of the effect of specific gravity of seed tubers on the growth of the crop or individual plants in the field or how the specific gravity of individual tubers changes during storage.

### 2.6.3. Number of stems per plant

The number of stems that each seed tuber produces can vary considerably within a stock (Svensson 1966; Firman & Shearman 2007). The mean number of stems per seed tuber is mainly determined by seed tuber weight (as discussed in Section 2.3.1), but the mechanisms determining the exact number of stems that an individual seed tuber produces remain to be determined. Growers in the UK typically plant a stock of seed tubers that has been graded into size classes at 10 mm intervals (e.g. 30 to 40 mm) although some plant 5 mm classes or ungraded seed tubers. Within each stock there is variation in the weight of the seed tubers and the number of stems that each seed tuber produces (Svensson 1966). Svensson (1966) measured the weight of tubers within 22 graded seed tuber stocks and found that the COV of seed tuber weight ranged from 20-30 %. The variation in the number of stems per plant was also measured, with the COV ranging from 27-42 %, equating to a range of between 1 and 7 stems for a stock producing an average of three stems per seed tuber. Firman & Shearman (2007) found similar variation within a stock of Maris Piper although the COV was not calculated.

The variation in seed tuber weight within a graded seed tuber stock and the number of stems per plant have rarely been reported in the literature. As a result it is unclear how much variation occurs within and between stocks and whether this has any influence on the uniformity of the crop. Tuber shape may influence the variation encountered as longer tubers of a given diameter will have more variable weights than round tubers of the same diameter.

Wurr *et al.* (1992b) graded 17 stocks of Record seed tubers into 10 g divisions and subsequently sprouted them in the greenhouse, or planted them in the field. The length, breadth, width and volume of the seed tubers were also recorded. The number of above-ground stems was found to be predicted most accurately from the seed tuber weight.

Firman (1997c) graded seed tubers into 5 g classes ranging from 15-20 g to 110-115 g and recorded the number of stems per plant. As the seed tuber weight increased the number of stems increased but the relationship differed between years and depending on the physiological age of the seed tubers. At the lower end of the 30-40 mm grade, a 20 g seed tuber produced an average of 2.5 stems whereas at the upper end, a 60 g seed tuber produced an average of 3.2 stems. The effect of seed tuber size on the variation in the number of stems per plant and on tuber size and variation were not reported.

While the relationship between mean seed tuber weight and the number of stems per plant is linear, the number of stems does not increase proportionally to the seed tuber weight (Allen *et al.* 1992a). For example, Firman & Daniels (2011) reported that for King Edward in 2010, seed tubers with an average weight of 40 g produced two stems and seed tubers with an average weight of 120 g produced four stems. Thus the lighter seed tubers produced one stem per 20 g of seed tuber, whereas the heavier seed tubers produced one stem per 30 g. This pattern of larger seed tubers producing fewer stems for a given weight was found across different varieties, different seed tuber stocks and in different years suggesting that it occurs consistently, but the precise relationships varied substantially. For example, there was considerable variation between years in late-produced (i.e. chronologically young, but not necessarily of the same chronological age) Pentland Dell. To produce an average of two stems per plant in 2008, a mean seed tuber weight of 30 g was required; in 2009 25 g was sufficient and in 2010 only 15 g was required.

Moorby (1967) planted single or multiple seed tubers in the same position and reported that the total weight of the above-ground stems at each position was only slightly higher when more stems grew, indicating that the average stem weight was decreased. Cother & Cullis (1985) surveyed individual plants from commercial crops and found that the total above-ground stem weight increased as the number of stems per plant increased, but the

average weight per stem decreased as the number of stems increased so that the average weight of stems from four-stemmed plants was approximately half that of single-stemmed plants.

Gill *et al.* (1989) attempted to artificially manipulate the number of stems per plant by removing sprouts from tubers of Maris Piper prior to planting by coring single eyes from seed tubers and planting several cores in the same location. Tubers with four eyes at planting, produced 6.6 stems, those with only one eye produced 4.3 stems. Four 10 g cores produced 5.0 stems and four 20 g cores produced 6.0 stems. Thus, even in an experimental setting it was not possible to produce uniform stem populations and the use of seed tuber cores introduced other variables, for example by advancing emergence due to wounding.

Firman & Shearman (2007) harvested individual Maris Piper plants from two stocks and plotted various relationships for all the plants with one, two, three or four stems. The one-stemmed plants produced the fewest tubers (equivalent to *c.* 200,000/ha) but as the number of stems increased, the number of tubers per stem decreased so that four-stemmed plants produced the equivalent of *c.* 500,000/ha. For the early produced seed tuber stock, as the number of stems per plant decreased, the mean tuber size increased, from 54 mm for four-stemmed plants to 63 mm for single-stemmed plants. A similar pattern was found for the late produced stock. As a result, if the variation in stems per plant could be reduced, then the variation in mean tuber size per plant would also decrease, resulting in a lower COV of tuber size. There were no consistent patterns found for either  $\sigma$  or COV for plants with different numbers of stems.

Firman (1997a) physically damaged Estima seed tubers that had been sprouted for different lengths of time and investigated what effect this had on the number of stems per plant. For unsprouted seed tubers, damage had little effect on the distribution of stems, but for seed tubers stored at 15 °C for 14 days the mean number of stems increased and this was even

more pronounced for seed tubers stored to accumulate 300 degree days  $> 4\text{ }^{\circ}\text{C}$ . For undamaged seed tubers, storage at  $15\text{ }^{\circ}\text{C}$  for 14 days increased the variation in stems per seed tuber and the mean was slightly increased. The undamaged seed stored to accumulate 300 degree days  $> 4\text{ }^{\circ}\text{C}$  also produced more variable numbers of stems per plant and the mean decreased slightly. The sprouting treatments had no effect on total yield, but planting damaged seed tubers reduced yield by 10 %. The mean tuber size was reduced when seed tubers were damaged, but the COV of tuber size was not affected.

#### 2.6.4. Yield per stem

There are apparently no descriptions of variation in the yield of individual stems previously published within typical crops. Svensson (1972) examined the growth of individual stems within hills formed from different numbers of single-shoot seed tubers. In one experiment the tubers were planted at the same density but either as individual seed tubers or groups of three or five seed tubers and in a second experiment were planted at the same plant density and thus different stem densities. Comparisons were made between the growth of the central stems in each plant and those surrounding them. When planted at the same density, the mean yield of the central stems was consistently lower than that of the surrounding stems, but the difference was relatively small and the variation between stems in the same position was extremely high with COVs ranging from 55-116 %, with no discernible trend between treatments. The size and number of tubers on the individual stems was not reported.

Considering that the seed tuber substrate is mobilised from the seed tuber and can affect the growth of the crop, it is possible that variations in the amount of substrate that individual stems receive from the seed tuber may explain some of the variation in stem yields encountered within crops. Since seed tuber weight and the number of stems per seed tuber can vary considerably, individual stems will receive varying amounts of nutrition from the

mother tuber. If a relatively small seed tuber produces a relatively high number of stems, it would be expected that initially they will grow at a slower rate compared to those that grow from a relatively large seed tuber that produces a relatively low number of stems. For example, if a 20 g seed tuber produced 3 stems and a 40 g seed tuber produced 2 stems, the stems from a 40 g seed tuber would have three times as much seed tuber substrate than those growing from a 20 g seed tuber. Morris (1966) measured the growth of sprouts on seed tubers of various weights (200 g, 100 g and 50 g) and with various numbers of shoots (1, 2 or 4) stored at 15 °C for 10 weeks. The sprouts on lighter seed tubers grew more slowly than those on heavier seed tubers, and as the number of sprouts per seed tuber increased, the growth of each stem decreased. Further work with pot-grown plants found that the average dry weight of sprouts at emergence decreased as the number of sprouts increased (Morris 1967).

Whether seed tuber weight and the number of stems have an effect on the growth of the stems in the field is unclear.

Svensson (1966) calculated the variation in seed tuber substrate per stem within crops, but assumed that stems growing from the same seed tuber shared the seed tuber substrate equally, which may not be the case. In a review of the causes of variation in size between plants in monocultures, Benjamin & Hardwick (1986) discussed the importance of the weight of plants at the start of growth for establishing hierarchies in size between individuals and understanding how and why this varies in potato crops may provide opportunities to increase uniformity.

#### 2.6.5. Emergence

Emergence, the point in time at which the tip of a growing shoot reaches the soil surface is “the culmination of a large number of preceding events” (Benjamin 1990). The interval from planting to 50 % emergence has frequently been reported in the literature, based on consecutive counts of the number of plants that have emerged every 2-4 days (e.g. Allen *et al.*

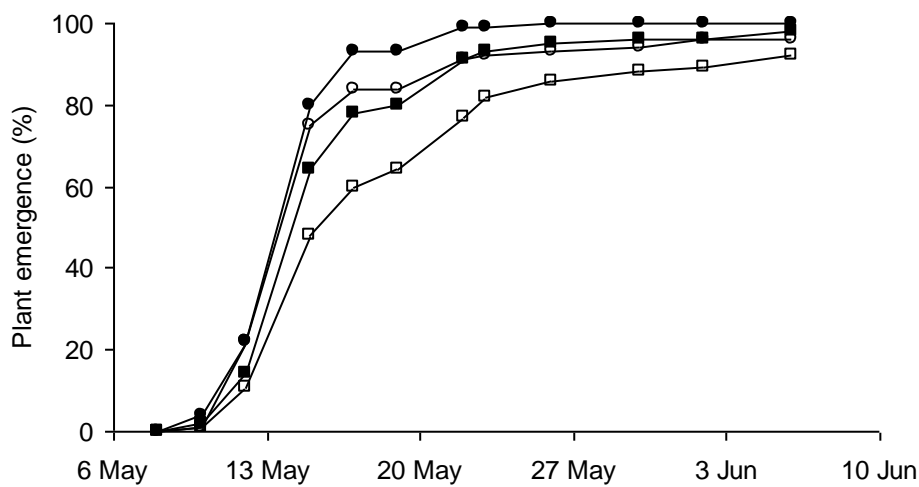
1992a; Firman & Daniels 2011). The interval from planting to emergence is largely determined by the soil temperature, since the growth of shoots is stimulated as temperatures increase up to 20-25 °C (Sands 1989; Firman *et al.* 1992). After planting, the growth rate of sprouts is initially slow but increases as the length of the sprout increases and they subsequently grow at a rate of *c.* 10-15 mm/day provided that soil temperature and moisture are adequate (Firman *et al.* 1992). Physiologically older seed emerges earlier (O'Brien *et al.* 1983; Allen & O'Brien 1986), because the sprouts are more developed at planting.

Variation in emergence has rarely been reported in the literature and no studies have specifically investigated factors that affect variation in emergence, nor whether the variation has any consequences for variation in tuber size. This discussion will therefore be limited to discussing factors which affect the time to 50 % emergence which could potentially also affect variation in the dates of emergence for individual plants and stems. It will be complemented by the findings of research in other crops, particularly root vegetables, in which variation in emergence and its effect on variation in plant size has been studied.

Potato plants emerge from the soil asynchronously over a period of between 5 and 30 days (Svensson 1966; Firman & Shearman 2007; Figure 15) but it is uncertain whether stems emerge at a similar rate to plants. As listed in Table 1, Svensson (1966) reported variation in emergence as the COV of the interval from planting to emergence for individual plants. The standard deviation is likely to provide a better description of the variation in emergence however, since if the rate is the same, but the time to 50 % emergence increases, the COV will decrease. Emergence in other crops has been described by fitting a Gompertz function to the cumulative number of plants that have emerged on different dates (Forcella *et al.* 2000). The date of 50 % emergence marks the start of the growth of the crop and considerable effort has been made to understand factors which affect the interval from planting to 50 % emergence since crops that emerge earlier have a greater opportunity to intercept solar radiation and

produce a higher yield (Allen *et al.* 2001). The same principle is expected to apply to individual plants and stems within the crop, since earlier emerging plants will produce a canopy sooner than those that emerge later. Differences in leaf area soon after emergence would be expected to persist and lead to differences in yield since radiation interception (and therefore absolute growth) is proportional to ground cover (as discussed in Section 2.2.2.).

**Figure 15.** The effect of seed tuber stock and rate of nitrogen on plant emergence in Maris Piper. Early-produced seed (chronologically old), normal N (200 kg/ha), ●; early-produced seed, high N (365 kg/ha), ■; late-produced seed (chronologically young), normal N, ○; late-produced seed, high N, □. Reproduced with permission from Firman & Shearman (2007).



Moorby (1967) reported that larger seed tubers emerged earlier, but Allen *et al.* (1992a) noted that this may be due to the effective planting depth differing if different sized tubers are planted at the same depth. The findings of Firman & Daniels (2011) showed that this effect is variable. For some varieties, seed tuber size had no effect on the interval from planting to 50 % emergence and some seed tuber stocks did not show this response either (Firman & Daniels 2011).

#### 2.6.5.1. Planting depth

Planting depth can affect the interval from planting to emergence, with deeper planted seed tubers taking longer to emerge (Svensson 1966). This could be caused by the effects of



temperature varying at different depths (Orchard & Wurr 1977), by the sprouts taking longer to reach the surface since they have further to grow, or a combination of the two. Booth & Allen (1990) surveyed three commercial crops where different seed sizes had been planted and measured the depth of planting, defined as the length of non-pigmented stem. The maximum planting depth was approximately twice that of the minimum planting depth at two sites, but at one the minimum planting depths were 3 and 6 cm. The average COV of planting depth was 15.9 % and was not consistently related to the variation in seed tuber size. Hogge (1991) also surveyed planting depth in commercial crops and the average COV of planting depth was 17.5 %.

Stalham *et al.* (2002) and Stalham (2003) planted FL 1953 in two years and Estima in one year at depths of 10, 15 or 20 cm and found that crops took *c.* 2.5 days longer to reach 50 % emergence at 20 cm than at 10 cm. If the increased distance was the only determinant, a 10 cm difference would be expected to result in a larger difference of *c.* 6.5 days (Firman *et al.* 1992). Pavek & Thornton (2009) planted Russet Burbank and Umatilla Russet at depths of 10 or 20 cm in two years and additionally at 15 and 25 cm in one year. The temperature at each depth and the interval from planting to 95 % emergence were recorded. Daily minimum and maximum soil temperatures were less variable at 25 cm than at 10 cm and the average temperature at 10 cm was 1.0 °C higher than at 25 cm. Sixty days after planting the number of growing degree days > 4 °C was *c.* 10 % lower at 25 cm than at 10 cm. The interval from planting to emergence was typically increased by planting at 20 cm compared to 10 cm but the difference varied between years and between varieties. The differences were more variable in Russet Burbank, ranging from there being no effect, to the interval being 9 days longer whilst the differences in Umatilla Russet ranged from 3-7 days. The number of growing degree days > 4 °C from planting to 95 % emergence varied between planting depths with shallower planting depths requiring fewer than deeper planting depths. Again, the

varieties differed in their response to the difference in the number growing degree days  $> 4^{\circ}\text{C}$  required to reach 95 % emergence between planting depths with Umatilla Russet requiring a relatively similar number at different depths and the deeper planted Russet Burbank requiring relatively more than the shallower planted.

#### 2.6.5.2. Dormancy

Within a seed tuber stock there can be considerable variation in the duration of dormancy, defined as the time from harvesting until a tuber produces a sprout when exposed to favourable environmental conditions (van Ittersum 1992). Considering the effect of the time from tuber initiation to re-planting on the number of stems per seed tuber, the biological validity of the harvest date is uncertain. In most crop species, seed dormancy has been selected against (Benjamin 1990), but dormancy is an essential trait of potato tubers, since it allows the tubers to be stored. Tuber size can affect the duration of dormancy, with larger tubers breaking dormancy before smaller ones, but the effect diminishes with increasing tuber weight and is variety specific (van Ittersum 1992; Firman 1997d; Firman 2002). The causes of variation in dormancy within seed tuber stocks are poorly understood and nor is it known whether variation in dormancy is related to variation in emergence. Potential causes of variation could be related to the date of tuber initiation, the position of seed tuber on the mother plant (i.e. primary, lateral or branch tubers) and the position of the tuber in the ridge, since this could affect the accumulated degree days experienced prior to storage.

Blauer *et al.* (2013b) treated cut seed tubers of five varieties by immersing them in different concentrations (0.5, 1, 2 and 4 mg/L) of gibberellic acid (GA) for five minutes. They found that emergence was significantly advanced in each of the varieties, with higher concentrations of GA tending to result in more rapid emergence. Since GA is known to be stimulate subsequent starch degradation (Davies & Viola 1988) and sprout growth (Suttle 2004), the findings of Blauer *et al.* (2013b) suggest that under equal environmental conditions, some

variation in the mean date of emergence may be due to variations in dormancy.

Consequently, some of the variation in emergence within a crop may be related to the time at which the dormancy of a tuber bud is broken and elongation begins.

#### 2.6.5.3. Soil conditions

Cloddy soils with large ped sizes can delay emergence (Firman & Daniels 2011) and therefore local variations in soil conditions could potentially affect the uniformity of emergence. The reason for the differences observed by Firman & Daniels (2011) is unclear however. Possible causes are that the sprouts were slower to penetrate through the cloddy soil, or that poor contact between the seed tuber and the soil slowed water uptake. Conversely, in one year, Firman & Daniels (2011) found finely sieved clay (i.e. containing no peds) delayed emergence and this could have been associated with limited supply of oxygen to the sprouts, which has been shown to delay emergence in other crops (Benjamin 1990). Firman & Daniels (2011) also found that emergence was delayed in a clay soil relative to a sandy-clay loam regardless of ped size, but the cause of this was not ascertained.

#### 2.6.5.4. In other crops

As mentioned previously, no studies have specifically investigated the effects of different rates of emergence on the potato crop, but it has been studied in other crops propagated from true seeds (Benjamin 1990). It is unclear what if any extrapolations can be made from these studies since the factors determining pre- and post-emergence growth in potato may differ, but there are probably at least some similarities. Benjamin (1982) examined the effect of population density, uniformity of emergence and uniformity of seed size on the COV of carrot root weight. The COV of root dry weight was decreased when emergence was more synchronous at both high and low densities, but the effect was relatively small compared to the increase that planting at higher densities caused. Similar trends were observed in leek

crops with the date of seedling emergence accounting for 25 % of the variation in mature weight, more than the position of a row within a bed and the within-row spacing (Benjamin 1984).

Gan *et al.* (1992) examined the effect the date of emergence of individual wheat plants on their yield. There was a strong linear relationship between the date of emergence of individual plants and their final yield, with plants that emerged earlier typically yielding twice that of plants that emerged 6 days later.

Adding nitrogen fertilisers to soils has been found to decrease the proportion of seeds that emerge in various crops and has been reported to be due to the osmotic effect of the fertiliser (Benjamin 1990). The uniformity of emergence was rarely examined in these experiments, except for Henriksen (1978) who found that applying nitrogen prior to emergence decreased the uniformity of emergence in onion and also decreased the percentage of seeds that emerged. Firman & Shearman (2007) reported a similar effect for two stocks of Maris Piper fertilised with 165 kg N/ha or 330 kg N/ha. Emergence began at similar dates, but was more protracted and reached a lower final percentage emergence in the treatments with higher nitrogen (Figure 15).

#### 2.6.6. Competition between plants

The effect of missing plants on the yield of potato crops was first examined by Stewart (1921) who concluded that they decreased yield, but that neighbouring plants compensated, so that the yield loss was not directly related to the number of missing plants. Hirst *et al.* (1973) removed 0-24 % of plants at random from crops either at emergence or flowering and determined the effect on yield. For every 1 % of plants removed at emergence, yield decreased linearly by 0.33 % but for every 1 % removed at flowering, yield was decreased by 0.83 %.

A series of experiments were conducted at Rothamsted during the 1980s that examined how the yield of plants was affected by neighbouring plants. Hide *et al.* (1995) examined the ability of healthy plants of Pentland Crown to compensate for plants grown from seed tubers inoculated with gangrene (*Phoma foveata*) or missing plants. The highest yielding plants were healthy plants neighboured by two missing plants, which had a yield *c.* 80 % higher than healthy plants neighboured by two other healthy plants. The lowest yielding plants were diseased plants neighboured by two healthy plants, which had a yield *c.* 50 % lower than healthy plants with equivalent neighbours. Competition mainly occurred within rows, with the yield of healthy plants only increasing *c.* 13 % when there were gaps in both adjacent rows. Interactions between plants that were not immediate neighbours also occurred, with the yield of healthy plants increasing by *c.* 25 % when plants next to their immediate neighbours were missing (76 cm away) compared to when those plants were healthy. The number of stems was not affected by neighbouring plants or by inoculation with gangrene and although the number of tubers did differ slightly between planting positions, the changes were relatively small in comparison to the differences in yield. Consequently, the differences in ware yield (defined as tubers > 150 g) between treatments were greater than the differences in total yield. There were also differences in the tuber size distribution, but these were not described quantitatively.

Hide *et al.* (1996) inoculated Pentland Squire with *Erwinia carotovora* subsp. *atroseptica* and Desiree with *R. solani* so as to induce blackleg and stem canker respectively. As Hide *et al.* (1995) found, the highest yielding plants were those with two missing plants as neighbours, and the lowest yielding were diseased plants with two healthy neighbours. Blackleg infected plants had a yield *c.* 50 % lower than healthy plants when both had healthy neighbours, similar to the effect of gangrene found by Hide *et al.* (1995). For equivalently positioned plants, stem canker had a smaller effect on yield, only decreasing it by *c.* 25 %. Stem canker

decreased the number of stems per plant by *c.* 10 % and had a similar effect on the number of tubers. However, infected plants had a similar percentage yield of ware sized tubers as healthy plants, because they had fewer small tubers and consequently it was concluded that stem canker did not affect ware yield. Blackleg decreased the number of stems per plant by *c.* 30 % and the number of tubers per plant by *c.* 50 % which compensated for the decrease in yield on the percentage of yield as ware tubers. As found by Hide *et al.* (1995), the effect of missing plants in adjacent rows on yield was minimal (*c.* 10 % higher in Desiree and *c.* 5 % higher in Pentland Squire), indicating that competition mainly occurred within the row. In both experiments, plants with two missing neighbours had more tubers, but the magnitude of the change was lower than the increase in yield, so they had a higher proportion of yield as tubers > 150 g.

#### 2.6.7. Within-row spacing

As discussed in Section 2.3, altering the average distance between plants is one method through which the stem density of a crop can be modified and in turn affect the mean tuber size of a crop. When seed tubers of a given size and chronological age are planted at closer intervals, the stem density is increased and for an equal yield, the mean tuber size will be decreased. Within crops, the distance between neighbouring plants can vary considerably from the intended mean spacing and this could potentially increase the variation in tuber size of the crop. Mechanical planters differ in the accuracy at which they plant seed tubers and it is necessary to establish the level of inaccuracy permissible without adversely affecting total and marketable yields.

Davies (1954) examined four arrangements of irregularity in within-row spacing (ranging from uniform spacing to all doubles, with two intermediate arrangements) at different mean spacings (*c.* 15, 35, 55 and 75 cm) over three years and with several varieties. The effect of the mean spacing on yield was generally greater than that of irregular spacing and substantial

decreases in yield as a result of irregular spacing were only observed at the wide mean spacings. Grading data were not presented for each combination of treatments, but the tuber size distributions for combined mean spacings with different levels of irregularity were similar.

Jarvis *et al.* (1976) surveyed a commercial crop in the United Kingdom and observed that the spacing between plants in a row was normally distributed, therefore allowing the variation to be described by the COV. Jarvis *et al.* (1976) also conducted a series of field trials using two varieties (King Edward and Pentland Crown), three mean spacings (20, 30 and 40 cm) and four levels of variability in within-row spacing (COVs of 0, 20, 40 and 60 %). The tubers were passed over a 44 mm grid and, for another set of experiments, graded into five classes. When only passed over a 44 mm grid, a reanalysis of the reported data revealed there was no effect of increasing the COV of within-row spacing on the percentage of marketable yield.

Pascal *et al.* (1977) conducted trials examining the effect of irregular spacing on the total and marketable yield at nine sites in Scotland. At most sites, regular spacing resulted in a slightly higher yield than irregular spacing but the differences were not significant. There were some significant effects on the yield within individual grades, but they were inconsistent.

Booth & Allen (1989, 1990) performed a similar set of experiments to Jarvis *et al.* (1976). The treatments consisted of all combinations of three mean spacings (23, 27 and 35 cm in 1988 and 32, 38 and 47 cm in 1989) and COVs of within-row spacing of 0, 20, 40 and 60 %. In 1988, more regular spacing tended to increase the total yield, but the absence of statistical analysis precludes establishing whether these differences were significant. The effect of irregular spacing on the proportion of yield within 40-65 mm was inconsistent, and the proportion of yield > 40 mm was consistently between 91 and 93 % across all treatments. In 1989, irregular spacing significantly decreased total yield and this was particularly pronounced at the widest mean spacing. However irregular spacing had no effect on the

proportion of yield within 40-65 mm and at the narrowest spacing, increasing the variation in within-row spacing increased the proportion of tubers within 40-65 mm. The COV of tuber size was not reported in either year, so it is not possible to determine whether there were more subtle effects on the tuber size distribution.

Entz & LaCroix (1984) examined the effect of irregular spacing on the growth of Russet Burbank at two sites for two years. The same mean spacing was used with COVs of within-row spacing of 0, 25, 50 or 75 %. In one year, at one site, the 75 % COV treatment significantly decreased total yield but in all the other combinations, no effects were found on total yield, marketable yield or the yield of oversize tubers.

Sieczka *et al.* (1986) compared uniform, moderately non-uniform and extremely non-uniform treatments with a mean spacing of either 23 or 31 cm in Katahdin and Kennebec. For the 31 cm mean spacing, the moderately non-uniform treatment consisted of three seed tubers planted with 13 cm gaps between them, followed by three 46 cm gaps. The extremely non-uniform treatment consisted of five seed tubers planted with 8 cm gaps between them followed by two 91 cm gaps. There were significant differences in total yield between the treatments, with the moderately non-uniform having a slightly higher yield than uniform spacing and the extremely non-uniform spacing having a slightly lower yield. Mean tuber weight was unaffected by the treatments and the grading was similar between treatments, although no statistical analysis of the tuber size distribution was reported. Considering the extreme treatment was considerably less uniform than that encountered in commercial crops, the authors concluded that the lack of uniformity in spacing is a relatively unimportant factor in determining variation in tuber size.

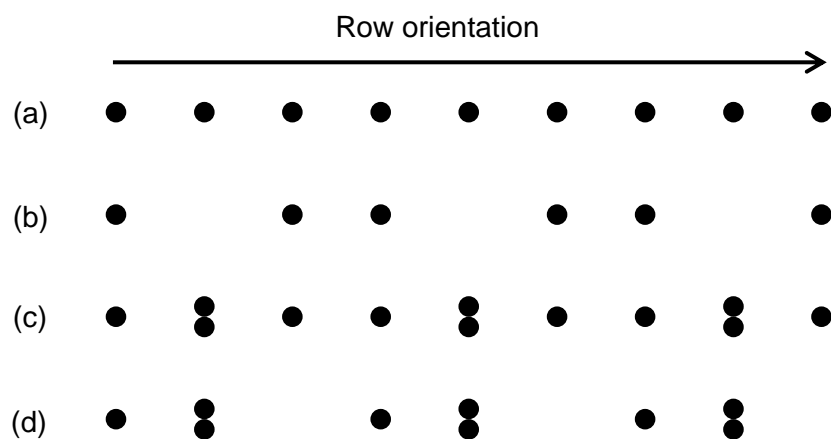
Halderson *et al.* (1992) investigated the effect of different percentages (0, 20, 40 and 60 %) of double planted seed pieces on the overall yield and marketable yield of Russet Burbank. As



the percentage of doubles increased, the yield of tubers < 113 g increased and because the total yield was unaffected, the marketable yield decreased.

Pavek & Thornton (2006) examined the effect of various planting errors on the economic return of crops. The treatments were uniform spacing, a missing plant surrounded by two neighbours, a double surrounded by two neighbours, a missing plant preceded by one plant and followed by a double and a final treatment where the effect of a missing plant in a neighbouring row was examined. These groups of plants were repeated either 8 or 10 times within each plot. Compared to the uniform treatment, the marketable yield was significantly reduced by the missing plant treatment and also reduced where the missing plant was followed by a double. This was partly due to the total yield being 10 % and 5 % lower in these treatments, but in the missing plant treatment there was also a higher yield of oversize tubers. It is not possible to establish whether or not the higher yield of oversize tubers was a result of a decrease in uniformity however, since the mean tuber size and variation in tuber size were not distinguished.

**Figure 16. The spatial arrangements of seed tuber pieces examined by Pavek & Thornton (2006). (a) uniform spacing; (b) missing plants; (c) doubles; (d) missing plants and doubles.**



#### 2.6.7.1. Surveys of commercial crops

Booth & Allen (1990) surveyed several commercial crops in the UK and recorded the distances between plants over three 30 m lengths. The mean spacing was generally different from the intended mean spacing; 6 out of 12 crops were planted wider than intended, 3 were planted closer than intended and 3 were within 1 cm of the target spacing. The COV of within-row spacing was similar in all 12 crops – between 34 and 41 %. Pavek & Thornton (2005) surveyed 70 commercial crops in Washington, USA and found that the COV of within-row spacing averaged 34 % and ranged from 18 to 69 %. They concluded that a large proportion of the variation was due to missing plants caused by planters not placing a seed piece.

#### 2.6.7.2. Belt and cup planters

The level of irregularity of spacing that can be tolerated may influence growers' decisions as to what planting machinery to purchase. Cup planters are considered to place seed tubers more accurately than belt planters, but operate more slowly (Witney & McRae 1992). Consequently, growers using cup planters may take longer to plant their crops than those using belt planters or be less able to wait for ideal soil conditions for planting, both of which may reduce yields (Jarvis 1978).

Belt planters have been suggested to place smaller seed tubers within a seed tuber stock more closely together than larger seed tubers which could increase the uniformity of the crop as the larger seed tubers may produce more stems (Witney and McRae 1992), although no experimental evidence has been published to support this. Cup planters require more tightly graded seed tubers than belt planters to ensure accurate planting. If they are not correctly calibrated, doubles and misses are more likely to occur which may have an adverse effect on uniformity (Anon 2013).

#### 2.6.8. Growth of individual tubers

The principles that govern the growth of individual tubers are relatively poorly understood, largely due to their subterranean growth habit. With the exception of studies with small sample sizes (e.g. Gray 1973; Wurr 1977; Schneiders *et al.* 1988; Struik *et al.* 1988) it has not been possible to determine the size of tubers without destructively harvesting plants. Collectively, these studies found that the growth of individual tubers on each plant was variable and that the largest at one time was not necessarily the largest at a later date.

Other studies exposed plants to  $^{14}\text{C}\text{O}_2$  and measured the radioactivity present in the tubers to quantify their growth rate. Moorby (1968) grew plants in pots, and found that the amount of  $^{14}\text{C}$  in the tubers was poorly correlated to their weight, meaning that larger tubers did not grow commensurately faster than small tubers. Consequently, the largest tuber at one time was not necessarily the largest at another. Oparka (1985) grew Maris Piper in the field and exposed plants to  $^{14}\text{C}\text{O}_2$  at six times through the growing season. Two weeks after tuber initiation, the amount of  $^{14}\text{C}$  correlated strongly ( $R^2 = 0.95$ ) with the tuber weight indicating that larger tubers were growing more rapidly than smaller tubers. At later harvests, the correlation had weakened slightly ( $R^2 = 0.80$ ) but still indicated that the largest tubers were growing most rapidly, and thus that they were also the largest earlier in the season.

X-ray computed tomography has recently been used to measure the volume of tubers developing in soil (Ferreira *et al.* 2010; Perez-Torres *et al.* 2015) but as with previous non-destructive studies, the plants were grown in pots and the tuber volumes were small ( $< 40 \text{ cm}^3$ ) in comparison to those achieved under field conditions. It is apparently not possible to use this technique in the field at present.

### 2.6.9. Monitoring individual plant growth

Studying the growth of individual plants over time requires non-destructive measurements of their size so that changes can be measured over time. The percentage of the ground covered by leaves is frequently used to characterise the development of the potato crop and to predict its yield potential (Burstall & Harris 1983; Allen *et al.* 2001). Historically, this has been measured using a quadrat containing 100 sub-divisions and counting the number of sub-divisions that contain > 50 % leaves (Burstall & Harris 1983). More recently, image analysis tools have been developed that allow growers to take digital photographs of their crop using smartphones and receive information on how their crop is developing (Allison *et al.* 2013). Bumgarner *et al.* (2012) used digital photography and image analysis to estimate the fresh shoot weight of lettuce crops and found strong correlations existed, allowing the fresh shoot weight to be predicted from photographs.

### 2.7. Hypotheses and knowledge gaps

Beyond the pathological causes of increased variation in tuber size (Section 2.4.2.2) the agronomic, physiological and genetic causes of variation in tuber size are obscure. Given the heterogeneity between plants reported to occur in the potato crop it is likely that this has some influence on uniformity, but the extent of any influence and the relative importance of different factors are undetermined. The central hypotheses explored in this work are that: mean tuber size per plant increases as yield increases and decreases as number of tubers per plant increases; decreasing the COV of mean tuber size (or weight) per plant decreases the COV of tuber size and improves uniformity.

This led to the formation of three hypotheses which were tested in Expts 1-3. Considering average seed tuber weight affects the number of stems per plant and the number of stems per plant affects mean tuber size of crops, it was hypothesised that decreasing variation in seed

tuber weight in Expt 1 would decrease variation in the number of stems per plant and in turn mean tuber weight per plant. Emergence is known to affect the performance of potato crops and variation in emergence can affect uniformity of other crops; in Expt 2 treatments were chosen that were expected to affect variation in emergence with the expectation that when it was less variable, variation in yield per plant would decrease variation in mean tuber weight per plant. While numerous experiments on the effects of variable within-row spacing on yield have been conducted, the influence on plant-to-plant variation and uniformity has not been established. It was hypothesised that some variation in within-row spacing is tolerable, particularly when the space per plant does not vary, but beyond a limit, increases in variation in within-row spacing would increase variation in yield per plant and mean tuber weight per plant. In Expt 3, seven treatments ranging from uniform to extremely variable spacing were examined with the aim of determining the threshold at which variation in within-row spacing affected plant-to-plant variation and uniformity.

Beyond these specific hypotheses, several more general areas were explored in this work relating to fundamental areas of potato crop development that are poorly understood. In particular, stem-to-stem variation has never been characterised and as the true unit of population it is probable that this has some influence on uniformity. Due to the roots and stolons of stems from each plant interlocking, the collection of data on stems is considerably slower than for plants, making replicated experiments difficult to conduct. Instead, the growth of stems were measured in detail over the course of the season in surveys to determine the extent of variation in yield, number of tubers and mean tuber weight of stems and relationships were explored to establish what factors may affect stem growth. Since there is probably a relationship between above-ground stem weight and yield per stem, where possible, above-ground stems were harvested in the experiments and weighed individually to establish whether treatments have an effect on the weight distribution.

Of particular interest is the role of the seed tuber in establishing the potato crop since the extent to which it affects growth post-emergence is unclear. While the dry weight of the seed tubers declines and nutrients are translocated to the developing leaves there are apparent contradictions with the importance of this to overall growth, since high-yielding crops can be grown from small seed tubers. No detailed descriptions of the growth of the potato crop during the first 3 weeks of development are available and considering that tubers are initiated during or shortly after this time, this represents a large gap in our understanding.

As the area of study is commercially orientated, crops were also surveyed to establish the extent of variation in less controlled conditions and where seed tuber size, emergence and within-row spacing all vary simultaneously. As noted in Section 2.5, within-field variation in potato crops is poorly characterised in relation to how it affects uniformity. An exhaustive investigation was outside the scope of this work but one crop exhibiting variable growth was surveyed and the findings placed into context with plant-to-plant and stem-to-stem variation by relating them to other work on within-field variation.

### 3. Materials and methods

#### 3.1. General methods

A summary of the experiments and surveys performed is given in Table 4 listing the variety, seed tuber size, treatments or objectives, number of replicates, planting date and harvest dates relative to the mean date of emergence of all treatments. In this section, general methods surveys are discussed, followed by specific experimental methods in Section 3.2 and specific survey methods in Section 3.3. Except where stated otherwise, the methods used were based on current practice at NIAB-CUF (e.g. Firman & Daniels 2011).

**Table 4. Summary of the experiments and surveys including variety, seed tuber size, treatments or objectives, replicates, planting and harvest dates (days after 50 % emergence.)**

| Name      | Variety   | Seed tuber size                     | Treatments or objectives  | Replicates | Planting date | Harvest dates (DAE)                 |
|-----------|---|-------------------------------------|---|------------|---------------|-------------------------------------|
| Expt 1    | Maris Piper                                       | See treatments                      | 4 distributions of seed tuber weight and 1 stem thinning treatment:   | 4          | 9/4/2013      | 61, 113                             |
| Expt 2    | Maris Piper                                       | 30-40 mm                            | Control; seed tubers warmed prior to planting; warmed seed tubers mixed with control seed; seed tubers planted in identical orientations; plants shaded for the first week of growth. | 4          | 24/4/2013     | 47, 86, 128                         |
| Expt 3    | Maris Piper                                       | 30-40 mm                            | 7 planting arrangements with different levels of variation in within-row spacing  | 4          | 16/4/2013     | 66, 108                             |
| Expt 4    | Maris Piper                                       | See treatments                      | 8 treatments combining every combination of low and high variation in seed tuber weight, sprout length and within-row spacing   | 4          | 16/4/2014     | 44, 76, 112                         |
| Expt 5    | Markies and Marfona                               | 35-45 mm                            | 2 varieties planted at either uniform or variable within-row spacing  | 4          | 8/4/2014      | 94                                  |
| Expt 6    | Maris Piper                                       | See treatments                      | Graded seed tubers (40-50 mm) and ungraded seed tubers  | 6          | 8/4/2014      | 103                                 |
| Expt 7    | Maris Piper                                       | See treatments                      | 2 seed sizes (35-45 mm and 45-55 mm) from 2 contrasting soil types (from survey sites 3a and 3b)  | 4          | 9/4/2014      | 19                                  |
| Expt 8    | Maris Piper                                       | See treatments                      | 4 different seed tuber weights planted at wide spacing  | 10         | 8/4/2014      | 121                                 |
| Survey 1  | Maris Piper                                       | 30-40 mm                            | Effects of plant-to-plant variation on variation in tuber size  | n.a.       | n.d.          | c.100                               |
| Survey 2  | Maris Piper                                       | 30-40 mm                            | Causes and consequences of stem-to-stem variation   | n.a.       | 9/4/2013      | 5, 12, 23, 33, 44, 58, 78, 105, 131 |
| Survey 3a | Maris Piper                                       | 35-45 mm                            | Effects of contrasting soil types on variation in tuber size  | n.a.       | n.d.          | c. 12, 40, 84                       |
| Survey 3b | Maris Piper                                       | 35-45 mm                            | Effects of contrasting soil types on variation in tuber size  | n.a.       | n.d.          | c. 4, 35, 77                        |
| Survey 3c | Maris Piper                                       | 50-55 mm                            | Effects of large seed tuber size on plant-to-plant variation  | n.a.       | n.d.          | c. 15, 60, 100                      |
| Survey 3d | Desiree   | Ungraded                            | Consequences of ungraded seed on plant-to-plant variation   | n.a.       | n.d.          | c. 15, 50, 75                       |
| Survey 4  | Maris Piper, Desiree, Russet Burbank, King Edward | 30-40 mm (35-45 mm for King Edward) | Causes and consequences of stem-to-stem variation in multiple varieties   | n.a.       | 9/4/2014      | 7, 14, 28, 50, 120                  |
| Survey 5  | Maris Piper                                       | 30-35 g                             | Effects of specific gravity of seed tubers on initial growth  | n.a.       | 25/4/2014     | 14                                  |
| Survey 6  | Desiree   | 1-2 g                               | Growth of plants grown from minitubers from 0 – 21 DAE  | n.a.       | 2/5/2014      | n.a.                                |

### 3.1.1. Site history, preparation, pesticides, fertilisers, planting and irrigation

The experiments were conducted at Cambridge University Farm located at an elevation of *c.* 25 m at 52 ° 13' N, 0 ° 05' E. The soil types ranged from clay loams to sandy clay loams. The experimental area in 2013 was planted with barley in 2012 and the area in 2014 was planted with winter wheat in 2013. The cereal residues were ploughed in mid-March and roto-ridged within one week. Seed tubers were planted by hand at a depth of *c.* 15 cm from the base of the seed tuber to the top of the ridge with a steel dibber. After planting, the ridge was reformed with a rake.

Contact and residual herbicides were applied pre-emergence and comprised a mixture of glufosinate-ammonium applied at 450 g/ha, flufenacet at 600 g/ha and metribuzin at 438 g/ha. Manual weeding was performed where performance of the herbicides was poor. Nitrogen fertiliser was applied pre-emergence at a rate of 200 kg/ha as ammonium nitrate solution. Other fertilisers were not applied due to the high fertility of the site from historical applications of farmyard manure. Fungicides containing the active ingredients fluopicolide, propamocarb hydrochloride, fluazinam, metalaxyl-M, mancozeb and cymoxanil were applied *c.* weekly after emergence to prevent late blight.

Irrigation was applied from a boom as required according to the CUF irrigation scheduling model (Stalham *et al.* 1999) so that the soil moisture deficit did not exceed *c.* 25 mm. The model used an adapted version of the Penman-Monteith equation to predict evapotranspiration based on the percentage ground cover of the crop and meteorological conditions. The amount of irrigation applied to each experiment and survey is listed in Table 5 along with the amount of rainfall that occurred from planting until final harvest.



**Table 5. Amount of rainfall from planting to final harvest and irrigation applied to each experiment and survey. Data were not available for commercial crops.**

| Experiment or Survey | Rainfall from planting to final harvest (mm) | Irrigation applied (mm) | Total (mm) |
|----------------------|--|-------------------------|------------|
| Expt 1               | 197  | 195                     | 392        |
| Expt 2               | 215  | 195                     | 410        |
| Expt 3               | 180  | 225                     | 405        |
| Expt 4               | 295  | 97                      | 392        |
| Expt 5               | 270  | 97                      | 367        |
| Expts 6 & 8          | 295  | 117                     | 412        |
| Expt 7               | 42   | 0                       | 42         |
| Survey 2             | 235  | 195                     | 430        |
| Survey 4             | 295  | 123                     | 418        |
| Survey 5             | 99   | 0                       | 99         |
| Surveys 1 & 3        | n.d.   | n.d.                    | n.d.       |

### 3.1.2. Data collection

#### 3.1.2.1. Seed tuber weight

Prior to planting, seed tubers used in harvest rows were selected at random, weighed to the nearest gram and placed in egg cartons in the sequence to be planted so that the weight of each seed tuber in each planting position was known. Individual seed tuber weights were not recorded in Expts 2 and 3 and Survey 1. In Survey 3, seed tuber weights were recorded when plants were harvested if they were still intact.

#### 3.1.2.2. Monitoring plant growth

##### 3.1.2.2.1. Date of emergence

The date of emergence of plants and stems was defined as the first day that a sprout was visible at the surface. Except for Expt 3, the dates of emergence for individual plants within harvest rows of experiments were recorded daily from the onset of emergence. In Expt 3 the number of plants emerged within the harvest rows was recorded every 3-4 days. In Surveys 2 and 4, individual stems were tagged with a ring of coloured wire (c. 4 cm in diameter) on the first day each was visible. Tagging was conducted daily and the colour of the wire corresponded to the date on which the stem emerged. The date on which the first stem of a plant emerged was used as the date of emergence of the plant. In Surveys 1 and 3 the dates of

emergence for individual plants were not determined and an approximate date of 50 % emergence was provided by the grower. The date when 50 % of plants had emerged was used as the cardinal date for determining when to carry out later activities on each experiment or survey.

#### 3.1.2.2.2. Ground cover

Digital photography and a quadrat were used to measure ground cover of individual plants and plots respectively. Plants were photographed from above using a digital camera (Canon 1100D, Japan) attached to a mobile rig where the camera was 90 cm above the plant. Fabric was attached to the rig so that the leaves of the focal plant were shaded and observations were made when the wind speed was sufficiently low that there was minimal movement of the leaves. The camera model was chosen as it had a short recovery time between taking consecutive photographs (< 1 s) and the resolution of the images was deliberately set low (3 megapixels) to expedite image processing and storage. Where neighbouring plants were touching, photographs were manually masked using GIMP 2.8 (Kimball *et al.* 2013) so only the leaves of the focal plant were visible. The photographs were analysed using ImageJ 1.48 (Schneider 2012; Rasband 2013) to determine the number of green pixels in each photograph. The macro contained the ‘colour threshold’ and ‘minimum’ procedures and the number of green pixels was converted to ground cover by comparing to an object of a known size photographed from the same height using the ‘analyse particles’ procedure.

The ground cover of plots was measured weekly by holding a quadrat (90 by 76.2 cm, with 100 subdivisions) directly above an area containing three plants in each plot and counting the number of squares in the quadrat that contained > 50 % green leaves (Burstall & Harris 1983).

### 3.1.2.3. Harvesting

All plant material was harvested by hand and each plant harvested separately unless stated otherwise. With the exception of Expts 7 and 8 and Survey 5 where samples were taken before plants began to compete, all samples were collected from an area guarded by at least one plant across the rows and two plants within the row to mitigate edge effects.

Above-ground stems were cut at the base and those from the same plant were bound with a labelled elastic band. Tubers and below-ground stems were dug using a hand fork and soil adhering to the surface was removed before they were stored in paper bags.

When plants were growing a short distance from each other (10-20 cm) special attention was given to ensure that tubers were from the target plant by examining them to distinguish between their stolon and apical ends. Tubers were assumed to be from the target plant if the stolon end of the tuber pointed towards where the stems emerged. In some instances it was not possible to determine which plant a particular above-ground stem originated from, as stems emerged *c.* 5 cm from where the seed tuber was planted. However, upon harvesting tubers this could be determined by observing the position of the base of the below-ground stem. Below-ground stems were harvested along with the tubers, and the number of stems was checked against the data previously collected for the above-ground stems. In the rare cases where the number of above-ground and below-ground stems did not correspond, data for above-ground stems was adjusted by moving stems from neighbouring plants, based on the assumption that the diameter of the below-ground stems was directly related to the weight of the above-ground stems.

When harvests could not be completed within a day, they were harvested block by block and all the above-ground stems were harvested before the tubers to minimize the effect of the protracted harvest period. Rotten or rodent-damaged tubers were substituted with sound

tubers of a similar weight and shape from the guard areas of plots. Between harvesting and analysis, all material was stored in the dark at 2-3 °C unless stated otherwise.

#### 3.1.2.4. Measurements

Tubers were weighed individually to the nearest gram unless the average weight was < 100 g when they were weighed to the nearest 0.1 g. After being weighed individually, samples from each plot were bulked and graded into 5 or 10 mm classes using a mechanical square-mesh grader. 5 mm classes were used for samples with a mean tuber size < 40 mm to ensure that there were sufficient classes to which a normal distribution could be fitted. Above-ground stems were weighed to the nearest 5 g except when the average weight was < 100 g when they were weighed to the nearest 0.1 g. Below-ground stems were weighed to the nearest 0.1 g.

The planting depth was estimated by measuring from the base of the stem to where the stem began to be pigmented. The below-ground stem weight was defined as the weight of non-pigmented stem, after roots, stolons and tubers had been removed. The orientation of the seed tuber was determined by the position of the apical end of the seed tuber relative to the soil surface. It was recorded as horizontal, vertical pointing downwards, vertical pointing upwards, 45° pointing downwards or 45° pointing upwards. The origin of the stem was recorded as either growing from the apical end of the seed tuber, the middle of the seed tuber or the stolon end of the seed tuber. Tubers were defined as a swelling at the end of a stolon that was at least twice the diameter of the stolon.

Dry weights were determined by drying in a ventilated fan oven with 90 % recirculated air at 90 °C for 48 hours. 1 kg sub-samples of above-ground stems and tubers from individual plots were used to determine dry weights. Tuber sub-samples were taken from the 5 or 10 mm size grade containing the greatest proportion of yield. At early harvests of the surveys, where 1 kg

of material was not present, all the material was dried. Prior to drying, tubers were washed and cut into pieces. Seed tubers were washed, cut into quarters and dried individually.

### 3.1.3. Data analysis

#### 3.1.3.1. Statistical analysis

All statistical analyses were performed using GenStat 16.1 (VSN International 2013). Linear regressions were performed using the 'fit' directive and non-linear regression was performed using the 'fitcurve' directive. Analysis of variance was performed using the 'anova' directive and t-tests were performed using the 'ttest' procedure. The mean tuber size and COV of tuber size for individual plots were calculated by fitting a normal distribution to the yield of tubers within size grades using the 'distribution' directive (an adapted version of the method used by Travis 1987). The interval from planting to 50 % emergence was calculated by fitting a curve using the 'fitnonlinear' directive to the cumulative percentage of plants or stems that had emerged at each date. The curve was then used to calculate the dates at which 50 % of plants or stems had emerged. The uniformity of emergence was defined by calculating the date at which 20 % and 80 % of the plants or stems had emerged and then calculating the difference between these two values.

Data for individual plants and stems is presented on a fresh weight basis as the quantity of material mean it was not possible to determine the dry weight of each plant individually.

Where experimental results were analysed using ANOVA, the probability of the differences being significant is given in the table as either n.s. = no significant difference, < 0.05 = significant at the 95 % confidence interval, < 0.01 = significant at the 99 % confidence interval and < 0.001 = significant at the 99.9 % confidence interval. Where results were analysed using multiple regression, relationships were only considered significant if each

explanatory variable had a significant effect in the regression (i.e. a t-probability < 0.05). All  $R^2$  values presented are the adjusted  $R^2$ .

### 3.1.3.2. Mean tuber weight

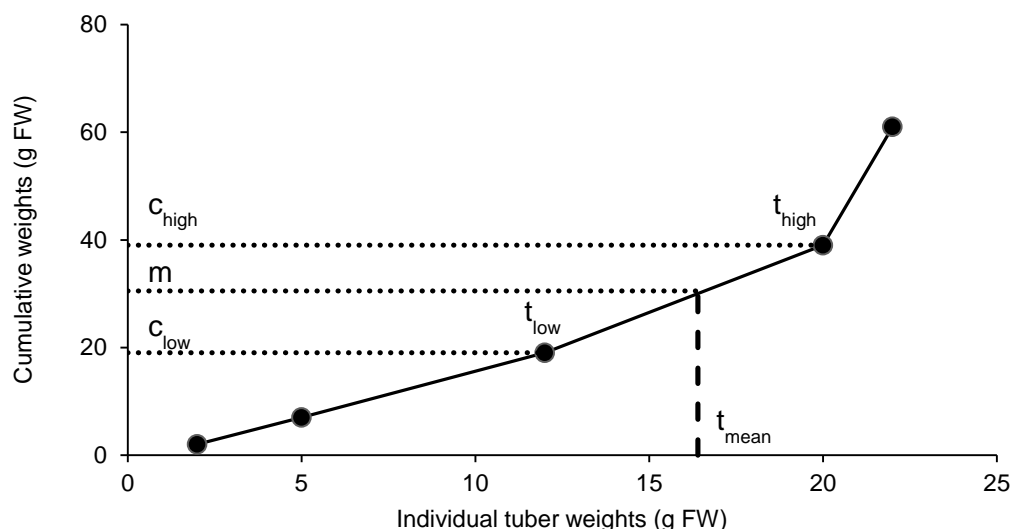
A statistic was required to describe the tuber size of plants and stems that was equivalent to the mean tuber weight or mean tuber size of crops described by Sands & Regel (1983) and Travis (1987) respectively but which could be calculated for small datasets. This was termed the mean tuber weight and was calculated using a custom procedure which estimated the tuber weight at the mid-point of the yield. This statistic reduced the distorting effect of small tubers on the mean tuber weight that occurred when the arithmetic mean (i.e. yield divided by the number of tubers) was calculated, in a similar manner to when the mean tuber size was calculated for a larger sample following the method of Travis (1987). For each set of tubers, the tubers ( $t_i$ ) were sorted by weight and the cumulative weights ( $c_i$ ) calculated. The total weight was halved and this value defined as the mid-point of the yield ( $m$ ). The two cumulative weights above and below  $m$  could then be distinguished as  $c_{low}$  and  $c_{high}$  and the corresponding individual tuber weights between which the mean tuber weight lay could be identified as  $t_{low}$  and  $t_{high}$ . Once these parameters were identified, the mean tuber weight was calculated using equation 1.

#### **Equation 1. Equation used to calculate the mean tuber weight**

$$t_{mean} = t_{low} + ((m - c_{low}) / t_{high}) \times (t_{high} - t_{low})$$

The procedure is shown diagrammatically in Figure 17 for a data set containing tubers weighing 2, 5, 12, 20 and 22 g and an example calculation is shown in Table 6. For comparison, the arithmetic mean for this data set =  $61/5 = 12.2$

**Figure 17.** An example of the procedure used to calculate the mean tuber weight demonstrating how the parameters used in equation 1 are related to each other.



**Table 6.** A worked example of the method used to calculate the mean tuber weight.

| Individual tubers<br>( $t_i$ ) | Cumulative<br>weights ( $c_i$ ) | Calculations  |
|--------------------------------|---------------------------------|---|
| 2                              | 2                               | $m = 61 / 2 = 30.5$   |
| 5                              | 7                               | $c_{low} = 19$ $t_{low} = 12$   |
| 12                             | 19                              | $c_{high} = 39$ $t_{high} = 20$   |
| 20                             | 39                              | $t_{mean} = t_{low} + ((m - c_{low}) / t_{high}) \times (t_{high} - t_{low})$ |
| 22                             | 61                              | $t_{mean} = 12 + ((30.5 - 19) / 20) \times (20 - 12) = 16.6$                  |

If the individual tuber weights were substituted for the upper limit of tuber size grades and the cumulative weights substituted for cumulative weights in those size grades, then the procedure could be used to calculate the mean tuber size of a crop and produce a similar value to that obtained if a normal distribution was fitted using the ‘distribution’ directive in Genstat. The procedure could not calculate a value when the number of tubers per stem or per plant was less than 3. For stems with only one tuber, the mean tuber weight was taken to be identical to the weight of the single tuber and for plants and stems with two tubers, the arithmetic mean was used.

### 3.1.3.3. Variation in stem weight

As well as describing variation in stem weights as the COV, a measure was required that accounted for their relative weights as larger stems made up a greater proportion of the total weight than smaller stems. Individual values were sorted into discrete classes depending on their weight. The lower and upper limits of each class were defined as the cubes of 1-15 i.e.

1-8, 8-27, 27-64 *etc.* The weight of all the stems within each class was then summed and a normal distribution fitted to the combined weights using the class number as the x variable. The COV was calculated from the normal distribution in a similar manner to calculating the COV of tuber size.

#### 3.1.3.4. Proxy stem diameter

A proxy measurement for the stem diameter was calculated by dividing the fresh weight of the below-ground stem by the planting depth. This measure was used instead of a direct measurement of the stem diameter because stems were not uniform cylinders and thus direct measurements of the diameter were relatively subjective and error-prone.

#### 3.1.3.5. Seed tuber substrate per stem

The amount of seed tuber substrate per stem was estimated from the relative diameter of stems growing from each seed tuber. First, the total proxy diameter of all the stems growing from each seed tuber was calculated and then the diameter of each stem was divided by the total diameter. The relative diameter of each stem was then multiplied by the weight of the seed tuber.

#### 3.1.3.6. Dry weight lost from seed tubers

The amount of dry weight lost from the seed tubers was estimated by subtracting the dry weight when harvested from an estimate of the dry weight at planting (calculated from the average percentage dry matter of tubers from the same seed tuber stock).

#### 3.1.3.7. Space per plant

The space per plant within the row was calculated as the average distance from each plant to its two neighbouring plants (Martin *et al.* 2005). In the experiments, the positions were



defined at planting by the positioning of the seed tuber, whereas in the surveys, the positions were defined as the central point around which the stems emerged from the soil.

#### 3.1.3.8. Comparison of plants with different amounts of space within the row

In Expts 3, 4 and 5 there were large differences in the space per plant within the row in the same plot of some treatments. To examine how this affected the growth of these plants, the yield, number of tubers and mean tuber weight of the plants with less space was calculated relative to the total plot. The same values were also calculated for plants in equivalent positions in evenly spaced plots and the means for each treatment were compared using ANOVA. The first and last plants within the plot were excluded from these analyses as they had an intermediate amount of space.

#### 3.1.3.9. Tuber weight and tuber size

Where necessary, tuber weights were converted into tuber size by a cubic root transformation (Hide *et al.* 1997; Marshall 2000) such that:

$$\text{Tuber size (mm)} = 10 \sqrt[3]{\text{tuber weight (g)}}$$

### 3.2. Experimental methods

#### 3.2.1. Experimental design

Each experimental treatment was replicated four times (six in Expt 6 and ten in Expt 8) and arranged in a randomised block design.

#### 3.2.2. Experiment 1 – Effects of variation in seed tuber weight and stem thinning

Treatments comprised four levels of variation in seed tuber weight and a treatment where stems were thinned so that each plant had only one stem. The level of variation in seed tuber weight in the control treatment was typical of current commercial practice and the others comprised two less variable treatments and one more variable treatment.

250 seed tubers graded 30-40 mm were weighed individually to the nearest gram and the mean and COV of tuber weight calculated. The COV of weight of the 30-40 mm seed tubers was 24 % and this was used as the control treatment. Higher and lower COVs were used to calculate distributions of seed tuber weights that were more and less variable than the control treatment as shown in Table 7. From these distributions, the number of seed tubers within 2 g classes was calculated for each harvest. Each seed tuber was randomly allocated to a position within each harvest. Guard rows were planted with seed with the same seed weight distribution as each harvested area. In the thinning treatment, 30-40 mm seed tubers were planted at a within-row spacing of 10 cm and the stems were thinned to one per plant at 11 and 22 DAE.

**Table 7. Details of treatments examined in Expt 1.**

| Treatment     | Average seed tuber weight (g FW) | COV of seed tuber weight (%) | Range in seed tuber weight (g FW) |
|---------------|----------------------------------|------------------------------|-----------------------------------|
| Control       | 33                               | 24                           | 18-47                             |
| Uniform       | 33                               | 2                            | 30-35                             |
| Less variable | 33                               | 11                           | 26-41                             |
| More variable | 33                               | 40                           | 12-51                             |
| Thinned       | 33                               | 24                           | 18-47                             |

Each plot measured 9 by 3.05 m, consisting of four rows, 76.2 cm wide, each with 30 plants at a within-row spacing of 30 cm. Each plant in the first four treatments was photographed 12 DAE. Two harvests of 24 plants were taken 61-63 and 113-114 DAE. At the second harvest tubers were left in the ground for 15 days before being dug after above-ground stems had been harvested.

Due to the practical difficulty of harvesting individual plants in the thinned treatment (plants were too closely spaced to separate), measurements were made on the plot as a whole, rather than on individual plants as for the other treatments. Ground cover was recorded with a quadrat as for the other treatments, but not with photography. The above-ground stems and tubers were weighed individually as for the other treatments, but comparisons were only made between the measurements for entire plots of the other treatments.

### 3.2.3. Experiment 2 – Effects of variation in emergence

The experiment consisted of five treatments expected to result in differences in the uniformity of emergence as listed in Table 8.

**Table 8. Details of treatments examined in Expt 2.**

| Treatment | Description            | Method  |
|-----------|------------------------|---|
| 1         | Control                | Seed tubers planted from storage at 3 °C.   |
| 2         | Mixed                  | Alternate seed tubers planted from storage at 3 °C and after 6 days storage in darkness at 15 °C. |
| 3         | Warmed                 | Seed tubers planted after 6 days storage in darkness at 15 °C.                                    |
| 4         | Shaded                 | Seed tubers planted from storage at 3 °C. Planting area heavily shaded during emergence.          |
| 5         | Seed tuber orientation | Seed tubers planted from storage at 3 °C with the apical end of the tuber lying horizontal.       |

Each plot measured 9 by 3.05 m, consisting of four rows, 76.2 cm wide, each with 30 plants at a within-row spacing of 30 cm. For treatments 1-4, seed tubers were planted paying no attention to their orientation, but for treatment 5, special attention was paid to ensure that all seed tubers were planted with the apical end of the tuber horizontal to the soil surface. Four layers of shade netting were suspended above the soil in treatment 4 during the period of emergence between 23 May and 3 June. The shade netting covering treatment 4 meant it was not possible to record the dates of emergence for plants in that treatment. After the shade netting had been removed from treatment 4 (7 DAE of the other treatments), all the plants in harvest rows were photographed.

The first harvest of 12 plants was taken 47 DAE and plants were not harvested individually. The total number of plants and stems was counted and all tubers > 10 mm were dug and graded by size. A second harvest of 12 plants was taken 86 DAE and a third harvest of 20 plants was taken 128 DAE. At the third harvest, the canopy had senesced and so only the tubers were harvested, but the number of above-ground stems was recorded for each plant. At the third harvest, tubers were stored for four weeks at ambient temperature prior to analysis.

### 3.2.4. Experiment 3 – Effects of variation in within-row spacing

The experiment consisted of seven treatments with different variations in the distance between each plant and the space per plant (the average of the distance to the two neighbouring plants) as listed in Table 9. The average within-row spacing was 30 cm in all treatments.

**Table 9. Distance between neighbouring plants, COV of distance between plants and COV of space per plant in Expt 3.**

| Treatment | Distance between plants (cm)               | COV of distance between plants (%) | COV of space per plant (%) |
|-----------|--|------------------------------------|----------------------------|
| 1         | 30, 30, 30, 30, 30, 30 <i>etc.</i>         | 0                                  | 0                          |
| 2         | 30, 40, 20, 30, 40, 20 <i>etc.</i>         | 28                                 | 14                         |
| 3         | 20, 40, 20, 40, 20, 40 <i>etc.</i>         | 34                                 | 0                          |
| 4         | 30, 50, 10, 30, 50, 10 <i>etc.</i>         | 56                                 | 28                         |
| 5         | 20, 20, 40, 40, 20, 20, 40, 40 <i>etc.</i> | 34                                 | 24                         |
| 6         | 30, 59, 1, 30, 59, 1 <i>etc.</i>           | 81                                 | 41                         |
| 7         | 10, 80, 20, 10, 10, 80, 20, 10 <i>etc.</i> | 98                                 | 61                         |

Each plot measured 16.2 m by 76.2 cm, consisting of a single row containing 54 plants. At either end of each area to be harvested, two plants were spaced at 30 cm. The plots were planted in between rows planted at uniform within-row spacing as in treatment 1.

Two harvests of 24 plants were taken 66-73 DAE and 108-114 DAE. Plants were harvested individually except for treatment 6 where it was not possible to distinguish between plants spaced 1 cm apart, so stems and tubers from these plants were combined.

### 3.2.5. Experiment 4 – Effects of variation in seed tuber weight, sprout length and within-row spacing

The experiment consisted of eight treatments that were combinations of either a low or high level of variation in three factors; seed tuber weight, sprout length and within-row spacing. Seed tubers weighing 35-45 g were used for the treatment with a low level of variation in seed tuber weight and seed tubers graded to 25-45 mm (mean weight 40 g) were used as the treatment with a high level of variation. The COV of seed tuber weight was 7.5 and 39.8 % respectively. Seed tubers with sprouts 2-4 mm long were used for the treatment with low

variation in sprout length and seed tubers with sprouts < 2 mm and > 4 mm were used as the treatment with a high level of variation. Uniform 30 cm spacing was used as the treatment with a low level of variation in within-row spacing and consecutive spacing of 10, 20, 80 and 10 cm was used for the high level of variation in within-row spacing (as in treatment 7 of Expt 3).

The seed tubers were moved from 3 °C to storage in darkness at 15 °C on 7 April 2014 to encourage sprout growth. One week later, seed tubers in each of the weight classes were split into groups depending on the length of the longest visible sprout. Once grouped, seed tubers were returned to storage at 15 °C. The seed tubers were picked at random, weighed individually and placed in egg cartons in the order to be planted.

Each plot measured 15 by 2.29 m, consisting of three rows 76.2 cm wide, each with 50 plants. In the treatment with a high level of variation in within-row spacing, only seed tubers in the central row of the plot were planted at variable spacing and guard plants at either end of each harvested area and the first and last plant of the harvested area were planted at a spacing of 30 cm. The first and third rows of the high variation in within-row spacing treatment were planted at uniform 30 cm spacing. The length of the longest sprout was measured for 4 samples of 25 tubers from each of the variation in seed size and sprout length treatments and the values are summarised in Table 10.

**Table 10. Average and variation in sprout length of treatments in Expt 4 at planting.**

|                                | Variation in seed tuber weight |      |          | Variation in sprout length |      |          | S.E.<br>(12 D.F.) |
|--------------------------------|--------------------------------|------|----------|----------------------------|------|----------|-------------------|
|                                | Low                            | High | <i>P</i> | Low                        | High | <i>P</i> |                   |
| Sprout length (mm)             | 2.31                           | 2.39 | n.s.     | 2.34                       | 2.36 | n.s.     | 0.107             |
| Variation in sprout length (%) | 59.7                           | 56.3 | n.s.     | 26.1                       | 89.9 | <0.001   | 2.91              |

Observations were only made on the central row of each plot. Harvests of 10, 14 and 18 plants were taken 44-45, 76-79 and 112-119 DAE respectively. The dry weight of above-ground stems and tubers was determined at each harvest.

### 3.2.6. Experiment 5 – Effects of variation in within-row spacing on two varieties

Treatments consisted of two varieties (Markies and Marfona) with contrasting canopy morphologies, planted at either uniform or variable within-row spacing.

Each plot measured 6.6 by 2.29 m, consisting of three rows 76.2 cm wide, each with 22 plants. The same planting arrangements were used as in Expt 4 with the outer rows of the variable within-row spacing treatment planted at uniform spacing. One harvest of 18 plants was taken from the central row from 94-96 DAE. The canopy of Marfona had senesced prior to harvesting so above-ground stems were not harvested but the number of stems per plant was recorded.

### 3.2.7. Experiment 6 – Comparison of graded and ungraded seed tubers

Treatments consisted of seed tubers graded 40-50 mm and ungraded seed tubers (c. 25-55 mm) with a similar average weight as summarised in Table 11.

**Table 11. Average weight, COV of weight and range of weights of seed tubers used in Expt 6.**

| Measurement                       | Graded seed tubers | Ungraded seed tubers |
|-----------------------------------|--------------------|----------------------|
| Average seed tuber weight (g FW)  | 64.6               | 62.3                 |
| COV of seed tuber weight (%)      | 25.3               | 64.3                 |
| Range in seed tuber weight (g FW) | 24-98              | 15-207               |

Each plot measured 3.6 by 3.05 m, consisting of four rows 76.2 cm wide, each with 12 plants at a within-row spacing of 30 cm. One harvest of 16 plants was taken from the central rows of each plot 103-105 DAE.

### 3.2.8. Experiment 7 – Comparison of seed tuber sizes originating from contrasting soil types

Treatments consisted of two seed sizes grown on contrasting soil types within the same field and where a difference in the growth of the mother crop had been observed (see Section 4.6.1). In September 2013, after the canopy had been desiccated with diquat and the skins of the tubers had set, 35-45 mm and 45-55 mm tubers were collected from the location of Survey

3a (a relatively light soil) and Survey 3b (a relatively heavy soil) and placed in plastic nets. After one week of storage at ambient temperature to cure the seed tubers, they were stored at 3 °C until April 2014.

Each plot measured 1.8 by 3.05 m, consisting of four rows, 76.2 cm wide, each with 6 plants at a within-row spacing of 30 cm. Each plant was photographed 6 and 9 DAE. The entire area of each plot consisting of 24 plants was harvested 19 DAE. The rows had not begun to compete and so it was not necessary to have guard rows or guard plants in this experiment. The above-ground stems were harvested separately for each plant and a sub-sample from each plot was dried. The below-ground portion of the plants was not harvested.

### 3.2.9. Experiment 8 – Effects of seed tuber weight on the growth of widely spaced plants

Treatments consisted of four seed tuber weights: 20-25 g, 35-40 g, 50-55 g and 65-70 g. Each plot consisted of a single plant spaced at a distance of 1.52 m from neighbouring plants both within and between rows. Plants were photographed 8, 15, 22, 31, 38 and 45 DAE. A single harvest was taken 121 DAE and the yield of each plant was recorded.

## 3.3. Survey methods

### 3.3.1. Survey 1

One large sample of neighbouring plants was taken from a commercial crop of Maris Piper. The site was located one mile north-east of the village of Hales, Norfolk at 52° 31' 41 N, 1° 31' 57 E. The above-ground stems from each plant a 7.5 m length of row from four rows, was harvested on 29 August 2012 (c. 100 DAE). On 12 September, the distance from each plant to its neighbours was measured before the tubers were harvested and graded by hand in 5 mm increments.

### 3.3.2. Survey 2

Two blocks 19.95 by 12.19 m, consisting of 16 rows, 76.2 cm wide with 57 plants at a within-row spacing of 35 cm were planted. Prior to planting, the dry weight of 100 seed tubers was determined. Nine harvests each of 126 plants were made 5, 12, 23, 33, 44, 58, 78, 105 and 131 DAE. Each harvest consisted of 9 plants in 14 rows and alternate harvests were taken from each of the two blocks. Immediately prior to the first three harvests, all plants in the survey area were photographed. With the exception of the eighth harvest, measurements were made on each stem.

At the first four harvests, individual plants were carefully dug by hand and placed in a sealed polythene bag. From the fifth harvest onwards, the above-ground stems were cut at the base and labelled with a coloured wire so that the above-ground and below-ground stems from each plant could be distinguished from each other. The underground portion of the plant and the surrounding soil was harvested by hand with particular care to ensure that tubers remained attached to stems. If tubers became detached during harvest and the stolon they were attached to could be determined, they were both labelled with a piece of coloured wire allowing them to be identified at analysis. If it was not possible to determine which stem the tubers were attached to, the tuber weights were recorded, but the data collected on the plant was excluded from the analysis of individual stems. The underground portion of the plant and the surrounding soil was placed in a paper bag. In the laboratory, soil surrounding the stems and tubers was removed allowing tubers attached to each stem to be identified. At the final harvest the canopy had senesced and it was not possible to remove the plants from the soil intact. To harvest the stems separately, soil surrounding tubers was removed in the field using trowels and brushes. Measurements made on each plant at each harvest are listed in Table 12.



**Table 12. Measurements made at each harvest of Survey 2.**

|   | Harvest |    |    |    |    |    |    |     |     |
|---|---------|----|----|----|----|----|----|-----|-----|
|   | 1       | 2  | 3  | 4  | 5  | 6  | 7  | 8   | 9   |
| Days after emergence                        | 5       | 12 | 23 | 33 | 44 | 58 | 78 | 105 | 131 |
| Number of stems                             | ●       | ●  | ●  | ●  | ●  | ●  | ●  | ●   | ●   |
| Fresh weight of above-ground stems          | ●       | ●  | ●  | ●  | ●  | ●  | ●  | ●   |     |
| Dry weight of above-ground stems            | ●       | ●  | ●  | ●  | ●  | ●  | ●  | ●   |     |
| Dry weight of individual above-ground stems |         |    |    |    | ●  | ●  | ●  | ●   |     |
| Fresh weight of below-ground stems          | ●       | ●  | ●  | ●  | ●  |    |    |     |     |
| Dry weight of below-ground stems            | ●       | ●  | ●  | ●  | ●  |    |    |     |     |
| Date of emergence of stems                  | ●       | ●  | ●  | ●  | ●  | ●  | ●  | ●   | ●   |
| Planting depth                              | ●       | ●  | ●  | ●  | ●  |    |    |     |     |
| Orientation of seed tuber                   |         | ●  | ●  | ●  | ●  |    |    |     |     |
| Position of stem on seed tuber              | ●       | ●  | ●  | ●  | ●  |    |    |     |     |
| Dry weight of seed tubers                   | ●       | ●  | ●  | ●  | ●  |    |    |     |     |
| Number of tubers                            |         |    | ●  | ●  | ●  |    |    |     |     |
| Number of tubers > 10 mm diameter           |         |    | ●  | ●  | ●  | ●  | ●  | ●   | ●   |
| Weight of individual tubers                 |         |    |    | ●  | ●  | ●  | ●  | ●   | ●   |
| Leaf area of individual stems               |         |    |    |    | ●  |    |    | ●   |     |
| Dry weight of tubers                        |         |    | ●  | ●  | ●  | ●  | ●  | ●   | ●   |
| Dry weight of individual tubers             |         |    |    |    |    |    |    |     | ●   |
| Size grading of tubers                      |         |    |    | ●  | ●  | ●  | ●  | ●   | ●   |

At harvests 1-4, stem dry weights were determined by bulking sub-samples of stems of similar fresh weights. For harvests 5-8 individual stem dry weights were determined for a sub-sample of 50 stems. At the final harvest, the dry weight of individual tubers from five randomly selected rows was determined. The size grade of each tuber that had its dry weight determined was recorded to the nearest 5 mm.

Leaf area was determined for a sub-sample of 25 stems by removing all the leaves, randomly selecting 50 leaves and punching a disc of 2.66 cm<sup>2</sup> from each leaf. The stem material, leaf discs and leaves were then dried separately and the leaf area calculated by dividing the total

dry weight of leaves by the dry weight of leaf discs and multiplying that value by the total area of the leaf discs (Firman & Allen 1989).

### 3.3.3. Survey 3

In three commercial crops, six rows between wheelings were chosen soon after 100 % emergence. Table 13 lists the location, variety and harvest dates for each of the crops surveyed. Two sites (3a and 3b) in the first crop were chosen on contrasting soil types identified from a soil electrical conductivity scan made the previous autumn. Site 3a was a relatively heavy soil with a higher proportion of clay than Site 3b. Three harvests of 12 plants (10 for 3c due to wider within-row spacing) were marked out in one row of each ridge and a stem on the first plant of each harvest area was labelled with coloured wire so it could be identified later in the season. In the area to be harvested, the distance between each plant was measured. At the first harvest, plants were kept intact and placed in a polythene bag. At subsequent harvests the above-ground stems of each plant were harvested individually, but at the third harvest of crop 3c this was impractical as the canopy was extensive and the stems could not be removed without damaging them, so this was not performed.

**Table 13. Details of the commercial crops sampled and the dates of harvests in Survey 3.**

| Code | Name                  | Location            | Variety     | Harvest |        |        |
|------|-----------------------|---------------------|-------------|---------|--------|--------|
|      |                       |                     |             | 1       | 2      | 3      |
| 3a   | Hales Hospital, heavy | 52.5205 N, 1.5184 E | Maris Piper | 7 Jun   | 5 Jul  | 18 Aug |
| 3b   | Hales Hospital, light | 52.5205 N, 1.5184 E | Maris Piper | 7 Jun   | 8 Jul  | 19 Aug |
| 3c   | R.9                   | 52.5222 N, 0.4715 E | Maris Piper | 27 Jun  | 15 Aug | 21 Sep |
| 3d   | Stevenson             | 51.8104 N, 0.2890 E | Desiree     | 17 Jun  | 24 Jul | 20 Aug |

At the first harvest, measurements of the above-ground stem weight, below-ground stem weight and planting depth were made on each stem. If present total number of tubers and number of tubers > 10 mm were also recorded. The dry weight was determined for sub-samples of stems of different fresh weights and of each seed tuber.

The following measurements were only made at sites 3a and 3b to allow comparisons between the sites. At the second harvest, the plants in one row at each site were harvested intact and the tubers from each stem were separated. The dry weight of above-ground stems and tubers from each row were determined at the second and third harvests.

#### 3.3.4. Survey 4

Similar methods were used as in Survey 2 to examine the growth of individual stems in the varieties Maris Piper, Desiree, Russet Burbank and King Edward. Prior to planting, the dry weight of 100 seed tubers of each variety was determined.

Six blocks were planted each containing one plot of each variety, with each plot measuring 7.2 by 3.81 m, consisting of five rows 76.2 cm wide, each with 24 plants at a within-row spacing of 30 cm. Each harvest consisted of 60 plants.

The harvest dates and the interval from 50 % emergence for the harvested areas of each variety are listed in Table 14. The first two harvests were timed to sample the crop approximately one and two weeks after emergence and the third at the end of tuber initiation. The fifth harvest was scheduled to take place *c.* 80 DAE but rainfall prevented harvesting the plants intact and by the time conditions allowed harvesting, the canopies had senesced so no further harvests were taken.

**Table 14. Sampling dates and the intervals from 50 % emergence for each harvest in Survey 4. The intervals from 50 % emergence was calculated separately for each harvest area.**

| Harvest |      | Maris Piper | Desiree | Russet Burbank | King Edward |
|---------|------|-------------|---------|----------------|-------------|
| 1       | Date | 21 May      | 21 May  | 21 May         | 19 May      |
|         | DAE  | 7           | 7       | 8              | 7           |
| 2       | Date | 28 May      | 28 May  | 28 May         | 26 May      |
|         | DAE  | 13          | 15      | 15             | 15          |
| 3       | Date | 12 Jun      | 9 Jun   | 11 Jun         | 10 Jun      |
|         | DAE  | 29          | 26      | 27             | 29          |
| 4       | Date | 3 July      | 3 July  | 4 Jul          | 4 Jul       |
|         | DAE  | 50          | 50      | 51             | 52          |
| 5       | Date | 14 Sep      | 10 Sep  | 11 Sep         | 12 Sep      |
|         | DAE  | 123         | 119     | 120            | 124         |

Measurements made at each harvest are listed in Table 15. Each plant was also photographed four days after the first harvest. The diameter of stems were only measured on plants in the central row of each plot. A pair of calipers was used to measure the shortest diameter around the circumference to the nearest 0.1 mm where they emerged from the soil.

**Table 15. Measurements at each harvest of Survey 4.**

| Measurement   | Harvest |   |   |   |   |
|---|---------|---|---|---|---|
|   | 1       | 2 | 3 | 4 | 5 |
| Number of stems   | ●       | ● | ● | ● | ● |
| Fresh weight of above-ground stems                        | ●       | ● | ● | ● |   |
| Dry weight of above-ground stems                          | ●       | ● | ● | ● |   |
| Fresh weight of below-ground stems                        | ●       | ● | ● | ● |   |
| Dry weight of below-ground stems                          | ●       | ● | ● | ● |   |
| Fresh weight of roots and stolons (20 plants only)        | ●       | ● |   |   |   |
| Dry weight of roots and stolons (20 plants only)          | ●       | ● |   |   |   |
| Diameter of stems in H1 and H2 plots (20 plants only)     | ●       |   |   |   |   |
| Diameter of stems in H3, H4 and H5 plots (20 plants only) |         |   | ● |   |   |
| Photographs of all plants                                 | ●       | ● |   |   |   |
| Dry weight of seed tubers                                 | ●       | ● | ● |   |   |
| Date of emergence of stems                                | ●       | ● | ● | ● | ● |
| Planting depth  | ●       | ● | ● | ● |   |
| Number of tubers < 10 mm                                  |         |   | ● | ● |   |
| Number of tubers > 10 mm                                  |         |   | ● | ● | ● |
| Fresh weight of tubers                                    |         |   | ● | ● | ● |
| Dry weight of tubers                                      |         |   | ● | ● | ● |
| Size grading of tubers                                    |         |   |   | ● | ● |

### 3.3.5. Survey 5

Two hundred seed tubers with a fresh weight of 30-35 g were separated according to their specific gravity (which correlates with percentage dry matter (Schippers 1976)) using a modified version of the brine method (Clark 1940). Sucrose was used as the solute to avoid any potentially phytotoxic effects of brine. 11 solutions were made with specific gravities ranging from 1.02 to 1.10 containing from 51 to 238 g of sucrose per litre.

Seed tubers were washed to remove soil adhering to the surface and dried before being weighed to the nearest 0.1 g. Tubers were placed in the most concentrated sucrose solution first and if the tuber floated this was recorded and the seed tuber was then rinsed and dried. If the tuber sank it was rinsed before being placed into a less concentrated sucrose solution. The process was repeated until the most concentrated solution that each tuber floated in was determined. Half of the seed tubers were then dried to determine their dry weight and the remaining half were planted in a random order while noting their weight and specific gravity. Plants were harvested 14 DAE. The planting depth and above- and below-ground stem weights were measured for each stem. Sub-samples of the above-ground and below-ground stems were dried and the seed tubers were dried individually.

#### 3.3.6. Survey 6

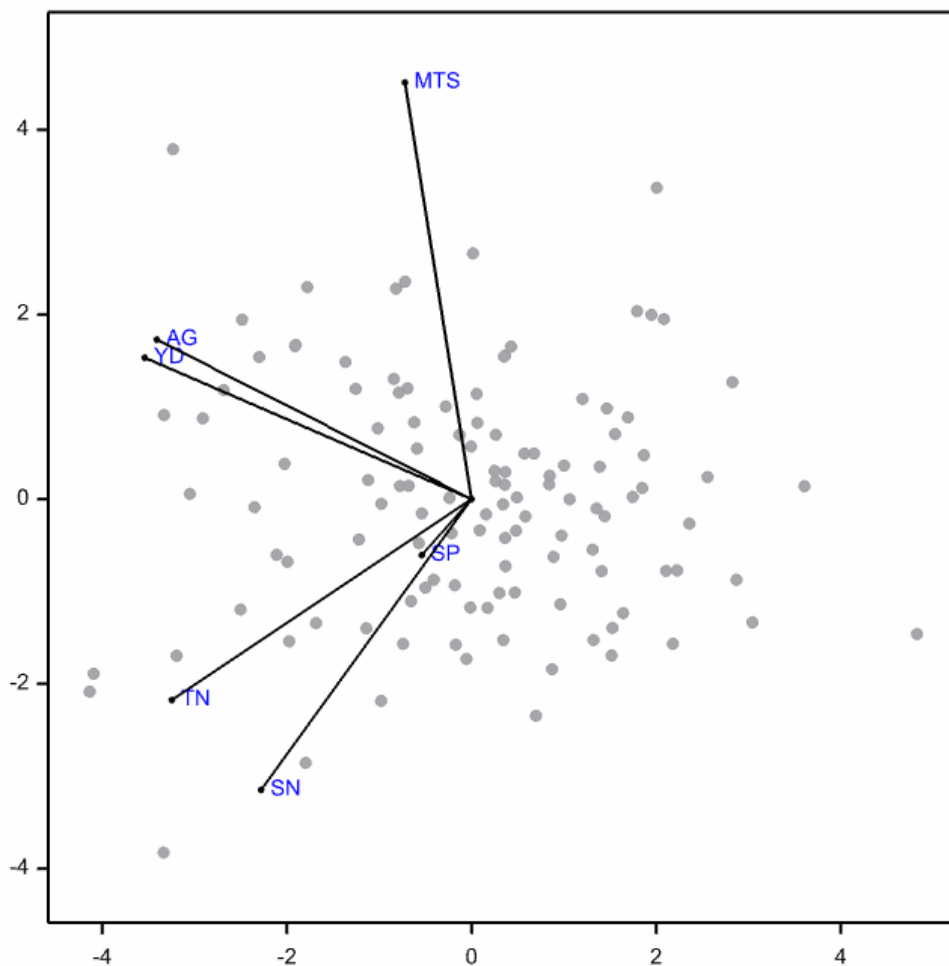
One hundred plants of Desiree grown from 1-2 g mini-tubers were planted at a within-row spacing of 25 cm. The number of plants emerged was recorded every 3-4 days from the onset of emergence. Each plant was photographed at 4, 11 and 18 DAE.

## 4. Results

### 4.1. Survey 1

A biplot of the variables measured for each plant showed that the above-ground stem weight was closely related to yield and that the number of stems was related to the number of tubers (Figure 18). Mean tuber size was negatively related to the number of stems per plant, while the space per plant had very little influence on the other variables (Figure 18). The parameters of crop growth and plant-to-plant variation in Survey 1 are listed in Table 16.

**Figure 18. Biplot of the variables measured for individual plants in Survey 1. AG = above-ground stem weight; MTS = mean tuber size; SN = number of stems; SP = space per plant; TN = number of tubers; YD = yield.**

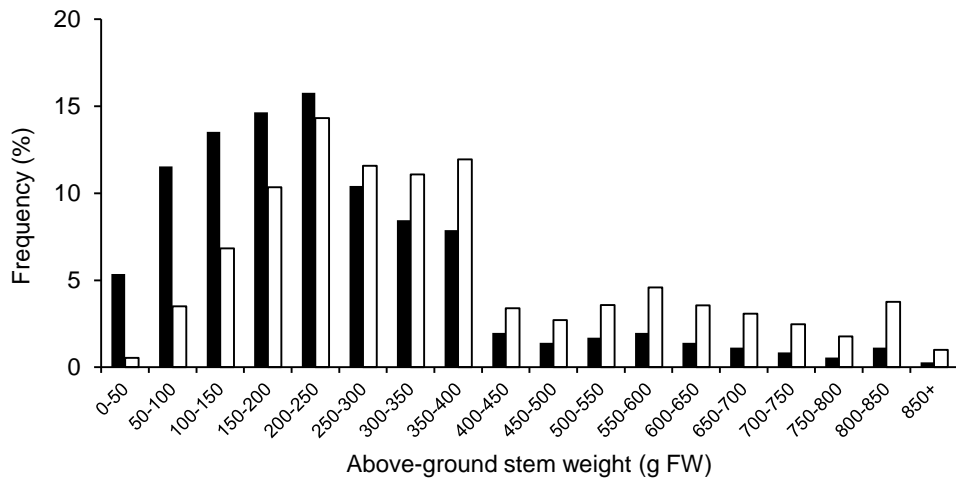


**Table 16. Overall parameters of crop growth and plant-to-plant variation in Survey 1.**

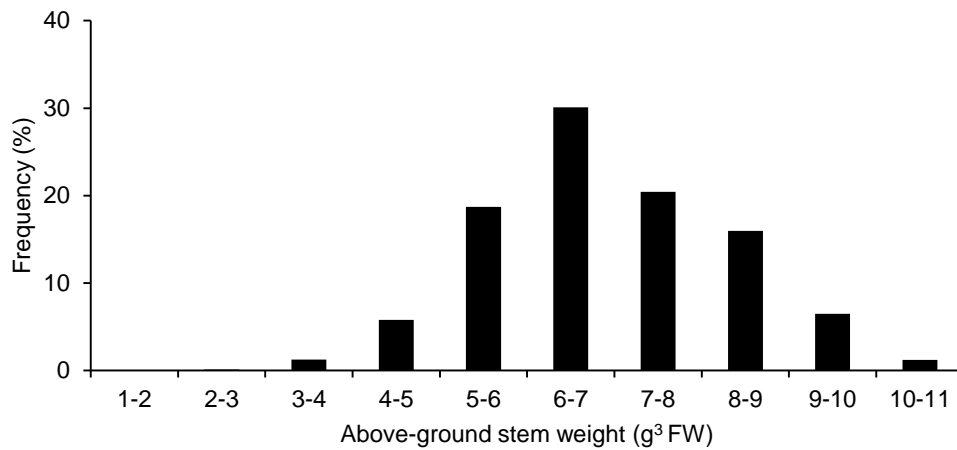
|                                |         |       |
|--------------------------------|---------|-------|
| Number of stems (000/ha)       |         | 126.3 |
| Number of tubers (000/ha)      |         | 588.0 |
| Yield (t FW/ha)                |         | 70.9  |
| Mean tuber size (mm)           |         | 56.2  |
| COV of tuber size (%)          |         | 14.9  |
| Number of stems per plant      | Mean    | 3.02  |
|                                | COV (%) | 39.5  |
| Yield per plant (g FW)         | Mean    | 1698  |
|                                | COV (%) | 33.1  |
| Number of tubers per plant     | Mean    | 14.1  |
|                                | COV (%) | 31.7  |
| Mean tuber size per plant (mm) | Mean    | 55.5  |
|                                | COV (%) | 6.8   |

Large above-ground stems (> 400 g FW) occurred at a low frequency but made up a relatively large percentage of the total weight of the canopy (Figure 19). The distribution of above-ground stem weights could be normalised by sorting the individual values into classes, summing the weight within each class and dividing the weight in each class by the total above-ground weight (Figure 20). Consistent with the biplot, there was a strong correlation between the total above-ground stem weight and yield of each plant, but plants with higher above-ground stem weights produced less yield per gram of above-ground stem than plants with lower above ground stem weights (Figure 21). This correlation would be expected if the fresh weight of the above-ground stems increased as leaf area increased and if yield increased as the leaf area of the stems increased. The slope of the relationship would be expected if leaves made up a smaller proportion of the weight of larger above-ground stems due to a larger proportion being portioned to structural tissues. Considering this relationship, it is probable that the distribution of above-ground stem weights reflected the distribution of yield of stems.

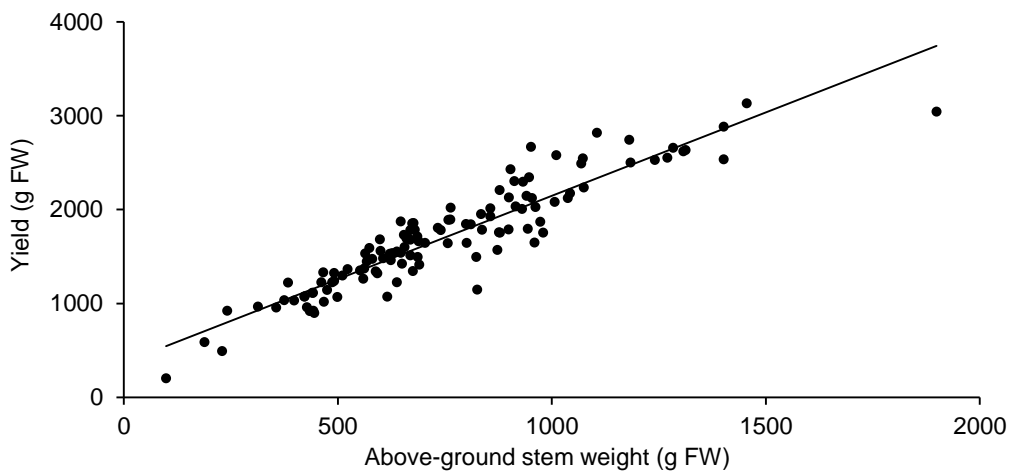
**Figure 19. Above-ground stem weights in Survey 1. Number (■) and weight (□). n = 355.**



**Figure 20. Transformed and weighted above-ground stem weights in Survey 1. Mean = 6.91 g<sup>3</sup>, COV = 19.7 %.**



**Figure 21. Relationship between above-ground stem weight (AG) and yield (YD) of individual plants in Survey 1.  $YD = 1.777 (\pm 0.0674) \times AG + 371 (\pm 54.1)$ ,  $R^2 = 0.86$ .**





Yield increased as the number of stems per plant increased but the relationship was weak and explained little of the variation in yield (Table 17). The number of tubers increased as the number of stems and yield increased and a regression incorporating both variables explained a large proportion of the variation in the number of tubers per plant (Table 17). When considered separately, yield, number of stems and number of tubers were poorly correlated with the mean tuber size of individual plants, but in combination they explained a large proportion of the variation (Table 17). Since the number of tubers was strongly correlated with yield and the number of stems, it was not unexpected that the addition of the number of stems to a regression already incorporating the number of tubers and yield only slightly increased the correlation coefficient, although the number of stems did still have a significant effect in the regression (Table 17).

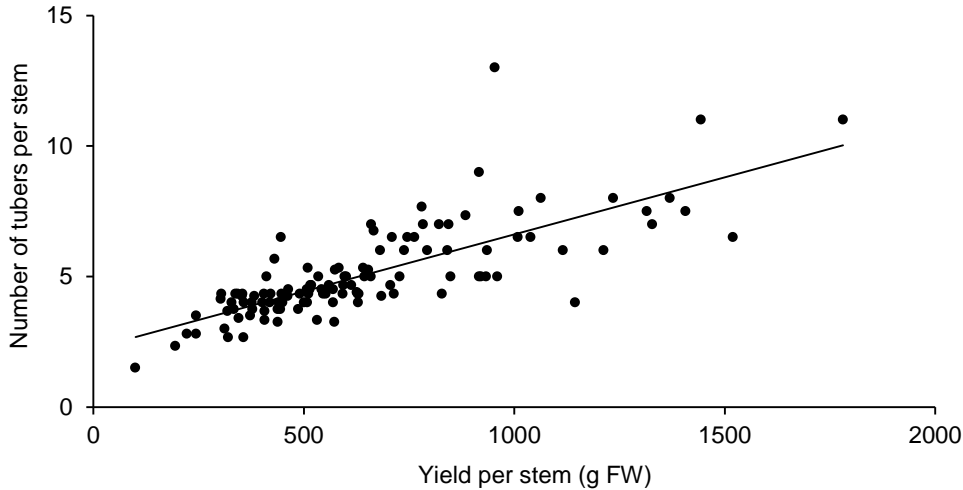
**Table 17. Relationships between the number of stems (SN), yield (YD, g FW) and number of tubers (TN) and between these variables and mean tuber size (MTS, mm) of individual plants in Survey 1.**

| Explanatory variable(s) |    |    | Response variable | Relationship   | $R^2$ | $P$    |
|-------------------------|----|----|-------------------|--|-------|--------|
| SN                      | TN | YD |                   |  |       |        |
| ●                       |    |    | YD                | $163 (\pm 39.9) \times SN + 1206 (\pm 130.0)$  | 0.12  | <0.001 |
| ●                       |    |    | TN                | $2.75 (\pm 0.236) \times SN + 5.78 (\pm 0.767)$  | 0.54  | <0.001 |
|                         |    | ●  | TN                | $0.00530 (\pm 0.000573) \times YD + 5.1 (\pm 1.02)$  | 0.42  | <0.001 |
| ●                       |    | ●  | TN                | $0.00364 (\pm 0.000434) \times YD + 2.15 (\pm 0.200) \times SN + 1.39 (\pm 0.802)$                                   | 0.71  | <0.001 |
| ●                       |    |    | MTS               | $-1.24 (\pm 0.266) \times SN + 59.24 (\pm 0.865)$  | 0.15  | <0.001 |
|                         | ●  |    | MTS               | $-0.217 (\pm 0.0747) \times TN + 58.6 (\pm 1.11)$  | 0.06  | <0.01  |
|                         |    | ●  | MTS               | $0.00295 (\pm 0.000567) \times YD + 50.5 (\pm 1.01)$   | 0.18  | <0.001 |
| ●                       |    | ●  | MTS               | $-1.96 (\pm 0.212) \times SN + 0.00447 (\pm 0.000461) \times YD + 53.85 (\pm 0.851)$                                 | 0.53  | <0.001 |
|                         | ●  | ●  | MTS               | $-0.788 (\pm 0.0558) \times TN + 0.00714 (\pm 0.000454) \times YD + 54.49 (\pm 0.678)$                               | 0.70  | <0.001 |
| ●                       | ●  | ●  | MTS               | $-0.54 (\pm 0.236) \times SN + -0.663 (\pm 0.0778) \times TN + 0.00688 (\pm 0.000460) \times YD + 54.77 (\pm 0.677)$ | 0.71  | <0.001 |

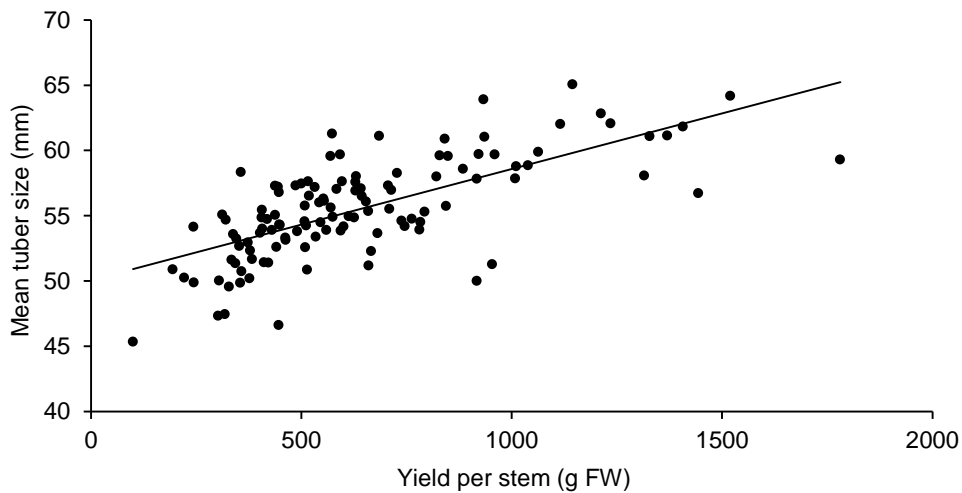
The multiple regressions were conceptually simplified by dividing the yield and number of tubers by the number of stems. From the relationship between the yield per stem and the number of tubers per stem it was apparent that although the number of tubers per stem increased as the yield per stem increased, the increase was not proportional, and so when the yield per stem doubled from 500 g to 1000 g, the number of tubers only increased by 50 % from 4.4 to 6.6 (Figure 22). As a consequence of the relationship between the yield per stem

and the number of tubers per stem, the mean tuber size increased as the yield per stem increased although the relationship was relatively weak (Figure 23).

**Figure 22. Relationship between yield per stem (YDS) and number of tubers per stem (TNS) in Survey 1. n = 118.  $TNS = 0.00437 (\pm 0.000333) \times YDS + 2.26 (\pm 0.236)$ ,  $R^2 = 0.59$ .**

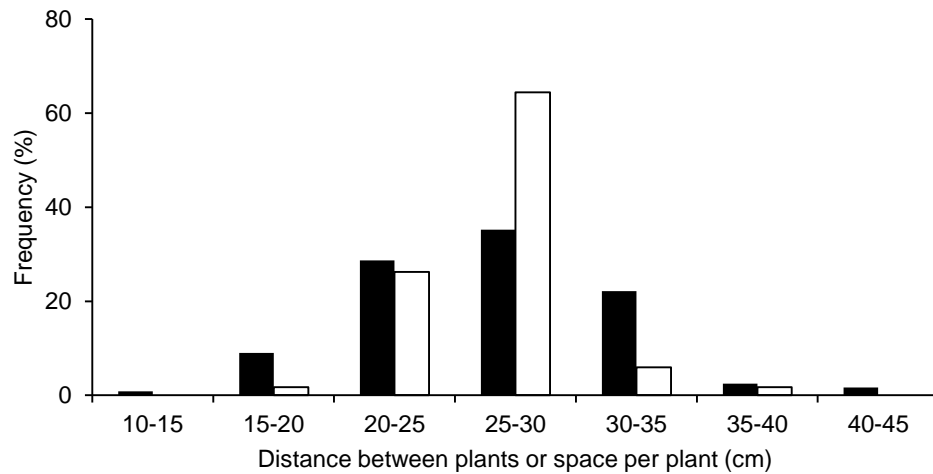


**Figure 23. Relationship between yield per stem (YDS) and mean tuber size (MTS) in Survey 1. n = 118.  $MTS = 0.000852 (\pm 0.000826) \times YDS + 50.06 (\pm 0.587)$ ,  $R^2 = 0.47$ .**

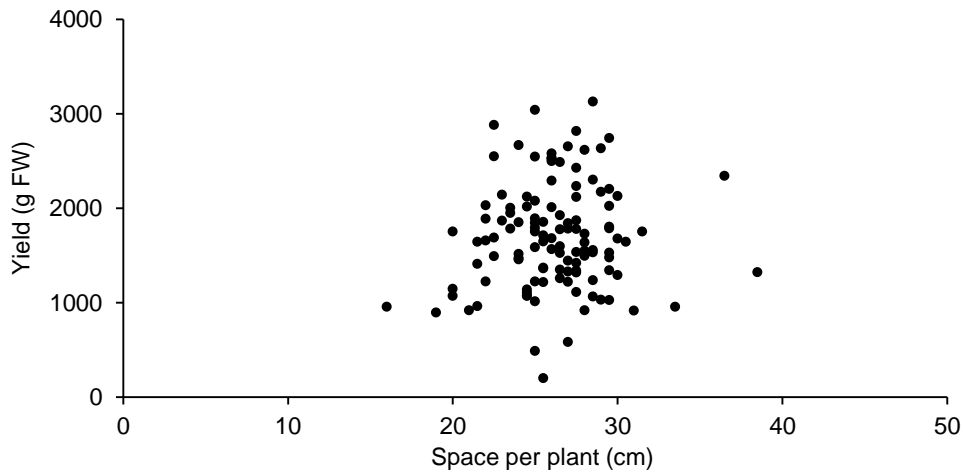


The COV of within-row spacing was *c.* 20 % but the COV of space per plant was lower at *c.* 12 % and the space per plant for almost all plants was within 5 cm of the mean (Figure 24). Although some plants had 50 % less space than others (20 cm rather than 30 cm) they did not produce a lower yield (Figure 25) or have a lower mean tuber size (data not shown).

**Figure 24. Distance between plants (■) and space per plant (□) in Survey 1. Distance: mean = 26.2 cm, COV = 20.7 %, n=122. Space: mean = 26.2 cm, COV = 12.3 %, n = 118.**



**Figure 25. Relationship between the space within the row per plant and yield per plant in Survey 1. There was no significant correlation.**



Considering the wide variation in above-ground stem weights and the relationship between the average yield per stem and the mean tuber size it was considered probable that the heavier above-ground stems produced a higher yield, and that tuber number did not increase sufficiently to counter the increase in yield, resulting in higher yielding stems producing larger tubers. Since variation in the mean tuber size of individual plants would be expected to contribute to the overall variation in tuber size within a crop, reducing variation in the yield of individual stems would theoretically reduce the COV of tuber size. This could be achieved by reducing variation in the number of stems per plant, yield per plant or by these two variables

correlating with each other so that the average yield per stem did not increase as yield increased.

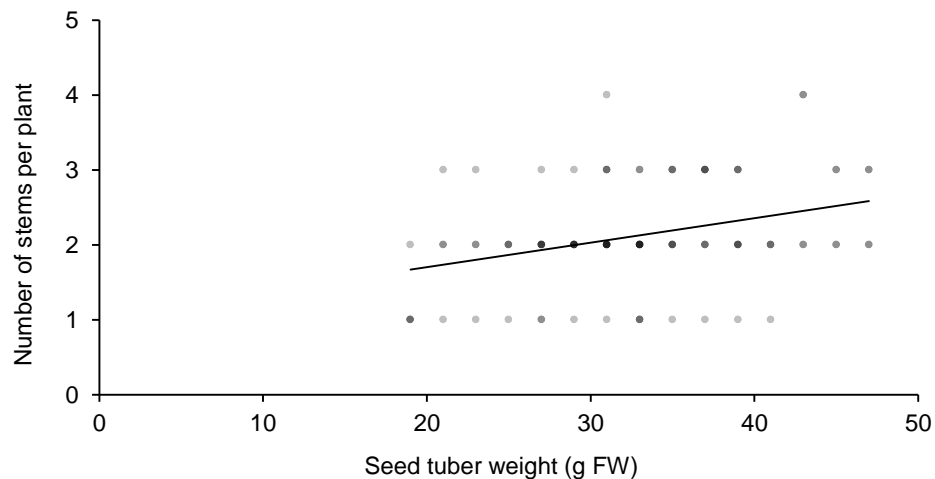
#### 4.2. Experiment 1 – Effects of variation in seed tuber weight and stem thinning

Unexpectedly, the thinned treatment reached 50 % emergence *c.* 2.5 days later than the other treatments but none of the treatments had an effect on the interval from 20 to 80 % emergence (Table 18). Initially ground cover was higher in the thinned treatment, but the difference was small and from *c.* 20 DAE there were no differences in ground cover between the treatments (data not shown). The seed tubers produced fewer stems than anticipated and as a result the thinned treatment had *c.* 40 % more stems than the other treatments (Table 18). As a consequence of this difference, the thinned treatment had a lower mean above-ground stem weight, a higher number of tubers and a lower mean tuber size at both harvests (Table 18). Changing variation in seed tuber weight had no effect on the number of stems, number of tubers, mean tuber size or the COV of tuber size (Table 18). The thinning treatment had no effect on yield or the COV of tuber size. Numerically the COV of tuber size was lower than the control, but this may have been at least partly due to the difference in mean tuber size between the treatments (Table 18). The COV of tuber size increased from *c.* 13 % at the first to *c.* 17 % at the second harvest in each of the variation in seed tuber weight treatments (Table 18). The treatments had no effect on the COV of above-ground stem weight at the first harvest and at the second harvest, in some plots > 20 % of stems had begun to senesce so the value could not be determined accurately (Table 18).

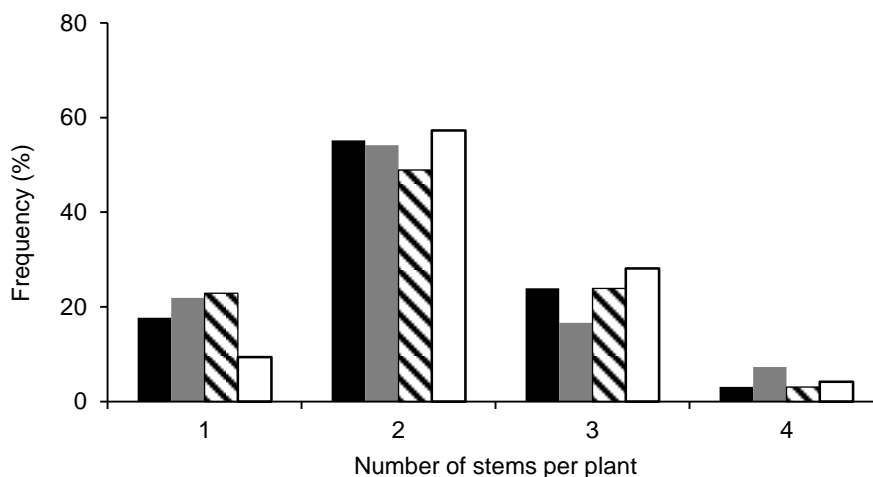
Variation in seed tuber weight had no effect on the average or COV of ground cover per plant 12 DAE (Table 19). The correlation between seed tuber weight and the number of stems per plant in the control treatment was weak (Figure 26) and as a result neither increasing nor decreasing variation in seed tuber weight had any effect on the COV of the number of stems per plant (Table 19; Figure 27). At the first harvest, increasing variation in seed tuber weight

increased the COV of yield per plant compared to the control, but decreasing variation in seed tuber weight had no effect (Table 19). By the second harvest however, the COV of yield per plant had increased in the control treatment and decreased in the more variable treatment and they were not significantly different. A small number of plants (*c.* 5 %) suffered from an unidentified disorder (daughter tubers were tested for the presence of common viruses but none were detected) that stunted their growth resulting in lower yields and lower numbers of tubers (*c.* 60 % lower yield and *c.* 40 % fewer tubers than the average). Due to the ability of neighbouring plants to compensate for weak plants, this did not appear to affect overall yield, but would have affected the COV of yield per plant within individual plots. Variation in seed tuber weight had no effect on the COV of the number of tubers per plant, or the COV of the mean tuber weight per plant at either harvest (Table 19).

**Figure 26. Relationship between seed tuber weight (ST) and number of stems per plant (SN) in the control treatment of Expt 1 at the first harvest (61 DAE). Darker points indicate where multiple plants had the same seed tuber weight and number of stems. Fitted line:  $SN = 0.0326 (\pm 0.00987) \times ST + 1.05 (\pm 0.332)$ ,  $R^2 = 0.09$ ,  $p = < 0.001$**



**Figure 27. Number of stems per plant for the variation in seed weight treatments at the first harvest of Expt 1. Control, black bars; more variable, grey bars; less variable, hatched bars; uniform, white bars.**



The date of emergence explained *c.* 70 % of the variation in ground cover per plant 12 DAE in each of the treatments and for both of the harvest areas (Table 20). In the area of the first harvest, when variation in seed tuber weight was increased, more of the variation in ground cover per plant was explained by variation in seed tuber weight, but this was not significantly so for the second harvest (Table 20). Regressions including both the date of emergence and seed tuber weight explained more of the variation in ground cover per plant in the control and more variable treatments, compared to either factor by itself, but not when variation in seed tuber weight was reduced, due to the lack of a correlation between seed tuber weight and ground cover per plant (Table 20). Variation in the date of emergence only explained *c.* 30 % of the variation in yield per plant at either harvest and there were no significant differences in the correlation coefficients between treatments (Table 20). When variation in seed tuber weight was increased, it explained significantly more of the variation in yield at both harvests, indicating that above a certain threshold, variation in seed tuber weight affected the yield per plant (Table 20). Ground cover 12 DAE explained *c.* 60 % of the variation in yield per plant at the first harvest but only *c.* 40 % of the variation at the second harvest in each of the treatments (Table 20). That variation in emergence explained a large proportion of the variation in ground cover 12 DAE but relatively little of the variation in yield demonstrates that the relative size of plants changed between 12 and 61 DAE because if each had grown at

a uniform rate based on their size at 12 DAE, the correlation coefficient of the regressions predicting yield would be similar to those predicting ground cover 12 DAE. In general, the yield of individual plants became less closely related to either the date of emergence, seed tuber weight or ground cover at 12 DAE between the harvests suggesting that the relative size of individual plants continued to change from 61-113 DAE.





**Table 19. Effects of variation in seed tuber weight on plant-to-plant variation in Expt 1 at each harvest (1 and 2, 61 and 113 DAE respectively).**

|  | Harvest | Variation in seed tuber weight |                  |                  |         | <i>P</i> | S.E.<br>(9 D.F.) |
|--|---------|--------------------------------|------------------|------------------|---------|----------|------------------|
|  |         | Control                        | More<br>variable | Less<br>variable | Uniform |          |                  |
| Ground cover per plant (cm <sup>2</sup> ) 12 DAE | n.a.    | 185                            | 182              | 167              | 201     | n.s.     | 15.2             |
| COV of ground cover per plant 12 DAE (%)         | n.a.    | 39.9                           | 45.5             | 47.0             | 39.8    | n.s.     | 2.05             |
| COV of number of stems per plant (%)             | 1       | 33.8                           | 38.7             | 37.9             | 31.0    | n.s.     | 4.28             |
|  | 2       | 33.5                           | 40.2             | 35.5             | 38.0    | n.s.     | 3.04             |
| COV of yield per plant (%)                       | 1       | 20.1                           | 34.4             | 23.8             | 21.4    | <0.01    | 2.24             |
|  | 2       | 27.2                           | 28.1             | 23.8             | 23.2    | n.s.     | 2.27             |
| COV of number of tubers per plant (%)            | 1       | 29.1                           | 36.0             | 30.0             | 30.4    | n.s.     | 3.00             |
|  | 2       | 31.2                           | 33.1             | 33.6             | 28.0    | n.s.     | 2.81             |
| COV of mean tuber weight per plant (%)           | 1       | 26.9                           | 24.4             | 29.9             | 27.8    | n.s.     | 2.77             |
|  | 2       | 31.3                           | 39.7             | 31.3             | 33.3    | n.s.     | 3.14             |

**Table 20. Effect of variation in seed tuber weight on the average correlation coefficients of linear regressions between the explanatory variables listed and ground cover per plant 12 DAE and yield per plant at each harvest of Expt 1 (1 and 2, 61 and 113 DAE respectively).**

| Explanatory variable(s)              | Response<br>variable | Harvest | Variation in seed tuber weight |                  |                  |         | <i>P</i> | S.E.<br>(9 D.F.) |
|--------------------------------------|----------------------|---------|--------------------------------|------------------|------------------|---------|----------|------------------|
|                                      |                      |         | Control                        | More<br>variable | Less<br>variable | Uniform |          |                  |
| Date of emergence                    | Ground cover         | 1       | 0.58                           | 0.66             | 0.69             | 0.75    | n.s.     | 0.069            |
|                                      |                      | 2       | 0.67                           | 0.64             | 0.69             | 0.71    | n.s.     | 0.041            |
| Seed tuber weight                    | Ground cover         | 1       | 0.14                           | 0.36             | 0.11             | 0.01    | <0.01    | 0.053            |
|                                      |                      | 2       | 0.10                           | 0.21             | 0.05             | 0.00    | n.s.     | 0.062            |
| Date of emergence, seed tuber weight | Ground cover         | 1       | 0.65                           | 0.79             | 0.70             | 0.74    | n.s.     | 0.063            |
|                                      |                      | 2       | 0.80                           | 0.75             | 0.74             | 0.70    | n.s.     | 0.035            |
| Date of emergence                    | Yield                | 1       | 0.28                           | 0.30             | 0.30             | 0.47    | n.s.     | 0.078            |
|                                      |                      | 2       | 0.28                           | 0.22             | 0.28             | 0.27    | n.s.     | 0.088            |
| Seed tuber weight                    | Yield                | 1       | 0.18                           | 0.41             | 0.07             | 0.00    | <0.05    | 0.077            |
|                                      |                      | 2       | 0.09                           | 0.38             | 0.10             | 0.00    | <0.001   | 0.027            |
| Date of emergence, seed tuber weight | Yield                | 1       | 0.43                           | 0.64             | 0.33             | 0.45    | n.s.     | 0.082            |
|                                      |                      | 2       | 0.37                           | 0.44             | 0.35             | 0.24    | n.s.     | 0.101            |
| Ground cover 12 DAE                  | Yield                | 1       | 0.59                           | 0.64             | 0.49             | 0.65    | n.s.     | 0.063            |
|                                      |                      | 2       | 0.42                           | 0.40             | 0.41             | 0.36    | n.s.     | 0.079            |

#### 4.3. Experiment 2 – Effects of variation in emergence

Both seed tubers warmed prior to planting and warmed seed tubers mixed with unwarmed seed tubers reached 50 % emergence *c.* 2 days earlier than the control, but the orientation of seed tubers had no effect on emergence (Table 21). The interval from 20 to 80 % emergence was approximately doubled by mixing warmed and unwarmed seed tubers and increased by 50 % by warming seed tubers compared to the control, but the orientation of the seed tubers had no effect (Table 21). When the shade material was removed from the shaded treatment, 7 DAE of the other treatments, the average ground cover per plant was significantly lower than that of the other treatments and the COV of ground cover per plant was significantly higher (Table 21). The reason for these differences is unclear but they may both have been caused by the shade material delaying emergence and causing the stems to etiolate compared to the other treatments.

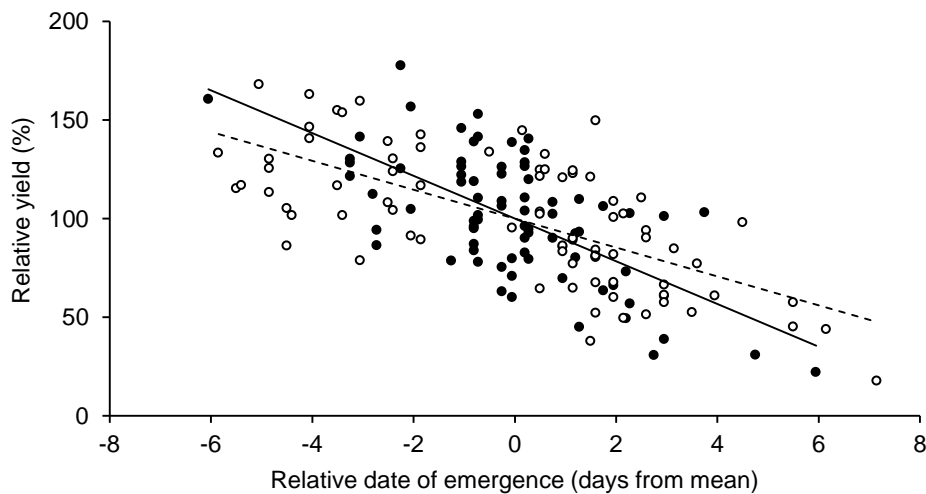
At the first harvest, the yield of the shaded treatment was *c.* 4 t/ha lower than the control and although a similar numerical difference occurred at later harvests, it was not significantly lower (Table 21). The number of tubers was *c.* 10 % lower in the shaded treatment at the first harvest compared to the control, but only the mixed and shaded treatments differed significantly (Table 21). The mean tuber size and the COV of tuber size were not affected by the treatments at any harvest (Table 21).

Despite the large difference in the interval from 20 to 80 % emergence between the control treatment and the mixed treatment, the COV of yield per plant did not significantly differ between the treatments (Table 22). The COV of yield per plant at the second and third harvests was lower than the COV of ground cover per plant 7 DAE in each of the treatments suggesting that relatively small plants grew faster than relatively large plants, thereby reducing the variation. This was particularly pronounced for the shaded treatment in which the COV of yield per plant was *c.* 60 % lower than the COV of ground cover per plant 7 DAE

(Tables 21-22). The COV of number of stems per plant, COV of number of tubers per plant, COV of yield per plant and the COV of mean tuber weight were unaffected by the treatments (Table 22).

At the second harvest, variation in the date of emergence explained significantly more of the variation in yield per plant in the mixed treatment than the control treatment, but at the third harvest the average correlation coefficients were not significantly different between any of the treatments (Table 23). Date of emergence explained *c.* 30 % of the variation in yield in each of the treatments (Table 23) but there was considerable variation in the yield of plants that emerged on the same day, indicating that other factors influenced the yield of individual plants (Figure 28).

**Figure 28. Relationship between relative date of emergence (EM, days from mean of each plot) and relative yield per plant (YD, percentage relative to the average of each plot) at the third harvest of Expt 2 for the control ● and mixed treatments ○. Fitted lines: Control, —  $YD = -10.9 (\pm 1.44) \times EM + 100.0 (\pm 2.73)$ ,  $R^2 = 0.42$ ; Mixed, - - -  $YD = -7.33 (\pm 0.900) \times EM + 100.0 (\pm 2.75)$ ,  $R^2 = 0.45$ .**



**Table 21. Effects of seed treatments on crop parameters at each harvest of Expt 2 (1-3, 47, 86 and 128 DAE respectively) † = S.E. based on 9 D.F.**

|   | Harvest | Control | Warmed | Mixed | Shaded | Orientation | <i>P</i> | S.E.<br>(12 D.F.) |
|---|---------|---------|--------|-------|--------|-------------|----------|-------------------|
| Interval from planting to 50 % emergence (days) | n.a.    | 32.8    | 31.1   | 31.5  | n.d.   | 33.2        | <0.01    | 0.33 †            |
| Interval from 20 to 80 % emergence (days)       | n.a.    | 2.45    | 3.50   | 4.82  | n.d.   | 2.46        | <0.01    | 0.422 †           |
| Ground cover per plant 7 DAE (cm <sup>2</sup> ) | n.a.    | 128.0   | 192.6  | 185.8 | 68.8   | 121.2       | <0.001   | 10.51             |
| COV of ground cover per plant 7 DAE (%)         | n.a.    | 43.7    | 33.4   | 49.5  | 78.0   | 45.6        | <0.001   | 2.58              |
| Number of stems (000/ha)                        | 1       | 105.8   | 109.5  | 112.2 | 97.6   | 108.6       | n.s.     | 5.60              |
|   | 2       | 105.8   | 104.9  | 109.5 | 109.5  | 105.8       | n.s.     | 4.87              |
|   | 3       | 104.4   | 103.1  | 113.5 | 103.1  | 103.4       | n.s.     | 3.75              |
| Number of tubers (000/ha)                       | 1       | 497     | 512    | 541   | 435    | 482         | <0.05    | 18.3              |
|   | 2       | 504     | 532    | 531   | 479    | 517         | n.s.     | 15.8              |
|   | 3       | 481     | 487    | 521   | 481    | 486         | n.s.     | 19.1              |
| Yield (t FW/ha)                                 | 1       | 22.4    | 24.0   | 23.5  | 18.2   | 22.3        | <0.001   | 0.64              |
|   | 2       | 56.5    | 57.9   | 58.5  | 52.5   | 57.3        | n.s.     | 2.62              |
|   | 3       | 72.8    | 72.3   | 74.7  | 70.9   | 72.8        | n.s.     | 3.95              |
| Mean tuber size (mm)                            | 1       | 41.0    | 41.1   | 40.1  | 40.6   | 40.7        | n.s.     | 0.41              |
|   | 2       | 54.6    | 54.7   | 55.1  | 55.6   | 54.9        | n.s.     | 0.77              |
|   | 3       | 60.7    | 59.8   | 59.4  | 60.5   | 59.7        | n.s.     | 1.08              |
| COV of tuber size (%)                           | 1       | 14.0    | 12.5   | 13.8  | 13.3   | 12.7        | n.s.     | 0.57              |
|   | 2       | 15.1    | 15.9   | 15.8  | 16.3   | 15.4        | n.s.     | 0.83              |
|   | 3       | 17.8    | 17.1   | 16.4  | 16.4   | 16.1        | n.s.     | 0.50              |

**Table 22. Effects of seed treatments on plant-to-plant variation in Expt 2 at the second and third harvests (86 and 128 DAE respectively).**

|  | Harvest | Control | Warmed | Mixed | Shaded | Orientation | <i>P</i> | S.E.<br>(12 D.F.) |
|--|---------|---------|--------|-------|--------|-------------|----------|-------------------|
| COV of number of stems per plant (%)   | 2       | 31.6    | 38.0   | 33.9  | 26.5   | 32.5        | n.s.     | 2.86              |
|  | 3       | 34.1    | 29.9   | 29.4  | 33.0   | 27.1        | n.s.     | 3.02              |
| COV of yield per plant (%)             | 2       | 25.5    | 26.4   | 38.5  | 24.4   | 32.4        | n.s.     | 3.80              |
|  | 3       | 31.4    | 27.3   | 33.8  | 32.1   | 28.9        | n.s.     | 3.27              |
| COV of number of tubers per plant (%)  | 2       | 30.7    | 32.5   | 32.5  | 29.9   | 30.5        | n.s.     | 3.48              |
|  | 3       | 32.2    | 26.5   | 26.8  | 30.0   | 26.9        | n.s.     | 2.67              |
| COV of mean tuber weight per plant (%) | 2       | 35.5    | 29.3   | 26.7  | 26.7   | 23.4        | n.s.     | 3.72              |
|  | 3       | 33.9    | 30.6   | 28.5  | 31.2   | 27.2        | n.s.     | 4.37              |

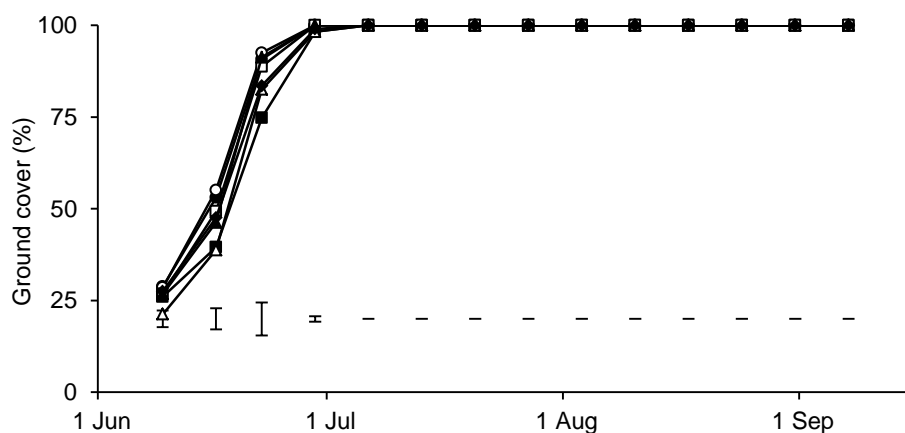
**Table 23. Effect of seed treatments on average correlation coefficients of linear regressions explaining variation in yield from the date of emergence in Expt 2 at the second and third harvests (86 and 128 DAE respectively).**

| Harvest | Control | Warmed | Mixed | Shaded | Orientation | <i>P</i> | S.E.<br>(9 D.F.) |
|---------|---------|--------|-------|--------|-------------|----------|------------------|
| 2       | 0.08    | 0.28   | 0.55  | n.d.   | 0.26        | <0.05    | 0.099            |
| 3       | 0.32    | 0.15   | 0.43  | n.d.   | 0.28        | n.s.     | 0.094            |

#### 4.4. Experiment 3 – Effects of variation in within-row spacing

None of the treatments had any effect on the interval from planting to 50 % emergence or from 20 to 80 % emergence (Table 24). The interval from 20 to 80 % emergence was relatively protracted in all of the treatments in comparison to in Expts 1 and 2 grown from the same seed tuber stock and planted at a similar date. Ground cover was slightly slower to develop in some of the non-uniform treatments in comparison to uniform spacing (treatment 1), but the differences were relatively small and all treatments developed complete canopies by the beginning of July, which persisted until the final harvest (Figure 29). There were no significant differences in the number of stems or the number of tubers between treatments at either harvest (Table 24). Yield was not affected by any of the treatments at the first harvest, but at the second, the yield of treatment 6 (in which two-thirds of the plants were spaced 1 cm apart) was significantly lower than treatments 3, 4 and 7 but not significantly different to the evenly spaced plants in treatment 1 (Table 24). The fresh weight of above-ground stems, the COV of above-ground stem weight, the mean tuber size and the COV of tuber size were not affected by treatments at either harvest (Table 24). Overall, the COV of tuber size increased from *c.* 15 % at the first harvest to *c.* 18 % at the second harvest (Table 24).

**Figure 29. Ground cover in Expt 3. Treatments: 1, ●; 2, ○; 3, ■; 4, □; 5, ▲; 6, △; 7, ◆. Bars represent S.E. (18 D.F.).**



The COV of number of stems per plant, number of tubers per plant, yield per plant and mean tuber weight were not significantly affected by any of the treatments at either harvest (Table 25). However, comparing the yield, number of tubers and mean tuber weight of individual plants in the most extreme treatments (1 and 7) revealed some differences in growth. In treatment 7, plants with less space in the row (12.5 cm on average) produced *c.* 50 % of the total yield and total number of tubers at the first harvest, indicating that they grew similarly to plants in the same treatment with more space (Table 26). The relative yield and relative number of tubers of plants with less space did not differ compared to evenly spaced plants in treatment 1, although the standard error was exceptionally high (Table 26). At the second harvest, the plants with less space in the row produced a lower proportion of the total yield and fewer tubers than those with more space, but the mean tuber weight per plant did not differ significantly as the differences in yield and in the number of tubers were of similar magnitude (Table 26). That there was no change in the mean tuber weight of plants with different amounts of space may explain why there was no difference in the COV of tuber size between these treatments.

Overall the results suggest that the growth of plants and stems within the crop was affected relatively little by differences in the amount of space per plant since even the substantial difference in planting arrangement between treatments 1 and 7 resulted in only minor differences in growth. That there were no significant differences in the COV of yield per plant or COV of number of tubers per plant between the treatments suggests that factors other than the space per plant influenced these variables.

**Table 24. Effects of variable within-row spacing on parameters of crop growth in Expt 3 at each harvest (1 and 2, 66 and 108 DAE respectively). Means were separated using Tukey's range test and means which were significantly different at the 95 % confidence level are distinguished by having different letters following the mean.**

|  | Harvest | Treatment |         |        |        |         |        |        | P     | S.E.<br>(18 D.F.) |
|--|---------|-----------|---------|--------|--------|---------|--------|--------|-------|-------------------|
|  |         | 1         | 2       | 3      | 4      | 5       | 6      | 7      |       |                   |
| Interval from planting to 50 % emergence (days)                            | n.a     | 34.8      | 34.7    | 34.2   | 34.6   | 33.7    | 34.1   | 34.0   | n.s.  | 0.61              |
| Interval from 20 to 80 % emergence (days)                                  | n.a     | 4.4       | 4.9     | 4.4    | 4.6    | 3.9     | 4.1    | 3.7    | n.s.  | 0.59              |
| Number of stems (000/ha)   | 1       | 101.0     | 91.8    | 100.5  | 101.4  | 102.1   | 98.7   | 106.9  | n.s.  | 4.33              |
|  | 2       | 104.2     | 99.2    | 105.5  | 108.3  | 107.4   | 100.1  | 110.1  | n.s.  | 4.64              |
| Number of tubers (000/ha)  | 1       | 518       | 472     | 521    | 506    | 504     | 459    | 467    | n.s.  | 24.3              |
|  | 2       | 519       | 514     | 518    | 544    | 547     | 480    | 530    | n.s.  | 25.6              |
| Yield (t FW/ha)  | 1       | 43.4      | 38.1    | 41.0   | 41.2   | 41.9    | 37.8   | 39.7   | n.s.  | 1.91              |
|  | 2       | 68.6 ab   | 69.6 ab | 74.1 b | 73.1 b | 70.4 ab | 62.2 a | 75.1 b | <0.01 | 2.05              |
| Above-ground stem weight (t FW/ha)   | 1       | 44.9      | 40.3    | 45.6   | 43.0   | 42.4    | 42.1   | 42.7   | n.s.  | 2.43              |
|  | 2       | 28.4      | 28.5    | 32.3   | 30.7   | 30.1    | 28.7   | 29.5   | n.s.  | 1.94              |
| Mean tuber size (mm)   | 1       | 50.9      | 50.0    | 50.2   | 50.5   | 50.7    | 50.0   | 51.3   | n.s.  | 0.54              |
|  | 2       | 58.9      | 59.6    | 60.9   | 59.9   | 59.6    | 59.1   | 61.2   | n.s.  | 0.57              |
| COV of tuber size (%)  | 1       | 14.9      | 15.2    | 15.5   | 15.3   | 14.9    | 14.7   | 15.7   | n.s.  | 0.64              |
|  | 2       | 16.9      | 17.9    | 17.9   | 17.3   | 18.4    | 18.3   | 18.8   | n.s.  | 0.74              |
| Mean above-ground stem weight (g FW)                                       | 1       | 449       | 449     | 454    | 435    | 423     | 430    | 403    | n.s.  | 20.0              |
|  | 2       | 266       | 277     | 300    | 271    | 279     | 287    | 270    | n.s.  | 20.1              |
| COV of above-ground stem weight (%)  | 1       | 67.1      | 64.7    | 63.6   | 67.1   | 66.6    | 66.6   | 68.9   | n.s.  | 3.39              |
|  | 2       | 72.4      | 70.4    | 64.5   | 76.7   | 74.5    | 66.8   | 79.1   | n.s.  | 3.75              |
| Transformed and weighted mean above-ground stem weight ( $\sqrt[3]{g}$ FW) | 1       | 8.33      | 8.34    | 8.37   | 8.33   | 8.14    | 8.20   | 8.16   | n.s.  | 0.146             |
|  | 2       | 7.09      | 7.14    | 7.27   | 7.25   | 7.24    | 7.21   | 7.27   | n.s.  | 0.187             |
| Transformed and weighted COV of above-ground stem weight (%)               | 1       | 18.5      | 18.0    | 18.0   | 18.9   | 18.6    | 18.6   | 18.7   | n.s.  | 0.91              |
|  | 2       | 20.5      | 19.5    | 17.0   | 19.5   | 20.5    | 17.9   | 21.2   | n.s.  | 0.95              |



**Table 25. Effects of variable within-row spacing on plant-to-plant variation in Expt 3 at each harvest (1 and 2, 66 and 108 DAE respectively) of Expt 3. Treatment 6 was excluded from the analysis as plants were not harvested separately.**

|   | Harvest | Treatment |      |      |      |      |      | <i>P</i> | S.E.<br>(15 D.F.) |
|---|---------|-----------|------|------|------|------|------|----------|-------------------|
|   |         | 1         | 2    | 3    | 4    | 5    | 7    |          |                   |
| COV of number of stems<br>per plant (%)   | 1       | 43.0      | 39.7 | 40.2 | 37.3 | 35.5 | 33.5 | n.s.     | 2.87              |
|   | 2       | 34.1      | 35.9 | 32.5 | 41.8 | 36.5 | 36.3 | n.s.     | 2.81              |
| COV of number of tubers<br>per plant (%)  | 1       | 37.3      | 36.3 | 37.2 | 36.7 | 39.4 | 37.4 | n.s.     | 3.23              |
|   | 2       | 31.9      | 38.6 | 31.5 | 40.5 | 31.9 | 37.8 | n.s.     | 2.65              |
| COV of yield per plant<br>(%)             | 1       | 31.8      | 36.5 | 33.8 | 43.3 | 34.9 | 40.8 | n.s.     | 3.10              |
|   | 2       | 29.5      | 33.4 | 32.5 | 36.1 | 32.2 | 39.6 | n.s.     | 2.59              |
| COV of mean tuber<br>weight per plant (%) | 1       | 27.0      | 29.0 | 35.2 | 27.1 | 28.9 | 34.9 | n.s.     | 3.06              |
|   | 2       | 27.9      | 31.8 | 30.7 | 29.4 | 34.4 | 28.7 | n.s.     | 3.34              |

**Table 26. Comparison of the yield, number of tubers and mean tuber weight of plants in Expt 3 with an average of 12.5 cm space within the row in treatment 7 with equivalently placed plants with an average of 30 cm space within the row in treatment 1.**

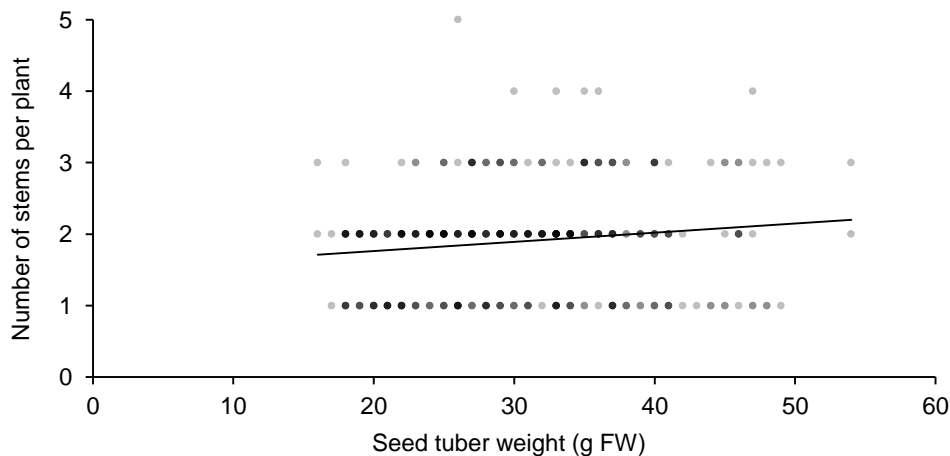
|   | Harvest | Treatment |      | <i>P</i> | S.E.<br>(3 D.F.) |
|---|---------|-----------|------|----------|------------------|
|   |         | 1         | 7    |          |                  |
| Yield (% of plot)                               | 1       | 47.0      | 49.5 | n.s.     | 2.43             |
|   | 2       | 49.2      | 44.6 | <0.01    | 0.57             |
| Number of tubers (% of<br>plot)                 | 1       | 47.0      | 51.8 | n.s.     | 1.95             |
|   | 2       | 48.7      | 44.7 | <0.01    | 0.28             |
| Mean tuber weight (%<br>relative to whole plot) | 1       | 100.5     | 95.4 | n.s.     | 4.31             |
|   | 2       | 100.9     | 99.4 | n.s.     | 2.01             |

## 4.5. Survey 2

### 4.5.1. Seed tuber weight and the number of stems per plant

The number of stems per plant correlated weakly with the weight of seed tubers at each harvest, with the relationship shown in Figure 30 being typical of the later harvests. Across the nine harvests, the average number of stems per plant was 1.93 and the COV of the number of stems per plant was 40.0 %.

**Figure 30. Relationship between seed tuber weight (ST) and number of stems per plant (SN) pooled from the first three harvests of Survey 2. Darker points indicate where multiple plants had the same seed tuber weight and number of stems. Fitted line:  $SN = 0.0132 (\pm 0.00476) \times ST + 1.50 (\pm 0.149)$ .  $R^2 = 0.02$ ,  $p < 0.01$ .**

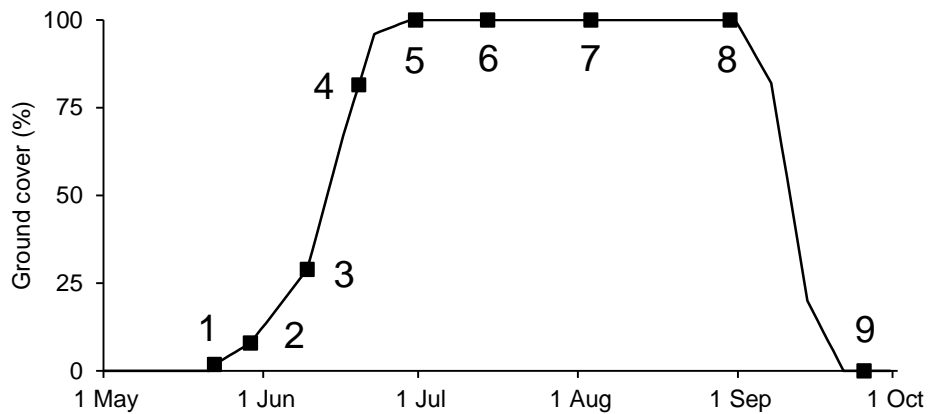


### 4.5.2. Emergence and ground cover

Over 99 % of plants emerged, but the date of emergence was not recorded for *c.* 5 % of the stems as they emerged after tagging was completed, or were not distinguishable from other stems on the same plant on the day they emerged. These stems were excluded from analyses examining the influence of emergence on growth. Averaged across the nine harvests, the interval from planting to 50 % plant emergence was 38.3 days and the interval from 20 to 80 % emergence was 3.6 days. For stems, the interval from planting to 50 % emergence and the interval from 20 to 80 % emergence was *c.* 1 day longer than for plants. The COV of planting depth at the first two harvests was *c.* 16 %, but planting depth did not explain any of the variation in the date of emergence of plants or stems, and neither did emergence correlate

with either seed tuber weight or the number of stems per plant (data not shown). The ground cover over the course of the season is shown in Figure 31.

**Figure 31. Ground cover in Survey 2 in relation to dates of the nine harvests.**



#### 4.5.3. Initial growth of plants

The percentage dry matter of seed tubers decreased by *c.* 50 % between planting and the first harvest and continued to decline between subsequent harvests, falling to 3.3 % by the fifth harvest (Table 27). At harvests 2-4, the percentage dry matter correlated very weakly ( $R^2 = 0.03$ ) with the seed tuber weight at planting and at the fifth harvest there was no significant relationship (data not shown). The above-ground stem weight increased *c.* 6-fold between the first and the second and the second and third harvests, but the ground cover per plant only increased *c.* 4-fold (Table 27). The COV of the above-ground stem weight and ground cover per plant were both lower at the second and third harvests than at the first harvest (Table 27). The proxy diameter of the below-ground stems increased by *c.* 25 % between the first and second harvests, but doubled between the second and third harvests (Table 27).

**Table 27. Plant-to-plant variation in percentage dry matter of seed tubers and estimated dry weight lost from seed tubers at planting (P) and harvests 1-5 and plant-to-plant variation of other variates at harvests 1-3 of Survey 2.**

|   | Sample                          | Mean  | COV (%) |
|---|---------------------------------|-------|---------|
| Percentage dry matter of seed tubers              | P                               | 26.5  | 9.6     |
|   | 1                               | 15.8  | n.d.    |
|   | 2                               | 11.2  | 26.2    |
|   | 3                               | 7.5   | 22.7    |
|   | 4                               | 5.3   | 27.3    |
| Estimated dry weight lost from seed tubers (g DW) | 5                               | 3.3   | 15.2    |
|   | 1                               | 3.57  | n.d.    |
|   | 2                               | 4.53  | 30.3    |
|   | 3                               | 5.74  | 25.1    |
|   | 4                               | 6.37  | 25.7    |
| Above-ground stem weight (g FW)                   | 5                               | 7.29  | 25.7    |
|   | 1                               | 4.43  | 76.8    |
|   | 2                               | 26.4  | 44.4    |
|   | 3                               | 159.3 | 34.6    |
|   | Ground cover (cm <sup>2</sup> ) | 1     | 47.6    |
| 2   |                                 | 211   | 37.8    |
| 3   |                                 | 771   | 25.5    |
| Proxy diameter of below-ground stems (g FW/cm)    | 1                               | 0.35  | 27.3    |
|   | 2                               | 0.43  | 31.9    |
|   | 3                               | 0.81  | 31.1    |

Date of emergence explained 67 % of the variation in the above-ground stem weight at the first harvest and *c.* 50 % at the second and third harvests (Table 28). Seed tuber weight only had a weak effect on the above-ground stem weight at the first three harvests, but improved the fit of regressions when combined with date of emergence (Table 28). The dry weight lost from individual seed tubers was not determined at the first harvest, but at the second and third harvests, the amount of dry weight lost from the seed tubers improved the fit of regressions compared to date of emergence and seed tuber weight alone (Tables 28-29).

**Table 28. Relationships between date of emergence (EM, relative to the first day that a stem emerged), seed tuber weight (ST, g FW) and the above-ground stem weight per plant (AG, g FW) at the first three harvests of Survey 2.  $AG = m EM + n ST + c$ .**

| Harvest | EM | ST | <i>m</i> | S.E.   | <i>n</i> | S.E.   | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----|----|----------|--------|----------|--------|----------|-------|----------|-----------------------|
| 1       | ●  |    | -1.375   | 0.0881 | n.a.     | n.a.   | 17.98    | 0.869 | <0.001   | 0.67                  |
|         |    | ●  | n.a.     | n.a.   | 0.094    | 0.0360 | 1.6      | 1.13  | <0.01    | 0.05                  |
| 2       | ●  | ●  | -1.384   | 0.0813 | 0.089    | 0.0193 | 15.33    | 0.986 | <0.001   | 0.72                  |
|         | ●  |    | -3.56    | 0.347  | n.a.     | n.a.   | 61.3     | 3.49  | <0.001   | 0.46                  |
|         |    | ●  | n.a.     | n.a.   | 0.54     | 0.120  | 10.2     | 3.73  | <0.001   | 0.13                  |
| 3       | ●  | ●  | -3.44    | 0.314  | 0.470    | 0.314  | 46.0     | 4.21  | <0.001   | 0.56                  |
|         | ●  |    | -14.9    | 1.33   | n.a.     | n.a.   | 305      | 13.5  | <0.001   | 0.50                  |
|         |    | ●  | n.a.     | n.a.   | 2.72     | 0.624  | 77       | 19.4  | <0.001   | 0.13                  |
|         | ●  | ●  | -14.7    | 1.16   | 2.60     | 0.410  | 224      | 17.3  | <0.001   | 0.62                  |

**Table 29. Relationships between date of emergence (EM, relative to the first day that a stem emerged), dry weight lost from the seed tuber (WL, g DW) and the above-ground stem weight per plant (AG, g FW) at the second and third harvests of Survey 2.  $AG = m EM + n WL + c$ .**

| Harvest | <i>m</i> | S.E.  | <i>n</i> | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----------|-------|----------|-------|----------|------|----------|-----------------------|
| 2       | n.a.     | n.a.  | 5.87     | 0.559 | -0.2     | 2.64 | <0.001   | 0.47                  |
|         | -2.60    | 0.287 | 4.34     | 0.287 | 32.2     | 4.12 | <0.001   | 0.68                  |
| 3       | n.a.     | n.a.  | 22.3     | 2.87  | 32       | 16.9 | <0.001   | 0.33                  |
|         | -13.37   | 0.998 | 18.6     | 1.85  | 184      | 15.6 | <0.001   | 0.73                  |

The total proxy diameter of the below-ground stems increased as seed tuber weight and number of stems per plant increased (Table 30). The strength of the relationships were similar at the first and second harvests but weaker at the third harvest (Table 30).

**Table 30. Relationships between the number of stems per plant (SN), seed tuber weight (ST, g FW) and the proxy diameter of below-ground stems per plant (PSD, g FW/cm) at the first three harvests of Survey 2.  $PSD = m SN + n ST + c$ .**

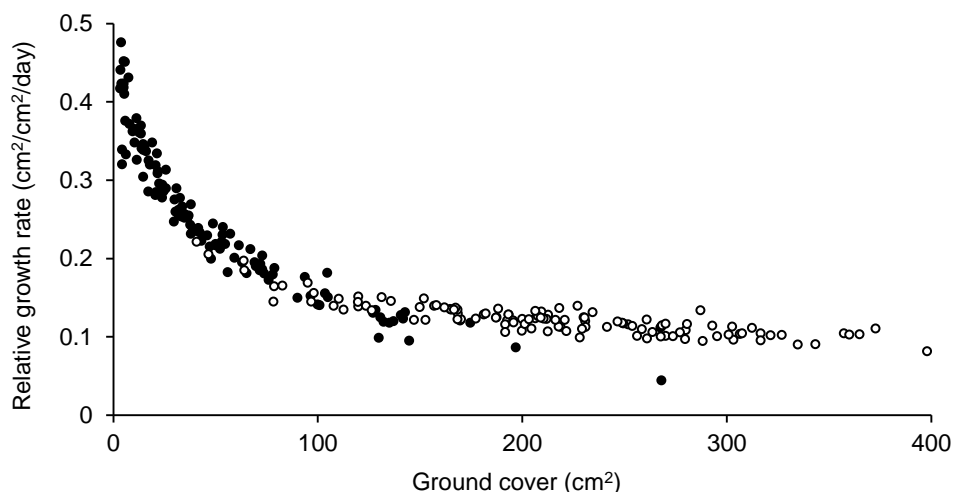
| Harvest | SN | ST | <i>m</i> | S.E.    | <i>n</i> | S.E.     | <i>c</i> | S.E.   | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----|----|----------|---------|----------|----------|----------|--------|----------|-----------------------|
| 1       | ●  |    | 0.0661   | 0.00985 | n.a.     | n.a.     | 0.231    | 0.0198 | <0.001   | 0.26                  |
|         |    | ●  | n.a.     | n.a.    | 0.00802  | 0.000757 | 0.111    | 0.0238 | <0.001   | 0.47                  |
| 2       | ●  | ●  | 0.0610   | 0.00629 | 0.00769  | 0.000572 | 0.072    | 0.0209 | <0.001   | 0.70                  |
|         | ●  |    | 0.113    | 0.0130  | n.a.     | n.a.     | 0.208    | 0.0271 | <0.001   | 0.37                  |
|         |    | ●  | n.a.     | n.a.    | 0.0110   | 0.00114  | 0.099    | 0.0354 | <0.001   | 0.42                  |
| 3       | ●  | ●  | 0.088    | 0.0103  | 0.00894  | 0.000941 | -0.010   | 0.0309 | <0.001   | 0.64                  |
|         | ●  |    | 0.152    | 0.0285  | n.a.     | n.a.     | 0.526    | 0.0572 | <0.001   | 0.18                  |
|         |    | ●  | n.a.     | n.a.    | 0.0167   | 0.00267  | 0.305    | 0.0834 | <0.001   | 0.24                  |
|         | ●  | ●  | 0.135    | 0.0250  | 0.0153   | 0.00243  | 0.097    | 0.0846 | <0.001   | 0.38                  |

At the first three harvests, the ground cover per plant correlated strongly ( $R^2 = 0.87-0.95$ ; data not shown) with the above-ground stem weight demonstrating that this was an effective way to estimate the weight of above-ground stems non-destructively.

The relative growth rate of ground cover of plants sampled at the third harvest decreased as the ground cover per plant increased (Figure 32). Between the first and second harvests the

relative growth rate of the smallest plants was extremely high, increasing by *c.* 30-50 % each day whereas the largest plants only grew by *c.* 10 % each day (Figure 32). This difference in the relative growth rate explains why the COV of the above-ground stem weight and ground cover per plant decreased between the first and second harvests (Table 27). Plants of similar size at the first and second harvests grew at similar rates in the interval between harvests despite the increasing day length (Figure 32). Although the ground cover at the first or second harvest was the predominant cause of variation in relative growth rate, it is notable that comparatively small variations in relative growth rate (e.g. 0.10 vs. 0.15) for plants with similar ground cover resulted in relatively large differences in overall growth over a period of 11 days (as between the second and third harvests).

**Figure 32. Relative growth rate of ground cover of plants sampled at the third harvest of Survey 2 between the first and second harvests (●) and between the second and third harvests (○).**



The different relative growth rates between the first and second harvests meant that ground cover at the first harvest was a relatively poor predictor (using linear regression) of the above-ground stem weight at the second and third harvests (Table 31). A square root transformation of ground cover at the first harvest improved the fit of the linear relationships and other terms could then be added (Table 31). Plants with the same ground cover at the first or second harvest but with a higher number of stems or those growing from larger seed tubers had higher above-ground stem weights at the subsequent harvests and regressions including all

three factors explained *c.* 90 % of the variation in the above-ground stem weight at the next harvest (Table 31).

**Table 31. Correlation coefficients of relationships (Untransformed GC  $R^2$ ) explaining variation in the above-ground stem weight per plant at the second and third harvests (AG at H2/H3) from ground cover at the first harvest (GC at H1), ground cover at the second harvest (GC at H2), seed tuber weight (ST) and the number of stems per plant (SN) and the same relationships, when the square root of the ground cover was used (Transformed GC  $R^2$ )**

| Explanatory variables | Response variable | Untransformed | Transformed |
|-----------------------|-------------------|---------------|-------------|
|                       |                   | GC $R^2$      | GC $R^2$    |
| GC at H1              | AG at H2          | 0.73          | 0.80        |
| GC at H1, ST          | AG at H2          | 0.80          | 0.86        |
| GC at H1, SN          | AG at H2          | 0.80          | 0.85        |
| GC at H1, SN, ST      | AG at H2          | 0.84          | 0.89        |
| GC at H1              | AG at H3          | 0.51          | 0.66        |
| GC at H1, ST          | AG at H3          | 0.60          | 0.75        |
| GC at H1, SN          | AG at H3          | 0.63          | 0.75        |
| GC at H1, SN, ST      | AG at H3          | 0.70          | 0.82        |
| GC at H2              | AG at H3          | 0.84          | 0.82        |
| GC at H2, ST          | AG at H3          | 0.87          | 0.86        |
| GC at H2, SN          | AG at H3          | 0.89          | 0.85        |
| GC at H2, SN, ST      | AG at H3          | 0.91          | 0.89        |

#### 4.5.4. Initial growth of stems

The majority (*c.* 85-90 %) of stems originated from the apical end of seed tubers and at the first three harvests, the average weight of above-ground stems originating from the centre or stolon end of seed tubers did not differ appreciably (data not shown). The above-ground stem weight approximately quadrupled between the first and second harvests and the COV decreased from 84 % to 64 % (Table 32). Between the second and third harvests, above-ground stem weight increased six-fold but the COV was relatively unchanged (Table 32). The proxy diameter of below-ground stems increased by *c.* 10 % between the first and second harvests and the COV was similar (Table 32). The proxy diameter of below-ground stems doubled between the second and third harvests, but the COV was similar to at the first two harvests (Table 32).

**Table 32. Stem-to-stem variation at the first three harvests of Survey 2.**

|  | Harvest | Mean | COV (%) |
|--|---------|------|---------|
| Above-ground stem weight (g FW)                | 1       | 2.83 | 84.1    |
|  | 2       | 13.6 | 64.3    |
|  | 3       | 84.0 | 59.1    |
| Proxy diameter of below-ground stems (g FW/cm) | 1       | 0.19 | 45.0    |
|  | 2       | 0.22 | 45.0    |
|  | 3       | 0.43 | 49.8    |

Date of emergence explained  $\geq 50$  % of the variation in above-ground stem weight at the first three harvests (Table 33). At the first two harvests, the number of stems per plant had only a very weak effect on the above-ground stem weight, but the effect was stronger at the third harvest (Table 33). The proxy below-ground stem diameter correlated relatively weakly with above-ground stem weight at the first harvest, but the relationship strengthened at subsequent harvests (Table 33). Multiple regressions, combining these factors explained a greater proportion of the variation than individual factors and the correlation coefficients were relatively stable between harvests, with date of emergence and proxy below-ground stem diameter explaining the greatest proportion of the variation in above-ground stem weight (Table 34).



**Table 33. Relationships between date of emergence (EM, relative to the first day that a stem emerged), the number of stems per plant (SN), proxy below-ground stem diameter (PSD, g FW/cm) and above-ground stem weight (AG, g FW) at the first three harvests of Survey 2.  $AG = mx + c$  where  $x = EM, SN$  or  $PSD$ .**

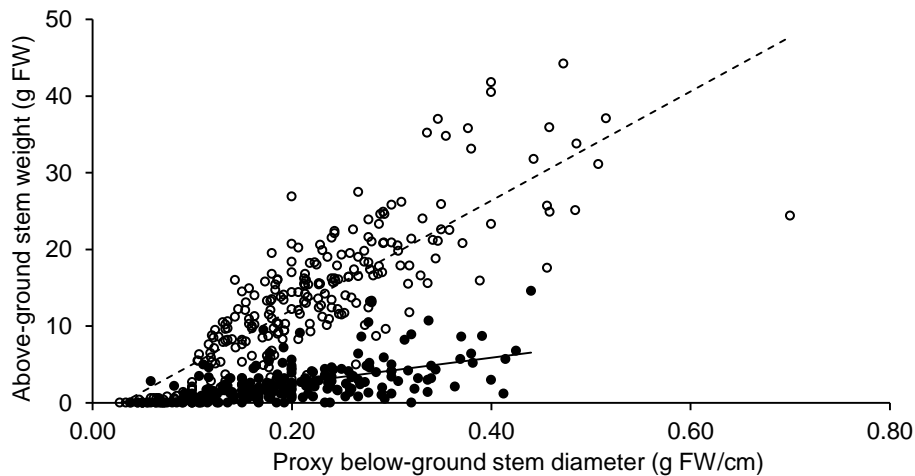
| Harvest | EM | SN | PSD | $m$    | S.E.   | $c$   | S.E.  | $P$    | $R^2$ |
|---------|----|----|-----|--------|--------|-------|-------|--------|-------|
| 1       | ●  |    |     | -0.886 | 0.0496 | 11.80 | 0.513 | <0.001 | 0.62  |
|         |    | ●  |     | -0.99  | 0.193  | 4.52  | 0.445 | <0.001 | 0.10  |
|         |    |    | ●   | 16.8   | 1.49   | -0.81 | 0.311 | <0.001 | 0.35  |
| 2       | ●  |    |     | -2.31  | 0.131  | 38.7  | 1.43  | <0.001 | 0.57  |
|         |    | ●  |     | -3.22  | 0.686  | 20.7  | 1.62  | <0.001 | 0.08  |
|         |    |    | ●   | 71.1   | 3.33   | -2.10 | 0.804 | <0.001 | 0.65  |
| 3       | ●  |    |     | -10.02 | 0.675  | 197.2 | 7.65  | <0.001 | 0.50  |
|         |    | ●  |     | -35.1  | 3.95   | 160.2 | 8.98  | <0.001 | 0.25  |
|         |    |    | ●   | 212.0  | 6.39   | -6.6  | 3.05  | <0.001 | 0.82  |

**Table 34. Multiple regressions between date of emergence (EM, relative to the first day that a stem emerged), the number of stems per plant (SN), proxy below-ground stem diameter (PSD, g FW/cm) and above-ground stem weight (AG, g FW) at the first three harvests of Survey 2.  $AG = m EM + nx + c$  where  $x = SN$  or  $PSD$ .**

| Harvest | EM | SN | PSD | $m$    | S.E.   | $n$   | S.E.  | $c$   | S.E.  | $P$    | $R^2$ |
|---------|----|----|-----|--------|--------|-------|-------|-------|-------|--------|-------|
| 1       | ●  | ●  |     | -0.861 | 0.0468 | -0.67 | 0.129 | 12.95 | 0.531 | <0.001 | 0.67  |
|         | ●  |    | ●   | -0.798 | 0.0401 | 11.5  | 1.07  | 8.54  | 0.506 | <0.001 | 0.76  |
| 2       | ●  | ●  |     | -2.24  | 0.128  | -1.83 | 0.448 | 41.9  | 1.60  | <0.001 | 0.60  |
|         | ●  |    | ●   | -1.52  | 0.102  | 48.4  | 2.97  | 19.3  | 1.54  | <0.001 | 0.80  |
| 3       | ●  | ●  |     | -9.05  | 0.598  | -24.1 | 2.86  | 237.9 | 8.23  | <0.001 | 0.62  |
|         | ●  |    | ●   | -4.01  | 0.447  | 169.6 | 7.34  | 56.3  | 7.36  | <0.001 | 0.86  |

The changes in the relationships between the proxy below-ground stem diameter and above-ground stem weight are of particular interest considering the relationships between proxy below-ground stem diameter and seed tuber weight of plants (Section 4.5.3). Between the first and second harvests, proxy below-ground stem diameter increased by  $c$ . 10 % whereas above-ground stem weight increased by  $c$ . 400 % (Table 32, Figure 33) and the correlation coefficient approximately doubled (Table 33). The change in the slope of the relationship between the first and second harvests suggests that the proxy below-ground stem diameter affected the growth of the above-ground stems because if the above-ground stem weight was determining the proxy below-ground stem diameter, the slope would have been relatively similar between harvests (Figure 33).

**Figure 33. Relationship between proxy below-ground stem diameter (PSD, g FW/cm) and above-ground stem weight (AG, g FW) at the first (—●—) and second (- -○- -) harvests of Survey 2. See Table 33 for details of fitted lines.**



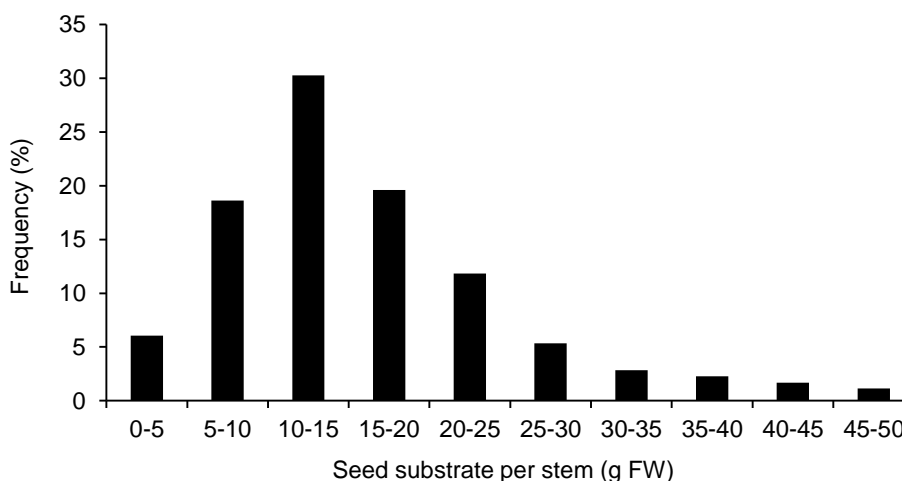
#### 4.5.4.1. Seed tuber substrate per stem

The amount of seed tuber substrate per stem was estimated at the first three harvests from the proxy diameter of each below-ground stem and seed tuber weight as described in Section 3.1.3.5. The mean seed tuber substrate was similar at each harvest (Table 35), with the differences caused by variations in the number of stems per plant. The COV of seed tuber substrate per stem was estimated to be highly variable at *c.* 55 % at each harvest (Table 35). The distribution had a long tail, caused by single-stemmed plants growing from relatively large seed tubers (Figure 34).

**Table 35. Average and COV of seed tuber substrate per stem (g FW) at the first three harvests of Survey 2.**

| Harvest | Mean | COV (%) |
|---------|------|---------|
| 1       | 16.2 | 57.8    |
| 2       | 15.4 | 52.3    |
| 3       | 16.1 | 55.7    |

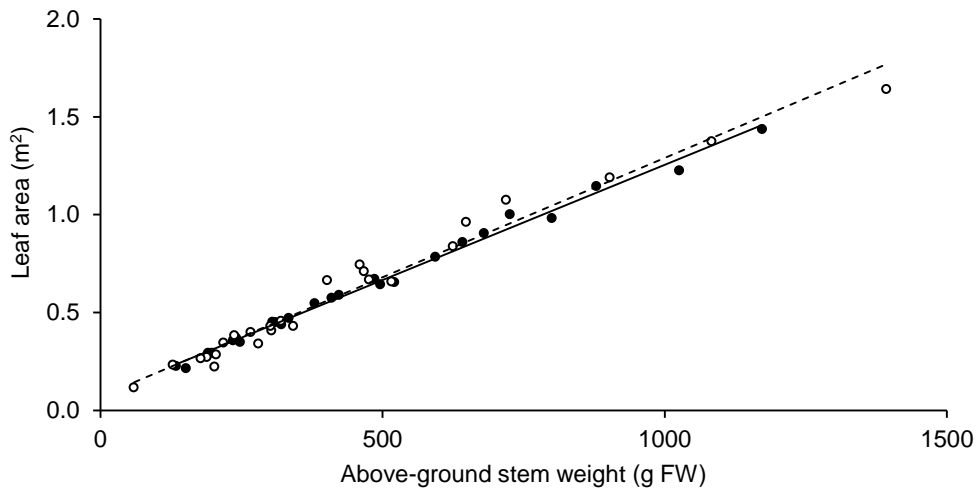
**Figure 34. Seed tuber substrate per stem pooled for the first three harvests of Survey 2.**



#### 4.5.5. Leaf area per stem

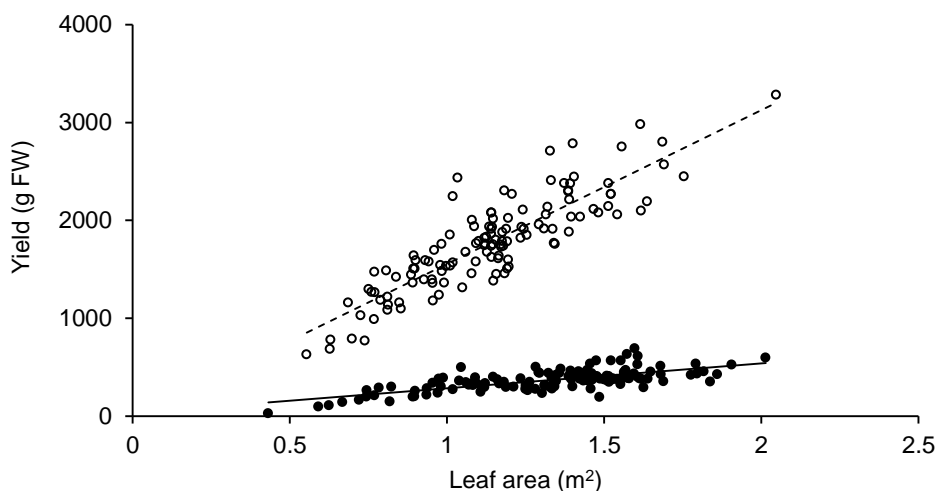
At the fifth and eighth harvests, above-ground stem weight correlated very strongly with leaf area per stem and the relationships were similar at the two harvests (Figure 35) despite mean above-ground stem weight being *c.* 20 % lower at the later harvest (Table 39). The slope of the relationships meant that larger stems had a low leaf area per gram than smaller stems, with an increase of the above-ground stem weight from 500 to 1000 g associated with an 88 % increase in the leaf area (Figure 35).

**Figure 35. Relationship between above-ground stem weight (AG) and leaf area per stem (LA) at the fifth (●) and eighth (○) harvests of Survey 2. Fitted lines: Fifth harvest, —  $LA = 0.001177 (\pm 0.0000211) \times AG + 0.077 (\pm 0.0116)$ ,  $R^2 = 0.99$ ; Eighth harvest, - - -  $LA = 0.001219 (\pm 0.0000418) \times YD + 0.072 (\pm 0.0224)$ ,  $R^2 = 0.97$ .**



The relationships listed in Figure 35 were used to calculate leaf area per plant at the fifth and eighth harvests from above-ground stem weight of each stem. At both harvests, the relationships were close to being proportional indicating that yield doubled for each doubling of leaf area, but the relationship was relatively weak at the fifth harvest compared to the eighth harvest (Figure 36). This may be because the canopy had recently closed at the time of the fifth harvest, and differences in the overall ground cover at different locations in the crop may have affected the allocation between the tubers and the above-ground stems. The above-ground stems of plants with relatively large neighbours (and thus relatively little space left to grow into) may have grown more slowly and consequently allocated a greater proportion of photosynthate to the tubers.

**Figure 36. Relationship between leaf area per plant (LA) and yield per plant (YD) at the fifth (●) and eighth (○) harvests of Survey 2. Fitted lines: Fifth harvest, —  $YD = 256 (\pm 22.6) \times LA + 29 (\pm 30.7)$ ,  $R^2 = 0.50$ ; Eighth harvest, - - -  $YD = 1572 (\pm 80.8) \times LA - 18 (\pm 94.4)$ ,  $R^2 = 0.75$ .**



#### 4.5.6. Overall yield and tuber size

At the fourth harvest, when yield was very low, the COV of tuber size was *c.* 20 % (Table 36). The COV was lower at the fifth, sixth and seventh harvests at *c.* 15 % but higher at the eighth and ninth harvests (*c.* 17 %) although it was not possible to determine whether these changes over time were due to chance (Table 36). At the final harvest, yield was *c.* 70 t/ha and mean tuber size *c.* 66 mm (Table 36).

**Table 36. Yield, mean tuber size and the COV of tuber size at harvests 4-9 of Survey 2.**

|                       | Harvest |      |      |      |      |      |
|-----------------------|---------|------|------|------|------|------|
|                       | 4       | 5    | 6    | 7    | 8    | 9    |
| Yield (t FW/ha)       | 3.8     | 13.6 | 29.8 | 45.4 | 63.9 | 71.2 |
| Mean tuber size (mm)  | 27.0    | 38.3 | 49.6 | 55.4 | 65.1 | 65.9 |
| COV of tuber size (%) | 19.9    | 14.8 | 14.6 | 14.8 | 16.9 | 17.2 |

#### 4.5.7. Yield per plant

The average above-ground stem weight increased until the seventh harvest but declined at the eighth harvest (Table 37). The COV of above-ground stem weight was stable between harvests 4-8 at 30-32 % and the COV of yield per plant was slightly lower at each successive harvest, except at the fourth harvest where it was substantially higher (Table 37). The higher COVs at the fourth harvest were probably caused by differences in allocation as discussed in Section 4.5.5. The lower COV of yield per plant than the COV of above-ground stem at

harvests 4-8 was due to larger plants having proportionally lower leaf areas for a given weight than smaller plants, also as discussed in Section 4.5.5.

**Table 37. Average and COV of above-ground stem weight and yield per plant at harvests 4-9 of Survey 2.**

|                                 |         | Harvest |      |      |      |      |      |
|---------------------------------|---------|---------|------|------|------|------|------|
|                                 |         | 4       | 5    | 6    | 7    | 8    | 9    |
| Above-ground stem weight (g FW) | Mean    | 476     | 864  | 942  | 968  | 698  | n.d. |
|                                 | COV (%) | 31.6    | 30.2 | 30.2 | 32.1 | 31.1 | n.d. |
| Yield (g FW)                    | Mean    | 102     | 367  | 800  | 1233 | 1772 | 1912 |
|                                 | COV (%) | 47.4    | 29.9 | 26.9 | 26.9 | 27.0 | 25.6 |

With the exception of the sixth harvest, seed tuber weight had a significant effect on yield per plant at each harvest but only explained *c.* 10-15 % of variation in yield per plant (Table 38). The slopes of relationships between seed tuber weight and yield per plant were relatively shallow, such that a doubling of seed tuber weight from 20 to 40 g increased the yield by *c.* 33 % (Table 38). Date of emergence explained a greater proportion of the variation in the yield per plant than seed tuber weight at each harvest (Table 38). The proportion of variation in yield that could be explained by date of emergence decreased between the fourth and sixth harvests, probably due to differences in the date when complete canopy development occurred at different locations within the crop (Table 38). Ground cover at the second harvest plant explained *c.* 70 % of variation in yield per plant at the fourth and fifth harvests, but less at later harvests, although it still explained *c.* 50 % of variation at the final harvest (Table 38).

**Table 38. Relationships between seed tuber weight (ST, g FW), date of emergence (EM, relative to the first day that a stem emerged), ground cover at the second harvest (GC, cm<sup>2</sup>) and yield per plant (YD, g FW) at harvests 4-9 of Survey 2.  $YD = mx + c$  where  $x = ST, EM$  or  $GC$ .**

| Harvest | ST | EM | GC | <i>m</i> | S.E.   | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----|----|----|----------|--------|----------|------|----------|-----------------------|
| 4       | ●  |    |    | 2.01     | 0.537  | 43.0     | 16.2 | <0.001   | 0.10                  |
|         |    | ●  |    | -12.7    | 1.00   | 229      | 10.4 | <0.001   | 0.56                  |
|         |    |    | ●  | 0.439    | 0.0260 | 12.4     | 5.79 | <0.001   | 0.70                  |
| 5       | ●  |    |    | 4.9      | 1.19   | 215      | 38.1 | <0.001   | 0.11                  |
|         |    | ●  |    | -30.3    | 2.86   | 669      | 29.5 | <0.001   | 0.47                  |
|         |    |    | ●  | 1.096    | 0.0622 | 143      | 13.7 | <0.001   | 0.71                  |
| 6       | ●  |    |    | 4.0      | 2.42   | 679      | 75.3 | n.s.     | 0.01                  |
|         |    | ●  |    | -44.5    | 6.43   | 1219     | 61.6 | <0.001   | 0.27                  |
|         |    |    | ●  | 1.83     | 0.130  | 397      | 31.1 | <0.001   | 0.61                  |
| 7       | ●  |    |    | 15.1     | 3.39   | 764      | 109  | <0.001   | 0.13                  |
|         |    | ●  |    | -82.7    | 9.51   | 2047     | 96.5 | <0.001   | 0.38                  |
|         |    |    | ●  | 3.02     | 0.226  | 628      | 49.0 | <0.001   | 0.59                  |
| 8       | ●  |    |    | 26.3     | 5.17   | 970      | 162  | <0.001   | 0.17                  |
|         |    | ●  |    | -102     | 13.6   | 2753     | 135  | <0.001   | 0.31                  |
|         |    |    | ●  | 4.07     | 0.364  | 910      | 82.9 | <0.001   | 0.50                  |
| 9       | ●  |    |    | 26.7     | 5.60   | 1111     | 173  | <0.001   | 0.15                  |
|         |    | ●  |    | -121     | 15.2   | 3189     | 163  | <0.001   | 0.34                  |
|         |    |    | ●  | 4.47     | 0.376  | 1128     | 72.7 | <0.001   | 0.53                  |

#### 4.5.8. Yield per stem

The average above-ground stem weight increased until the sixth harvest and then began to decline (Table 39). The COV of above-ground stem weight was similar from the third to the sixth harvest but was higher at the seventh and eighth harvests (Table 39). At the fourth harvest, when the average yield per stem was very low, the COV of yield per stem was relatively high at *c.* 70 %, but at subsequent harvests the COV of yield per stem was lower at *c.* 50-60 % (Table 39).

**Table 39. Average and COV of above-ground stem weight and yield per stem at harvests 4-9 of Survey 2.**

|                                 |         | Harvest |      |      |      |      |      |
|---------------------------------|---------|---------|------|------|------|------|------|
|                                 |         | 4       | 5    | 6    | 7    | 8    | 9    |
| Above-ground stem weight (g FW) | Mean    | 244     | 462  | 502  | 467  | 363  | n.d. |
|                                 | COV (%) | 58.4    | 62.5 | 59.5 | 69.5 | 70.1 | n.d. |
| Yield (g FW)                    | Mean    | 52.1    | 193  | 432  | 605  | n.d. | 986  |
|                                 | COV (%) | 69.6    | 56.2 | 50.5 | 61.5 | n.d. | 57.5 |

From the fourth to the ninth harvest, the number of stems per plant and date of emergence consistently explained *c.* 60 % of the variation in yield per stem, similar to the relationships between these explanatory variables and the above-ground stem weight at the first three

harvests (Table 40). The relative influence of emergence declined from the early harvests but was relatively similar from the fifth harvest onwards, once the canopy had closed (Table 40).

**Table 40. Relationships between date of emergence (EM, relative to the first day that a stem emerged) and the number of stems per plant (SN) and yield per stem (YDS, g FW) at harvests 4-9 of Survey 2.**  
 $YDS = m EM + n SN + c$

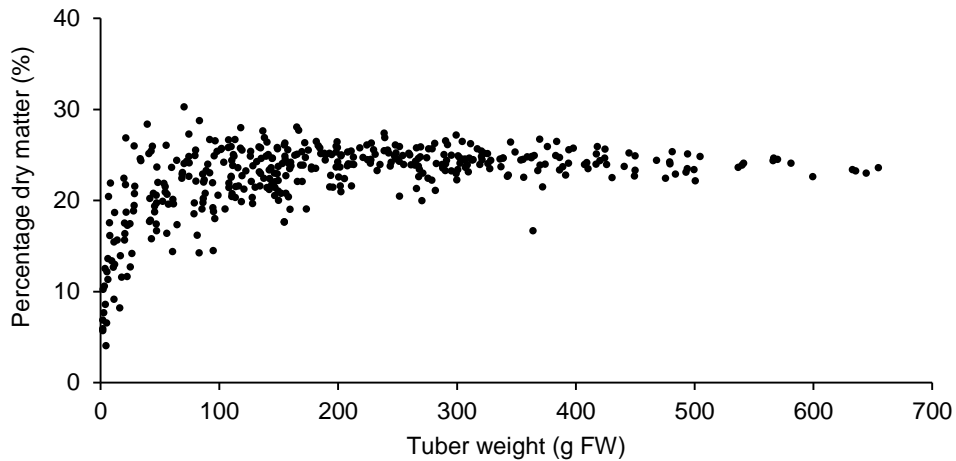
| Harvest | EM | SN | <i>m</i> | S.E.  | <i>n</i> | S.E. | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----|----|----------|-------|----------|------|----------|------|----------|-----------------------|
| 4       | ●  |    | -7.73    | 0.436 | n.a.     | n.a. | 140.0    | 5.10 | <0.001   | 0.57                  |
|         |    | ●  | n.a.     | n.a.  | -18.0    | 2.73 | 92.6     | 6.51 | <0.001   | 0.15                  |
| 5       | ●  | ●  | -7.31    | 0.402 | -12.5    | 1.79 | 163.3    | 5.72 | <0.001   | 0.64                  |
|         | ●  |    | -19.9    | 1.54  | n.a.     | n.a. | 422      | 18.0 | <0.001   | 0.42                  |
| 6       |    | ●  | n.a.     | n.a.  | -86.7    | 7.90 | 332      | 13.9 | <0.001   | 0.33                  |
|         | ●  | ●  | -15.6    | 1.54  | -52.1    | 7.50 | 455      | 17.1 | <0.001   | 0.52                  |
| 7       | ●  |    | -34.7    | 4.00  | n.a.     | n.a. | 791      | 42.2 | <0.001   | 0.26                  |
|         |    | ●  | n.a.     | n.a.  | -186     | 17.0 | 828      | 38.0 | <0.001   | 0.36                  |
| 8       | ●  | ●  | -33.8    | 2.87  | -180     | 12.8 | 1164     | 40.2 | <0.001   | 0.62                  |
|         | ●  |    | -60.5    | 5.38  | n.a.     | n.a. | 1312     | 63.0 | <0.001   | 0.38                  |
| 9       |    | ●  | n.a.     | n.a.  | -232     | 64.6 | 1156     | 62.0 | <0.001   | 0.28                  |
|         | ●  | ●  | -57.4    | 4.44  | -195     | 19.5 | 1728     | 66.5 | <0.001   | 0.58                  |
| 8       | ●  |    | n.d.     | n.d.  | n.d.     | n.d. | n.d.     | n.d. | n.d.     | n.d.                  |
|         |    | ●  | n.d.     | n.d.  | n.d.     | n.d. | n.d.     | n.d. | n.d.     | n.d.                  |
| 9       | ●  | ●  | n.d.     | n.d.  | n.d.     | n.d. | n.d.     | n.d. | n.d.     | n.d.                  |
|         | ●  |    | -93.3    | 9.81  | n.a.     | n.a. | 2122     | 120  | <0.001   | 0.31                  |
| 9       |    | ●  | n.a.     | n.a.  | -401     | 36.9 | 1822     | 88.1 | <0.001   | 0.35                  |
|         | ●  | ●  | -75.5    | 7.93  | 346      | 31.4 | 2676     | 108  | <0.001   | 0.57                  |

#### 4.5.9. Percentage dry matter

At the final harvest, the percentage dry matter of individual tubers varied widely from c. 5-30 % (Figure 37). Percentage dry matter was lowest and most variable amongst the smallest tubers (< 50 g) but relatively similar amongst larger tubers (> 200 g). There were no significant correlations between percentage dry matter of tubers and yield per stem or the number of tubers per stem (data not shown). Despite variation in the percentage dry matter of individual tubers, dry weight of individual stems correlated very strongly ( $R^2 > 0.99$ ) with fresh weight, indicating that there was no systemic bias associated with examining fresh weight rather than dry weight yield (data not shown).



**Figure 37. Relationship between fresh weight of tubers and percentage dry matter at the ninth harvest of Survey 2.**



#### 4.5.10. Yield per stem and tuber weight

The number of tubers per stem increased as yield per stem increased at all harvests at which tubers were present but, differences in the yield per stem only explained *c.* 35-50 % of the variation in the number of tubers per stem (Table 41). The number of tubers per stem did not increase in proportion to yield per stem, and as a result, mean tuber weight per stem correlated strongly with yield per stem at each harvest (Table 41). The maximum tuber weight per stem also correlated strongly with yield per stem at each harvest indicating that the largest tubers in the crop were more likely to originate from higher yielding stems (Table 41).

**Table 41. Relationships to explain variation in number of tubers (TN), mean tuber weight (MTW, g FW) and maximum tuber weight (MXT, g FW) per stem from yield per stem (g FW) at harvests 4-9 of Survey 2.**

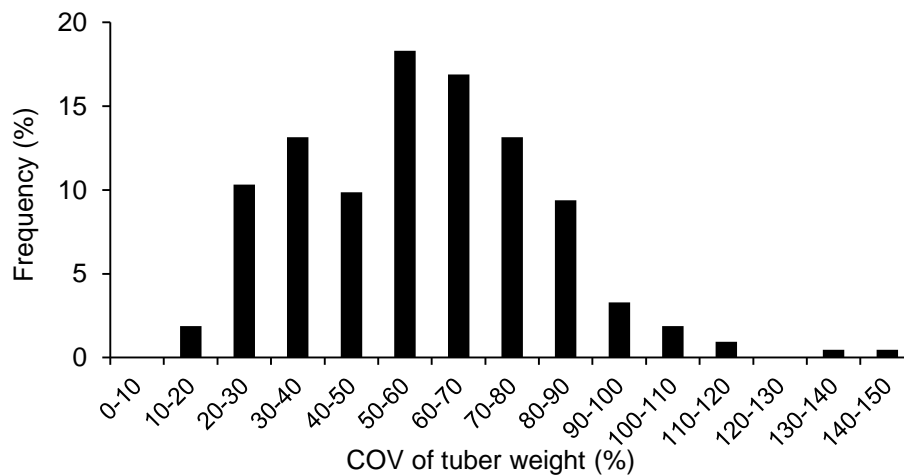
| Harvest | TN | MTW | MXT | <i>m</i> | S.E.     | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----|-----|-----|----------|----------|----------|-------|----------|-----------------------|
| 4       | ●  |     |     | 0.0309   | 0.00268  | 3.10     | 0.170 | <0.001   | 0.35                  |
|         |    | ●   |     | 0.1743   | 0.00557  | 2.28     | 0.353 | <0.001   | 0.80                  |
| 5       |    |     | ●   | 0.2526   | 0.00750  | 3.74     | 0.476 | <0.001   | 0.82                  |
|         | ●  | ●   |     | 0.01181  | 0.000907 | 3.10     | 0.200 | <0.001   | 0.41                  |
| 6       |    |     | ●   | 0.1294   | 0.00591  | 14.6     | 1.31  | <0.001   | 0.67                  |
|         | ●  | ●   |     | 0.1631   | 0.00888  | 21.3     | 1.96  | <0.001   | 0.59                  |
| 7       |    |     | ●   | 0.00467  | 0.000364 | 3.33     | 0.176 | <0.001   | 0.43                  |
|         | ●  | ●   |     | 0.1455   | 0.00548  | 28.6     | 2.65  | <0.001   | 0.77                  |
| 8       |    |     | ●   | 0.1834   | 0.00759  | 46.9     | 3.67  | <0.001   | 0.73                  |
|         | ●  | ●   |     | 0.00324  | 0.000244 | 3.23     | 0.175 | <0.001   | 0.44                  |
| 9       |    |     | ●   | 0.1331   | 0.00582  | 49.7     | 4.22  | <0.001   | 0.71                  |
|         | ●  | ●   |     | 0.1965   | 0.00749  | 59.1     | 5.32  | <0.001   | 0.76                  |
| 8       | ●  | ●   |     | n.d.     | n.d.     | n.d.     | n.d.  | n.d.     | n.d.                  |
|         |    |     | ●   | n.d.     | n.d.     | n.d.     | n.d.  | n.d.     | n.d.                  |
| 9       |    |     | ●   | n.d.     | n.d.     | n.d.     | n.d.  | n.d.     | n.d.                  |
|         | ●  | ●   |     | 0.00202  | 0.000139 | 3.22     | 0.158 | <0.001   | 0.49                  |
| 9       |    |     | ●   | 0.1513   | 0.00476  | 61.4     | 5.41  | <0.001   | 0.82                  |
|         |    |     | ●   | 0.2087   | 0.00749  | 96.8     | 8.51  | <0.001   | 0.78                  |

There was considerable variation in the weight of tubers on individual stems and also in the variation of tuber weight on individual stems such that the tubers on some stems were of similar weights whereas on others they were highly variable (Table 42; Figure 38). Overall, both measures of variation were relatively similar between harvests (Table 42) and for individual stems, the COV of tuber weight did not correlate with either yield or number of tubers (data not shown).

**Table 42. Average COV of tuber weight per stem and COV of the COV of tuber weight per stem at harvest 4-9 of Survey 2.**

|                                  |         | Harvest |      |      |      |      |
|----------------------------------|---------|---------|------|------|------|------|
|                                  |         | 4       | 5    | 6    | 7    | 9    |
| COV of tuber weight per stem (%) | Mean    | 54.8    | 51.0 | 53.6 | 55.3 | 57.9 |
|                                  | COV (%) | 41.8    | 46.3 | 39.4 | 46.8 | 39.8 |

**Figure 38. Variation in individual tuber weights on each stem at the ninth harvest of Survey 2.**



#### 4.6. Survey 3

##### 4.6.1. Surveys 3a & 3b

Although there were no significant differences in the number of stems at individual harvests, the plants growing on the heavy soil consistently had numerically fewer stems on average than those growing on the light soil (Table 43). When the data from each of the harvests was combined, the difference was significant ( $p = 0.01$  from a two-sample t-test with 22 D.F.) with the heavy soil having  $117,000 \pm 2,930$  stems/ha compared to  $137,700 \pm 7,140$  stems/ha on the light soil. Across the three harvests, the plant population did not differ between the soil types (the heavy soil had  $31,700 \pm 3,470$  plants/ha and the light soil had  $32,200 \pm 3,810$  plants/ha) and thus the difference in number of stems was due to differences in the number of stems per seed tuber.

At the first two harvests, the dry weight of the above-ground stems was significantly lower on the heavy soil than the light soil (Table 43). This was associated with 50 % emergence occurring *c.* 8 days later on the heavy soil, but the difference at the second harvest may have other contributory factors as the difference resulting from emergence would be expected to decrease over time. At the second harvest, the canopy had reached 100 % ground cover on the light soil, but not on the heavy soil (data not shown). At the third harvest, the dry weight

of the above-ground stems did not differ significantly between soil types although the canopies were still distinct in that the fresh weight was lower, and the percentage dry matter was higher on the heavy soil than the light soil (data not shown). The reduced ground cover probably explains why the heavy soil produced a significantly lower yield at the second and third harvests (Table 43). The numerical difference in yield between the soil types increased between the second and third harvests and at the third harvest the yield was *c.* 25 % lower on the heavy soil than the light soil (Table 43). The number of tubers was also *c.* 25 % lower on the heavy soil and was the result of lower numbers of tubers per stem as well as the lower number of stems (Table 43). At the second harvest, the differences in yield and tuber number compensated for each other and resulted in the mean tuber size not differing between the soil types, but at the third harvest the mean tuber size was *c.* 2 mm larger on the heavy soil than the light soil (Table 43). The COV of tuber size did not differ significantly between the two soil types, but was more variable on the heavy soil at the third harvest, ranging from 11.9-17.2 % compared to 12.4-13.9 % on the light soil. The COV of tuber size was lower at the third harvest than at the second (Table 43), which was unexpected since variation in tuber size generally increases over the course of the season (Wurr *et al.* 1993). At the second harvest, the tubers from the heavy soil had a significantly higher percentage dry matter than those from the light soil, but there was no difference at the third harvest (Table 43).

**Table 43. Parameters of crop growth at each harvest of Surveys 3a and 3b. Data are presented as the mean of six samples and differences between the means were distinguished by a two-sample t-test with 10 D.F.**

|                                    | Harvest | Heavy |        | Light |        | <i>P</i> |
|------------------------------------|---------|-------|--------|-------|--------|----------|
|                                    |         | Mean  | S.E.   | Mean  | S.E.   |          |
| Crop age at harvest (DAE)          | 1       | 4     | n.a.   | 12    | n.a.   | n.a.     |
|                                    | 2       | 35    | n.a.   | 40    | n.a.   | n.a.     |
|                                    | 3       | 77    | n.a.   | 84    | n.a.   | n.a.     |
| Number of stems (000/ha)           | 1       | 118.4 | 6.01   | 153.5 | 18.32  | n.s.     |
|                                    | 2       | 113.7 | 4.58   | 127.0 | 4.65   | n.s.     |
|                                    | 3       | 119.0 | 5.23   | 132.4 | 9.24   | n.s.     |
| Number of tubers (000/ha)          | 1       | n.d.  | n.d.   | n.d.  | n.d.   | n.d.     |
|                                    | 2       | 340   | 12.4   | 453   | 16.6   | <0.001   |
|                                    | 3       | 329   | 13.1   | 451   | 18.9   | <0.001   |
| Number of tubers > 10 mm per stem  | 1       | n.d.  | n.d.   | n.d.  | n.d.   | n.d.     |
|                                    | 2       | 3.01  | 0.141  | 3.57  | 0.093  | <0.01    |
|                                    | 3       | 2.78  | 0.098  | 3.45  | 0.150  | <0.01    |
| Yield (t FW/ha)                    | 1       | n.d.  | n.d.   | n.d.  | n.d.   | n.d.     |
|                                    | 2       | 7.7   | 0.29   | 12.5  | 0.48   | <0.001   |
|                                    | 3       | 38.8  | 1.44   | 52.6  | 0.34   | <0.001   |
| Above-ground stem weight (t DW/ha) | 1       | 0.043 | 0.0044 | 0.178 | 0.0030 | <0.01    |
|                                    | 2       | 1.24  | 0.057  | 2.44  | 0.164  | <0.001   |
|                                    | 3       | 2.57  | 0.172  | 2.81  | 0.029  | n.s.     |
| Tuber percentage dry matter (%)    | 1       | n.d.  | n.d.   | n.d.  | n.d.   | n.d.     |
|                                    | 2       | 14.9  | 0.16   | 13.0  | 0.21   | <0.001   |
|                                    | 3       | 22.9  | 0.21   | 22.0  | 0.37   | n.s.     |
| Mean tuber size (mm)               | 1       | n.d.  | n.d.   | n.d.  | n.d.   | n.d.     |
|                                    | 2       | 34.2  | 0.53   | 35.3  | 0.38   | n.s.     |
|                                    | 3       | 56.0  | 0.55   | 53.7  | 0.54   | <0.05    |
| COV of tuber size (%)              | 1       | n.d.  | n.d.   | n.d.  | n.d.   | n.d.     |
|                                    | 2       | 16.3  | 0.45   | 15.3  | 0.29   | n.s.     |
|                                    | 3       | 14.6  | 0.84   | 13.5  | 0.23   | n.s.     |

There were no differences in the COV of number of stems, COV of number of tubers, COV of yield or COV of mean tuber weight between the soil types at any harvest (Table 44). The COV of yield per plant at the second and third harvests was lower than the COV of above-ground stem weight at the first harvest at both sites, suggesting that between the first and second harvest, relatively small plants grew at a faster rate than relatively large plants (Table 44). Consistent with the differences in canopy development previously noted, the mean above-ground stem weight was lower on the heavy soil than the light soil at the second and third harvests (Table 44). The COV of above-ground stem weight was very high (> 80 %) on both soil types at the first harvest but lower at the second and third harvests (Table 44). The COV of above-ground stem weight was lower on the heavy soil than the light soil at the second harvest but not at the third. The low mean value for above-ground stem

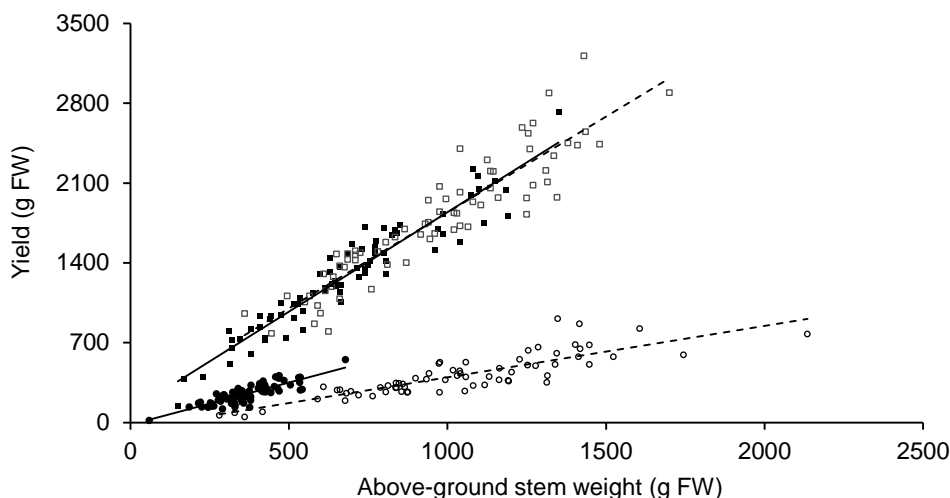
weight meant that a value for the transformed COV of above-ground stem weight at the first harvest could not be determined, and there were no differences in the transformed COV of above-ground stem weights between soil types at the second and third harvests (Table 44).

**Table 44. Plant-to-plant variation and stem-to-stem variation at each harvest of Survey 3a and 3b. Data are presented as the mean of six samples and differences between the means were distinguished by a two-sample t-test with 10 D.F.**

|  | Harvest | Heavy |       | Light |       | <i>P</i> |
|--|---------|-------|-------|-------|-------|----------|
|  |         | Mean  | S.E.  | Mean  | S.E.  |          |
| COV of number of stems per plant (%)   | 1       | 30.6  | 1.41  | 36.6  | 2.39  | n.s.     |
|  | 2       | 29.3  | 1.88  | 33.5  | 3.54  | n.s.     |
|  | 3       | 35.1  | 3.00  | 31.9  | 3.80  | n.s.     |
| COV of number of tubers per plant (%)  | 1       | n.d.  | n.d.  | n.d.  | n.d.  | n.d.     |
|  | 2       | 26.2  | 3.03  | 30.4  | 2.19  | n.s.     |
|  | 3       | 31.5  | 2.93  | 31.1  | 3.04  | n.s.     |
| COV of yield per plant (%) (above-ground stem weight per plant for H1)             | 1       | 52.7  | 1.98  | 57.8  | 4.57  | n.s.     |
|  | 2       | 34.0  | 3.84  | 44.5  | 3.64  | n.s.     |
|  | 3       | 37.0  | 2.67  | 30.2  | 3.27  | n.s.     |
| COV of mean tuber weight per plant (%)   | 1       | n.d.  | n.d.  | n.d.  | n.d.  | n.d.     |
|  | 2       | 31.7  | 2.21  | 32.8  | 2.70  | n.s.     |
|  | 3       | 30.7  | 5.36  | 22.3  | 2.41  | n.s.     |
| Mean above-ground stem weight (g FW)   | 1       | 3.40  | 0.318 | 12.30 | 1.028 | <0.001   |
|  | 2       | 99.4  | 3.77  | 253.9 | 12.04 | <0.001   |
|  | 3       | 177.2 | 11.9  | 225.1 | 20.8  | n.s.     |
| COV of above-ground stem weight (%)  | 1       | 80.4  | 4.12  | 95.1  | 10.11 | n.s.     |
|  | 2       | 50.7  | 2.43  | 62.5  | 4.30  | <0.05    |
|  | 3       | 56.7  | 3.89  | 61.1  | 5.34  | n.s.     |
| Transformed and weighted mean above-ground stem weight ( $\sqrt[3]{\text{g FW}}$ ) | 1       | n.d.  | n.d.  | n.d.  | n.d.  | n.d.     |
|  | 2       | 4.89  | 0.049 | 6.82  | 0.130 | <0.001   |
|  | 3       | 5.94  | 0.134 | 6.52  | 0.178 | <0.05    |
| Transformed and weighted COV of above-ground stem weight (%)                       | 1       | n.d.  | n.d.  | n.d.  | n.d.  | n.d.     |
|  | 2       | 14.9  | 0.53  | 17.5  | 1.72  | n.s.     |
|  | 3       | 16.6  | 1.57  | 18.1  | 1.56  | n.s.     |

At the second and third harvests, yield per plant correlated strongly with above-ground stem weight (Figure 39). At the second harvest, the relationships differed between soil types, but at the third harvest, despite the differences in overall yield and canopy structure previously discussed, the relationships were very similar. Plants with the same above-ground stem weight produced similar yields on both soil types (Figure 39) but this was probably a chance observation. With the exception of the second harvest on the heavy soil, yield per plant increased as the number of stems per plant increased, but explained at most 21 % of the variation (Table 46).

**Figure 39. Relationship between above-ground stem weight (AG) and yield (YD) at the second and third harvests. Heavy soil, second harvest, ●; light soil, second harvest, ○; heavy soil, third harvest, ■; light soil, third harvest, □. See Table 45 for details of fitted lines.**



**Table 45. Fitted lines in Figure 39.  $YD = m AG + c$ .**

| Harvest/site | $m$   | S.E.   | $c$ | S.E. | $P$    | $R^2$ |
|--------------|-------|--------|-----|------|--------|-------|
| 2H           | 0.739 | 0.0551 | -20 | 20.8 | <0.001 | 0.72  |
| 2L           | 0.452 | 0.0337 | -56 | 36.4 | <0.001 | 0.73  |
| 3H           | 1.744 | 0.0652 | 100 | 47.6 | <0.001 | 0.91  |
| 3L           | 1.681 | 0.0852 | 161 | 85.3 | <0.001 | 0.85  |

The number of tubers per plant increased as the number of stems increased at both sites and at the third harvest,  $c$ . 50 % of the variation in the number of tubers was accounted for by differences in the number of stems (Table 46). The number of tubers per plant also increased as yield increased and regressions including both the number of stems and yield explained  $c$ . 75 % of the variation (Table 46). At the second harvest, there was no significant relationship between the number of stems per plant or the number of tubers per plant and mean tuber weight per plant (Table 46). At the third harvest, mean tuber weight per plant decreased as the number of stems per plant increased but little of the variation was explained by the relationship (Table 46). On the heavy soil, there was no significant relationship between the number of tubers per plant and mean tuber weight per plant, but on the light soil there was a weak relationship (Table 46). Multiple regressions including yield and the number of stems per plant explained  $c$ . 50 % of variation in mean tuber weight per plant at

both harvests and on both soil types (Table 46). Yield and the number of tubers per plant explained *c.* 75 % of variation in mean tuber weight per plant at both harvests and on both soil types (Table 46).

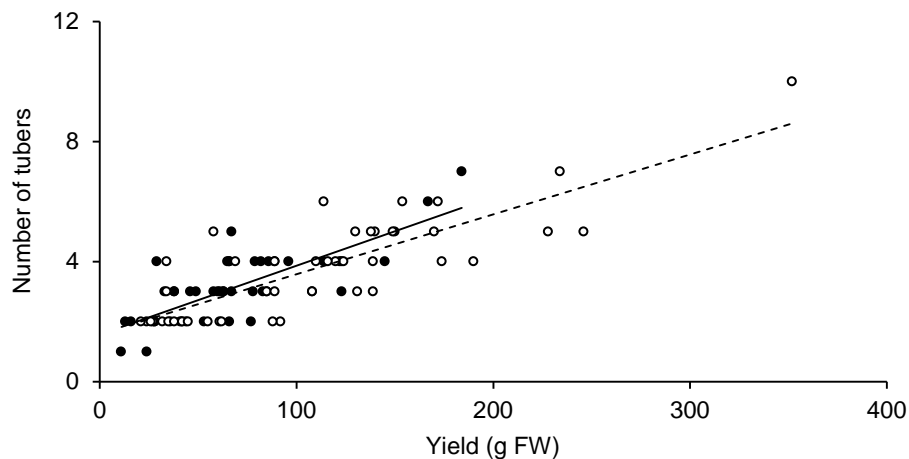
**Table 46. Relationships to explain variation in yield per plant (YD, g FW), the number of tubers per plant (TN) and mean tuber weight per plant (MTW, g FW) from the number of stems per plant (SN), the number of tubers per plant and yield per plant in Survey 3a (H) and 3b (L).**

| Explanatory variable(s) |    |    | Response variable | Harvest / site | Relationship  | P      | R <sup>2</sup> |
|-------------------------|----|----|-------------------|----------------|---|--------|----------------|
| SN                      | TN | YD |                   |                |   |        |                |
| ●                       |    |    | YD                | 2H             | 20 (±10.8) × SN + 197 (±40.7)                                 | n.s.   | 0.03           |
|                         |    |    |                   | 2L             | 61 (±15.3) × SN + 161 (±64.2)                                 | <0.001 | 0.19           |
| ●                       |    |    | YD                | 3H             | 179 (±36.7) × SN + 645 (±156)                                 | <0.001 | 0.21           |
|                         |    |    |                   | 3L             | 108 (±41.6) × SN + 1298 (±193)                                | <0.05  | 0.08           |
| ●                       |    |    | TN                | 2H             | 1.82 (±0.282) × SN + 4.7 (±1.06)                              | <0.001 | 0.32           |
|                         |    |    |                   | 2L             | 2.21 (±0.300) × SN + 5.4 (±1.26)                              | <0.001 | 0.45           |
| ●                       |    |    | TN                | 3H             | 2.09 (±0.216) × SN + 3.13 (±0.919)                            | <0.001 | 0.52           |
|                         |    |    |                   | 3L             | 2.20 (±0.259) × SN + 5.3 (±1.20)                              | <0.001 | 0.50           |
| ●                       |    | ●  | TN                | 2H             | 1.49 (±0.222) × SN + 0.0168 (±0.00219) × YD + 1.41 (±0.924)   | <0.001 | 0.60           |
|                         |    |    |                   | 2L             | 1.34 (±0.235) × SN + 0.0141 (±0.00173) × YD + 3.14 (±0.925)   | <0.001 | 0.73           |
| ●                       |    | ●  | TN                | 3H             | 1.36 (±0.178) × SN + 0.00408 (±0.000471) × YD + 0.49 (±0.734) | <0.001 | 0.75           |
|                         |    |    |                   | 3L             | 1.73 (±0.196) × SN + 0.00432 (±0.000542) × YD - 0.3 (±1.12)   | <0.001 | 0.74           |
| ●                       |    |    | MTW               | 2H             | -1.7 (±1.00) × SN + 36.4 (±3.77)                              | n.s.   | 0.02           |
|                         |    |    |                   | 2L             | 0.3 (±1.10) × SN + 35.7 (±4.63)                               | n.s.   | 0.00           |
| ●                       |    |    | MTW               | 3H             | -8.5 (±3.73) × SN + 182 (±15.8)                               | <0.05  | 0.05           |
|                         |    |    |                   | 3L             | -10.9 (±2.61) × SN + 192 (±12.1)                              | <0.001 | 0.19           |
|                         | ●  |    | MTW               | 2H             | -0.15 (±0.322) × TN + 31.7 (±3.79)                            | n.s.   | 0.00           |
|                         |    |    |                   | 2L             | 0.62 (±0.330) × TN + 27.9 (±4.91)                             | n.s.   | 0.04           |
|                         | ●  |    | MTW               | 3H             | -1.5 (±1.32) × TN + 166 (±16.2)                               | n.s.   | 0.00           |
|                         |    |    |                   | 3L             | -2.16 (±0.916) × TN + 177 (±14.3)                             | <0.05  | 0.06           |
|                         |    | ●  | MTW               | 2H             | 0.0603 (±0.00764) × YD + 13.9 (±2.21)                         | <0.001 | 0.42           |
|                         |    |    |                   | 2L             | 0.0449 (±0.00581) × YD + 18.6 (±2.59)                         | <0.001 | 0.48           |
|                         |    | ●  | MTW               | 3H             | 0.0410 (±0.00907) × YD + 92 (±13.3)                           | <0.001 | 0.19           |
|                         |    |    |                   | 3L             | 0.0293 (±0.00726) × YD + 93 (±13.4)                           | <0.001 | 0.18           |
| ●                       |    | ●  | MTW               | 2H             | -3.06 (±0.718) × SN + 0.0663 (±0.00710) × YD + 23.3 (±2.99)   | <0.001 | 0.52           |
|                         |    |    |                   | 2L             | -3.14 (±0.797) × SN + 0.0554 (±0.00587) × YD + 26.8 (±3.13)   | <0.001 | 0.58           |
|                         |    |    |                   | 3H             | -20.3 (±3.22) × SN + 0.0663 (±0.00850) × YD + 139 (±13.2)     | <0.001 | 0.45           |
| ●                       |    | ●  | MTW               | 3L             | -15.4 (±2.05) × SN + 0.0419 (±0.00567) × YD + 138 (±11.7)     | <0.001 | 0.54           |
|                         |    |    |                   | 2H             | -2.25 (±0.197) × TN + 0.1047 (±0.00616) × YD + 27.4 (±1.82)   | <0.001 | 0.77           |
|                         | ●  | ●  | MTW               | 2L             | -2.13 (±0.281) × TN + 0.0846 (±0.00671) × YD + 32.7 (±2.65)   | <0.001 | 0.73           |
|                         |    |    |                   | 3H             | -13.4 (±1.12) × TN + 0.1189 (±0.00847) × YD + 141.3 (±9.00)   | <0.001 | 0.70           |
|                         | ●  | ●  | MTW               | 3L             | -8.27 (±0.604) × TN + 0.0767 (±0.00512) × YD + 132.0 (±7.55)  | <0.001 | 0.78           |

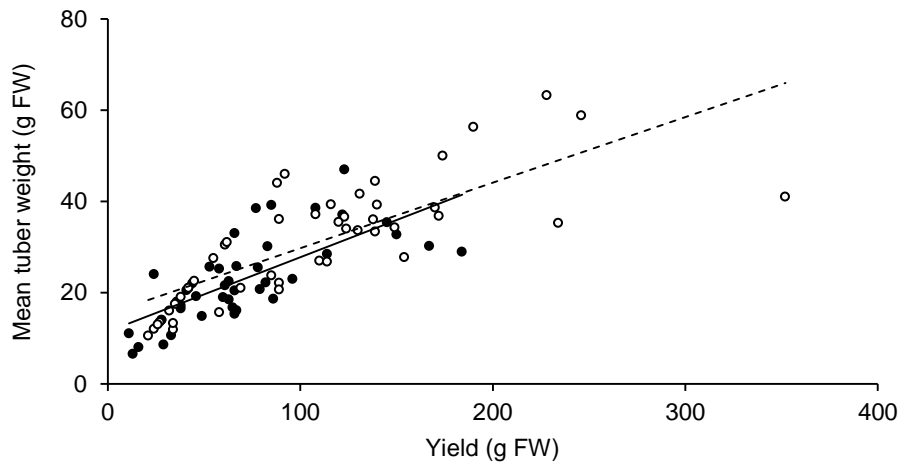


At the second harvest, 12 plants from each soil type were split into individual stems. Stems with a similar yield produced a similar number of tubers and had a similar mean tuber weight regardless of soil type (Figs 40-41). However, amongst stems with the same number of tubers, yield varied widely, for example stems with four tubers had yields ranging from c. 30-200 g (Figure 40). The overall differences associated with soil type thus appear to have been caused by an increase in the average yield per stem with a simultaneous increase in the number of tubers per stem, rather than a change in the relationship between these variables. A possible explanation is that stems with a similar leaf area at tuber initiation produced a similar yield and number of tubers regardless of soil type, and the differences observed were the result of the average leaf area per stem (i.e. ground cover) being lower on the heavy soil during tuber initiation.

**Figure 40. Relationships between yield (YDS) and number of tubers (TNS) per stem at the second harvest of Surveys 3a and 3b. Heavy soil, ●; Light soil, ○. Fitted lines: Heavy soil, —  $TNS = 0.0231 (\pm 0.00288) \times YDS + 1.54 (\pm 0.229)$ ,  $R^2 = 0.59$ ,  $n = 45$ ; Light soil, - - -  $TNS = 0.0287 (\pm 0.00427) \times YDS + 2.75 (\pm 0.550)$ ,  $R^2 = 0.50$ ,  $n = 45$ .**

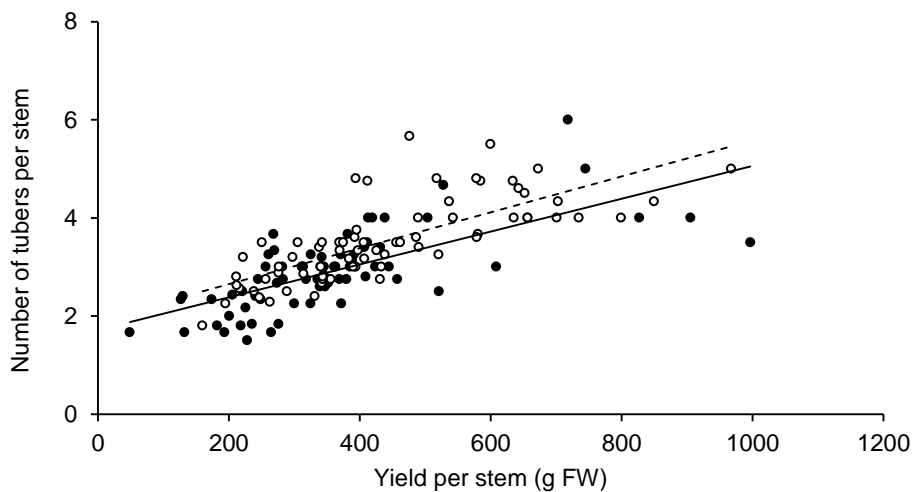


**Figure 41. Relationships between yield (YDS) and mean tuber weight (MTW) per stem at the second harvest of Surveys 3a and 3b. Heavy soil, ●; Light soil, ○. Fitted lines: Heavy soil, —  $MTW = 0.162 (\pm 0.0242) \times YDS + 11.7 (\pm 1.93)$ ,  $R^2 = 0.50$ ,  $n = 45$ ; Light soil, - - -  $MTW = 0.144 (\pm 0.0182) \times YDS + 15.4 (\pm 2.35)$ ,  $R^2 = 0.58$ ,  $n = 45$ .**

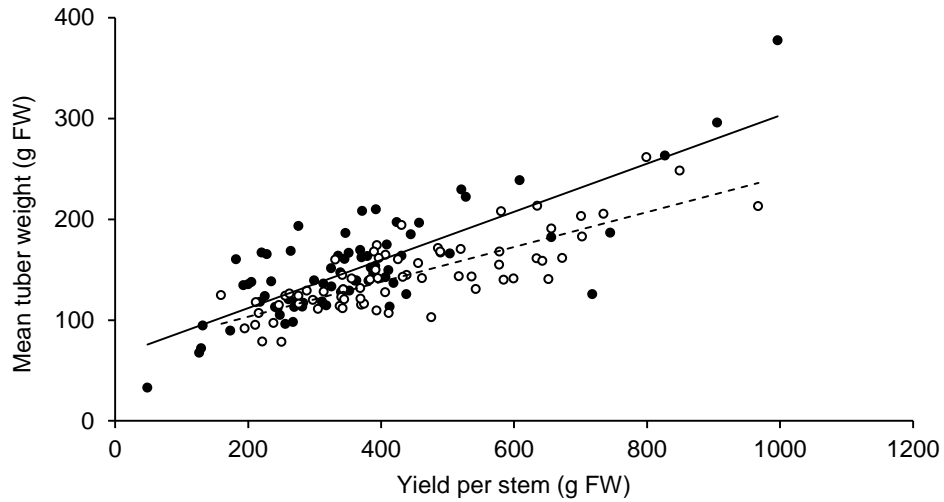


At the third harvest, plants with similar yields per stem had a similar number of tubers per stems regardless of soil type, but plants from light soil had higher yields per stem and more tubers per stem than from the light soil (Figure 42). These relationships were consistent with the observations of individual stems made at the second harvest.

**Figure 42. Relationships between yield per stem (YDS) and the number of tubers per stem (TNS) of individual plants at the third harvest of Surveys 3a and 3b. Heavy soil, ●; Light soil, ○. Fitted lines: Heavy soil, —  $TNS = 0.00333 (\pm 0.000400) \times YDS + 1.72 (\pm 0.161)$ ,  $R^2 = 0.49$ ,  $n = 72$ ; Light soil, - - -  $TNS = 0.00372 (\pm 0.000394) \times YDS + 1.88 (\pm 0.18)$ ,  $R^2 = 0.55$ .**

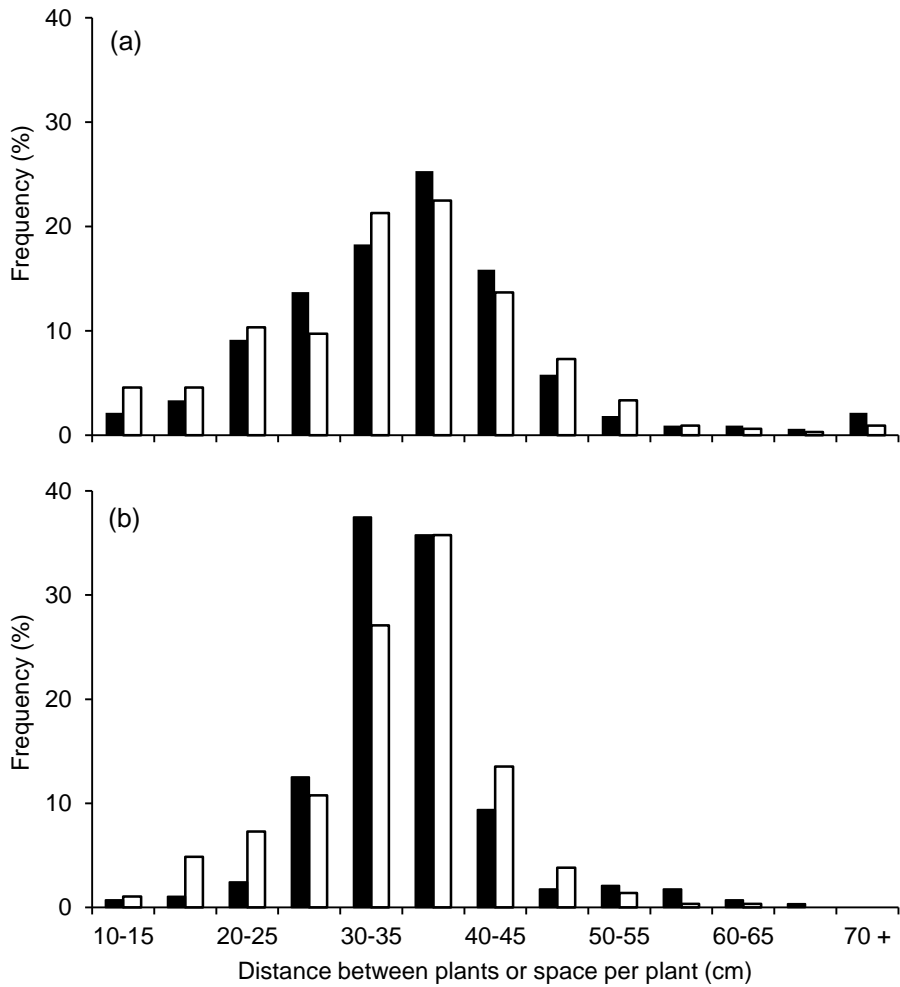


**Figure 43. Relationships between yield per stem (YDS) and mean tuber weight (MTW) of individual plants at the third harvest of Surveys 3a and 3b. Heavy soil, ●; Light soil, ○. Fitted lines: Heavy soil, —  $MTW = 0.239 (\pm 0.0217) \times YDS + 63.9 (\pm 8.72), R^2 = 0.63$ ; Light soil, - - -  $MTW = 0.171 (\pm 0.0153) \times YDS + 69.9 (\pm 7.14), R^2 = 0.64$ .**

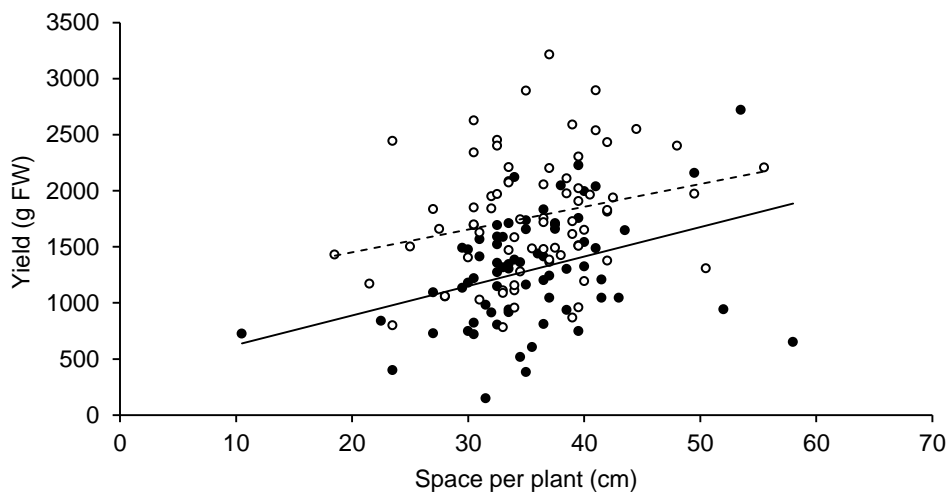


The COV of distance between plants was *c.* 30 % on both soil types, but the COV of space per plant was lower at *c.* 20 %, and > 80 % of plants were within 10 cm of the mean spacing (Figure 44). At the third harvest there was a significant relationship between space per plant and yield per plant on both soil types but the correlation was very weak and for those plants within 10 cm of the mean there appeared to be no effect on yield per plant suggesting that variation in space per plant was a relatively minor cause of variation in yield between plants (Figure 45).

**Figure 44. (a) Distance between plants and (b) space per plant in Surveys 3a and 3b. Heavy soil (■); light soil, (□). Heavy soil, distance: mean = 35.0 cm, COV = 32.7 %. Light soil, distance: mean = 34.1 cm, COV = 33.1 %. Heavy soil, space: mean = 35.1 cm, COV = 19.9 %. Light soil, space: mean = 34.2 cm, COV = 22.0 %.**



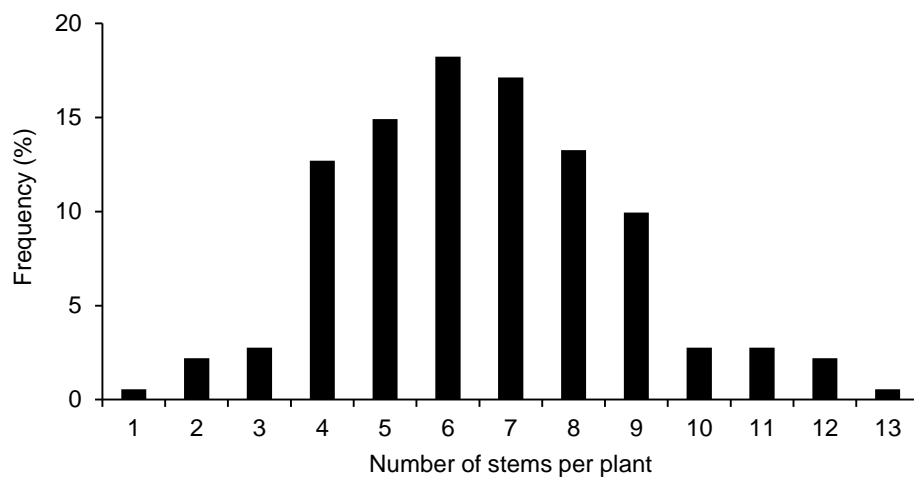
**Figure 45. Relationship between space per plant (SP) and yield per plant (YD) at the third harvest of Surveys 3a and 3b. Heavy soil, ●; Light soil, ○ Fitted lines: Heavy soil, —  $YD = 0.0053 (\pm 0.00156) \times SP + 28.5 (\pm 2.14)$ ,  $R^2 = 0.13$ ,  $p < 0.001$ ; Light soil, - - -  $YD = 0.00358 (\pm 0.00136) \times SP + 29.3 (\pm 2.52)$ ,  $R^2 = 0.08$   $p < 0.05$ .**



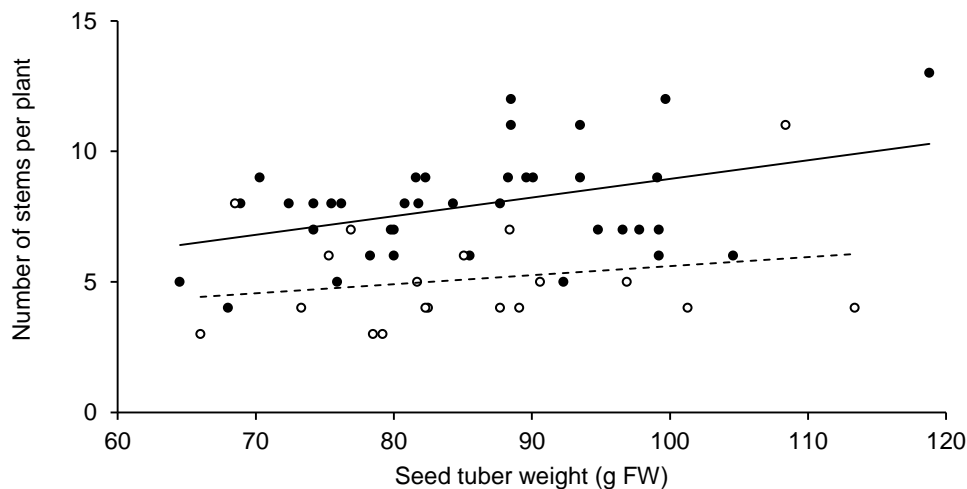
#### 4.6.2. Survey 3c

At the first harvest, the average seed tuber weight was 85 g and as a result of the use of tightly graded seed tubers (50-55 mm) the COV of seed tuber weight was relatively low at 14.1 %. Despite the use of tightly graded seed tubers, there was considerable variation in the number of stems per plant, ranging from 1-13 stems per plant across all the harvests (Figure 46). At the first harvest, approximately one third of plants had at least one stem that was infected by *R. solani* as evidenced by symptoms of stem canker. This was despite seed tubers having been treated with the fungicide pencycuron at planting. Infected plants produced fewer stems than those without symptoms (5.1 vs. 7.9) and the COV of the number of stems per plant was higher for infected plants (39 vs. 25 %). Variation in seed tuber weight explained little of the variation in the number of stems per plant for healthy plants at the first harvest, and the correlation was not significant for plants infected by *R. solani* (Figure 47).

**Figure 46. Number of stems per plant in Survey 3c for all harvests. Mean = 6.55, COV = 33.8 %.**



**Figure 47. Relationship between seed tuber weight (ST) and number of stems per plant (SN) at the first harvest of Survey 3c. Healthy plants, ●; plants infected by *R. solani*, ○. Fitted lines: Healthy plants, —  $SN = 0.071 (\pm 0.0266) \times ST + 1.8 (\pm 2.30)$ ,  $R^2 = 0.14$ ,  $p = 0.01$ ,  $n = 38$ . Infected plants, - - -  $SN = 0.035 (\pm 0.0381) \times ST + 2.1 (\pm 3.29)$ ,  $p = 0.37$ ,  $n = 19$ .**

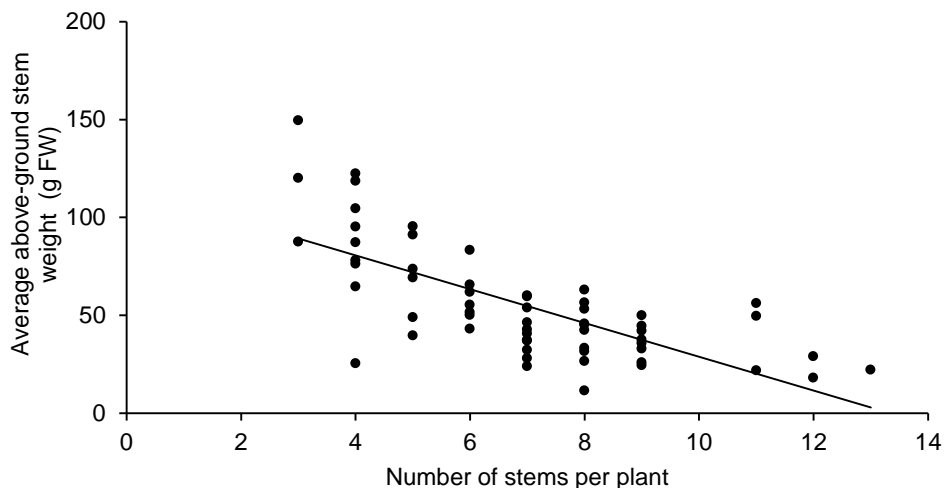


At each harvest, there was either no correlation, or a very weak correlation, between the number of stems and total weight (either above-ground stem weight or yield) of plants (Table 47). Consequently, the average weight of stems decreased as the number of stems per plant increased (Figs 48-49, data for second harvest not shown).

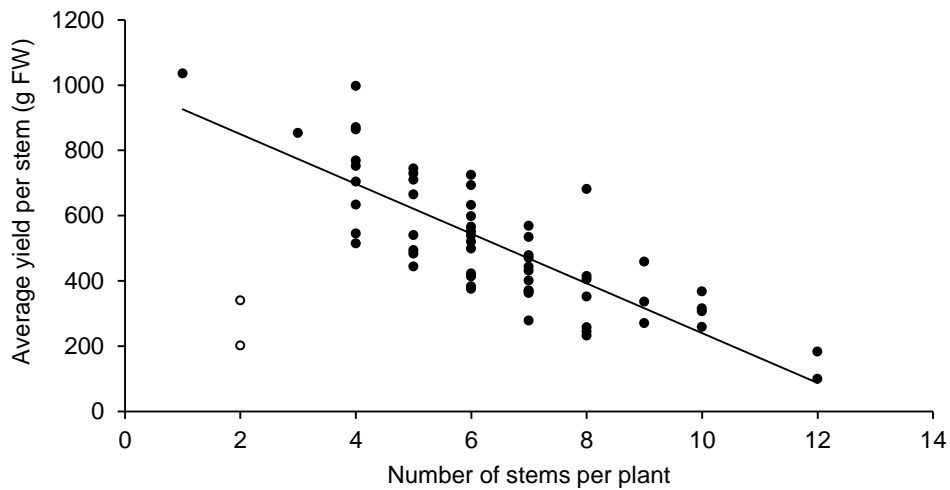
**Table 47. Relationships between the number of stems per plant (SN) and above-ground stem weight per plant (AG, g FW) at the first harvest and yield per plant (YD, g FW) at the second and third harvests of Survey 3c.**

| Harvest | Relationship                                      | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---|----------|-----------------------|
| 1       | $AG = -0.5 (\pm 5.81) \times SN + 339 (\pm 42.6)$ | n.s.     | 0.00                  |
| 2       | $YD = 73 (\pm 28.5) \times SN + 1414 (\pm 191)$   | <0.05    | 0.09                  |
| 3       | $YD = 70 (\pm 49.5) \times SN + 2435 (\pm 332)$   | n.s.     | 0.02                  |

**Figure 48. Relationship between the number of stems per plant (SN) and average above-ground stem weight (AG) at the first harvest of Survey 3c. Fitted line:  $AG = -8.6 (\pm 1.13) \times SN + 115.2 (\pm 8.25)$ ,  $R^2 = 0.50$ .**



**Figure 49. Relationship between the number of stems per plant (SN) and average yield per stem (YDS) at the third harvest of Survey 3c. Two outliers (○) were excluded from the regression. Fitted line:  $YDS = -76.2 (\pm 7.26) \times SN + 1002 (\pm 49.3)$ ,  $R^2 = 0.65$ .**



At the second harvest, the canopy was extensive, having a fresh weight over 50 t/ha (Table 48) and 25 % of the stems were physically damaged at their base, seemingly by the combination of the wind and weight of the canopy (Figure 50). The length of stems had increased further by the third harvest and it was not possible to remove individual stems from the canopy. The leaves of stems that were physically damaged at the base were wilted, presumably decreasing stem growth rate and yield.

**Figure 50. A severe example of damage observed at the base of stems at the second harvest of Survey 3c.**



**Table 48. Overall parameters of crop growth and plant-to-plant variation at each harvest of Survey 3c.**

|   |         | Harvest |       |       |
|---|---------|---------|-------|-------|
|   |         | 1       | 2     | 3     |
| Number of stems (000/ha)  |         | 160.1   | 157.8 | 143.9 |
| Number of tubers (000/ha)   |         | n.d.    | 663   | 607   |
| Yield (t FW/ha)   |         | n.d.    | 45.7  | 67.1  |
| Above-ground stem weight (t FW/ha)  |         | 8.44    | 53.4  | n.d.  |
| Mean tuber size (mm)  |         | n.d.    | 46.7  | 54.9  |
| COV of tuber size (%)   |         | n.d.    | 15.4  | 17.5  |
| Number of stems per plant   | Mean    | 6.93    | 6.52  | 6.32  |
|   | COV (%) | 34.4    | 31.6  | 35.4  |
| Yield per plant (kg FW)   | Mean    | n.d.    | 1.88  | 2.88  |
|   | COV (%) | n.d.    | 24.0  | 30.3  |
| Number of tubers per plant  | Mean    | n.d.    | 27.2  | 26.7  |
|   | COV (%) | n.d.    | 26.0  | 28.8  |
| Mean tuber weight per plant (g FW)  | Mean    | n.d.    | 94.3  | 152.0 |
|   | COV (%) | n.d.    | 36.4  | 35.4  |
| Above-ground stem weight (g FW)   | Mean    | 48.3    | 346   | n.d.  |
|   | COV (%) | 73.3    | 65.3  | n.d.  |
| Transformed and weighted above-ground stem weight ( $\sqrt[3]{\text{g FW}}$ ) | Mean    | 4.06    | 7.61  | n.d.  |
|   | COV (%) | 19.8    | 20.9  | n.d.  |

The number of tubers per plant was closely related to variations in the number of stems per plant at the second and third harvests (Table 49). At the second harvest, yield had no significant effect on the number of tubers per plant but at the third harvest, the number of tubers per plant increased as yield per plant increased (Table 49). Mean tuber weight decreased as the number of stems and number of tubers per plant increased and increased as the yield per plant increased at the second and harvests, but individually these variables explained relatively little of the variation (Table 49). The average yield per stem and multiple regressions including the number of stems or tubers per plant and yield explained a large proportion of the variation in mean tuber weight at the second and third harvests (Table 49; Figure 51).

**Table 49. Relationships to explain variation in the number of tubers per plant (TN) and mean tuber weight per plant (MTW, g FW) from the number of stems per plant (SN), number of tubers per plant and yield per plant (YD, g FW) in Survey 3c.**

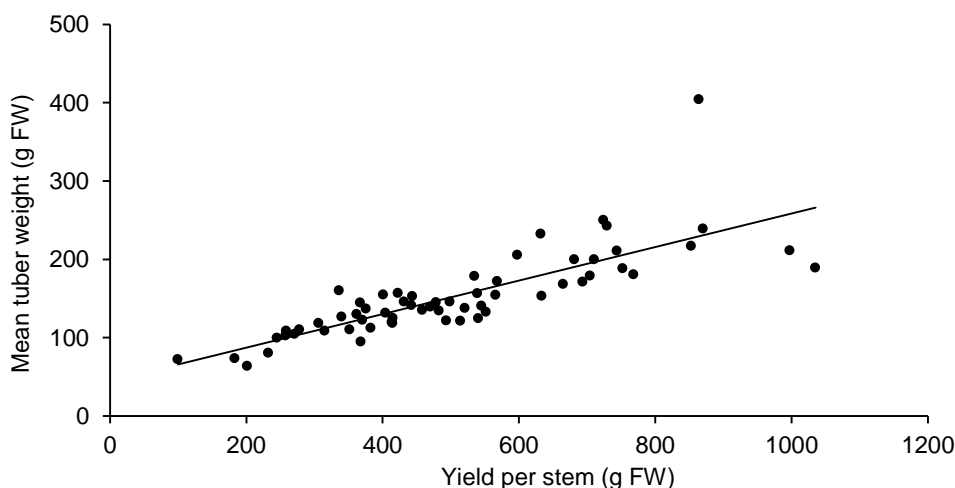
| Explanatory variable (s) |    |    | Response variable | Harvest | Relationship   | P      | R <sup>2</sup> |
|--------------------------|----|----|-------------------|---------|--|--------|----------------|
| SN                       | TN | YD |                   |         |  |        |                |
| ●                        |    |    | TN                | 2       | $3.03 (\pm 0.244) \times \text{SN} + 7.8 (\pm 1.64)$   | <0.001 | 0.73           |
| ●                        |    |    | TN                | 3       | $2.84 (\pm 0.248) \times \text{SN} + 8.7 (\pm 1.66)$   | <0.001 | 0.68           |
| ●                        |    | ●  | TN                | 2       | No significant effect of yield   | n.s.   | n.a.           |
| ●                        |    | ●  | TN                | 3       | $2.65 (\pm 0.213) \times \text{SN} + 0.00272 (\pm 0.000547) \times \text{YD} + 2.1 (\pm 1.94)$ | <0.001 | 0.77           |
| ●                        |    |    | MTW               | 2       | $-9.0 (\pm 1.95) \times \text{SN} + 152 (\pm 13.0)$  | <0.001 | 0.26           |



|   |   |     |     |   |   |        |      |
|---|---|-----|-----|---|---|--------|------|
| ● |   | MTW | 3   | $-10.3 (\pm 2.80) \times \text{SN} + 217 (\pm 18.8)$  | <0.01   | 0.17   |      |
|   | ● | MTW | 2   | $-2.93 (\pm 0.514) \times \text{TN} + 174 (\pm 14.4)$ | <0.001  | 0.35   |      |
|   | ● | MTW | 3   | $-2.23 (\pm 0.858) \times \text{TN} + 212 (\pm 23.8)$ | <0.05   | 0.09   |      |
|   |   | ●   | MTW | 2   | $0.0308 (\pm 0.00920) \times \text{YD} + 37 (\pm 17.8)$   | <0.001 | 0.15 |
|   |   | ●   | MTW | 3   | $0.0335 (\pm 0.00668) \times \text{YD} + 56 (\pm 20.1)$   | <0.001 | 0.28 |
| ● |   | ●   | MTW | 2   | $-12.6 (\pm 1.46) \times \text{SN} + 0.0489 (\pm 0.00643) \times \text{YD} + 84 (\pm 13.0)$     | <0.001 | 0.63 |
| ● |   | ●   | MTW | 3   | $-13.1 (\pm 2.06) \times \text{SN} + 0.0395 (\pm 0.00528) \times \text{YD} + 121 (\pm 18.7)$    | <0.001 | 0.57 |
|   | ● | ●   | MTW | 2   | $-4.21 (\pm 0.302) \times \text{TN} + 0.0547 (\pm 0.00472) \times \text{YD} + 105.8 (\pm 9.84)$ | <0.001 | 0.81 |
|   | ● | ●   | MTW | 3   | $-4.93 (\pm 0.569) \times \text{TN} + 0.0529 (\pm 0.00500) \times \text{YD} + 131 (\pm 16.0)$   | <0.001 | 0.68 |

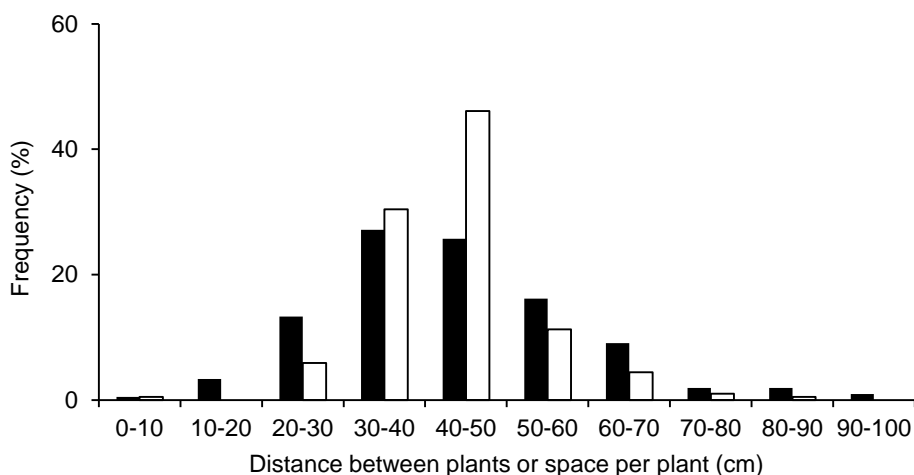
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**Figure 51. Relationship between average yield per stem (YDS) and mean tuber weight (MTW) at the third harvest of Survey 3c. Fitted line:  $MTW = 0.214 (\pm 0.0205) \times YDS + 45 (\pm 11.1)$ ,  $R^2 = 0.64$ .**



The crop was planted with a cup planter but there was still considerable variation in the distance between plants with *c.* 10 % of plants having less than half the mean distance and *c.* 10 % twice the mean distance (Figure 52). There was less variation in the space per plant with *c.* 90 % of the plants being  $\pm 50$  % of the mean (Figure 52). At the second and third harvests, the yield per plant did not increase as the space per plant increased suggesting that it was not a substantial cause of the variation in the yield per plant (data not shown).

**Figure 52. Distance between plants (■) and space per plant (□) in Survey 3c. Distance: mean = 43.0 cm, COV = 35.7 %. Space: mean = 42.7 cm, COV = 22.8 %.**

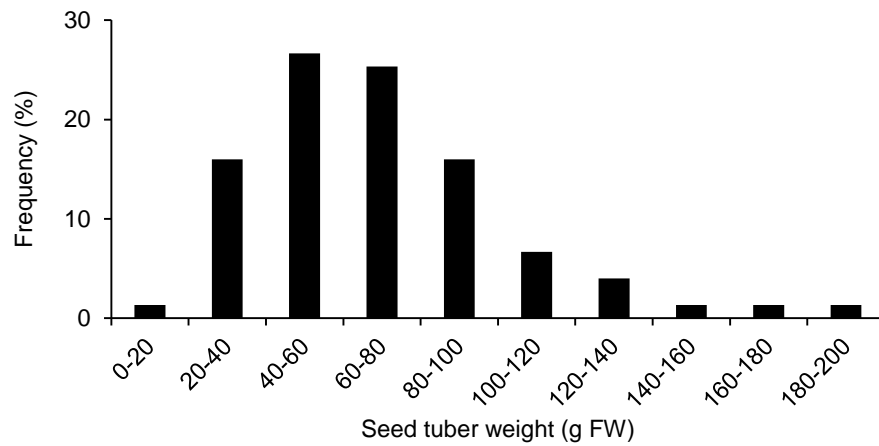


#### 4.6.3. Survey 3d

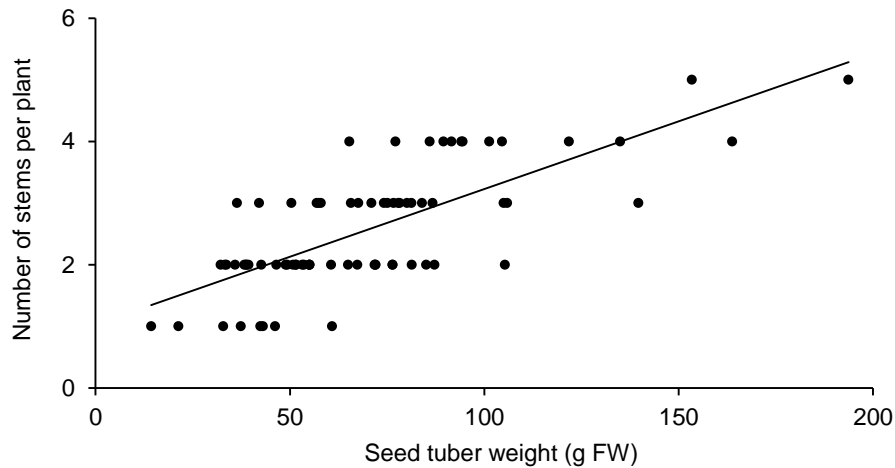
Seed tuber weight varied widely due to the use of ungraded seed tubers (Figure 53) and at the first harvest the number of stems per plant increased as seed tuber weight increased, but there

was a considerable range in the weight of seed tubers that produced the same number of stems (Figure 54). Despite wide variation in seed tuber weight, the COV of seed tuber substrate per stem was *c.* 40 % indicating that as well as producing more stems, the largest seed tubers produced relatively evenly-sized stems (Figure 55). There were few stems with < 10 g of seed tuber substrate (Figure 55).

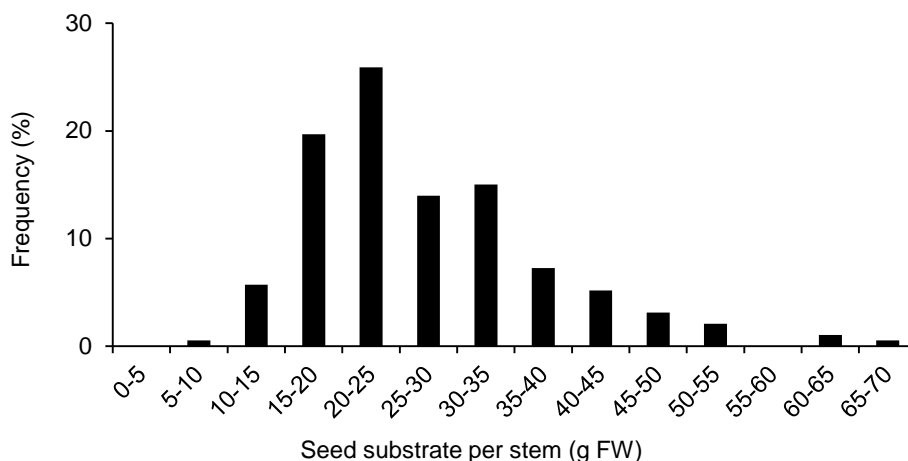
**Figure 53. Seed tuber weight at the first harvest of Survey 3d. Mean = 70.2 g, COV = 46.6 %.**



**Figure 54. Relationship between seed tuber weight (ST) and number of stems per plant (SN) at the first harvest of Survey 3d.  $SN = 0.0220 (\pm 0.00235) \times ST + 1.03 (\pm 0.182)$ ,  $R^2 = 0.54$ .**



**Figure 55. Seed tuber substrate per stem at the first harvest of Survey 3d. Mean = 27.3 g, COV = 37.9 %.**



**Table 50. Crop parameters at each harvest of Survey 3d.**

|   | Harvest |       |       |
|---|---------|-------|-------|
|   | 1       | 2     | 3     |
| Number of stems (000/ha)  | 104.0   | 115.2 | 121.5 |
| Above-ground stem weight (t FW/ha)                              | 6.3     | 33.7  | 25.9  |
| Number of tubers (000/ha)†                                      | 358.8   | 368.1 | 400.3 |
| Yield (t FW/ha)   | 0.19    | 37.6  | 59.9  |
| Mean above-ground stem weight (g FW)                            | 49.9    | 291   | 213   |
| COV of above-ground stem weight (%)                             | 40.7    | 51.6  | 44.3  |
| Transformed and weighted mean above-ground stem weight (g FW)   | 3.78    | 6.95  | 6.21  |
| Transformed and weighted COV of above-ground stem weight (g FW) | 12.9    | 16.7  | 13.9  |
| Mean tuber size (mm)  | n.d.    | 50.5  | 57.0  |
| COV of tuber size (%)   | n.d.    | 13.2  | 13.2  |

† At the first harvest the number of tubers included those < 10 mm in diameter but at the second and third harvests only those > 10 mm were included.

At the first harvest, the weight of above-ground stems per plant increased as the number of stems per plant increased and as seed tuber weight increased and both variables had a significant effect in a multiple regression (Table 51). The relationships between seed tuber weight, the number of stems per plant and above-ground stem weight meant that the average above-ground stem weight per plant did not change as the number of stems per plant increased (data not shown). The average percentage dry matter of seed tubers was 7.4 % and did not change as seed tuber weight increased demonstrating that seed tuber substrate was mobilised from seed tubers at a similar relative rate regardless of their size (data not shown).

At the second harvest, yield increased as the number of stems per plant increased, but the correlation coefficient was lower than at the first harvest (Table 51). Only *c.*70 % of seed

tubers were recovered intact at the second harvest, but for those plants with intact seed tubers, yield increased as weight of the seed tuber increased and variation in the weight of seed tubers explained *c.* 50 % of the variation in yield (Table 51). Unlike at the first harvest, the number of stems per plant did not have a significant effect on yield in a multiple regression also including seed tuber weight (Table 51). Plants with more stems had a lower average yield per stem whereas at the first harvest, the number of stems per plant had no effect on average above-ground stem weight (data not shown). At the third harvest, no seed tubers were recovered but yield still increased as the number of stems per plant increased (Table 51). As at the second harvest, the average yield per stem decreased as the number of stems per plant increased (data not shown).

**Table 51. Relationships between the number of stems per plant (SN) and seed tuber weight (ST, g FW) on plant size at each harvest of Survey 3d. AG = above-ground stem weight (g FW), YD = yield (g FW). H1, n = 75; H2, n = 52; H3, n = 72.**

| Explanatory variable(s) |    | Response variable | Harvest | Relationship  | <i>P</i> | <i>R</i> <sup>2</sup> |
|-------------------------|----|-------------------|---------|---|----------|-----------------------|
| SN                      | ST |                   |         |   |          |                       |
| ●                       |    | AG                | 1       | $47.8 (\pm 5.07) \times \text{SN} + 5 (\pm 13.9)$                                     | <0.001   | 0.54                  |
|                         | ●  | AG                | 1       | $1.52 (\pm 0.137) \times \text{ST} + 22 (\pm 10.6)$                                   | <0.001   | 0.62                  |
| ●                       | ●  | AG                | 1       | $22.3 (\pm 6.37) \times \text{SN} + 1.03 (\pm 0.190) \times \text{ST} - 1 (\pm 11.9)$ | <0.001   | 0.67                  |
| ●                       |    | YD                | 2       | $128 (\pm 29.7) \times \text{SN} + 554 (\pm 84.2)$                                    | <0.001   | 0.26                  |
|                         | ●  | YD                | 2       | $8.2 (\pm 1.16) \times \text{ST} + 401 (\pm 74.1)$                                    | <0.001   | 0.49                  |
| ●                       | ●  | YD                | 2       | No significant effect of SN   | n.a.     | n.a.                  |
| ●                       |    | YD                | 3       | $261 (\pm 42.5) \times \text{SN} + 643 (\pm 121.0)$                                   | <0.001   | 0.34                  |

At the second and third harvests there were on average *c.* 2.7 stems and *c.* 8.8 tubers per plant and the COV of both the number of stems and number of tubers per plant were *c.* 35 % (Table 52).

**Table 52. Plant-to-plant variation at the second and third harvests of Survey 3d.**

|                                    | Harvest | Mean  | COV (%) |
|------------------------------------|---------|-------|---------|
| Number of stems per plant          | 2       | 2.71  | 39.1    |
|                                    | 3       | 2.67  | 33.3    |
| Number of tubers per plant         | 2       | 8.73  | 34.6    |
|                                    | 3       | 8.86  | 33.8    |
| Yield per plant (g FW)             | 2       | 906   | 30.4    |
|                                    | 3       | 1346  | 29.5    |
| Mean tuber weight per plant (g FW) | 2       | 130.1 | 21.7    |
|                                    | 3       | 190.0 | 27.6    |

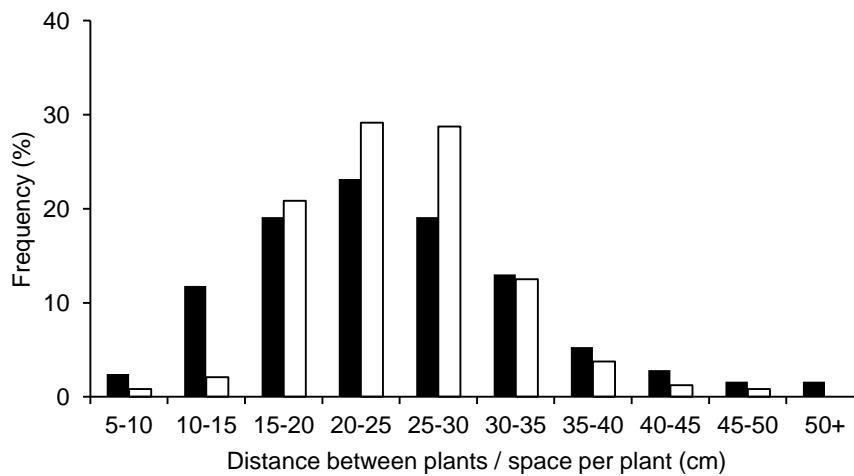
At the second and third harvests, the number of tubers per plant increased as the number of stems increased and as yield increased (Table 53). Regressions including both the number of stems and yield explained a large proportion of the variation in the number of tubers per plant (Table 53). Mean tuber weight correlated poorly with the number of stems, number of tubers and yield when considered separately, but regressions including both the number of stems and yield or the number of tubers and yield had higher correlation coefficients (Table 53). The relationships meant that mean tuber weight increased as yield increased and decreased as the number of stems and number of tubers increased.

**Table 53. Relationships to explain the number of tubers per plant (TN) and mean tuber weight per plant (MTW, g FW) from the number of stems per plant (SN), number of tubers per plant (TN) and yield per plant (YD, g FW) at the second and third harvests of Survey 3d.**

| Explanatory variable(s) |    |    | Response variable | Harvest | Relationship   | P      | R <sup>2</sup> |
|-------------------------|----|----|-------------------|---------|--|--------|----------------|
| SN                      | TN | YD |                   |         |  |        |                |
| ●                       |    |    | TN                | 2       | $2.29 (\pm 0.208) \times SN + 2.52 (\pm 0.604)$                                    | <0.001 | 0.64           |
| ●                       |    |    | TN                | 3       | $2.76 (\pm 0.224) \times SN + 1.43 (\pm 0.636)$                                    | <0.001 | 0.68           |
|                         |    | ●  | TN                | 2       | $0.00823 (\pm 0.000889) \times YD + 1.27 (\pm 0.841)$                              | <0.001 | 0.55           |
|                         |    | ●  | TN                | 3       | $0.00543 (\pm 0.000628) \times YD + 1.55 (\pm 0.881)$                              | <0.001 | 0.51           |
| ●                       | ●  |    | TN                | 2       | $1.58 (\pm 0.216) \times SN + 0.00459 (\pm 0.000833) \times YD + 0.30 (\pm 0.645)$ | <0.001 | 0.75           |
| ●                       | ●  |    | TN                | 3       | $2.06 (\pm 0.241) \times SN + 0.00267 (\pm 0.000547) \times YD - 0.28 (\pm 0.655)$ | <0.001 | 0.76           |
| ●                       |    |    | MTW               | 2       | $-6.7 (\pm 3.16) \times SN + 148.2 (\pm 9.19)$                                     | <0.05  | 0.05           |
| ●                       |    |    | MTW               | 3       | $-19.4 (\pm 6.58) \times SN + 242 (\pm 18.7)$                                      | <0.01  | 0.10           |
|                         | ●  |    | MTW               | 2       | $-2.8 (\pm 1.09) \times TN + 155 (\pm 10.1)$                                       | <0.05  | 0.08           |
|                         | ●  |    | MTW               | 3       | $-5.4 (\pm 1.99) \times TN + 238 (\pm 18.6)$                                       | <0.01  | 0.08           |
|                         |    | ●  | MTW               | 2       | $0.024 (\pm 0.0122) \times YD + 108 (\pm 11.6)$                                    | n.s.   | 0.04           |
|                         |    | ●  | MTW               | 3       | $0.044 (\pm 0.0149) \times YD + 132 (\pm 20.9)$                                    | <0.01  | 0.10           |
| ●                       | ●  |    | MTW               | 2       | $-16.2 (\pm 3.46) \times SN + 0.062 (\pm 0.0133) \times YD + 118 (\pm 10.3)$       | <0.001 | 0.27           |
| ●                       |    | ●  | MTW               | 3       | $-47.3 (\pm 5.95) \times SN + 0.107 (\pm 0.0135) \times YD + 174 (\pm 16.1)$       | <0.001 | 0.52           |
|                         | ●  | ●  | MTW               | 2       | $10.1 (\pm 1.14) \times TN + 0.108 (\pm 0.0125) \times YD + 121.3 (\pm 7.99)$      | <0.001 | 0.56           |
|                         | ●  | ●  | MTW               | 3       | $-19.7 (\pm 1.60) \times TN + 0.151 (\pm 0.0121) \times YD + 162 (\pm 12.0)$       | <0.001 | 0.71           |

There was variation in the distance between plants within the row but calculating the space per plant, rather than the distance between plants reduced the variability (Figure 56).

**Figure 56. Distribution of distance between plants (■) and space per plant (□) in Survey 3d. Distance: mean = 25.0 cm, COV = 36 %. Space: mean = 24.9 cm, COV = 25 %.**



The crop was planted with a belt planter and at the first harvest, space per plant increased as seed tuber weight increased but the relationship explained little of the variation in space per plant (data not shown). At the second and third harvests there were similarly weak relationships between space per plant and yield per plant (data not shown). At the second harvest, for plants for which seed tubers were recovered, space per plant had a significant effect on yield per plant, but in a multiple regression where seed tuber weight was included, the effect of space per plant was not significant (data not shown). Thus the weak effect of space per plant on yield appeared to have been due to larger seed tubers being planted at a wider spacing and also producing a higher yield, rather than increased space per plant increasing yield per plant.

Despite the wide variation in seed tuber weight, the COV of tuber size was relatively low at the second and third harvests (Table 50). While it was not possible to determine whether the crop would have been more uniform had it been grown from graded seed tubers, there are some possible explanations for why the crop was relatively uniform despite the use of ungraded seed tubers. At the first two harvests, when seed tubers were recovered intact, the fresh weight of plants and the number of stems per plant increased as the seed tuber weight increased. Since yield and the number of stems strongly influenced the number of tubers per plant, larger seed tubers produced plants with more tubers than those from small seed tubers. Consequently, yield and the numbers per plant were positively correlated and this reduced the variation in the mean tuber weight per plant compared to if the same extent of variation in yield and the number of tubers per plant had occurred without the factors correlating.

#### 4.7. Summary of work conducted in 2013

The results of Expts 1-3 were disappointing as none of the treatments had significant effects on plant-to-plant variation or variation in tuber size. The main hypothesis of variation in mean tuber weight per plant determining variation in tuber size therefore remained untested.



In Expt 1 it was evident that the relationship between seed tuber weight and number of stems per plant was very weak and therefore reducing variation in seed tuber weight had no effect on variation in number of stems per plant. There was some evidence that seed tuber weight affected the growth of plants however, since more of the variation in yield per plant was explained by seed tuber weight when the variation in seed tuber weight was increased. In Expt 2 earlier emerging plants did produce higher yields but increasing the duration of emergence was not sufficient to increase plant-to-plant variation. The seed tuber orientation and shaded treatments were intended to produce (or simulate) more uniform emergence but were unsuccessful in doing so. Considerable growth occurred prior to removing the shade material and this added credence to the seed tuber affecting the growth rate of plants post-emergence. The results of Expt 3 were the most unexpected since there were very large differences in the variation in space per plant between treatments. It was noticeable in the most extreme treatment that the stems grew into the large (80 cm) gap and this allowed plants with less space (10 cm) to still occupy a similar amount of space in the canopy as plants with more space in the row.

The high standard error of the COV of tuber size in Expts 1-3 made detecting any significant differences between treatments unlikely. The treatments were adapted and combined in Expt 4 in an attempt to reduce the standard error and make significant differences easier to detect. Two levels of each factor were chosen consisting of either high or low variation in seed tuber weight, sprout length (which was expected to affect variation in emergence) and within-row spacing. Varieties differ in their canopy growth habit and it was possible that the lack of any effect of the treatments in Expt 4 on uniformity was due to the canopy of Maris Piper being highly plastic and that other varieties may not have responded in the same manner. Expt 5 was designed to examine the hypothesis that varieties may respond differently to variation in within-row spacing by comparing uniform spacing with the most extreme treatment of Expt 3

in Markies and Marfona. In Survey 3d there was an extremely wide range in seed tuber weight and yet the crop was relatively uniform and this appeared to be due to plants growing from larger seed tubers producing more stems, more tubers and higher yields. This was unexpected and merited further attention, so in Expt 6, treatments were chosen to compare the effect of grading seed tubers on the uniformity of Maris Piper.

The results of Expt 1 indicated that factors other than seed tuber weight influenced the number of stems per seed tuber. Two potential influences that could affect physiology of the seed tubers were within-field variation within the seed crop and differences in the dry matter concentration of the seed tuber. Tubers were harvested from the sections of the crop examined in Surveys 3a & 3b and their initial growth was compared in Expt 7 with the expectation that tubers from the heavier soil, (where emergence was later) would produce fewer stems than those from the lighter soil. Two seed sizes were used so the effect of seed size on the initial growth rate of the canopy could also be quantified. In Survey 5, seed tubers of similar weights were classified according to their specific gravity (indicative of their dry matter concentration) with the expectation that seed tubers with a higher specific gravity would produce more stems than those with a lower specific gravity.

Survey 2 identified a strong correlation between the yield and the mean tuber weight per stem and identified several relationships which influenced the variation in yield per stem in Maris Piper. Specifically, loss of dry weight from the seed tuber influenced the initial growth of plants and the total thickness of stems per plant correlated with seed tuber weight indicating that seed tuber substrate per stem affected yield per stem. Survey 4 was designed to examine stem-to-stem variation in Desiree, Russet Burbank and King Edward as well as Maris Piper, and establish whether the relationships found in Survey 2 were consistent between years and varieties. It was suspected that seed tuber substrate was important for determining differences in the size of stems, but as it could not be manipulated experimentally, two other pieces of

work were established to further clarify the role of seed tuber substrate. In Expt 8, seed tubers were planted at very wide spacings (1.52 m) to allow plants growing without competition to be monitored non-destructively for longer than was possible in other work. In Survey 6, the growth of Desiree plants grown from minitubers (weighing 1-2 g) was examined non-destructively and compared to the growth of plants grown from 30-40 mm seed tubers in Survey 2.

#### 4.8. Experiment 4 – Effects of variation in seed tuber weight, sprout length and within-row spacing

##### 4.8.1. Emergence and ground cover

There were no differences in the interval from planting to 50 % emergence between treatments (Table 54) and all plants in harvest rows emerged (data not shown). Increasing variation in sprout length increased the interval from 20 to 80 % emergence by *c.* 50 % to 4.5 days, but increasing variation in seed tuber weight and within-row spacing had no effect (Table 54). The difference between sprouting treatments suggests that some variation in the interval from planting to emergence was caused by differences in the sprouting condition of seed tubers at planting and those with more developed sprouts emerged sooner.

**Table 54. Main effects of variation in seed tuber weight, sprout length and within-row spacing on the intervals from planting to 50 % emergence and from 20 to 80 % emergence in Expt 4.**

|   | Variation in seed tuber weight |      |          | Variation in sprout length |      |          | Variation in within-row spacing |      |          | S.E. (21 D.F.) |
|---|--------------------------------|------|----------|----------------------------|------|----------|---------------------------------|------|----------|----------------|
|   | Low                            | High | <i>P</i> | Low                        | High | <i>P</i> | Low                             | High | <i>P</i> |                |
| Interval from planting to 50 % emergence (days) | 27.7                           | 27.1 | n.s.     | 27.4                       | 27.4 | n.s.     | 27.4                            | 27.4 | n.s.     | 0.28           |
| Interval from 20 to 80 % emergence (days)       | 3.93                           | 3.63 | n.s.     | 3.06                       | 4.49 | <0.001   | 3.88                            | 3.67 | n.s.     | 0.132          |

Increasing variation in seed tuber weight and sprout length had no effect on average ground cover per plant 10 DAE, but both increased the COV of ground cover per plant from *c.* 30 to 40 % (Table 55). When variation in seed tuber weight was increased, more of the variation in

ground cover per plant could be explained by variation in seed tuber weight and less from variation in the date of emergence (Table 55). Regressions including both seed tuber weight and date of emergence explained *c.* 70 % of variation in ground cover per plant 10 DAE in both treatments (Table 55). When variation in sprout length was increased, there was no effect on the amount of variation in ground cover per plant explained by the weight of seed tubers but more of the variation in ground cover per plant could be explained by variation in date of emergence and also by the combination of seed tuber weight and date of emergence (Table 55). The effects of variation in within spacing were not considered in this analysis, as the plants in the more variable treatment had already begun to compete and so only the less variable treatment was sampled.

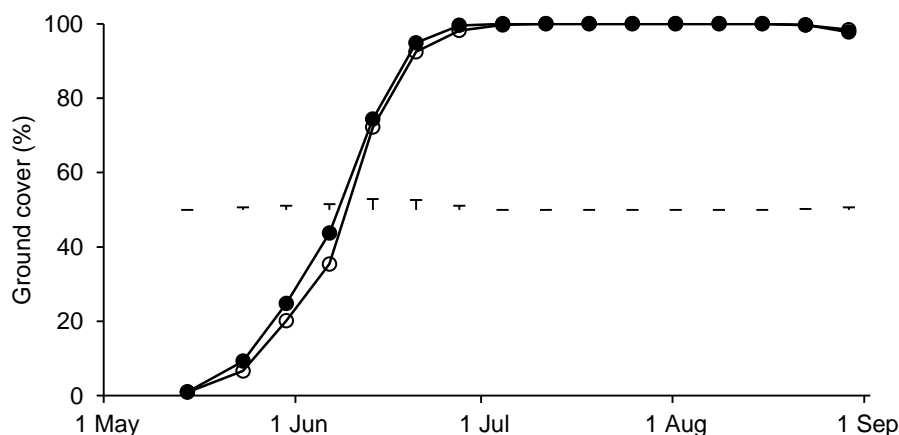
**Table 55. Main effects of variation in seed tuber weight and sprout length on the average and COV of ground cover (GC) per plant 10 DAE and on the correlation coefficients of relationships between ground cover and seed tuber weight (ST) and date of emergence (EM) in Expt 4.**

|  | Variation in seed tuber weight |                 |                     | Variation in sprout length |       |          | S.E.<br>(9 D.F.) |       |       |
|--|--------------------------------|-----------------|---------------------|----------------------------|-------|----------|------------------|-------|-------|
|  | Low                            | High            | <i>P</i>            | Low                        | High  | <i>P</i> |                  |       |       |
| GC per plant (cm <sup>2</sup> )  | 234                            | 233             | n.s.                | 221                        | 247   | n.s.     | 14.5             |       |       |
| COV of GC per plant (%)  | 32.8                           | 41.8            | <0.05               | 33.2                       | 41.4  | <0.05    | 2.47             |       |       |
| Correlation coefficient of relationships between <i>x</i> and GC per plant | } <i>x</i> = ST                | 0.03            | 0.36                | <0.001                     | 0.18  | 0.21     | n.s.             | 0.027 |       |
|  |                                | } <i>x</i> = EM | 0.65                | 0.46                       | <0.05 | 0.44     | 0.67             | <0.01 | 0.046 |
|  |                                |                 | } <i>x</i> = EM, ST | 0.67                       | 0.75  | n.s.     | 0.62             | 0.80  | <0.01 |

Increasing variation in within-row spacing decreased ground cover at 10, 17 and 24 DAE, but from 31 DAE there was no significant difference between treatments (Table 56; Figure 57).

Increasing variation in seed tuber weight and sprout length had no effect on ground cover at any time from 10 to 45 DAE (Table 56). This indicates that while increasing variation in within-row spacing had a small effect on the rate of initial canopy expansion, between 24 and 31 DAE the growth faster and after 31 DAE the canopies were indistinguishable. From 45 DAE until final harvest, all treatments had > 99 % ground cover (Figure 57). The integrated ground cover from emergence until final harvest did not differ between treatments (Table 57).

**Figure 57. Effect of variation in within-row spacing on ground cover in Expt 4. Low variation in within-row spacing, ●; high variation in within-row spacing, ○. Bars indicate S.E. based on 21 D.F.**



**Table 56. Main effects of variation in seed tuber weight, sprout length and within-row spacing on percentage ground cover from 10 to 45 DAE in Expt 4.**

| DAE | Variation in seed tuber weight |      |          | Variation in sprout length |      |          | Variation in within-row spacing |      |          | S.E. (21 D.F.) |
|-----|--------------------------------|------|----------|----------------------------|------|----------|---------------------------------|------|----------|----------------|
|     | Low                            | High | <i>P</i> | Low                        | High | <i>P</i> | Low                             | High | <i>P</i> |                |
| 10  | 7.7                            | 8.2  | n.s.     | 7.7                        | 8.2  | n.s.     | 9.3                             | 6.7  | <0.01    | 0.63           |
| 17  | 22.3                           | 22.6 | n.s.     | 22.4                       | 22.4 | n.s.     | 24.8                            | 20.1 | <0.01    | 1.10           |
| 24  | 40.4                           | 38.7 | n.s.     | 39.2                       | 39.8 | n.s.     | 43.7                            | 35.4 | <0.001   | 1.52           |
| 31  | 76.1                           | 70.4 | n.s.     | 71.8                       | 74.8 | n.s.     | 74.4                            | 72.2 | n.s.     | 2.85           |
| 38  | 96.2                           | 91.1 | n.s.     | 94.4                       | 92.9 | n.s.     | 94.9                            | 92.4 | n.s.     | 2.65           |
| 45  | 99.8                           | 98.0 | n.s.     | 99.5                       | 98.3 | n.s.     | 99.6                            | 98.2 | n.s.     | 1.11           |

**Table 57. Main effects of variation in seed tuber weight, sprout length and within-row spacing on integrated ground cover (% days) from planting until final harvest in Expt 4.**

| Variation in seed tuber weight |      |          | Variation in sprout length |      |          | Variation in within-row spacing |      |          | S.E. (21 D.F.) |
|--------------------------------|------|----------|----------------------------|------|----------|---------------------------------|------|----------|----------------|
| Low                            | High | <i>P</i> | Low                        | High | <i>P</i> | Low                             | High | <i>P</i> |                |
| 8398                           | 8305 | n.s.     | 8350                       | 8354 | n.s.     | 8429                            | 8275 | n.s.     | 62.6           |

#### 4.8.2. Overall crop parameters

At the second harvest, increasing variation in seed tuber weight decreased the number of stems and the number of tubers but this effect was not observed at other harvests (Table 58).

Increasing variation in sprout length increased the number of stems at the first and third harvests but not at the second harvest and had no effect on the number of tubers at any harvest (Table 58). The number of stems would not be expected to change during the season and so it is unclear why changing variation in the seed tuber weight and sprout length had these effects.

Increasing variation in within-row spacing had no effect on the number of stems at any

harvest, but decreased the number of tubers by *c.* 10 % at the second and third harvests (Table 58).

Increasing variation in seed tuber weight and sprout length had no effect on yield, weight of above-ground stems or total dry weight at any harvest (Table 58). Increasing variation in within-row spacing had no effect on yield at the first harvest but at the second and third harvest it decreased yield by *c.* 6 and 10 % respectively (Table 58). Increasing variation in within-row spacing had no effect on weight of above-ground stems at any harvest and total dry weight was only significantly decreased at the third harvest by *c.* 8 % (Table 58).

Considering there was no difference in integrated ground cover days between treatments (Table 58), the decrease in yield and dry matter production caused by increasing variation in within-row spacing was unexpected. It could either have been caused by decreased radiation use efficiency or by plants in neighbouring rows out-competing those in the harvest row. This could have decreased the leaf area of the plants in the harvest row, without causing any detectable decrease in ground cover.

Increasing variation in seed tuber weight increased mean tuber size by *c.* 1 mm at the second and third harvests (Table 58). This difference was relatively small and at the second harvest was consistent with differences observed in the number of stems and tubers combined with no difference in yield. Increasing variation in sprout length and within-row spacing had no effect on mean tuber size at any harvest (Table 58). The decrease in yield and the number of tubers when variation in within-row spacing was increased therefore compensated for each other, since a change in either of these variables by itself would be expected to affect mean tuber size.

**Table 58. Main effects of variation in seed tuber weight, sprout length and within-row spacing on parameters of crop growth at each harvest (1-3, 44, 76 and 112 DAE respectively) in Expt 4.**

|   | Harvest | Variation in seed tuber weight |      |          | Variation in sprout length |      |          | Variation in within-row spacing |      |          | S.E.<br>(21 D.F.) |
|---|---------|--------------------------------|------|----------|----------------------------|------|----------|---------------------------------|------|----------|-------------------|
|   |         | Low                            | High | <i>P</i> | Low                        | High | <i>P</i> | Low                             | High | <i>P</i> |                   |
| Number of stems (000/ha)  | 1       | 130                            | 133  | n.s.     | 123                        | 141  | <0.001   | 130                             | 134  | n.s.     | 3.1               |
|   | 2       | 139                            | 128  | <0.001   | 134                        | 132  | n.s.     | 133                             | 134  | n.s.     | 2.0               |
|   | 3       | 136                            | 130  | n.s.     | 129                        | 137  | <0.05    | 133                             | 133  | n.s.     | 2.5               |
| Number of tubers (000/ha)   | 1       | 638                            | 611  | n.s.     | 605                        | 644  | n.s.     | 643                             | 607  | n.s.     | 16.8              |
|   | 2       | 616                            | 567  | <0.001   | 595                        | 588  | n.s.     | 621                             | 562  | <0.001   | 14.0              |
|   | 3       | 563                            | 536  | n.s.     | 541                        | 557  | n.s.     | 579                             | 520  | <0.05    | 16.5              |
| Yield (t FW/ha)   | 1       | 20.4                           | 19.9 | n.s.     | 20.0                       | 20.3 | n.s.     | 21.0                            | 19.3 | n.s.     | 0.62              |
|   | 2       | 49.8                           | 48.7 | n.s.     | 49.4                       | 49.1 | n.s.     | 50.9                            | 47.6 | <0.05    | 1.11              |
|   | 3       | 71.9                           | 72.3 | n.s.     | 72.9                       | 71.3 | n.s.     | 75.0                            | 69.2 | <0.05    | 1.74              |
| Weight of above-ground stems (t FW/ha)  | 1       | 24.9                           | 23.7 | n.s.     | 24.1                       | 24.4 | n.s.     | 25.1                            | 23.5 | n.s.     | 1.02              |
|   | 2       | 32.6                           | 33.0 | n.s.     | 33.1                       | 32.5 | n.s.     | 33.4                            | 32.2 | n.s.     | 1.02              |
|   | 3       | 26.3                           | 27.2 | n.s.     | 27.0                       | 26.5 | n.s.     | 27.2                            | 26.4 | n.s.     | 0.84              |
| Total dry weight (t/ha)   | 1       | 5.4                            | 5.2  | n.s.     | 5.2                        | 5.4  | n.s.     | 5.5                             | 5.1  | n.s.     | 0.18              |
|   | 2       | 13.9                           | 13.9 | n.s.     | 14.0                       | 13.8 | n.s.     | 14.3                            | 13.5 | n.s.     | 0.34              |
|   | 3       | 19.9                           | 19.7 | n.s.     | 20.0                       | 19.6 | n.s.     | 20.6                            | 19.0 | <0.05    | 0.48              |
| Mean tuber size (mm)  | 1       | 37.5                           | 37.6 | n.s.     | 37.7                       | 37.4 | n.s.     | 37.8                            | 37.3 | n.s.     | 0.22              |
|   | 2       | 50.9                           | 51.8 | <0.05    | 51.2                       | 51.5 | n.s.     | 51.1                            | 51.6 | n.s.     | 0.28              |
|   | 3       | 58.6                           | 59.9 | <0.05    | 59.4                       | 59.1 | n.s.     | 59.1                            | 59.4 | n.s.     | 0.38              |
| COV of tuber size (%)   | 1       | 14.0                           | 14.0 | n.s.     | 13.6                       | 14.4 | <0.01    | 13.9                            | 14.1 | n.s.     | 0.21              |
|   | 2       | 13.8                           | 13.9 | n.s.     | 13.9                       | 13.9 | n.s.     | 13.7                            | 14.0 | n.s.     | 0.25              |
|   | 3       | 15.6                           | 15.8 | n.s.     | 15.4                       | 16.0 | n.s.     | 15.2                            | 16.1 | <0.05    | 0.23              |
| COV of above-ground stem weight (%)   | 1       | 49.2                           | 50.5 | n.s.     | 49.1                       | 50.6 | n.s.     | 48.4                            | 51.3 | n.s.     | 2.89              |
|   | 2       | 51.8                           | 52.8 | n.s.     | 53.2                       | 51.4 | n.s.     | 48.6                            | 56.0 | <0.05    | 1.92              |
|   | 3       | 63.6                           | 58.6 | n.s.     | 59.0                       | 63.2 | n.s.     | 56.0                            | 66.3 | <0.01    | 2.20              |
| Transformed and weighted average above-ground stem weight ( $\sqrt[3]{\text{g FW}}$ ) | 1       | 6.07                           | 5.93 | n.s.     | 6.11                       | 5.90 | n.s.     | 6.09                            | 5.92 | n.s.     | 0.111             |
|   | 2       | 6.54                           | 6.75 | n.s.     | 6.67                       | 6.62 | n.s.     | 6.61                            | 6.68 | n.s.     | 0.076             |
|   | 3       | 6.28                           | 6.39 | n.s.     | 6.39                       | 6.28 | n.s.     | 6.30                            | 6.37 | n.s.     | 0.070             |
| Transformed and weighted COV of above-ground stem weight (%)                          | 1       | 14.0                           | 13.7 | n.s.     | 13.2                       | 14.6 | n.s.     | 13.2                            | 14.5 | n.s.     | 0.79              |
|   | 2       | 15.6                           | 15.5 | n.s.     | 16.0                       | 15.1 | n.s.     | 14.7                            | 16.3 | n.s.     | 0.56              |
|   | 3       | 17.6                           | 16.5 | n.s.     | 16.9                       | 17.3 | n.s.     | 16.1                            | 18.0 | <0.05    | 0.59              |

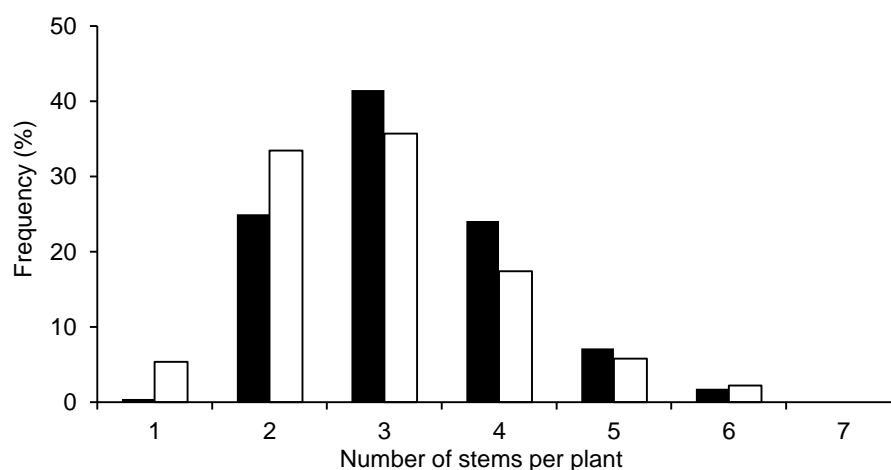
At the first harvest, increasing variation in sprout length increased the COV of tuber size but no differences were observed at later harvests (Table 58). Increasing variation in within-row spacing had no effect on the COV of tuber size at the first or second harvest but increased it by 0.9 % at the final harvest. Increasing variation in seed tuber weight had no effect on the COV of tuber size at any harvest (Table 58). None of the treatments had any effect on the COV of above-ground stem weight at the first harvest, but at the second harvest, increasing variation in within-row spacing increased it slightly (Table 58) and the effect was more pronounced at the third harvest, also being detected in the weighted distribution of above-ground stem weights (Table 58).

#### 4.8.3. Plant-to-plant variation

At the first two harvests, increasing variation in seed tuber weight increased the COV of the number of stems per plant, but there was no significant effect at the third harvest (Table 59). This effect was expected to occur since seed tuber weight affects the number of stems produced, but the relatively small difference between treatments (Figure 58) and the inconsistency of the effect demonstrates that other unidentified factors influenced the number of stems per plant and that variation in the number of stems per plant was insensitive to changes in seed tuber weight. Increasing variation in sprout length did not affect the COV of the number of stems per plant at any harvest (Table 59). At the first harvest, increasing variation in within-row spacing increased the COV of the number of stems per plant, but this was probably an anomalous result and was not found at later harvests (Table 59).



**Figure 58. Number of stems per plant at the second harvest of Expt 4. Low variation in seed tuber weight, ■; high variation in seed tuber weight, □.**

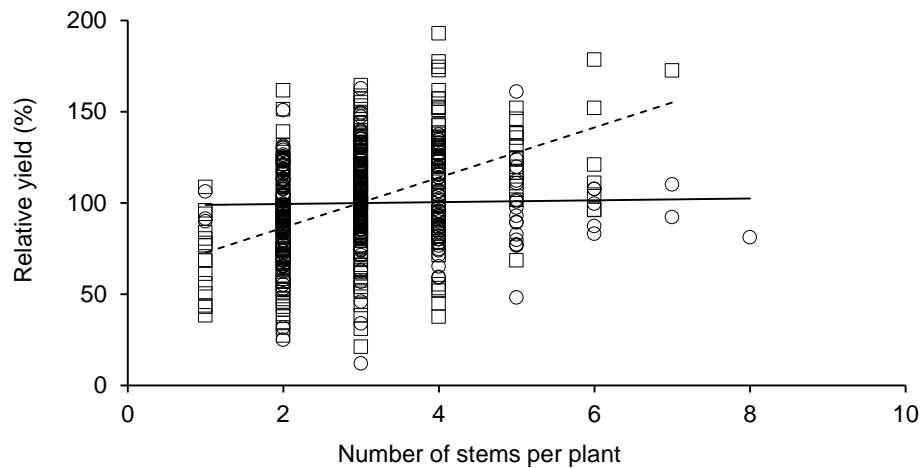


At each harvest, the COV of yield per plant increased as variation in the experimental factors increased. Numerically, the increase in the COV of yield per plant was largest when variation in seed tuber weight was increased and smallest when variation in sprout length was increased (Table 59). The difference between seed tuber weight and sprout length treatments remained at a similar level at all harvests, whereas increasing variation in within-row spacing had only a small effect at the first harvest and a larger effect at the second and third harvests (Table 59).

At the final harvest, the number of stems per plant had no effect on the relative yield per plant when the variation in seed tuber weight was low, but when variation in seed tuber weight was high, the relative yield increased as the number of stems per plant increased (Figure 59).

When regressions were conducted on individual plots and the correlation coefficients were analysed by ANOVA, the difference between the seed weight treatments was significant (Figure 59).

**Figure 59. Relationship between the number of stems per plant (SN) and relative yield (YD) per plant for the low variation in seed tuber weight (○) and high variation in seed tuber weight (□) at the third harvest of Expt 4. Fitted lines: low variation in seed tuber weight, —  $YD = 0.51 (\pm 1.27) \times SN + 98.4 (\pm 4.15)$ ,  $R^2 = 0.00$ ,  $p = n.s.$ ; High variation in seed tuber weight, - - -  $YD = 13.7 (\pm 1.59) \times SN + 59.0 (\pm 5.05)$ ,  $R^2 = 0.21$ ,  $p < 0.001$ . Correlation coefficients for regressions fitted to individual plots:  $0.00$  and  $0.21 \pm 0.0514$  with 21 D.F.  $p < 0.001$ .**



At each harvest, increasing variation in seed tuber weight increased the COV of the number of tubers per plant (Table 59). The difference between treatments was of a similar magnitude to the COV of yield per plant and was observed at the final harvest when there was no significant difference in the COV of the number of stems per plant between treatments (Table 59). Increasing variation in sprout length and within-row spacing had no effect on the COV of the number of tubers per plant at the first harvest but both increased it at the second and third harvests (Table 59). The effect of increasing variation in within-row spacing and sprout length on the COV of the number of tubers per plant was relatively small in comparison to the effect of increasing variation in seed tuber weight (Table 59). Since tubers would not have been initiated after the first harvest, the increase in the COV of the number of tubers per plant in the variable within-row spacing treatment between the first and second harvests may have been caused by some plants resorbing a larger proportion of tubers than others.

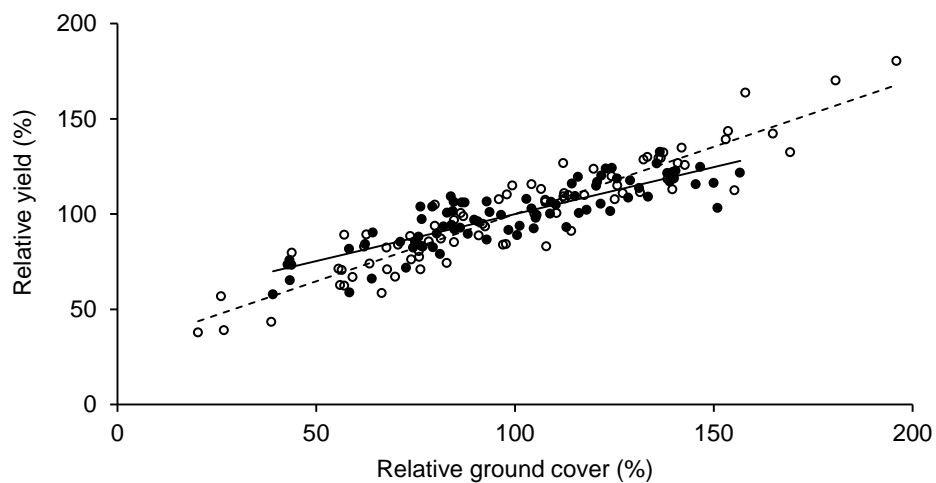
Increasing variation in seed tuber weight increased the COV of mean tuber weight per plant at the first harvest but not at other harvests (Table 59). Increasing variation in sprout length and

within-row spacing did not affect the COV of mean tuber weight per plant at the first two harvests but did at the third harvest (Table 59).

Although on average increasing sprout length increased the COV of tuber size at the first harvest, individual treatment combinations were not significantly different (Table 60).

Similarly, at the third harvest, although increasing variation in within-row spacing increased the COV of tuber size on average, only the two most extreme individual treatments (combining either all low levels of variation or all high levels of variation in the experimental factors) were significantly different from each other (Table 60). The difference between these two treatments was relatively large (2.5 %) in comparison to the overall difference between the low and high variation in within-row spacing treatments listed in Table 58 (0.9 %). It is apparent from this analysis that due to the variation between individual plots, only large differences in the COV of tuber size could be distinguished when there were few replicates and thus a large error. The differences in the COV of yield per plant and the COV of the number of tubers per plant were also larger between the two most extreme combinations of treatments than when each factor was considered separately (Table 60). The COV of yield per plant in the low-variation in within-row spacing treatment was lower than the COV of ground cover per plant 10 DAE in each of the treatments (Table 55, Table 60). For example, when variation in seed tuber weight was low, the COV of ground cover per plant 10 DAE was 33 % but the COV of yield per plant was 15-20 % at each harvest. This difference appears to be due to plants with a relatively high ground cover 10 DAE producing a proportionately lower yield than plants with a relatively low ground cover 10 DAE (Figure 60). Thus the population became less variable between 10 and 44 DAE.

Figure 60. Relationship between relative ground cover (GC) per plant 10 DAE and relative yield (YD) at the first harvest (44 DAE) of Expt 4. Low variation in seed tuber weight, ●; high variation in seed tuber weight ○. Fitted lines: Low variation in seed tuber weight, —  $YD = 0.493 (\pm 0.0335) \times GC + 50.7 (\pm 3.49)$ ,  $R^2 = 0.73$ ; High variation in seed tuber weight, - - -  $YD = 0.706 (\pm 0.0316) \times GC + 29.5 (\pm 3.36)$ ,  $R^2 = 0.86$ .



**Table 59. Main effects of variation in seed tuber weight, sprout length and within-row spacing on plant-to-plant variation at each harvest (1-3 at 44, 76 and 112 DAE respectively) in Expt 4.**

|  | Harvest | Variation in seed tuber weight |      |          | Variation in sprout length |      |          | Variation in within-row spacing |      |          | S.E.<br>(21 D.F.) |
|--|---------|--------------------------------|------|----------|----------------------------|------|----------|---------------------------------|------|----------|-------------------|
|  |         | Low                            | High | <i>P</i> | Low                        | High | <i>P</i> | Low                             | High | <i>P</i> |                   |
| COV of number of stems per plant (%)   | 1       | 27.2                           | 30.6 | <0.05    | 30.2                       | 27.6 | n.s.     | 26.9                            | 30.9 | <0.05    | 0.95              |
|  | 2       | 29.6                           | 37.0 | <0.01    | 32.4                       | 34.3 | n.s.     | 34.3                            | 32.3 | n.s.     | 1.50              |
|  | 3       | 32.6                           | 35.8 | n.s.     | 33.8                       | 34.6 | n.s.     | 32.3                            | 36.1 | n.s.     | 1.85              |
| COV of yield per plant (%)             | 1       | 19.2                           | 31.1 | <0.001   | 23.4                       | 26.9 | <0.05    | 23.4                            | 26.9 | <0.01    | 1.05              |
|  | 2       | 20.8                           | 35.2 | <0.001   | 25.3                       | 30.6 | <0.001   | 22.8                            | 33.1 | <0.001   | 0.96              |
|  | 3       | 22.4                           | 33.1 | <0.001   | 25.2                       | 30.3 | <0.05    | 24.2                            | 31.3 | <0.001   | 1.33              |
| COV of number of tubers per plant (%)  | 1       | 20.9                           | 28.4 | <0.001   | 24.8                       | 24.5 | n.s.     | 24.0                            | 25.3 | n.s.     | 1.07              |
|  | 2       | 20.8                           | 33.0 | <0.001   | 24.8                       | 29.0 | <0.01    | 25.2                            | 28.6 | <0.05    | 0.94              |
|  | 3       | 22.7                           | 31.1 | <0.001   | 25.1                       | 28.8 | <0.05    | 24.9                            | 28.9 | <0.05    | 1.19              |
| COV of mean tuber weight per plant (%) | 1       | 16.9                           | 21.2 | <0.05    | 17.9                       | 20.3 | n.s.     | 18.9                            | 19.2 | n.s.     | 1.40              |
|  | 2       | 20.7                           | 24.3 | n.s.     | 21.5                       | 23.5 | n.s.     | 24.1                            | 20.9 | n.s.     | 2.21              |
|  | 3       | 25.7                           | 24.5 | n.s.     | 22.9                       | 27.3 | <0.05    | 23.1                            | 27.1 | <0.05    | 1.29              |

**Table 60. Individual effects of variation in seed tuber weight, sprout length and within-row spacing on COV of tuber size, COV of yield per plant and COV of number of tubers per plant at each harvest (1-3 at 44, 76 and 112 DAE respectively) in Expt 4. Means were separated using Tukey's range test and means which were significantly different at the 95 % confidence level are distinguished by different letters following the value.**

|                                       | Harvest | Factor  | Level of variation |           |          |          |          |          |         |        | S.E.<br>(21 D.F.) |      |      |
|---------------------------------------|---------|---------|--------------------|-----------|----------|----------|----------|----------|---------|--------|-------------------|------|------|
|                                       |         |         | Seed               | Low       |          |          |          | High     |         |        |                   |      |      |
|                                       |         |         |                    | Sprouting | Low      |          | High     |          | Low     |        |                   | High |      |
|                                       |         |         |                    |           | Low      | High     | Low      | High     | Low     | High   |                   | Low  | High |
| COV of tuber size (%)                 | 1       | Spacing | 13.5               | 13.3      | 14.7     | 14.3     | 13.7     | 13.8     | 13.5    | 15.1   | 0.58              |      |      |
|                                       | 2       |         | 13.5               | 14.5      | 13.6     | 14.5     | 13.8     | 13.8     | 14.3    | 13.8   | 0.71              |      |      |
|                                       | 3       |         | 14.2 a             | 15.9 ab   | 16.0 ab  | 16.2 ab  | 15.7 ab  | 15.7 ab  | 15.0 ab | 16.7 b | 0.65              |      |      |
| COV of yield per plant (%)            | 1       | Spacing | 15.4 a             | 19.6 ab   | 18.4 a   | 23.4 abc | 28.6 bcd | 29.9 cd  | 29.3 cd | 36.4 d | 2.96              |      |      |
|                                       | 2       |         | 13.1 a             | 25.4 bc   | 17.2 ab  | 27.3 c   | 29.6 c   | 33.2 c   | 31.3 c  | 46.6 d | 2.70              |      |      |
|                                       | 3       |         | 16.3 a             | 23.6 ab   | 21.2 ab  | 28.5 ab  | 29.7 bc  | 31.2 bc  | 29.7 bc | 41.8 c | 3.76              |      |      |
| COV of number of tubers per plant (%) | 1       | Spacing | 22.3 ab            | 19.4 a    | 20.5 ab  | 21.3 ab  | 27.5 ab  | 30.0 b   | 27.5 ab | 30.4 b | 3.03              |      |      |
|                                       | 2       |         | 19.4 a             | 22.9 ab   | 18.8 a   | 22.1 ab  | 29.8 bc  | 27.1 abc | 32.6 c  | 42.4 d | 2.67              |      |      |
|                                       | 3       |         | 18.3 a             | 22.8 ab   | 24.2 abc | 25.6 abc | 26.1 abc | 33.1 bc  | 31.2 bc | 34.1 c | 3.36              |      |      |

#### 4.8.3.1. Effects on variation in tuber size

While each of the factors affected plant-to-plant variation, as evidenced by changes in the COV of yield per plant and the COV of the number of tubers per plant, these changes did not consistently result in a change in the COV of tuber size. If the changes in plant-to-plant variation were responsible for the increase in the COV of tuber size caused by increasing variation in within-row spacing at the third harvest, then there must have been other differences between the treatments which negated the effects of increased plant-to-plant variation when variation in seed tuber weight was increased and thus resulted in no effect on the COV of tuber size.

Linear regressions were performed on individual plots to determine the amount of variation in yield per plant that could be explained by variation in seed tuber weight, date of emergence and both of these variables in combination. Increasing variation in seed tuber weight increased the proportion of variation in yield per plant that could be explained by variation in seed tuber weight at each harvest and when seed tuber weight was more variable it explained c. 50 % of the variation in yield per plant (Table 61; Figure 61). Increasing variation in sprout length had no consistent effect on the proportion of yield explained by variation in seed tuber weight (Table 61). Increasing variation in within-row spacing decreased the proportion of variation in yield per plant that could be explained by seed tuber weight, although the effect was only significant at the second and third harvests (Table 61). This indicates that space per plant influenced yield per plant when the variation in within-row spacing was increased.

Date of emergence explained a relatively small proportion (typically less than 20 %) of the variation in yield per plant (Table 61). The proportion of yield explained by date of emergence was greater for the treatments with high variation in sprout length than low variation at each harvest indicating that the increase in the interval from 20-80 % emergence in the high variation treatment increased the relative importance of emergence in determining

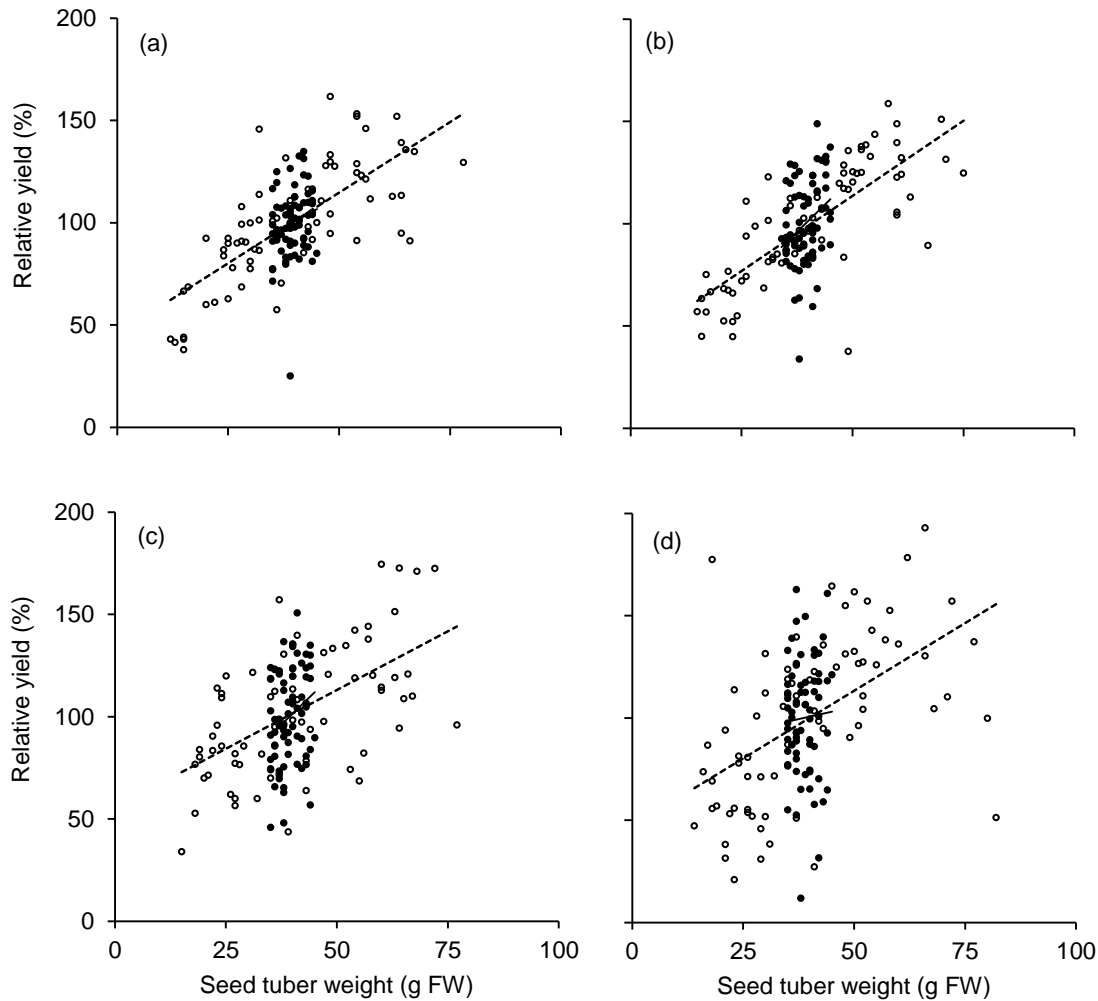
variation in yield per plant (Table 61). There were no consistent effects of emergence causing different amounts of variation in yield between the seed tuber weight and within-row spacing treatments (Table 61).

When both seed tuber weight and date of emergence were considered, a greater proportion of the variation in yield per plant could be explained (Table 61). The effects of treatments were consistent with when the variables were considered separately, with correlation coefficients being higher when variation in seed tuber weight and sprout length were increased, and lower when variation in within-row spacing was increased (Table 61). These results indicate that each of the experimental factors influence individual plant yields.

**Table 61. Main effects of variation in seed tuber weight, sprout length and within-row spacing on the correlation coefficients of linear regressions fitted to explain variation in yield per plant within each plot at each harvest (1-3, 44, 76 and 112 DAE respectively) of Expt 4.**

| Explanatory variable(s)              | Harvest | Variation in seed tuber weight |      |          | Variation in sprout length |      |          | Variation in within-row spacing |      |          | S.E. (21 D.F.) |
|--------------------------------------|---------|--------------------------------|------|----------|----------------------------|------|----------|---------------------------------|------|----------|----------------|
|                                      |         | Low                            | High | <i>P</i> | Low                        | High | <i>P</i> | Low                             | High | <i>P</i> |                |
| Seed tuber weight                    | 1       | 0.13                           | 0.55 | <0.001   | 0.32                       | 0.37 | n.s.     | 0.40                            | 0.28 | n.s.     | 0.057          |
|                                      | 2       | 0.03                           | 0.57 | <0.001   | 0.24                       | 0.36 | <0.05    | 0.40                            | 0.20 | <0.001   | 0.030          |
|                                      | 3       | 0.08                           | 0.45 | <0.001   | 0.26                       | 0.27 | n.s.     | 0.34                            | 0.19 | <0.01    | 0.036          |
| Date of emergence                    | 1       | 0.36                           | 0.19 | <0.01    | 0.18                       | 0.37 | <0.01    | 0.29                            | 0.26 | n.s.     | 0.044          |
|                                      | 2       | 0.16                           | 0.12 | n.s.     | 0.05                       | 0.23 | <0.001   | 0.16                            | 0.13 | n.s.     | 0.031          |
|                                      | 3       | 0.17                           | 0.08 | n.s.     | 0.07                       | 0.18 | <0.05    | 0.17                            | 0.07 | <0.05    | 0.032          |
| Seed tuber weight, date of emergence | 1       | 0.47                           | 0.70 | <0.01    | 0.46                       | 0.71 | <0.01    | 0.62                            | 0.55 | n.s.     | 0.054          |
|                                      | 2       | 0.15                           | 0.64 | <0.001   | 0.27                       | 0.51 | <0.001   | 0.53                            | 0.25 | <0.001   | 0.034          |
|                                      | 3       | 0.26                           | 0.50 | <0.001   | 0.33                       | 0.42 | n.s.     | 0.50                            | 0.25 | <0.001   | 0.042          |

**Figure 61.** Relationships between seed tuber weight (ST) and relative yield of individual plants at the third harvest of Expt 4, 112 DAE. Low variation in seed tuber weight, (—●—); high variation in seed tuber weight (- - ○ - -). (a) low variation in sprout length and low variation in within-row spacing; (b) high variation in sprout length and low variation in within-row spacing; (c) low variation in sprout length and high variation in within-row spacing; (d) high variation in sprout length and high variation in within-row spacing. See Table 62 for details of fitted lines.



**Table 62.** Fitted lines in Figure 61.  $YD = m ST + c$  where ST = seed tuber weight, YD = relative yield.

|     | Low variation in seed tuber weight |       |          |      |          |                       | High variation in seed tuber weight |       |          |       |          |                       |
|-----|------------------------------------|-------|----------|------|----------|-----------------------|-------------------------------------|-------|----------|-------|----------|-----------------------|
|     | <i>m</i>                           | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> | <i>m</i>                            | S.E.  | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
| (a) | 1.22                               | 0.686 | 51.9     | 27.2 | n.s.     | 0.03                  | 1.38                                | 0.150 | 45.7     | 6.33  | <0.001   | 0.54                  |
| (b) | 2.15                               | 0.759 | 15.6     | 30.0 | <0.01    | 0.09                  | 1.47                                | 0.145 | 40.2     | 6.29  | <0.001   | 0.59                  |
| (c) | 2.10                               | 0.935 | 17.3     | 36.9 | <0.05    | 0.05                  | 1.15                                | 0.197 | 55.6     | 8.71  | <0.001   | 0.32                  |
| (d) | 0.48                               | 1.190 | 81.4     | 46.1 | n.s.     | 0.00                  | 1.32                                | 0.243 | 47.2     | 10.50 | <0.001   | 0.29                  |

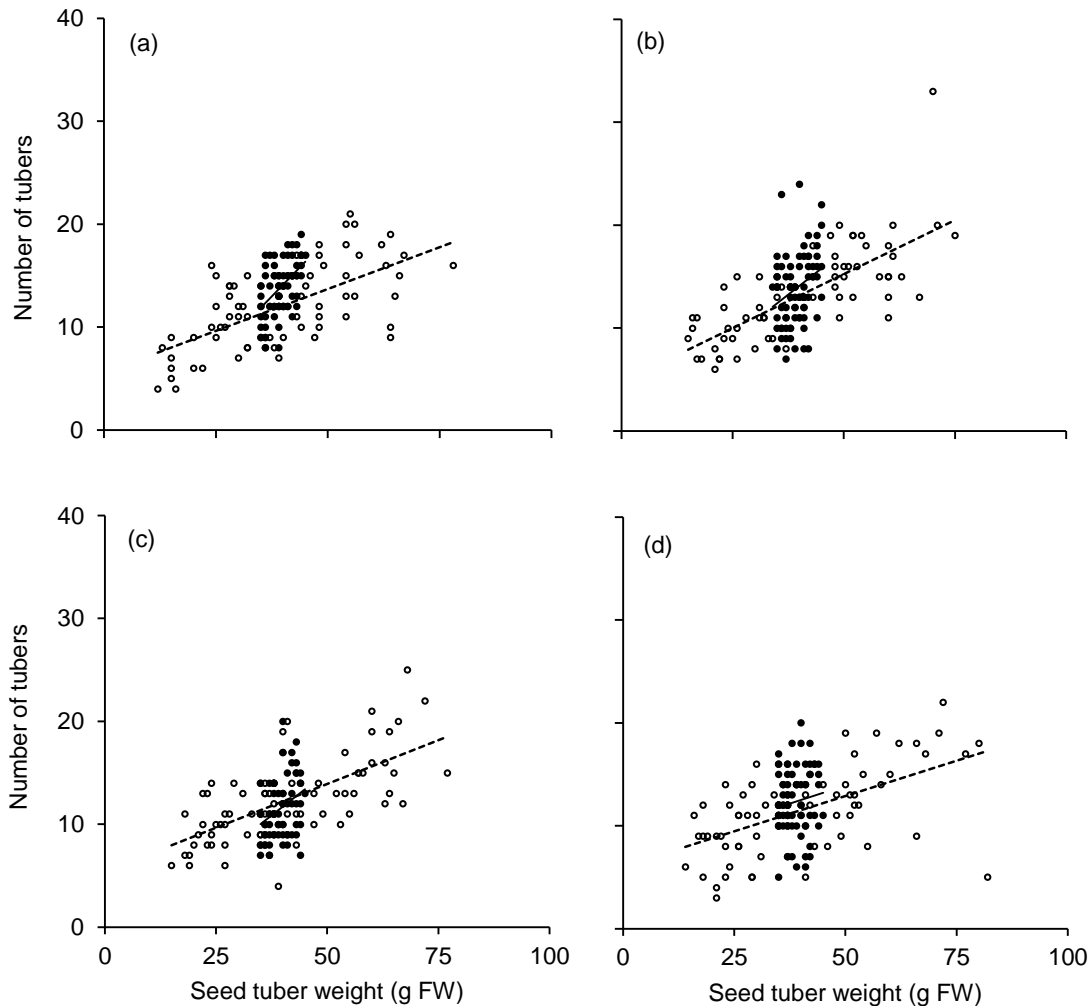


Increasing variation in seed tuber weight increased the correlation coefficients of linear regressions explaining the number of tubers per plant from seed tuber weight and yield per plant but the correlation coefficients did not consistently differ between the other treatments (Table 63). When variation in seed tuber weight was increased, both variation in yield and the number of tubers per plant were increased, but the three variables were positively correlated with each other i.e. smaller seed tubers produced relatively few tubers and a relatively low yield (Figs 61-62). This probably explains why the COV of mean tuber weight per plant did not increase detectably at the second and third harvests when variation in seed tuber weight was increased (Table 59) and consequently why the differences in plant-to-plant variation were not associated with any detectable change in the COV of tuber size.

**Table 63. Main effects of variation in seed tuber weight, sprout length and within-row spacing on the correlation coefficients of linear regressions fitted to explain variation in the number of tubers per plant within each plot at each harvest (1-3, 44, 76 and 112 DAE respectively) of Expt 4.**

| Explanatory variable | Harvest | Variation in seed tuber weight |      |          | Variation in sprout length |      |          | Variation in within-row spacing |      |          | S.E. (21 D.F.) |
|----------------------|---------|--------------------------------|------|----------|----------------------------|------|----------|---------------------------------|------|----------|----------------|
|                      |         | Low                            | High | <i>P</i> | Low                        | High | <i>P</i> | Low                             | High | <i>P</i> |                |
| Seed tuber weight    | 1       | 0.07                           | 0.45 | <0.001   | 0.23                       | 0.29 | n.s.     | 0.23                            | 0.28 | n.s.     | 0.043          |
|                      | 2       | 0.08                           | 0.49 | <0.001   | 0.22                       | 0.35 | <0.05    | 0.35                            | 0.22 | <0.05    | 0.041          |
|                      | 3       | 0.12                           | 0.47 | <0.001   | 0.29                       | 0.30 | n.s.     | 0.34                            | 0.25 | n.s.     | 0.041          |
| Number of stems      | 1       | 0.31                           | 0.36 | n.s.     | 0.41                       | 0.26 | n.s.     | 0.29                            | 0.38 | n.s.     | 0.068          |
|                      | 2       | 0.33                           | 0.50 | <0.05    | 0.41                       | 0.41 | n.s.     | 0.56                            | 0.27 | n.s.     | 0.118          |
|                      | 3       | 0.35                           | 0.50 | n.s.     | 0.45                       | 0.40 | n.s.     | 0.45                            | 0.40 | n.s.     | 0.057          |
| Yield                | 1       | 0.27                           | 0.55 | <0.001   | 0.41                       | 0.42 | n.s.     | 0.37                            | 0.45 | n.s.     | 0.050          |
|                      | 2       | 0.30                           | 0.69 | <0.001   | 0.49                       | 0.50 | n.s.     | 0.43                            | 0.56 | n.s.     | 0.053          |
|                      | 3       | 0.15                           | 0.54 | <0.001   | 0.29                       | 0.39 | <0.05    | 0.31                            | 0.38 | n.s.     | 0.045          |

**Figure 62. Relationships between seed tuber weight (ST) and number of tubers per plant at the third harvest of Expt 4, 112 DAE. Low variation in seed tuber weight, (—●—); high variation in seed tuber weight, (- -○- -). (a) low variation in sprout length and low variation in within-row spacing; (b) high variation in sprout length and low variation in within-row spacing; (c) low variation in sprout length and high variation in within-row spacing; (d) high variation in sprout length and high variation in within-row spacing. See Table 64 for details of fitted lines.**



**Table 64. Fitted lines in Figure 62.  $TN = m ST + c$ . Where ST = seed tuber weight, TN = number of tubers.**

|     | Low variation in seed tuber weight |       |          |      |          |                       | High variation in seed tuber weight |        |          |      |          |                       |
|-----|------------------------------------|-------|----------|------|----------|-----------------------|-------------------------------------|--------|----------|------|----------|-----------------------|
|     | <i>m</i>                           | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> | <i>m</i>                            | S.E.   | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
| (a) | 0.45                               | 0.094 | -4.0     | 3.71 | <0.001   | 0.24                  | 0.163                               | 0.0238 | 5.6      | 1.01 | <0.001   | 0.39                  |
| (b) | 0.34                               | 0.129 | 0.6      | 5.10 | <0.05    | 0.08                  | 0.210                               | 0.0234 | 4.8      | 1.02 | <0.001   | 0.53                  |
| (c) | 0.34                               | 0.111 | -1.9     | 4.38 | <0.01    | 0.11                  | 0.170                               | 0.0232 | 5.4      | 1.02 | <0.001   | 0.43                  |
| (d) | 0.14                               | 0.130 | 6.9      | 5.04 | n.s.     | 0.00                  | 0.137                               | 0.0247 | 6.0      | 1.07 | <0.001   | 0.30                  |

To examine further why increasing variation in within-row spacing increased the COV of tuber size, comparisons were made between the yield, number of tubers and the mean tuber weight of plants with less space in the row (an average of 12.5 cm each) in the more variable treatment with equivalently positioned, but evenly spaced plants (an average of 30 cm each)

in the less variable treatment (Section 3.1.3.8). Only the main effects of variable within-row spacing were examined since the other treatments contained a mixture of both spacing treatments and so would not be expected have any effect.

With evenly spaced plants, as expected the plants produced *c.* 50 % of the yield and tubers and the mean tuber weight was similar to the whole plot (Table 65). At the first harvest, plants with less space had a slightly decreased yield, but there was no significant difference in the number of tubers or mean tuber weight (Table 65). At the second harvest, the difference in yield had increased in comparison to that observed at the first harvest and the number of tubers and mean tuber weight of plants with less space both decreased (Table 65). Similar differences were observed at the final harvest; the plants with less space produced 42 % of the total yield and 47 % of the total number of tubers (Table 65). The mean tuber weight of plants with less space was 11 % lower than the average (Table 65). The plants with less space produced a disproportionate yield considering that they had 21 % of the space within the row but produced 42 % of the yield. The decrease in the number of tubers acted to counter the effect of the decreased yield on the mean tuber weight and meant that the overall effect on the COV of tuber size was relatively small.

**Table 65. Relative yield, number of tubers and mean tuber weight of plants with an average of 12.5 cm of space in the row in the high variation in within-row spacing treatment in comparison to plants in the equivalent position in the evenly spaced treatment with 30 cm each in the row (mean of sprouting and seed weight treatments).**

|   | Harvest | Variation in within-row spacing |      |          | S.E.<br>(27 D.F.) |
|---|---------|---------------------------------|------|----------|-------------------|
|   |         | Low                             | High | <i>P</i> |                   |
| Relative yield<br>(% of plot)                                       | 1       | 50.5                            | 47.1 | <0.05    | 1.11              |
|   | 2       | 49.8                            | 41.8 | <0.001   | 0.93              |
|   | 3       | 51.1                            | 41.7 | <0.001   | 1.00              |
| Relative number of tubers<br>(% of plot)                            | 1       | 50.7                            | 48.1 | n.s.     | 1.16              |
|   | 2       | 48.7                            | 44.5 | <0.01    | 0.94              |
|   | 3       | 50.0                            | 46.9 | <0.05    | 0.82              |
| Relative mean tuber weight<br>(% compared to mean of whole<br>plot) | 1       | 98.4                            | 98.8 | n.s.     | 1.48              |
|   | 2       | 101.1                           | 92.3 | <0.01    | 1.77              |
|   | 3       | 101.8                           | 89.0 | <0.001   | 1.57              |

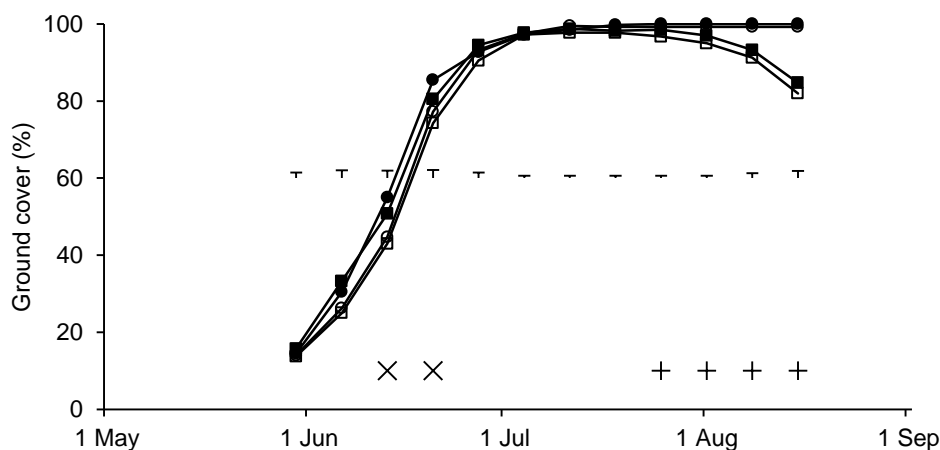
While increasing variation in within-row spacing only caused a small increase in the COV of yield per plant at the first harvest, differences became more pronounced as the season

progressed and probably contributed to the increase in the COV of tuber size at the third harvest. As the season progressed, the COV of yield per plant increased (Table 59), yield per plant correlated less strongly with seed tuber weight and the date of emergence (Table 61), plants with less space produced relatively lower yields and fewer, smaller tubers (Table 65) and at the third harvest the COV of above-ground stem weights was increased (Table 58). Overall, these results indicate that the relative yield of plants changed during the course of the season and that negative effects of variable within-row spacing became apparent late in the season.

#### 4.9. Experiment 5 – Effects of variation in within-row spacing on two varieties

Ground cover expansion was slower when variation in within-row spacing was increased but the differences were only significant *c.* 4-5 weeks after emergence (Figure 63). The canopy of Marfona began to senesce 4 weeks prior to harvest whereas Markies was still at 100 % ground cover (Figure 63).

**Figure 63. Ground cover in Expt 5. Markies, low variation in within-row spacing, ●; Markies, high variation in within-row spacing, ○; Marfona, low variation in within-row spacing, ■; Marfona, high variation in within-row spacing, □. Bars indicate S.E. based on 9 D.F. Significant differences ( $p < 0.05$ ) between within-row spacing treatments, ×; between varieties, +.**



The average seed tuber weight did not differ between the varieties, but COV of seed tuber weight was slightly higher in Marfona than Markies (Table 66). Marfona reached 50 % emergence 2 days earlier than Markies (Table 66) and all plants in the harvest rows emerged

(data not shown). Marfona produced *c.* 15 % fewer stems and *c.* 33 % fewer tubers than Markies and because there was no difference in yield between the varieties, the mean tuber size was over 10 mm larger in Marfona than Markies (Table 66). There was no difference in the COV of tuber size between the varieties (Table 66).

The interval from 20 to 80 % emergence, the COV of yield per plant, COV of mean tuber weight per plant and the COV of tuber size were all increased by increasing variation in within-row spacing (Table 66). The difference in the interval from 20 to 80 % emergence was relatively small (*c.* 0.7 days) and has no obvious explanation. The number of tubers was numerically *c.* 15 % lower when variation in the space per plant was increased but this difference was not significant ( $p = 0.06$ ). The COV of the number of tubers per plant was not affected by increasing variation in within-row spacing (Table 66). Yield was numerically *c.* 10 % lower when within-row spacing was more variable, but again this difference was not significant ( $p = 0.06$ ; Table 66). In Markies there was almost no difference in yield between treatments, but in Marfona the yield was numerically *c.* 15 % lower with variable within-row spacing (Table 67). The COV of yield per plant increased by *c.* 50 % when variation in within-row spacing was increased (Table 66). The COV of mean tuber weight per plant increased when variation in within-row spacing increased and this was consistent with the significant increase in the COV of yield per plant without any change in the COV of number of tubers per plant (Table 66). The increase in the COV of mean tuber weight per plant may explain the large difference in the COV of tuber size between treatments (Table 66).

**Table 66. Main effects of variety and variation in within-row spacing on parameters of crop growth and plant-to-plant variation in Expt 5.**

|   | Variety |         |          | Variation in within-row spacing |      |          | S.E.<br>(9 D.F.) |
|---|---------|---------|----------|---------------------------------|------|----------|------------------|
|   | Markies | Marfona | <i>P</i> | Low                             | High | <i>P</i> |                  |
| Seed tuber weight (g FW)                        | 54.4    | 54.3    | n.s.     | 54.4                            | 54.3 | n.s.     | 1.16             |
| COV of seed tuber weight (%)                    | 21.0    | 26.9    | <0.01    | 23.7                            | 24.3 | n.s.     | 1.07             |
| Interval from planting to 50 % emergence (days) | 40.6    | 37.9    | <0.001   | 38.3                            | 38.2 | n.s.     | 0.36             |
| Interval from 20 to 80 % emergence (days)       | 3.12    | 2.70    | n.s.     | 2.56                            | 3.26 | <0.01    | 0.144            |
| Number of stems (000/ha)                        | 106.6   | 89.0    | <0.05    | 97.8                            | 97.8 | n.s.     | 4.26             |
| Number of tubers (000/ha)                       | 393     | 261     | <0.001   | 348                             | 307  | 0.06     | 13.4             |
| Yield (t FW/ha)                                 | 58.8    | 57.4    | n.s.     | 60.8                            | 55.1 | 0.06     | 1.87             |
| Mean tuber size (mm)                            | 58.5    | 70.0    | <0.001   | 64.1                            | 64.4 | n.s.     | 0.54             |
| COV of tuber size (%)                           | 15.4    | 15.4    | n.s.     | 14.0                            | 16.8 | <0.001   | 0.38             |
| COV of number of stems per plant (%)            | 40.6    | 35.2    | n.s.     | 35.5                            | 40.3 | n.s.     | 2.28             |
| COV of number of tubers per plant (%)           | 33.9    | 35.2    | n.s.     | 34.3                            | 34.7 | n.s.     | 2.40             |
| COV of yield per plant (%)                      | 25.5    | 31.9    | n.s.     | 22.8                            | 34.7 | <0.01    | 2.09             |
| COV of mean tuber weight per plant (%)          | 34.6    | 32.0    | n.s.     | 27.4                            | 39.2 | <0.01    | 2.00             |

**Table 67. Individual effects of variety and variation in within-row spacing on parameters of crop growth and plant-to-plant variation in Expt 5. Means were separated using Tukey's range test and means which were significantly different at the 95 % confidence level are distinguished by different letters following the value.**

| Variation in within-row spacing        | Variety |         | Variation in within-row spacing |         | S.E.<br>(9 D.F.) |
|--|---------|---------|---------------------------------|---------|------------------|
|  | Markies | Marfona | Low                             | High    |                  |
| Yield (t FW/ha)                        | 58.2 a  | 58.8 a  | 62.8 a                          | 52.0 a  | 2.64             |
| Number of tubers (000/ha)              | 420 a   | 367 a   | 276 a                           | 246 a   | 26.8             |
| COV of tuber size (%)                  | 13.5 a  | 17.3 c  | 14.5 ab                         | 16.2 bc | 0.54             |
| COV of yield per plant (%)             | 21.7 a  | 29.3 ab | 23.9 ab                         | 40.0 b  | 2.96             |
| COV of number of tubers per plant (%)  | 33.2 a  | 34.5 a  | 33.2 a                          | 35.4 a  | 3.39             |
| COV of mean tuber weight per plant (%) | 28.6 ab | 40.7 b  | 26.3 a                          | 37.7 ab | 2.83             |

Plants with less space in the row (an average of 12.5 cm compared to 47.5 cm) produced c. 40 % of the total yield whereas when spacing was uniform, plants in the equivalent positions produced c. 50 % of the total yield as expected. However, plants with less space produced a similar proportion of the total number of tubers and consequently the mean tuber weight of the plants with less space was decreased (Table 68). Had the number of tubers decreased along with the decrease in yield, the effect on the mean tuber weight would have been reduced and the overall increase in the COV of tuber size may have been less.

**Table 68. Relative yield, number of tubers and mean tuber weight of plants with an average of 12.5 cm of space in the row in comparison to plants in the equivalent position in the evenly spaced treatment with 30 cm each in the row in Expt 5.**

|  | Variation in within-row spacing |      |          | S.E.<br>(11 D.F.) |
|--|---------------------------------|------|----------|-------------------|
|  | Low                             | High | <i>P</i> |                   |
| Relative yield (% of total)                      | 49.0                            | 40.5 | <0.01    | 1.78              |
| Relative number of tubers (% of total)           | 47.1                            | 49.6 | n.s.     | 1.10              |
| Relative mean tuber weight (% relative to total) | 104.6                           | 81.6 | <0.001   | 3.59              |

There were no significant differences in the correlation coefficients of linear regressions fitted to explain variation in yield per plant from the seed tuber weight and the date of emergence between the varieties. The correlation coefficients of linear regressions explaining yield from the weight of the seed tuber and from the seed tuber weight and date of emergence were significantly higher with uniform within-row spacing compared to irregular spacing (Table 69).

**Table 69. Effect of variety and variation in within-row spacing on the correlation coefficients of linear regressions fitted to explain variation in yield per plant from the seed tuber weight and date of emergence in Expt 5.**

|   | Variety |         |          | Variation in within-row spacing |      |          | S.E.<br>(9 D.F.) |
|---|---------|---------|----------|---------------------------------|------|----------|------------------|
|   | Markies | Marfona | <i>P</i> | Low                             | High | <i>P</i> |                  |
| Seed tuber weight                       | 0.20    | 0.29    | n.s.     | 0.34                            | 0.15 | <0.05    | 0.060            |
| Date of emergence                       | 0.23    | 0.18    | n.s.     | 0.26                            | 0.15 | n.s.     | 0.073            |
| Seed tuber weight and date of emergence | 0.49    | 0.38    | n.s.     | 0.55                            | 0.32 | <0.01    | 0.044            |

#### 4.10. Experiment 6 – Comparison of graded and ungraded seed tubers

The interval from planting to 50 % emergence and from 20 to 80 % emergence was similar for both treatments (Table 70) and all plants in the harvest rows emerged (data not shown).

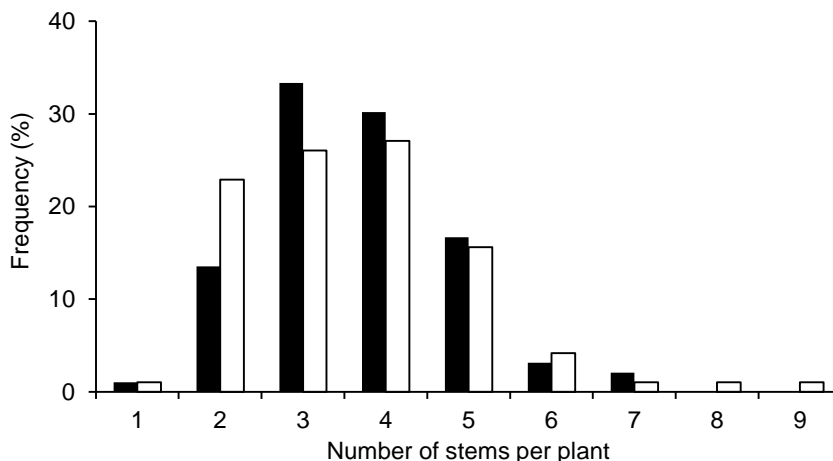
The treatments had no effect on yield, the number of stems, the number of tubers, mean tuber size (Table 70) or ground cover (data not shown).

The variation in the number of stems per plant was numerically slightly higher in the ungraded seed treatment than the graded seed treatment but not significantly different (Table 70). The ungraded seed tubers produced more plants with 2 stems and some plants with 8 or 9 stems but these were at a low frequency (Figure 64). For the ungraded seed tuber treatment,

more of the variation in the number of stems per plant could be explained by variation in seed tuber weight than in the graded seed (Table 71).

Increasing variation in seed tuber weight increased the COV of yield and the COV of number of tubers per plant from *c.* 22 to *c.* 34 % but did not affect the COV of mean tuber weight per plant (Table 70). The lack of a difference in the COV of mean tuber weight per plant between the treatments is probably due to the fact that yield and the number of tubers per plant both increased as seed tuber weight increased (Figs 66-67). Although there was no difference in the COV of mean tuber weight, the COV of tuber size was slightly increased in the ungraded seed tuber treatment (Table 70). This may be because the COV of mean tuber weight does not take into account the yield of individual plants, which determines the proportion of the total yield each plant contributes to the tuber size distribution. There was no significant difference in the COV of above-ground stem weights between treatments, nor in the transformed and weighted COV of above-ground stem weights (Table 70).

**Figure 64.** Number of stems per plant in Expt 6. Graded seed tubers, ■; ungraded seed tubers, □.





**Table 70. Effects of seed tuber grading on crop growth parameters and plant-to-plant variation in Expt 6.**

|   | Graded seed | Ungraded seed | <i>P</i> | S.E.<br>(5 D.F.) |
|---|-------------|---------------|----------|------------------|
| Interval from planting to 50 % emergence (days)                                       | 39.1        | 38.5          | n.s.     | 0.25             |
| Interval from 20-80 % emergence (days)  | 2.73        | 2.88          | n.s.     | 0.190            |
| Number of stems (000/ha)  | 160         | 158           | n.s.     | 5.7              |
| Number of tubers (000/ha)   | 596         | 592           | n.s.     | 13.3             |
| Yield (t FW/ha)   | 73.6        | 71.7          | n.s.     | 1.39             |
| Mean tuber size (mm)  | 57.6        | 57.9          | n.s.     | 0.64             |
| COV of tuber size (%)   | 14.5        | 15.3          | <0.05    | 0.17             |
| COV of number of stems per plant (%)  | 31.3        | 37.4          | n.s.     | 2.63             |
| COV of number of tubers per plant (%)   | 22.4        | 34.1          | <0.01    | 1.36             |
| COV of yield per plant (%)  | 21.0        | 33.5          | <0.01    | 1.64             |
| COV of mean tuber weight per plant (%)  | 24.0        | 22.9          | n.s.     | 2.21             |
| COV of above-ground stem weight (%)   | 53.9        | 48.7          | n.s.     | 2.11             |
| Transformed and weighted mean<br>above-ground stem weight ( $\sqrt[3]{\text{g FW}}$ ) | 6.30        | 6.24          | n.s.     | 0.066            |
| Transformed and weighted COV of<br>above-ground stem weight (%)                       | 15.7        | 13.8          | n.s.     | 0.60             |

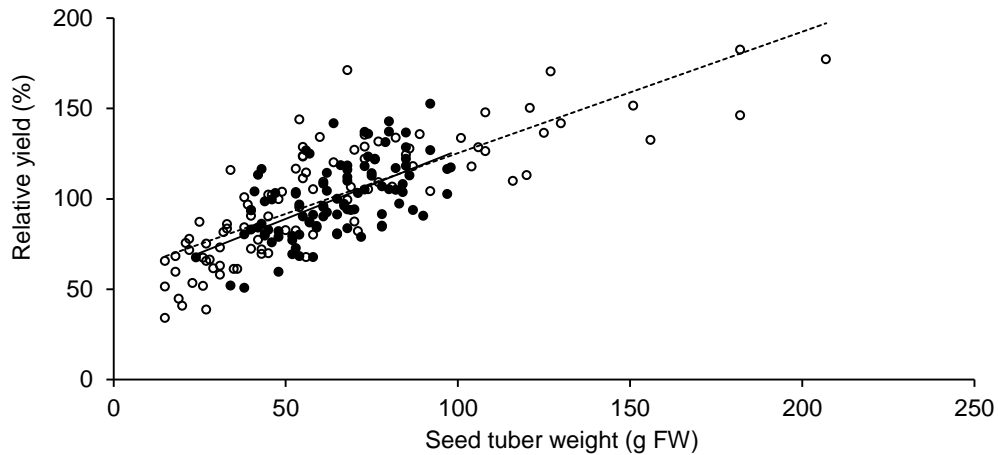
**Table 71. Average correlation coefficients of linear regressions fitted to plants within plots in Expt 6. ST = seed tuber weight, EM = date of emergence, SN = number of stems, YD = yield, TN = number of tubers.**

| ● | Explanatory variable(s) |    |    |    | Response<br>variable | Ungraded    |      | <i>P</i> | S.E.<br>(5 D.F.) |
|---|-------------------------|----|----|----|----------------------|-------------|------|----------|------------------|
|   | ST                      | EM | SN | YD |                      | Graded seed | seed |          |                  |
| ● |                         |    |    |    | YD                   | 0.37        | 0.64 | n.s.     | 0.083            |
|   |                         | ●  |    |    | YD                   | 0.08        | 0.13 | n.s.     | 0.081            |
| ● |                         | ●  |    |    | YD                   | 0.46        | 0.68 | n.s.     | 0.089            |
|   |                         |    | ●  |    | YD                   | 0.06        | 0.48 | <0.001   | 0.031            |
| ● |                         |    |    |    | SN                   | 0.14        | 0.50 | <0.01    | 0.053            |
| ● |                         |    |    |    | TN                   | 0.21        | 0.53 | n.s.     | 0.101            |
|   |                         |    |    | ●  | TN                   | 0.23        | 0.56 | <0.01    | 0.047            |

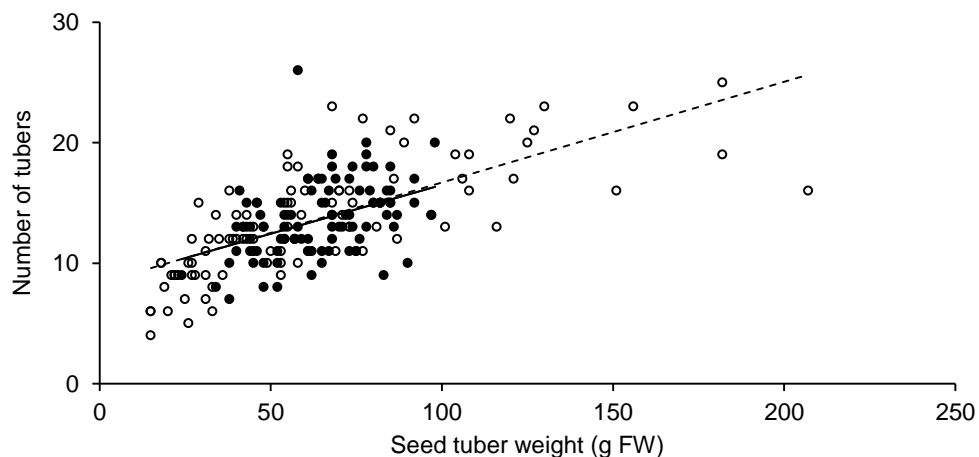
Emergence explained only *c.* 10 % of the variation in yield per plant in either treatment whereas variation in seed tuber weight explained *c.* 40-60 % of the variation (Table 71). The influence of seed tuber weight on yield per plant was highly variable between plots in the graded seed treatment with the correlation coefficient ranging from 0 to 0.70, whereas in the ungraded seed treatment it was consistently over 0.50 (data not shown). Overall, the amount of variation in yield explained by variation in the weight of the seed tuber did not differ significantly, but numerically more of the variation could be explained by variation in seed tuber weight in the ungraded seed treatment (Table 71). In the graded seed treatment, the number of tubers correlated significantly less strongly with yield than in the ungraded seed treatment (Table 71).



**Figure 66. Relationship between seed tuber weight (ST) and the relative yield (YD) per plant in Expt 6. Graded seed tubers, ●; ungraded seed tubers, ○. Fitted lines: Graded seed tubers, —  $YD = 0.756 (\pm 0.106) \times ST + 51.14 (\pm 7.08)$ ,  $R^2 = 0.34$ ; ungraded seed tubers, - - -  $YD = 0.671 (\pm 0.050) \times ST + 58.20 (\pm 3.72)$ ,  $R^2 = 0.65$ .**



**Figure 67. Relationship between seed tuber weight (ST) and number of tubers (TN) per plant in Expt 6. Graded seed tubers, ●; ungraded seed tubers, ○. Fitted lines: Graded seed tubers, —  $TN = 0.081 (\pm 0.0178) \times ST + 8.38 (\pm 1.190)$ ,  $R^2 = 0.17$ ; ungraded seed tubers, - - -  $TN = 0.083 (\pm 0.0082) \times ST + 8.35 (\pm 0.606)$ ,  $R^2 = 0.52$ .**



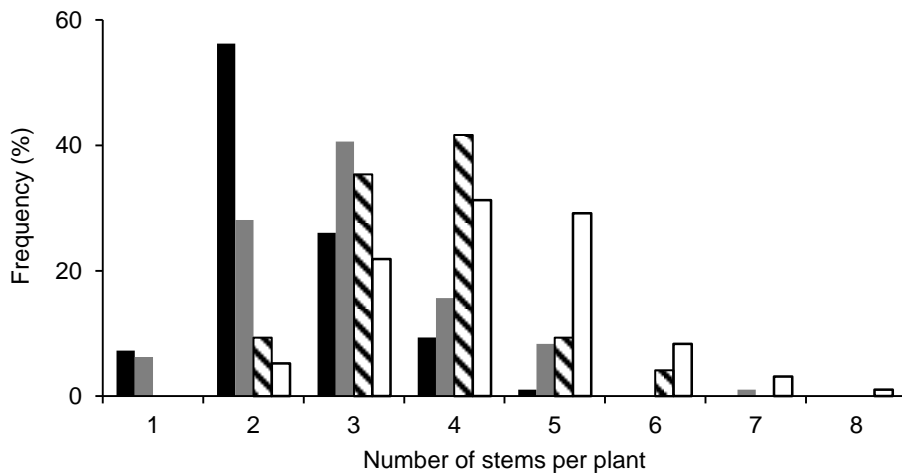
#### 4.11. Experiment 7 – Comparison of seed tuber sizes originating from contrasting soil types

The larger seed tubers had an average weight almost double that of the smaller seed tubers and had a slightly lower COV of seed tuber weight, but the seed tuber weight and COV of seed tuber weight did not differ between the soil types (Table 72). There were no effects of treatments on the interval from planting to emergence or from 20-80 % emergence (Table 72) and all of the plants emerged.

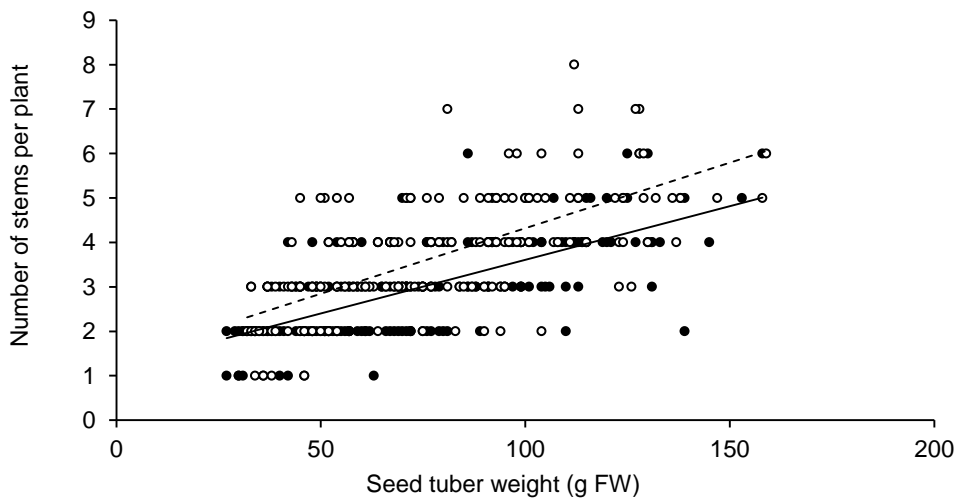
As expected, the larger seed produced more stems per plant than the smaller seed (Table 72; Figure 68). The seed tubers from the heavy soil produced *c.* 15 % fewer stems than the seed

tubers from the light soil (Table 72; Figure 68). The slope of the relationship between seed tuber weight and number of stems per plant was slightly higher for the seed tubers from light soil and the constant was also higher (Figure 69). The mother plants growing in the heavy soil emerged *c.* 1 week later than in light soil (as discussed in Section 4.6.1) and therefore initiated tubers *c.* 1 week later, resulting in the seed tubers being chronologically younger when planted, which may at least partly explain the decrease in the number of stems produced. The COV of the number of stems per plant was lower for the larger seed, which may be related to the lower COV of seed tuber weight (Table 72).

**Figure 68. Number of stems per plant in Expt 7. 35-45 mm seed tubers from heavy soil, black bars; 35-45 mm seed tubers from light soil, grey bars; 45-55 mm seed tubers from heavy soil, hatched bars; 45-55 mm seed tubers from light soil, white bars.**



**Figure 69. Relationship between seed tuber weight (ST) and number of stems per plant (SN) in Expt 7. Heavy soil, ●; light soil, ○. Fitted lines: Heavy soil, —  $SN = 0.0241 (\pm 0.00186) \times ST + 1.20 (\pm 0.151)$ ,  $R^2 = 0.47$ ; light soil, - - -  $SN = 0.0295 (\pm 0.00239) \times ST + 1.37 (\pm 0.195)$ ,  $R^2 = 0.44$ .**

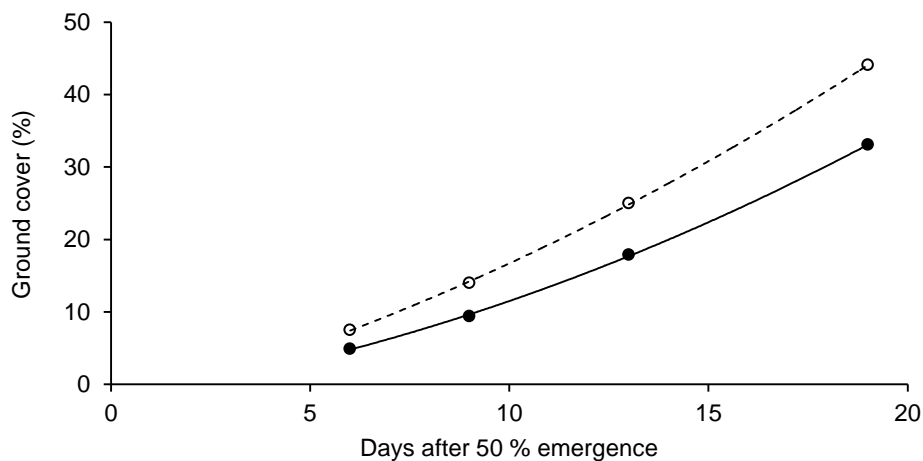


No differences in ground cover were observed between the seed tubers from contrasting soil types at any time despite the differences in the number of stems per plant (Table 72). The plants grown from larger seed tubers had higher ground cover at 6, 9, 13 and 19 DAE (Table 72; Figure 70) and at the harvest 19 DAE, the dry weight of the above-ground stems of plants grown from the larger seed tubers was *c.* 60 % higher (Table 72). These results demonstrate that seed tuber weight influenced the growth of the crops but the increase in above-ground stem weight was not proportional to the increase in seed tuber weight. Similarly, the *c.* 60 % higher above-ground stem weight of the larger seed only resulted in a *c.* 33 % higher ground cover (Table 72).

**Table 72. Main effects of soil type and seed tuber size on the average and COV of seed tuber weight, date of emergence and number of stems per plant, ground cover at 6, 9, 13 and 19 DAE and above-ground stem dry weight 19 DAE in Expt 7.**

|  | Soil type |       |          | Seed tuber size |             |          | S.E.<br>(9 D.F.) |
|--|-----------|-------|----------|-----------------|-------------|----------|------------------|
|  | Heavy     | Light | <i>P</i> | 35-45<br>mm     | 45-55<br>mm | <i>P</i> |                  |
| Seed tuber weight (g FW)                           | 75.7      | 76.0  | n.s.     | 52.0            | 99.7        | <0.001   | 0.84             |
| COV of seed tuber weight (%)                       | 25.6      | 23.4  | n.s.     | 27.1            | 21.9        | <0.001   | 0.71             |
| Interval from planting to 50 %<br>emergence (days) | 37.5      | 38.1  | n.s.     | 38.0            | 37.6        | n.s.     | 0.21             |
| Interval from 20-80 %<br>emergence (days)          | 2.28      | 2.34  | n.s.     | 2.39            | 2.23        | n.s.     | 0.193            |
| Number of stems per plant                          | 3.02      | 3.62  | <0.001   | 2.68            | 3.95        | <0.001   | 0.071            |
| COV of number of stems per<br>plant (%)            | 29.0      | 31.9  | n.s.     | 34.2            | 26.7        | <0.01    | 1.35             |
| Ground cover 6 DAE (%)                             | 6.3       | 6.0   | n.s.     | 4.9             | 7.5         | <0.05    | 0.57             |
| Ground cover 9 DAE (%)                             | 11.8      | 11.6  | n.s.     | 9.4             | 14.0        | <0.01    | 0.80             |
| Ground cover 13 DAE (%)                            | 22.6      | 20.3  | n.s.     | 17.9            | 25.0        | <0.01    | 1.13             |
| Ground cover 19 DAE (%)                            | 38.8      | 38.5  | n.s.     | 33.1            | 44.1        | <0.001   | 1.25             |
| Above-ground stem weight<br>(t DW/ha)              | 0.597     | 0.602 | n.s.     | 0.461           | 0.738       | <0.001   | 0.026            |

**Figure 70. Average ground cover (GC) of the two seed tuber sizes from 6-19 DAE in Expt 7. 35-45 mm, ●; 45-55 mm, ○. Fitted curves: 35-45 mm, — GC = -25.5 (±9.33) + 22.3 (±8.15) × 1.052 (±0.0116)<sup>DAE</sup>, R<sup>2</sup> = 0.999; 45-55 mm, - - - GC = -47.7 (±12.60) + 43.5 (±11.60) × 1.040 (±0.0071)<sup>DAE</sup> R<sup>2</sup> = 1.000.**



#### 4.12. Experiment 8 – Effects of seed tuber weight on the growth of widely spaced plants

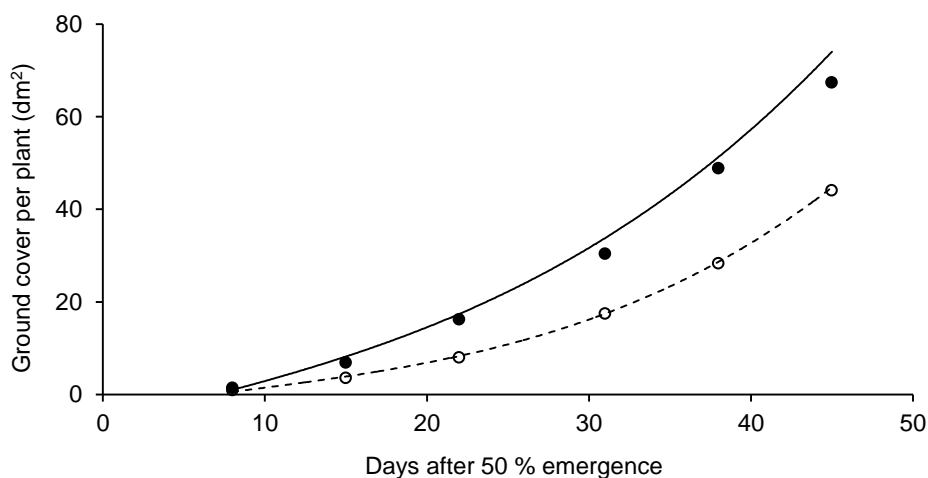
The plant canopies continued to expand throughout the season and after 45 DAE they were too large to measure using photography. The plants began to compete from *c.* 80 DAE and it was not possible to differentiate between the canopies of individual plants when the harvest was made. One plant grown from a 35-40 g seed tuber displayed foliar symptoms of primary virus Y infection and was visibly stunted, so this plant was excluded from the analysis.

There was no difference in the interval from planting to emergence between the treatments (Table 73). At 8 DAE the ground cover did not differ between treatments, but from 15 DAE ground cover was greater for plant with higher seed tuber weight (Table 73). At 15, 22 and 31 DAE the ground cover of plants grown from the smallest seed tubers was *c.* 50 % lower compared to the ground cover of plants grown from the largest seed tubers, but at 45 DAE the difference had reduced to *c.* 33 % (Table 73; Figure 71). Curves were fitted to the ground cover values of each plant at each date and the time at which individual plants reached a ground cover of 5, 10, 20 and 30 dm<sup>2</sup> was calculated from the curves. The interval between reaching each of those sizes was then calculated. The interval from 5 to 10 dm<sup>2</sup> and from 10 to 20 dm<sup>2</sup> decreased as seed tuber weight increased indicating that the seed tuber weight continued to influence the growth rate of plants (Table 74). There was no difference in the interval from 20 to 30 dm<sup>2</sup> however indicating that once the plants had reached a ground cover of 20 dm<sup>2</sup> the seed tuber no longer influenced their rate of growth (Table 74). Therefore the difference in ground cover at 45 DAE was caused by plants grown from larger seed tubers initially growing faster than those from smaller seed tubers but then subsequently growing at a similar rate dependent on their ground cover area.

**Table 73. Effects of seed tuber weight on the interval from planting to emergence, ground cover (GC) from 8-45 DAE, number of stems, yield and total dry weight for individual plants in Expt 8.**

|  | Seed tuber weight (g FW) |       |       |       | <i>P</i> | S. E.<br>(26 D.F.) |
|--|--------------------------|-------|-------|-------|----------|--------------------|
|  | 20-25                    | 35-40 | 50-55 | 65-70 |          |                    |
| Interval from planting to emergence (days) | 40.2                     | 39.9  | 40.5  | 40.7  | n.s.     | 0.47               |
| GC at 8 DAE (dm <sup>2</sup> )             | 0.92                     | 1.21  | 1.14  | 1.41  | n.s.     | 0.153              |
| GC at 15 DAE (dm <sup>2</sup> )            | 3.56                     | 5.20  | 5.55  | 6.86  | <0.001   | 0.405              |
| GC at 22 DAE (dm <sup>2</sup> )            | 8.00                     | 11.36 | 12.65 | 16.18 | <0.001   | 0.828              |
| GC at 31 DAE (dm <sup>2</sup> )            | 17.4                     | 22.4  | 24.4  | 30.4  | <0.001   | 1.17               |
| GC at 38 DAE (dm <sup>2</sup> )            | 28.3                     | 36.3  | 40.7  | 48.9  | <0.001   | 1.55               |
| GC at 45 DAE (dm <sup>2</sup> )            | 44.1                     | 53.2  | 58.7  | 67.4  | <0.001   | 1.40               |
| Number of stems per plant                  | 2.20                     | 2.76  | 2.60  | 3.80  | <0.001   | 0.259              |
| Yield per plant (kg FW)                    | 7.01                     | 8.20  | 8.62  | 9.61  | <0.001   | 0.279              |

**Figure 71.** Average ground cover per plant (GC) of the smallest and largest seed tuber weights from 8-45 DAE in Expt 8. 65-70 g, ●; 20-25 g, ○. Fitted curves: 65-70 g, — GC =  $-21.3 (\pm 5.58) + 16.3 (\pm 4.13) \times 1.038 (\pm 0.0046)^{\text{DAE}}$ ,  $R^2 = 0.998$ ; 20-25 g, - - - GC =  $-5.82 (\pm 0.574) + 4.18 (\pm 0.316) \times 1.057 (\pm 0.0016)^{\text{DAE}}$ ,  $R^2 = 1.000$ .



**Table 74.** Intervals for ground cover to increase from 5 to 10 dm<sup>2</sup>, 10 to 20 dm<sup>2</sup> and 20 to 30 dm<sup>2</sup> for plants grown from different sized seed tubers in Expt 8.

|   | Seed tuber weight (g FW) |       |       |       | P      | S. E.<br>(26 D.F.) |
|---|--------------------------|-------|-------|-------|--------|--------------------|
|   | 20-25                    | 35-40 | 50-55 | 65-70 |        |                    |
| Interval from 5 to 10 dm <sup>2</sup> (days)  | 6.89                     | 6.01  | 5.55  | 4.62  | <0.001 | 0.223              |
| Interval from 10 to 20 dm <sup>2</sup> (days) | 8.81                     | 8.52  | 7.96  | 7.28  | <0.001 | 0.140              |
| Interval from 20 to 30 dm <sup>2</sup> (days) | 5.91                     | 6.11  | 5.82  | 5.69  | n.s.   | 0.166              |

Yield increased as the weight of the seed tuber increased with plants grown from the smallest seed tubers producing *c.* 25 % less yield than those grown from the largest seed tubers (Table 73). These results demonstrate that the weight of the seed tuber affected the yield of plants but that the increase in yield was not proportional to the increase in seed tuber weight.

Analysis of the influence of date of emergence and seed tuber weight on ground cover of each plant showed that date of emergence only had a significant effect at 8 DAE (Table 75). At 8 DAE, weight of the seed tuber explained little of the variation in ground cover and a multiple regression containing both variables explained more of the variation than either alone (Table 75). At 15 DAE weight of the seed tuber explained substantially more of the variation in ground cover than at 8 DAE and including date of emergence allowed more of the variation to be explained (Table 75). As the age of the plants increased, weight of the seed tuber explained more of the variation in ground cover and from 31 DAE, date of emergence did not



have a significant effect when added to the regression (Table 75). Ground cover increased as the number of stems per plant increased, but the number of stems explained less of the variation than seed tuber weight (Table 75). In multiple regressions combining the number of stems and seed tuber weight, there was no significant effect of the number of stems except at 31 DAE, which may be anomalous (Table 75).

**Table 75. Correlation coefficients of linear regressions fitted to explain variation in ground cover between plants in Expt 9. EM = date of emergence, ST = seed tuber weight, SN = number of stems per plant.**

| Explanatory variable(s) |    |    | Ground cover |        |        |        |        |        |
|-------------------------|----|----|--------------|--------|--------|--------|--------|--------|
| EM                      | ST | SN | 8 DAE        | 15 DAE | 22 DAE | 31 DAE | 38 DAE | 45 DAE |
| ●                       |    |    | 0.26         | n.s.   | n.s.   | n.s.   | n.s.   | n.s.   |
|                         | ●  |    | 0.08         | 0.44   | 0.55   | 0.62   | 0.70   | 0.77   |
|                         |    | ●  | 0.08         | 0.24   | 0.30   | 0.52   | 0.35   | 0.24   |
| ●                       | ●  |    | 0.42         | 0.59   | 0.65   | n.s.   | n.s.   | n.s.   |
|                         | ●  | ●  | n.s.         | n.s.   | n.s.   | 0.74   | n.s.   | n.s.   |

#### 4.13. Survey 4

##### 4.13.1. Seed tuber weight

Although Maris Piper, Desiree and Russet Burbank were grown from the same size grade of seed tubers (30-40 mm), the mean weight varied due to differences in tuber shape, with Maris Piper having relatively round tubers, Desiree being more elongated and Russet Burbank even more so (Table 76). These differences in tuber shape also affected the variation in seed tuber weight which increased as the mean tuber weight increased (Table 76) because while the minimum tuber weights were similar, elongated tubers increased the maximum seed tuber weight (data not shown). King Edward was grown from a larger size grade (35-45 mm) and so had a higher mean seed tuber weight but the variation in seed tuber weight was similar to Maris Piper (Table 76). These differences in seed tuber weight must be considered when establishing the effects of seed tuber weight on the growth of plants within the crop.

**Table 76. Average and COV of seed tuber weight in Survey 4. Values are the mean of the five harvested areas.**

|             | Variety     |         |                |             |
|-------------|-------------|---------|----------------|-------------|
|             | Maris Piper | Desiree | Russet Burbank | King Edward |
| Mean (g FW) | 29.8        | 35.7    | 40.6           | 52.1        |
| COV (%)     | 25.3        | 30.0    | 34.0           | 25.4        |

#### 4.13.2. Emergence and planting depth

King Edward emerged *c.* 2 days earlier than other varieties and in all varieties the date when 50 % of stems emerged was *c.* 1 day after 50 % of plants had emerged (Table 77). The interval from 20 to 80 % of plants emerging was *c.* 3-4 days in all varieties and with the exception of King Edward where emergence of stems was more protracted, the duration of stem emergence was only slightly longer than for plants (Table 77). The mean planting depth was *c.* 1 cm shallower than intended and the COV of planting depth was *c.* 15 % in each of the varieties (Table 77). Variation in date of emergence of plants could not be explained by differences in seed tuber weight, the number of stems per plant or planting depth (data not shown). As in Survey 2, the date of emergence of *c.* 5 % of stems was not recorded and these stems were excluded from analyses examining effects of emergence.

**Table 77. Interval from planting to emergence and from 20 to 80 % emergence for plants and stems in Survey 4. Values are the mean of the five harvested areas (four for planting depth).**

|   |        | Variety     |         |                |             |
|---|--------|-------------|---------|----------------|-------------|
|   |        | Maris Piper | Desiree | Russet Burbank | King Edward |
| Interval from planting to 50 % emergence (days) | Plants | 35.2        | 34.8    | 34.9           | 32.9        |
|   | Stems  | 36.3        | 35.6    | 35.8           | 34.3        |
| Interval from 20 to 80% emergence (days)        | Plants | 4.04        | 3.21    | 3.81           | 3.97        |
|   | Stems  | 4.28        | 3.55    | 4.45           | 5.29        |
| Mean planting depth (cm)                        | Stems  | 14.6        | 13.9    | 13.4           | 14.0        |
| COV of planting depth (%)                       | Stems  | 13.4        | 15.2    | 15.8           | 17.0        |

#### 4.13.3. Number of stems per plant

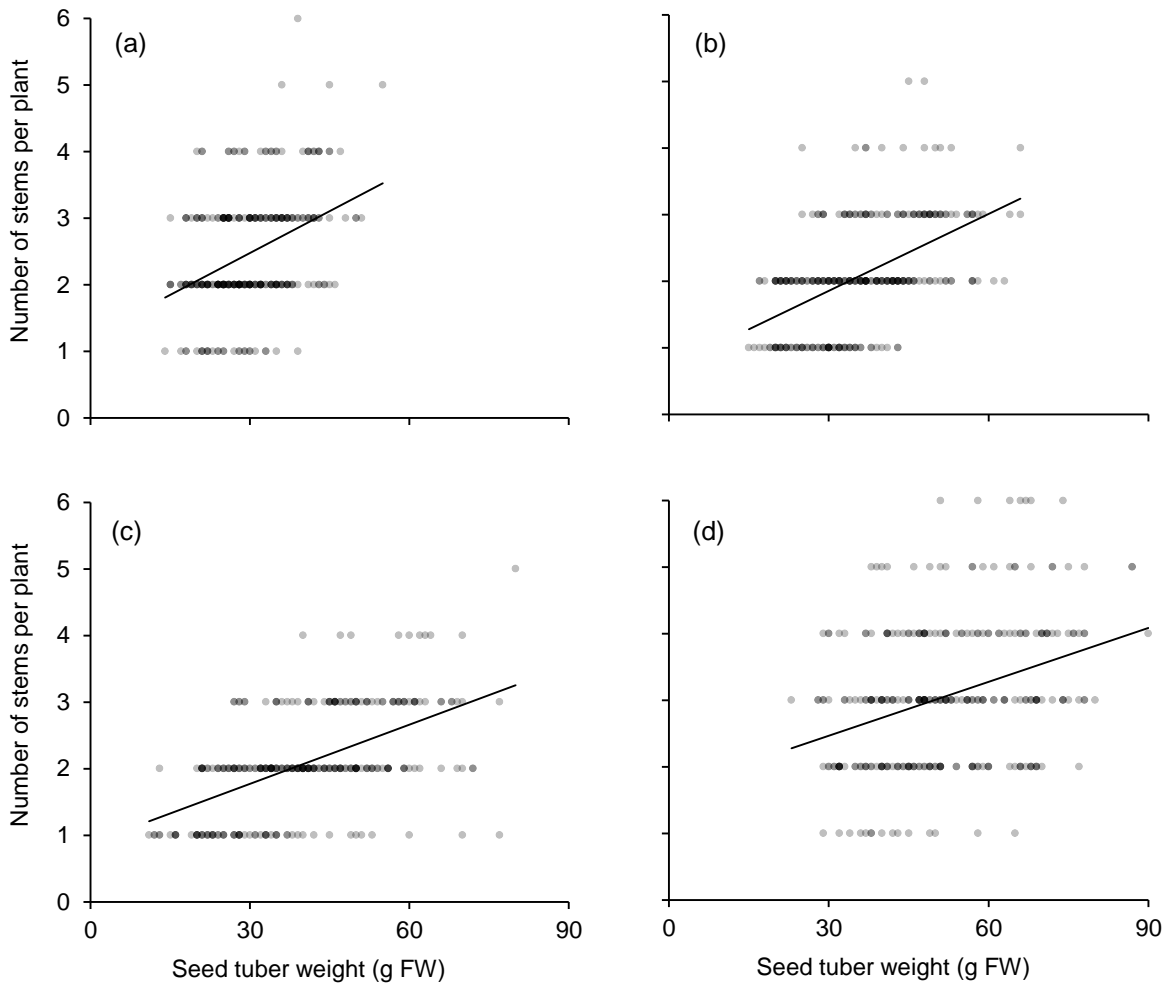
Desiree and Russet Burbank produced *c.* 2 stems per plant, Maris Piper *c.* 2.5 and King Edward *c.* 3. The COV of number of stems per plant was similar in all of the varieties at *c.* 35-40 % (Table 78). The number of stems per plant increased as the seed tuber weight increased in all of the varieties, but variation in the number of stems per plant was poorly explained by variation in seed tuber weight. Numerically, more of the variation in the number

of stems per plant could be explained in Desiree and Russet Burbank than in Maris Piper and King Edward (Figure 72; Table 79), but this may have been in part caused by the greater variation in seed tuber weight, rather than a genetic or physiological difference.

**Table 78. Average and COV of number of stems per plant in Survey 4. Values are the mean of the five harvested areas.**

|         | Variety     |         |                |             |
|---------|-------------|---------|----------------|-------------|
|         | Maris Piper | Desiree | Russet Burbank | King Edward |
| Mean    | 2.47        | 2.08    | 2.08           | 3.05        |
| COV (%) | 34.6        | 39.1    | 37.1           | 36.2        |

**Figure 72. Relationship between seed tuber weight and number of stems per plant in (a) Maris Piper, (b) Desiree, (c) Russet Burbank, (d) King Edward combined for all harvests in Survey 4. Darker points, indicate where multiple plants had the same seed tuber weight and number of stems. See Table 79 for details of fitted lines.**



**Table 79. Fitted lines in Figure 72.  $SN = m ST + c$ . Where  $ST$  = seed tuber weight,  $SN$  = number of stems.**

|     | $m$    | S.E.    | $c$  | S.E.  | $P$    | $R^2$ |
|-----|--------|---------|------|-------|--------|-------|
| (a) | 0.0419 | 0.00590 | 1.22 | 0.182 | <0.001 | 0.14  |
| (b) | 0.0385 | 0.00377 | 0.70 | 0.141 | <0.001 | 0.26  |
| (c) | 0.0296 | 0.00265 | 0.88 | 0.114 | <0.001 | 0.29  |
| (d) | 0.0270 | 0.00440 | 1.66 | 0.236 | <0.001 | 0.11  |

#### 4.13.4. Initial growth of plants

To establish the causes of variation in the yield of plants it was necessary to consider the causes of variation in plant size during the initial phases of growth, from emergence until *c.* 50 % ground cover, which in this survey was up until the date of the third harvest. During this phase of growth there was relatively little competition between plants and thus the causes of variation should be simpler to determine than after canopy closure.

The percentage dry matter of seed tubers decreased by *c.* 50 % between planting and the first harvest in all varieties except King Edward, although the amount of dry weight lost in King Edward was similar, due to the larger seed size (Table 80). The percentage dry matter of seed tubers continued to decrease between the first and third harvests and at the third harvest, the percentage dry matter was *c.* 4 % (Table 80). Relatively little dry weight was lost from the seed tubers between the second and third harvests by comparison with that lost between the first and the second harvests (Table 80). The above-ground stem weight increased *c.* 20-fold between the first and third harvests and the COV of above-ground stem weight decreased between each harvest except between the second and third harvests for Desiree (Table 80). The variation in ground cover per plant also decreased between the first and the second harvests (Table 80), by which point the overall ground cover was *c.* 15-19 % in each of the varieties (Figure 80). The proxy diameter of below-ground stems increased relatively little between the first and third harvests and the COV of the proxy diameter of below-ground stems was similar at each of the harvests (Table 80).

**Table 80. Average and COV of crop growth parameters of individual plants at the first three harvests (and at planting (P) for the percentage dry matter of seed tubers) of Survey 4.**

|   | Harvest |         | Maris Piper | Desiree | Russet Burbank | King Edward |
|---|---------|---------|-------------|---------|----------------|-------------|
| Percentage dry matter of seed tubers (%)          | P       | Mean    | 18.7        | 20.0    | 19.0           | 23.5        |
|   |         | COV (%) | 14.7        | 15.1    | 9.3            | 8.8         |
|   | 1       | Mean    | 7.94        | 7.98    | 10.8           | 15.6        |
|   |         | COV (%) | 29.0        | 27.2    | 23.4           | 21.6        |
|   | 2       | Mean    | 5.16        | 4.90    | 6.50           | 9.70        |
|   |         | COV (%) | 30.2        | 26.2    | 26.8           | 25.7        |
| 3   | Mean    | 3.66    | 4.08        | 4.39    | 5.35           |             |
|   | COV (%) | 14.0    | 11.6        | 16.3    | 27.8           |             |
| Estimated dry weight lost from seed tubers (g DW) | 1       | Mean    | 3.11        | 4.15    | 3.16           | 3.78        |
|   |         | COV (%) | 37.6        | 34.6    | 42.4           | 54.1        |
|   | 2       | Mean    | 4.15        | 5.15    | 5.30           | 7.13        |
|   |         | COV (%) | 27.9        | 27.9    | 32.6           | 35.7        |
|   | 3       | Mean    | 4.49        | 5.57    | 6.06           | 8.97        |
|   |         | COV (%) | 25.2        | 29.5    | 33.8           | 25.3        |
| Above-ground stem weight (g FW)                   | 1       | Mean    | 12.8        | 18.2    | 11.4           | 14.0        |
|   |         | COV (%) | 41.4        | 38.0    | 52.7           | 55.9        |
|   | 2       | Mean    | 46.9        | 74.8    | 59.8           | 72.7        |
|   |         | COV (%) | 36.8        | 27.3    | 39.6           | 36.4        |
|   | 3       | Mean    | 270         | 248     | 247            | 344         |
|   |         | COV (%) | 20.4        | 27.5    | 29.8           | 24.6        |
| Ground cover (cm <sup>2</sup> )                   | 1       | Mean    | 140         | 162     | 121            | 81.5        |
|   |         | COV (%) | 44.7        | 37.2    | 54.3           | 60.3        |
|   | 2       | Mean    | 333         | 378     | 404            | 436         |
|   |         | COV (%) | 30.9        | 23.1    | 34.9           | 32.3        |
|   | 3       | Mean    | n.d.        | n.d.    | n.d.           | n.d.        |
|   |         | COV (%) | n.d.        | n.d.    | n.d.           | n.d.        |
| Proxy diameter of below-ground stems (g FW/cm)    | 1       | Mean    | 0.38        | 0.71    | 0.33           | 0.51        |
|   |         | COV (%) | 25.2        | 35.2    | 33.8           | 33.8        |
|   | 2       | Mean    | 0.51        | 0.82    | 0.46           | 0.75        |
|   |         | COV (%) | 27.5        | 27.5    | 33.6           | 28.7        |
|   | 3       | Mean    | 1.07        | 1.23    | 0.88           | 1.37        |
|   |         | COV (%) | 22.5        | 30.8    | 32.4           | 26.3        |

The following sections describe how the variables listed in Table 80 were related to each other and how they were affected by seed tuber weight and emergence.

#### 4.13.4.1. Emergence

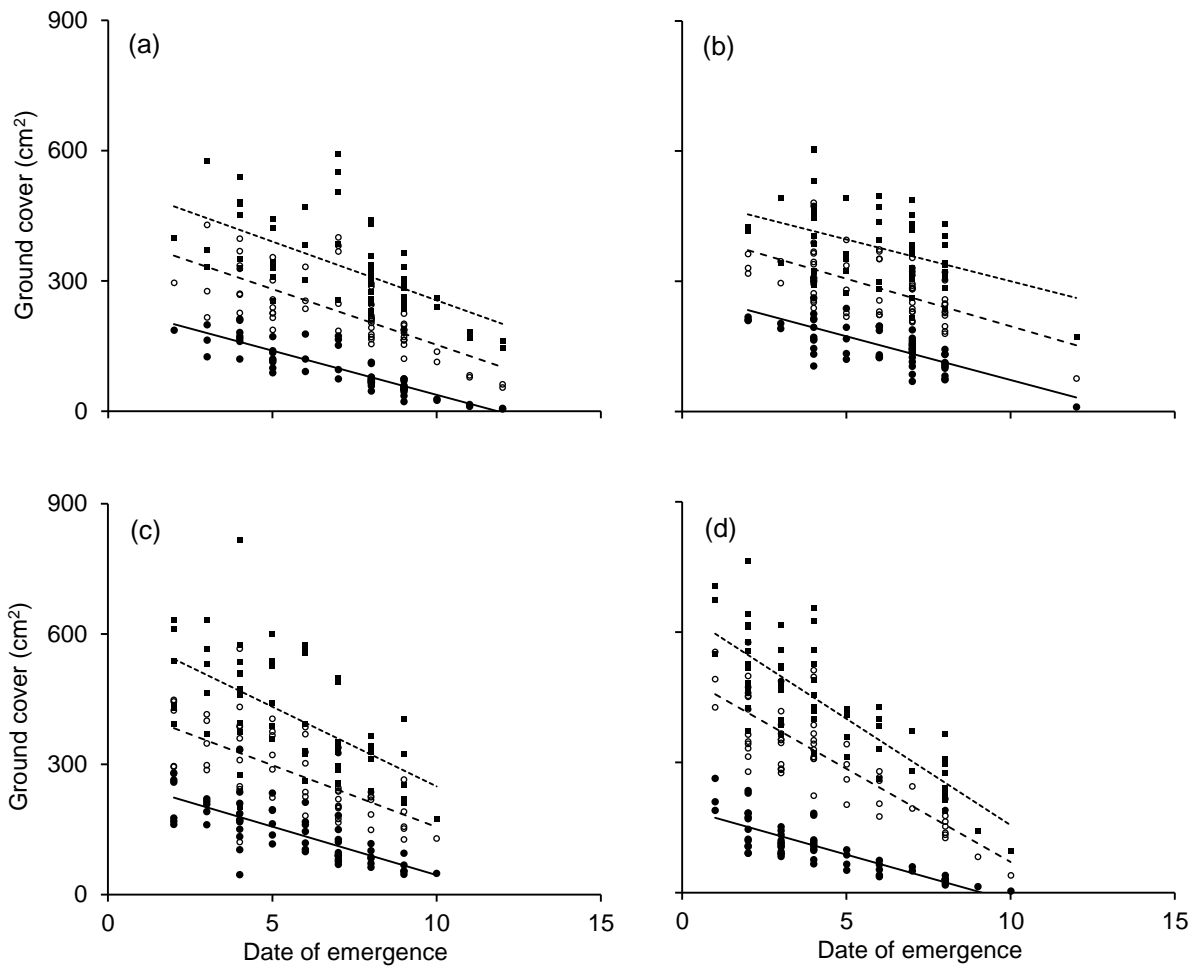
At the first harvest, differences in the date of emergence between plants explained > 50 % of the variation in above-ground stem weight in all varieties except Desiree (Table 81). The correlation coefficients were lower at the second harvest, although in King Edward the difference was relatively small (Table 81). At the third harvest, the correlation coefficients were similar to those at the second harvest in Desiree and Russet Burbank, but were lower in Maris Piper and King Edward (Table 81).

**Table 81. Relationships between the date of emergence (EM, relative to the first day that a stem emerged) and the above-ground stem weight (AG, g FW) per plant at the first three harvests of Survey 4.  $AG = m \cdot EM + c$ .**

| Variety | Harvest | <i>m</i> | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---------|----------|-------|----------|------|----------|-----------------------|
| Maris   | 1       | -1.76    | 0.186 | 23.5     | 1.22 | <0.001   | 0.60                  |
| Piper   | 2       | -4.43    | 0.750 | 78.4     | 5.63 | <0.001   | 0.36                  |
|         | 3       | -8.7     | 3.06  | 326      | 21.0 | <0.01    | 0.11                  |
| Desiree | 1       | -2.31    | 0.410 | 32.2     | 2.59 | <0.001   | 0.34                  |
|         | 2       | -4.5     | 1.26  | 101.7    | 7.84 | <0.001   | 0.17                  |
|         | 3       | -16.1    | 4.18  | 353      | 28.4 | <0.001   | 0.19                  |
| Russet  | 1       | -1.82    | 0.219 | 22.7     | 1.40 | <0.001   | 0.54                  |
| Burbank | 2       | -5.5     | 1.18  | 91.2     | 7.05 | <0.001   | 0.26                  |
|         | 3       | -19.0    | 4.07  | 384      | 30.4 | <0.001   | 0.26                  |
| King    | 1       | -2.56    | 0.233 | 26.7     | 1.24 | <0.001   | 0.68                  |
| Edward  | 2       | -8.86    | 0.944 | 110.5    | 4.57 | <0.001   | 0.60                  |
|         | 3       | -22.5    | 4.05  | 447      | 20.5 | <0.001   | 0.34                  |

At the first harvest, differences in the date of emergence explained > 50 % of the variation in the ground cover of plants sampled at the second harvest but over the following week, the correlations weakened in each of the varieties except King Edward (Figure 73). These differences between harvests suggest that other factors influenced the growth rate of plants, since if plants had grown at a continuous rate determined by their size, the correlation coefficients would be expected to remain similar during this phase of development.

**Figure 73.** Relationships between the date of emergence (relative to the first day that a stem emerged) and the ground cover per plant for plants in the second harvest of Survey 4 at the first harvest (—●—), four days later (- -○- -) and at the second harvest (--■--) in (a) Maris Piper, (b) Desiree, (c) Russet Burbank and (d) King Edward. See Table 82 for details of fitted lines.



**Table 82.** Fitted lines in Figure 73.  $GC = m EM + c$ . Where GC = ground cover and EM = date of emergence.

|                    | Time | $m$   | S.E. | $c$   | S.E. | $P$    | $R^2$ |
|--------------------|------|-------|------|-------|------|--------|-------|
| (a) Maris Piper    | H1   | -20.3 | 1.49 | 240   | 11.2 | <0.001 | 0.76  |
|                    | H1.5 | -25.7 | 3.21 | 410   | 24.1 | <0.001 | 0.52  |
|                    | H2   | -27.1 | 4.42 | 526   | 33.1 | <0.001 | 0.38  |
| (b) Desiree        | H1   | -20.2 | 2.63 | 274   | 16.4 | <0.001 | 0.50  |
|                    | H1.5 | -21.9 | 4.09 | 415   | 25.5 | <0.001 | 0.32  |
|                    | H2   | -19.3 | 5.38 | 492   | 33.5 | <0.001 | 0.17  |
| (c) Russet Burbank | H1   | -22.2 | 2.66 | 267   | 15.9 | <0.001 | 0.55  |
|                    | H1.5 | -28.5 | 4.54 | 440   | 27.2 | <0.001 | 0.40  |
|                    | H2   | -36.7 | 6.45 | 615   | 38.6 | <0.001 | 0.35  |
| (d) King Edward    | H1   | -21.2 | 1.90 | 193.1 | 9.23 | <0.001 | 0.68  |
|                    | H1.5 | -42.9 | 3.80 | 500   | 18.4 | <0.001 | 0.68  |
|                    | H2   | -49.0 | 4.71 | 645   | 22.9 | <0.001 | 0.64  |

#### 4.13.4.2. Seed tuber weight

At the first harvest, differences in seed tuber weight explained relatively little variation in the above-ground stem weight of plants, although the correlation coefficient was approximately



twice as strong in Desiree than in King Edward and Russet Burbank (Table 83). The relationships were stronger at the second harvest than at the first harvest and stronger at the third harvest than at the second harvest in all varieties (Table 83). At the third harvest, variation in seed tuber weight explained more variation in above-ground stem weight than date of emergence in all varieties (Table 83).

**Table 83. Relationships between seed tuber weight (ST, g FW) and the above-ground stem weight (AG, g FW) per plant at the first three harvests of Survey 4.  $AG = m ST + c$ .**

| Variety | Harvest | <i>m</i> | S.E.   | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---------|----------|--------|----------|------|----------|-----------------------|
| Maris   | 1       | 0.230    | 0.0783 | 5.8      | 2.46 | <0.01    | 0.11                  |
| Piper   | 2       | 1.26     | 0.253  | 7.5      | 8.13 | <0.001   | 0.29                  |
|         | 3       | 4.99     | 0.798  | 127      | 23.5 | <0.001   | 0.39                  |
| Desiree | 1       | 0.427    | 0.0693 | 2.4      | 2.67 | <0.001   | 0.38                  |
|         | 2       | 1.25     | 0.195  | 30.5     | 7.24 | <0.001   | 0.40                  |
|         | 3       | 4.43     | 0.587  | 92       | 21.6 | <0.001   | 0.49                  |
| Russet  | 1       | 0.203    | 0.0518 | 2.9      | 2.28 | <0.001   | 0.20                  |
| Burbank | 2       | 1.12     | 0.175  | 11.7     | 7.91 | <0.001   | 0.40                  |
|         | 3       | 3.78     | 0.497  | 94       | 21.2 | <0.001   | 0.49                  |
| King    | 1       | 0.269    | 0.0658 | -0.3     | 3.60 | <0.001   | 0.21                  |
| Edward  | 2       | 0.93     | 0.214  | 23       | 11.8 | <0.001   | 0.23                  |
|         | 3       | 4.76     | 0.756  | 110      | 38.2 | <0.001   | 0.40                  |

The combined proxy diameter of below-ground stems increased as seed tuber weight increased in all varieties at the first three harvests (Table 84). The combined proxy diameter of below-ground stems approximately doubled when seed tuber weight doubled (Table 84). Including the number of stems per plant in multiple regressions increased the correlation coefficients in all varieties at the first three harvests (Table 84) with the combined proxy below-ground stem diameter increasing as the number of stems increased (data not shown). These relationships indicate that there were strong allometric relationships between the weight of the seed tubers and the total size of the sprouts that they produced, despite the number of stems per plant correlating poorly with seed tuber weight (as discussed in Section 4.13.3.).

**Table 84. Relationships between seed tuber weight (ST, g FW) and the proxy diameter of below-ground stems (PSD, g FW/cm) per plant and the correlation coefficients of multiple regressions explaining the proxy diameter of below-ground stems from seed tuber weight and the number of stems per plant (ST, SN  $R^2$ ) at the first three harvests of Survey 4.  $PSD = m ST + c$ .**

| Variety | Harvest | $m$     | S.E.     | $c$    | S.E.   | $P$    | $R^2$ | ST, SN |
|---------|---------|---------|----------|--------|--------|--------|-------|--------|
|         |         |         |          |        |        |        |       | $R^2$  |
| Maris   | 1       | 0.00928 | 0.000903 | 0.098  | 0.0284 | <0.001 | 0.64  | 0.74   |
| Piper   | 2       | 0.0142  | 0.00157  | 0.062  | 0.0504 | <0.001 | 0.58  | 0.62   |
|         | 3       | 0.0234  | 0.00328  | 0.396  | 0.0965 | <0.001 | 0.46  | 0.61   |
| Desiree | 1       | 0.0210  | 0.00166  | -0.071 | 0.0639 | <0.001 | 0.73  | 0.93   |
|         | 2       | 0.0182  | 0.00149  | 0.174  | 0.0554 | <0.001 | 0.71  | 0.90   |
|         | 3       | 0.0282  | 0.00270  | 0.236  | 0.0993 | <0.001 | 0.65  | 0.80   |
| Russet  | 1       | 0.00621 | 0.000722 | 0.073  | 0.0318 | <0.001 | 0.55  | 0.78   |
| Burbank | 2       | 0.00936 | 0.000867 | 0.061  | 0.0391 | <0.001 | 0.66  | 0.80   |
|         | 3       | 0.0153  | 0.00183  | 0.259  | 0.0782 | <0.001 | 0.54  | 0.64   |
| King    | 1       | 0.00941 | 0.00109  | 0.011  | 0.0596 | <0.001 | 0.56  | 0.67   |
| Edward  | 2       | 0.0117  | 0.00123  | 0.112  | 0.0679 | <0.001 | 0.61  | 0.72   |
|         | 3       | 0.0209  | 0.00315  | 0.34   | 0.159  | <0.001 | 0.42  | 0.67   |

#### 4.13.4.3. Loss of dry weight from the seed tuber

The amount of dry weight lost from the seed tubers correlated with the seed tuber weight at planting in all varieties at the first three harvests (data not shown) and there was either no correlation, or occasionally a very weak correlation between the percentage dry matter of the seed tuber and weight at planting, indicating that seed tuber substrate was mobilised at a similar relative rate regardless of seed tuber weight (Table 85). The correlation coefficients of regressions explaining the variation in the above-ground stem weight from the amount of dry weight lost from the seed tuber were higher than those in which seed tuber weight was the explanatory variable, particularly at the first harvest, except for in Desiree (Tables 83 & 86). This indicates that the mobilisation of seed tuber substrate to the developing leaves influenced their growth.

**Table 85. Correlation coefficients and probabilities for the relationships between seed tuber weight at planting and seed tuber percentage dry matter at the first three harvests of Survey 4.**

| Variety        | Harvest |       |       |       |       |       |
|----------------|---------|-------|-------|-------|-------|-------|
|                | 1       |       | 2     |       | 3     |       |
|                | $R^2$   | $P$   | $R^2$ | $P$   | $R^2$ | $P$   |
| Maris Piper    | n.s.    | n.s.  | n.s.  | n.s.  | n.s.  | n.s.  |
| Desiree        | n.s.    | n.s.  | 0.14  | <0.01 | 0.07  | <0.05 |
| Russet Burbank | 0.08    | <0.05 | n.s.  | n.s.  | n.s.  | n.s.  |
| King Edward    | n.s.    | n.s.  | n.s.  | n.s.  | n.s.  | n.s.  |

**Table 86. Relationships between dry weight lost from the seed tuber (WL, g DW) and above-ground stem weight (AG, g FW) per plant at the first three harvests of Survey 4.  $AG = m WL + c$ .**

| Variety | Harvest | <i>m</i> | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---------|----------|-------|----------|------|----------|-----------------------|
| Maris   | 1       | 3.08     | 0.434 | 3.2      | 1.44 | <0.001   | 0.46                  |
| Piper   | 2       | 11.0     | 1.31  | 1.1      | 5.66 | <0.001   | 0.54                  |
|         | 3       | 32.4     | 4.78  | 125      | 22.1 | <0.001   | 0.42                  |
| Desiree | 1       | 3.98     | 0.357 | 1.7      | 1.57 | <0.001   | 0.68                  |
|         | 2       | 11.5     | 1.11  | 15.7     | 5.92 | <0.001   | 0.64                  |
|         | 3       | 31.6     | 3.51  | 72       | 20.4 | <0.001   | 0.58                  |
| Russet  | 1       | 3.79     | 0.317 | -0.6     | 1.09 | <0.001   | 0.71                  |
| Burbank | 2       | 11.59    | 0.96  | -1.7     | 5.34 | <0.001   | 0.71                  |
|         | 3       | 27.1     | 3.25  | 82       | 20.8 | <0.001   | 0.55                  |
| King    | 1       | 2.87     | 0.333 | 3.2      | 1.43 | <0.001   | 0.55                  |
| Edward  | 2       | 7.77     | 0.911 | 17.3     | 6.89 | <0.001   | 0.55                  |
|         | 3       | 28.1     | 3.21  | 92       | 29.7 | <0.001   | 0.56                  |

#### 4.13.4.4. Ground cover

At the first two harvests, ground cover per plant correlated strongly ( $R^2 = c. 0.90$ ) with above-ground stem weight per plant (data not shown). Measurements of ground cover per plant were made between the first two harvests on each plant in Survey 4 so changes in ground cover per plant (and thus above-ground stem weight) could be examined over time for the same plants.

The ground cover per plant at the second harvest correlated strongly with ground cover per plant at the date of the first harvest, but the correlations were weaker than when ground cover was measured between the first and second harvests (Table 87). Including seed tuber weight in multiple regressions increased the correlation coefficients of regressions explaining variation in ground cover from earlier measurements of ground cover in all varieties, but the increases were larger in Maris Piper and Desiree than in Russet Burbank and King Edward (Table 87). The number of stems per plant also had a significant effect when included in multiple regressions, but the correlation coefficients were lower than if seed tuber weight was included (data not shown) and, when seed tuber weight was included, the number of stems per plant did not have a significant effect on the growth of plants in the four days after the first harvest (i.e. up to H1.5; Table 87). The number of stems per plant had a significant effect between the first and second harvests, even when seed tuber weight was accounted for, in all

varieties except Maris Piper, but the increases in the correlation coefficients were small in comparison to regressions including seed tuber weight only (Table 87).

**Table 87. Correlation coefficients of regressions explaining ground cover per plant between the first and second harvests (GC at H1.5) and at the second harvest (GC at H2) for plants sampled at the second harvest of Survey 4 from ground cover at the first harvest (GC at H1), seed tuber weight (ST) and the number of stems per plant (SN).**

| Variables†                    | Variety     |         |                |             |
|-------------------------------|-------------|---------|----------------|-------------|
|                               | Maris Piper | Desiree | Russet Burbank | King Edward |
| GC at H1 ~ GC at H1.5         | 0.86        | 0.89    | 0.93           | 0.93        |
| GC at H1 ~ GC at H2           | 0.74        | 0.74    | 0.87           | 0.87        |
| GC at H1, ST ~ GC at H1.5     | 0.92        | 0.95    | 0.96           | 0.94        |
| GC at H1, ST ~ GC at H2       | 0.90        | 0.87    | 0.92           | 0.89        |
| GC at H1, ST, SN ~ GC at H1.5 | n.s.        | n.s.    | n.s.           | n.s.        |
| GC at H1, ST, SN ~ GC at H2   | n.s.        | 0.91    | 0.92           | 0.91        |

† Variables on the left hand side of ~ are explanatory variables and the response variable is on the right hand side.

The above-ground stem weight of plants at the third harvest increased as the ground cover measured at the date of earlier harvests increased but the correlation coefficients of regressions predicting the above-ground stem weight from ground cover at the date of the first harvest were weaker than those predicting it from ground cover at the date of the second harvest (Table 88). As for plants sampled at the second harvest, accounting for seed tuber weight increased the correlation coefficients of regressions from earlier measurements of ground cover, except for Maris Piper between the second and third harvests (Table 88). Again, the number of stems per plant had a significant effect in regressions (data not shown) but, when seed tuber weight was included, the effect was only consistently significant for King Edward (Table 88).

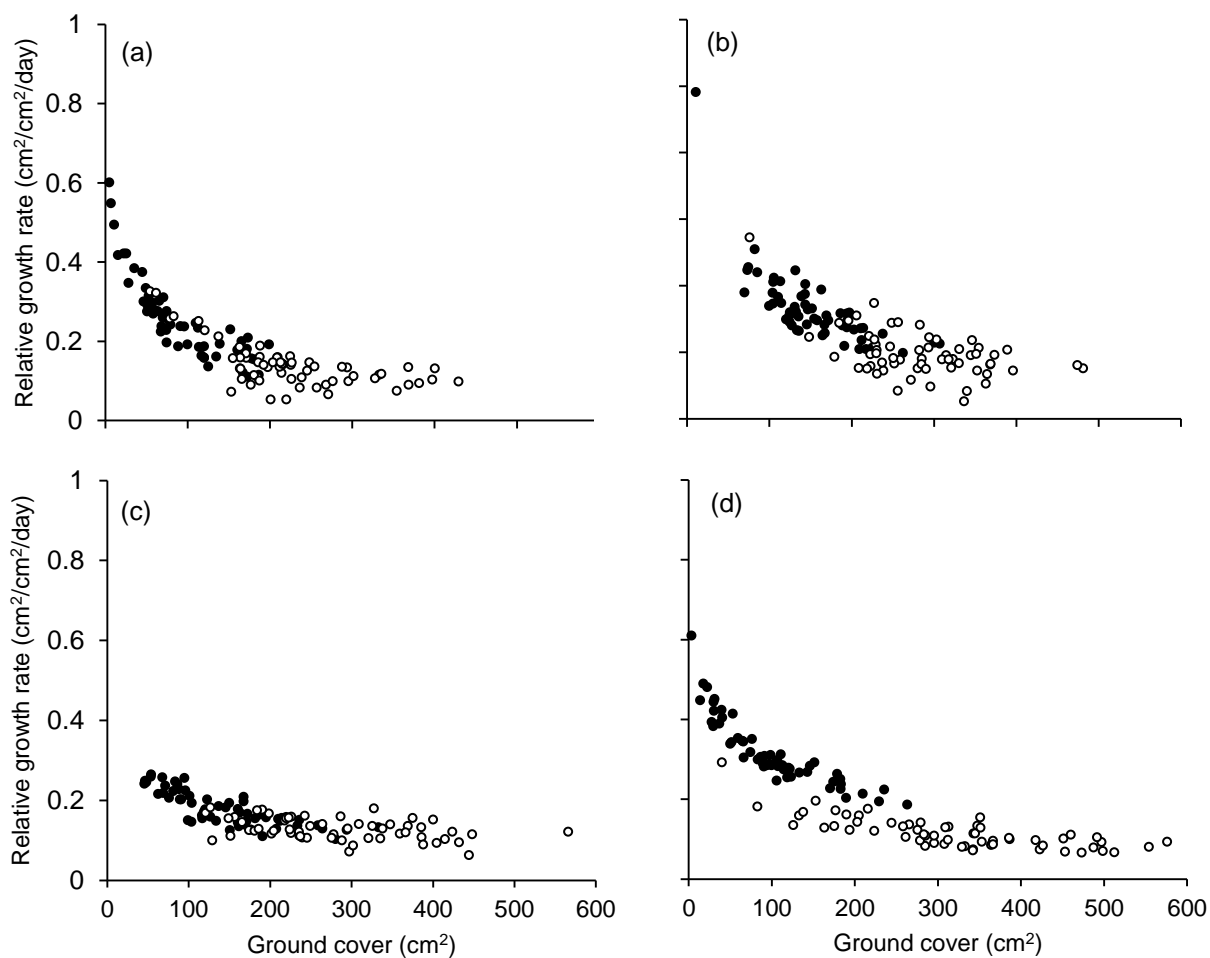
**Table 88. Correlation coefficients of regressions explaining the variation in above-ground stem weight per plant at the third harvest (AG at H3) of Survey 4 from ground cover at the first harvest (GC at H1), ground cover at the second harvest (GC at H2), seed tuber weight (ST) and the number of stems per plant (SN).**

| Variables†                  | Variety     |         |                |             |
|-----------------------------|-------------|---------|----------------|-------------|
|                             | Maris Piper | Desiree | Russet Burbank | King Edward |
| GC at H1 ~ AG at H3         | 0.55        | 0.67    | 0.55           | 0.63        |
| GC at H2 ~ AG at H3         | 0.87        | 0.89    | 0.86           | 0.91        |
| GC at H1, ST ~ AG at H3     | 0.76        | 0.86    | 0.87           | 0.80        |
| GC at H2, ST ~ AG at H3     | n.s.        | 0.92    | 0.93           | 0.93        |
| GC at H1, ST, SN ~ AG at H3 | 0.82        | n.s.    | n.s.           | 0.87        |
| GC at H2, ST, SN ~ AG at H3 | n.s.        | n.s.    | n.s.           | 0.95        |

† Variables on the left hand side of ~ are explanatory variables and the response variable is on the right hand side.

The relative growth rate of ground cover per plant between sampling dates decreased as the ground cover per plant increased (Figure 74). For plants that were very small ( $< 50 \text{ cm}^2$ ) at the first harvest, the relative growth rate over the following four days was very high, with ground cover increasing by *c.* 50 % each day (Figure 74). For plants with a ground cover  $> 300 \text{ cm}^2$  four days after the first harvest, the relative growth rate of ground cover over the following three days was *c.* 10 % per day (Figure 74). There were substantial variations in the relative growth rate amongst plants with similar ground covers at the earlier sampling which resulted in the relative size of plants changing over time (Figure 74).

**Figure 74. Relative growth rate of ground cover per plant between the first harvest and four days later (●) and between four days after the first harvest and the second harvest (○) for (a) Maris Piper; (b) Desiree; (c) Russet Burbank; (d) King Edward.**



4.13.4.5. Dry weight lost from the seed tuber and date of emergence

At the first three harvests, above-ground stem weight per plant was best explained by multiple regressions in which the amount of dry weight lost from the seed tuber and date of emergence were explanatory variables (Table 89). The combination of these two variables explained *c.* 80 % of the variation in above-ground stem weight at the first two harvests for all varieties and a similar proportion at the third harvest in Desiree and Russet Burbank, but less in Maris Piper and King Edward (Table 89).

**Table 89. Relationships between dry weight lost from the seed tuber (WL, g DW), date of emergence (EM, relative to the first day that a stem emerged) and the above-ground stem weight per plant (AG, g FW) at the first three harvests of Survey 4.  $AG = m WL + n EM + c$ .**

| Variety | Harvest | <i>m</i> | S.E.  | <i>n</i> | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---------|----------|-------|----------|-------|----------|------|----------|-----------------------|
| Maris   | 1       | 1.95     | 0.322 | -1.35    | 0.161 | 15.0     | 1.71 | <0.001   | 0.75                  |
| Piper   | 2       | 9.61     | 0.951 | -3.52    | 0.462 | 32.0     | 5.71 | <0.001   | 0.77                  |
|         | 3       | 33.4     | 4.14  | -9.6     | 2.11  | 182      | 23.0 | <0.001   | 0.58                  |
| Desire  | 1       | 3.41     | 0.304 | -1.40    | 0.244 | 12.6     | 2.28 | <0.001   | 0.79                  |
| e       | 2       | 11.45    | 0.785 | -4.47    | 0.583 | 42.4     | 5.46 | <0.001   | 0.82                  |
|         | 3       | 30.1     | 2.87  | -13.7    | 2.45  | 170      | 24.2 | <0.001   | 0.72                  |
| Russet  | 1       | 2.66     | 0.333 | -0.98    | 0.333 | 9.1      | 1.96 | <0.001   | 0.79                  |
| Burban  | 2       | 10.61    | 0.770 | -3.76    | 0.577 | 25.2     | 5.86 | <0.001   | 0.83                  |
| k       | 3       | 25.6     | 2.40  | 17.0     | 2.45  | 215      | 24.5 | <0.001   | 0.75                  |
| King    | 1       | 1.52     | 0.271 | -1.93    | 0.219 | 17.7     | 1.88 | <0.001   | 0.79                  |
| Edwar   | 2       | 5.15     | 0.700 | -6.28    | 0.767 | 62.8     | 7.28 | <0.001   | 0.79                  |
| d       | 3       | 23.4     | 2.89  | -14.4    | 2.96  | 200      | 33.6 | <0.001   | 0.69                  |

#### 4.13.5. Initial growth of stems

While understanding the growth of individual plants is of interest, the primary aim of Survey 4 was to characterise variation in the growth of individual stems. As multiple stems developed from each seed tuber, it was not possible to isolate all factors that could have affected the growth of stems, but the processes determining their growth are expected to be fundamentally similar to those of individual plants, as discussed in Section 4.13.4.

The variation in above-ground stem weight of individual stems was consistently higher than that of individual plants for all varieties (Table 80; Table 90). The COV of above-ground stem weight was lower at the second harvest than at the first and lower at the third harvest than at the second, indicating that smaller stems at the first harvest grew relatively faster than larger stems (Table 90), consistent with the differences in the relative growth rate of plants at this time (Figure 74). That emergence of stems was not substantially more prolonged than emergence of plants indicates that increased variation in other factors must have determined this increased variation in the size of stems.

**Table 90. Average and COV of above-ground stem weight and proxy diameter of below-ground stems for individual stems at the first three harvests of Survey 4.**

|  | Harvest |         | Maris Piper | Desiree | Russet<br>Burbank | King Edward |
|--|---------|---------|-------------|---------|-------------------|-------------|
| Above-ground stem<br>weight (g FW)                   | 1       | Mean    | 4.82        | 8.29    | 5.32              | 4.70        |
|  |         | COV (%) | 67.2        | 62.4    | 69.3              | 75.9        |
|  | 2       | Mean    | 17.8        | 35.9    | 28.0              | 23.3        |
|  |         | COV (%) | 60.3        | 50.2    | 53.2              | 59.4        |
|  | 3       | Mean    | 115         | 115     | 114               | 110         |
|  |         | COV (%) | 49.6        | 47.3    | 48.9              | 52.0        |
| Proxy diameter of<br>below-ground stems<br>(g FW/cm) | 1       | Mean    | 0.14        | 0.32    | 0.16              | 0.17        |
|  |         | COV (%) | 39.0        | 37.5    | 38.4              | 43.7        |
|  | 2       | Mean    | 0.19        | 0.39    | 0.22              | 0.24        |
|  |         | COV (%) | 45.2        | 35.9    | 38.1              | 45.1        |
|  | 3       | Mean    | 0.45        | 0.57    | 0.41              | 0.44        |
|  |         | COV (%) | 40.8        | 35.5    | 37.8              | 41.3        |

### 3.12.1.1. Emergence

The effect of emergence on above-ground stem weight of individual stems was similar to that of individual plants. At the first harvest, a large proportion of the variation in above-ground stem weight could be explained by variation in emergence, but this effect diminished at later harvests (Table 91). At the second harvest, some stems that emerged one week apart had similar weights in all varieties (Figure 75).

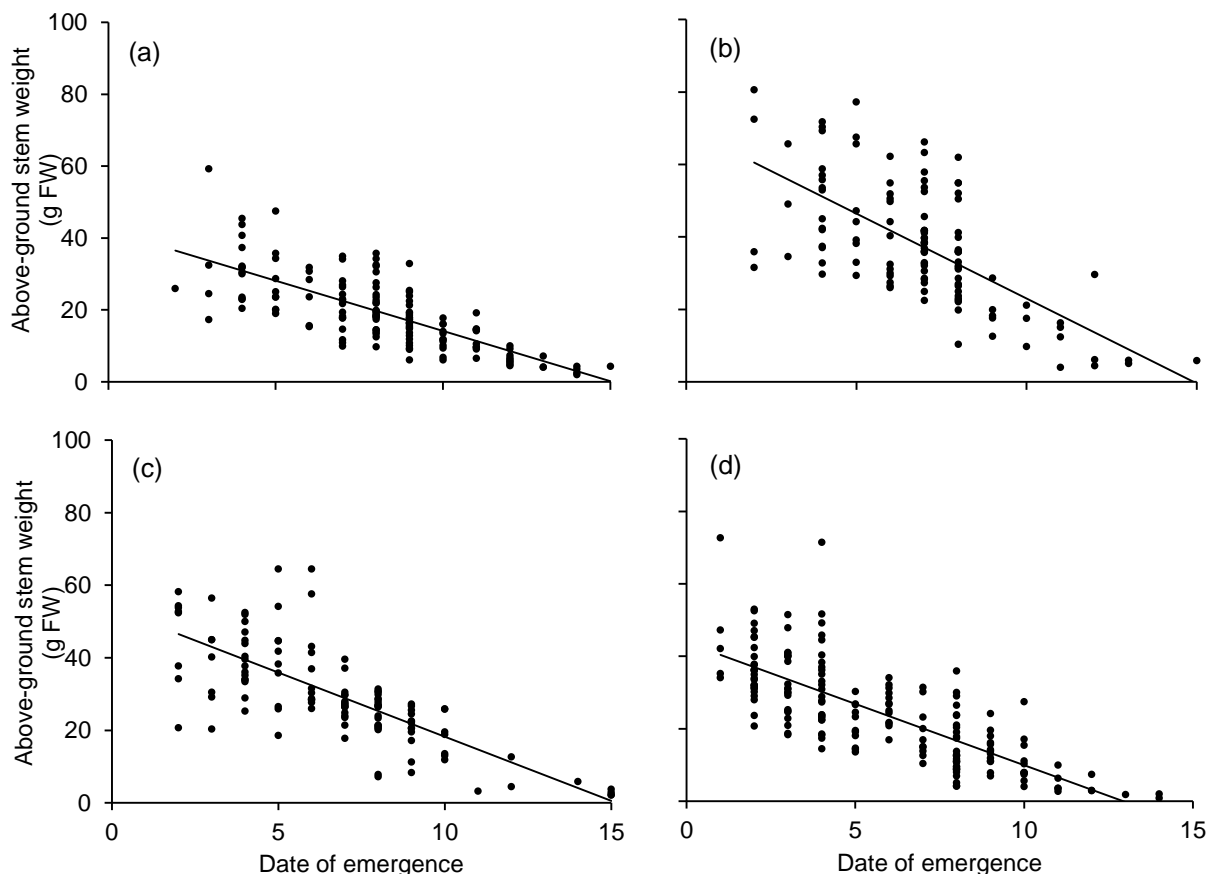
**Table 91. Relationships between date of emergence (EM, relative to the first day that a stem emerged) and above-ground stem weight (AG, g FW) for individual stems at the first three harvests of Survey 4.**

$AG = m EM + c.$

| Variety           | Harvest | <i>m</i> | S.E.   | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|-------------------|---------|----------|--------|----------|-------|----------|-----------------------|
| Maris<br>Piper    | 1       | -1.018   | 0.0568 | 12.57    | 0.440 | <0.001   | 0.69                  |
|                   | 2       | -2.80    | 0.209  | 42.1     | 1.80  | <0.001   | 0.55                  |
|                   | 3       | -13.4    | 1.54   | 224      | 12.3  | <0.001   | 0.37                  |
| Desiree           | 1       | -1.75    | 0.137  | 21.1     | 1.01  | <0.001   | 0.57                  |
|                   | 2       | -4.69    | 0.487  | 69.9     | 3.55  | <0.001   | 0.44                  |
|                   | 3       | -11.5    | 1.53   | 206      | 11.9  | <0.001   | 0.31                  |
| Russet<br>Burbank | 1       | -1.063   | 0.0602 | 13.29    | 0.461 | <0.001   | 0.72                  |
|                   | 2       | -3.54    | 0.281  | 53.6     | 2.07  | <0.001   | 0.57                  |
|                   | 3       | -14.9    | 1.38   | 241      | 11.5  | <0.001   | 0.49                  |
| King<br>Edward    | 1       | -0.991   | 0.0589 | 10.86    | 0.375 | <0.001   | 0.64                  |
|                   | 2       | -3.39    | 0.215  | 43.8     | 1.41  | <0.001   | 0.59                  |
|                   | 3       | -11.9    | 1.08   | 186.4    | 7.19  | <0.001   | 0.41                  |



**Figure 75. Relationships between date of emergence (relative to the first day that a stem emerged) and above-ground stem weight at the second harvest of Survey 4 for (a) Maris Piper, (b) Desiree, (c) Russet Burbank, (d) Desiree. See Table 91 for details of fitted lines.**



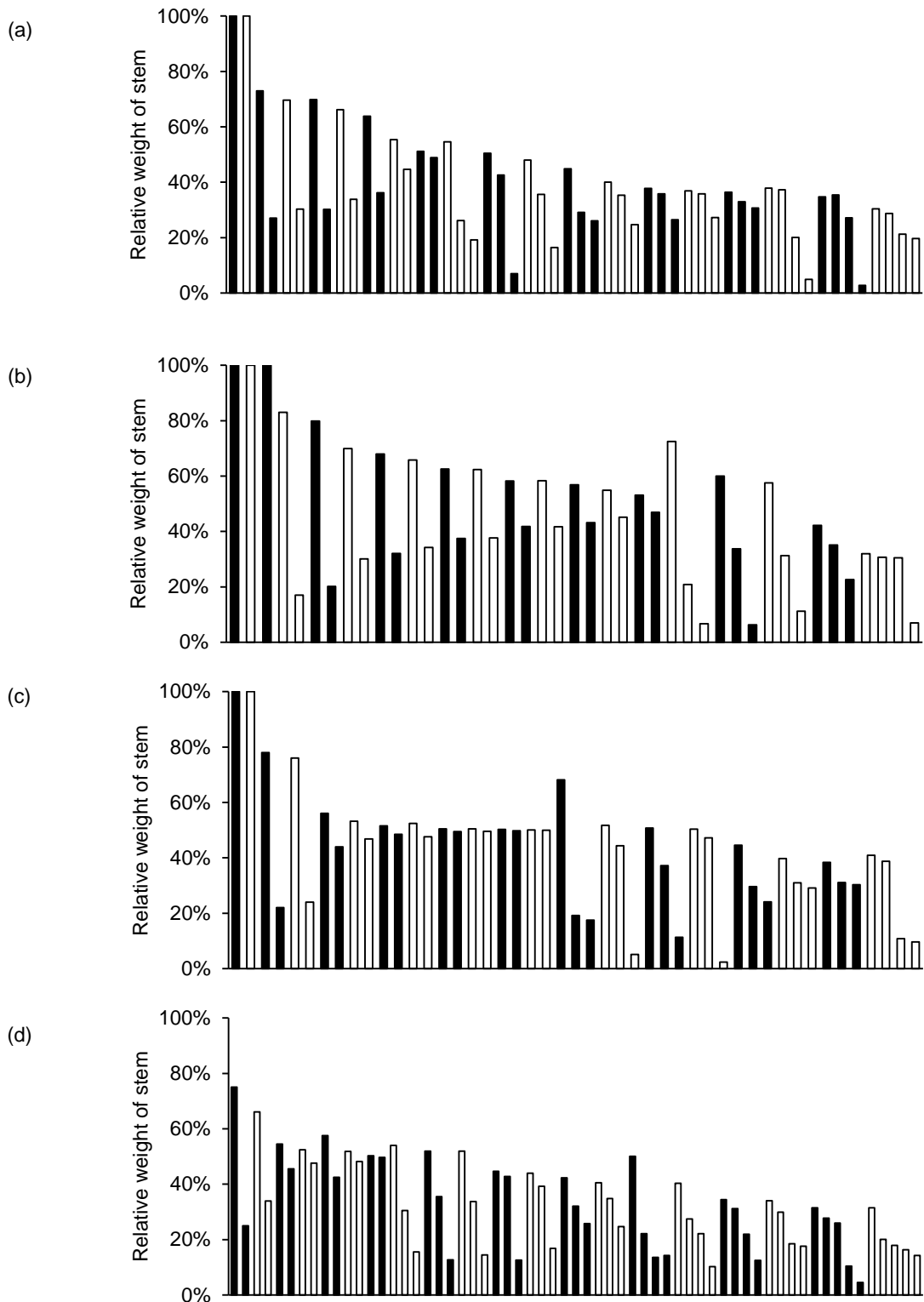
### 3.12.1.2. Number of stems per plant

The number of stems per plant accounted for very little of the variation in above-ground stem weight at the first two harvests and only *c.* 20-30 % at the third harvest (Table 92). It was anticipated that the number of stems would have a stronger effect than that observed as higher stem densities could result in smaller stems. One reason for the weak relationships was that the relative size of stems within plants was extremely variable (Figure 76). For example, some two-stemmed plants were composed of one large stem and one small stem, whereas others were composed of two similar sized stems (Figure 76).

**Table 92. Relationships between the number of stems per plant (SN) and the above-ground stem weight (AG, g FW) for individual stems at the first three harvests of Survey 4.  $AG = m \text{ EM} + c$ .**

| Variety | Harvest | <i>m</i> | S.E.  | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---------|----------|-------|----------|-------|----------|-----------------------|
| Maris   | 1       | -1.32    | 0.271 | 8.68     | 0.828 | <0.001   | 0.13                  |
| Piper   | 2       | -5.3     | 1.02  | 33.0     | 3.03  | <0.001   | 0.14                  |
|         | 3       | -34.9    | 4.63  | 207      | 12.9  | <0.001   | 0.29                  |
| Desiree | 1       | -2.09    | 0.454 | 13.6     | 1.24  | <0.001   | 0.13                  |
|         | 2       | -11.4    | 1.89  | 62.7     | 4.68  | <0.001   | 0.22                  |
|         | 3       | -30.2    | 6.06  | 188      | 15.3  | <0.001   | 0.16                  |
| Russet  | 1       | -0.70    | 0.422 | 7.0      | 1.07  | n.s.     | 0.01                  |
| Burbank | 2       | -4.4     | 1.45  | 38.8     | 3.75  | <0.01    | 0.06                  |
|         | 3       | -34.3    | 6.44  | 197      | 16.2  | <0.001   | 0.18                  |
| King    | 1       | -0.91    | 0.210 | 7.89     | 0.777 | <0.001   | 0.09                  |
| Edward  | 2       | -3.68    | 0.954 | 36.0     | 3.42  | <0.001   | 0.07                  |
|         | 3       | -22.1    | 3.38  | 187      | 12.5  | <0.001   | 0.18                  |

**Figure 76. Relative weights of above-ground stems of 20 plants of (a) Maris Piper (b) Desiree, (c) Russet Burbank and (d) King Edward at the third harvest of Survey 4. Individual plants have alternating black and white bars and are arranged according to the number of stems per plant and the relative size of the largest stem.**



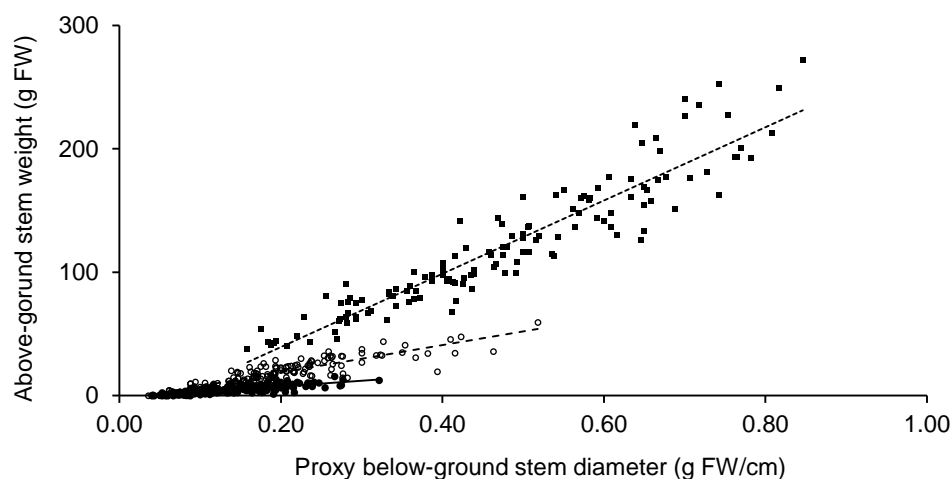
### 3.12.1.3. Proxy below-ground stem diameter

The proxy measurements of below-ground stem diameter correlated strongly with the direct measurements of stem diameter at the base of the stem made on a sub-sample of the plants at the first and third harvests (data not shown). The relationships between proxy stem diameter and above-ground stem weight were stronger at the second and third harvests than at the first harvest in all varieties (Table 93). At the third harvest, this could have been caused by the above-ground stem weight increasing the stem diameter rather than the stem diameter increasing the above-ground stem weight, but as shown in Figure 77 for Maris Piper, the increasing slope of the relationship at successive harvests indicated that the proxy below-ground stem diameter was not increasing in proportion to the increase in the above-ground stem weight. Consequently, the proxy below-ground stem diameter was apparently affecting the growth rate of the above-ground stems.

**Table 93. Relationships between the proxy below-ground stem diameter (PSD, g FW/cm) and the above-ground stem weight (AG, g FW) for individual stems at the first three harvests of Survey 4.  $AG = m \text{ PSD} + c$ .**

| Variety | Harvest | <i>m</i> | S.E. | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---------|----------|------|----------|-------|----------|-----------------------|
| Maris   | 1       | 45.9     | 2.83 | -1.75    | 0.434 | <0.001   | 0.63                  |
| Piper   | 2       | 110.5    | 4.48 | -3.38    | 0.943 | <0.001   | 0.79                  |
|         | 3       | 291.8    | 8.26 | -17.4    | 4.04  | <0.001   | 0.90                  |
| Desiree | 1       | 34.9     | 2.16 | -2.97    | 0.746 | <0.001   | 0.66                  |
|         | 2       | 110.9    | 5.65 | -7.8     | 2.36  | <0.001   | 0.76                  |
|         | 3       | 248.2    | 9.28 | -26.2    | 5.58  | <0.001   | 0.85                  |
| Russet  | 1       | 48.9     | 3.37 | -2.26    | 0.560 | <0.001   | 0.62                  |
| Burbank | 2       | 157.8    | 7.68 | -6.3     | 1.79  | <0.001   | 0.77                  |
|         | 3       | 314      | 16.2 | -13.2    | 7.03  | <0.001   | 0.74                  |
| King    | 1       | 34.9     | 2.45 | -1.26    | 0.457 | <0.001   | 0.53                  |
| Edward  | 2       | 109.0    | 5.10 | -2.6     | 1.33  | <0.001   | 0.71                  |
|         | 3       | 294.1    | 8.38 | -19.1    | 3.97  | <0.001   | 0.87                  |

**Figure 77. Relationships between the proxy below-ground stem diameter and above-ground stem weight for Maris Piper at the first three harvests of Survey 4. First harvest, —●—; second harvest, - -○- -; third harvest, ---■---. See Table 93 for details of fitted lines.**



Accounting for variations in emergence substantially increased the strength of the relationships between the proxy below-ground stem diameter and the above-ground stem weight at the first harvest in all of the varieties (Table 94). Thus, variation in the size of stems that emerged on the same day was largely explained by differences in the proxy below-ground stem diameter, that as discussed in Section 4.13.4.2, for whole plants, correlated strongly with seed tuber weight. Emergence also had a significant effect at the second and third harvests, but the amount by which it increased the correlation coefficient compared to the individual regressions listed in Table 93 decreased over time (Table 94).

**Table 94. Relationships between the proxy below-ground stem diameter (PSD, g FW/cm), date of emergence (EM, relative to the first day that a stem emerged) and above-ground stem weight (AG, g FW) of individual stems at the first three harvests of Survey 4.  $AG = m \text{ PSD} + n \text{ EM} + c$ .**

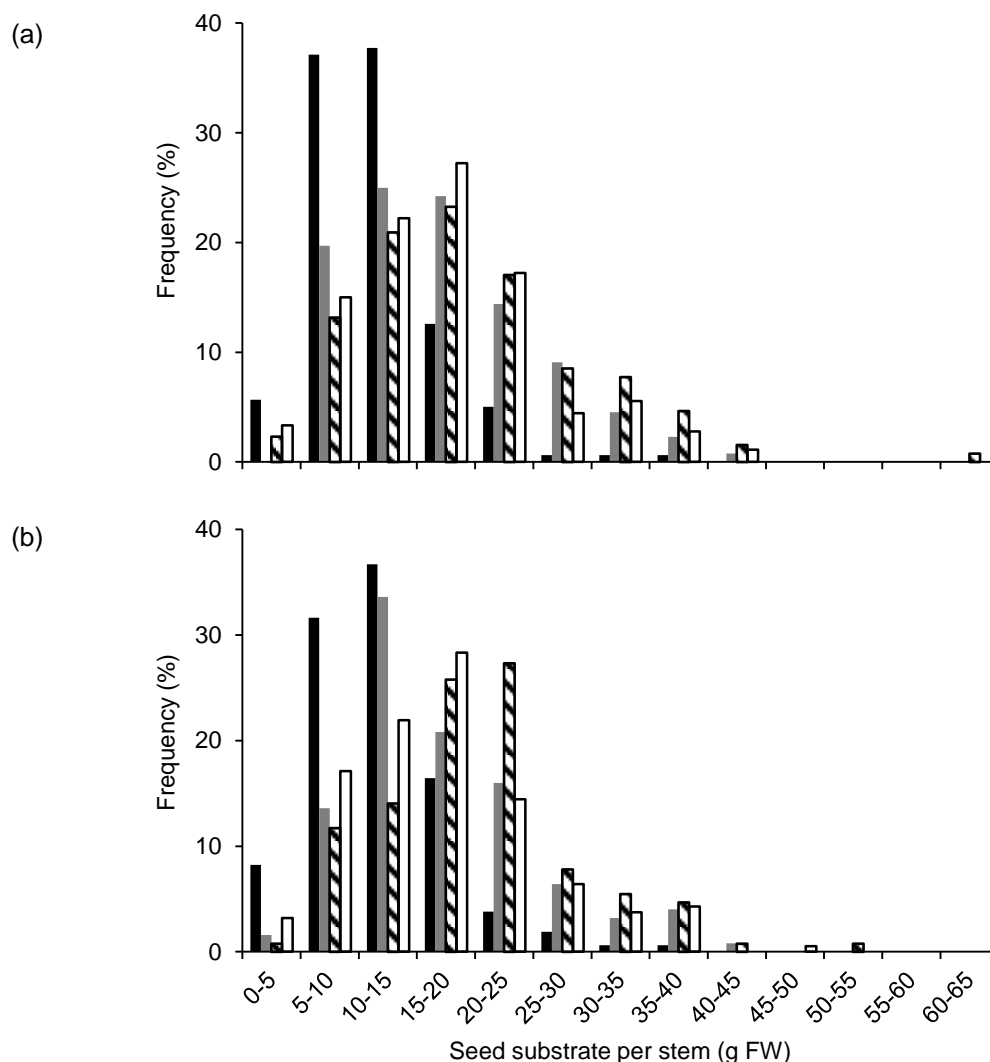
| Variety | Harvest | <i>m</i> | S.E. | <i>n</i> | S.E.   | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|---------|----------|------|----------|--------|----------|-------|----------|-----------------------|
| Maris   | 1       | 29.4     | 1.76 | -0.753   | 0.0369 | 6.26     | 0.458 | <0.001   | 0.89                  |
| Piper   | 2       | 81.7     | 3.86 | -1.59    | 0.118  | 15.6     | 1.53  | <0.001   | 0.89                  |
|         | 3       | 270      | 11.0 | -3.61    | 0.755  | 20.2     | 9.73  | <0.001   | 0.89                  |
| Desiree | 1       | 24.6     | 1.70 | -1.177   | 0.0924 | 8.8      | 1.04  | <0.001   | 0.84                  |
|         | 2       | 88.0     | 5.01 | -2.80    | 0.277  | 21.0     | 3.35  | <0.001   | 0.85                  |
|         | 3       | 219      | 11.0 | -3.96    | 0.830  | 21       | 10.9  | <0.001   | 0.84                  |
| Russet  | 1       | 27.0     | 2.44 | -0.784   | 0.0492 | 6.96     | 0.658 | <0.001   | 0.86                  |
| Burbank | 2       | 122.9    | 7.35 | -1.69    | 0.188  | 13.7     | 2.63  | <0.001   | 0.88                  |
|         | 3       | 231      | 18.3 | -8.2     | 1.05   | 88       | 14.2  | <0.001   | 0.78                  |
| King    | 1       | 23.0     | 1.64 | -0.756   | 0.0429 | 5.41     | 0.464 | <0.001   | 0.84                  |
| Edward  | 2       | 77.9     | 4.09 | -2.10    | 0.140  | 17.4     | 1.60  | <0.001   | 0.87                  |
|         | 3       | 271      | 11.6 | -2.27    | 0.673  | 5.2      | 8.54  | <0.001   | 0.86                  |

#### 3.12.1.4. Seed tuber substrate per stem

The amount of seed tuber substrate per stem was estimated at the first two harvests from the proxy diameter of each below-ground stem and the seed tuber weight as described in Section 3.1.3.5. The average seed tuber substrate was lowest for Maris Piper but relatively similar in the other varieties and for all varieties the values were similar at both harvests (Table 95).

The COV of seed tuber substrate per stem was 46-50 % for all varieties and the values were similar at both harvests (Figure 78; Table 95). Considering that the seed tuber weight affected the above-ground stem-weight of individual plants, this high level of variation in seed tuber substrate per stem represents a major source of variation in the above-ground stem weight of individual stems early in their development.

**Figure 78. Seed tuber substrate per stem for Maris Piper (black bars), Desiree (grey bars), Russet Burbank (hatched bars), King Edward (white bars) at (a) the first and (b) second harvest of Survey 4. Mean values and COVs are listed in Table 95.**



**Table 95. Seed tuber substrate per stem at the first and second harvests of Survey 4.**

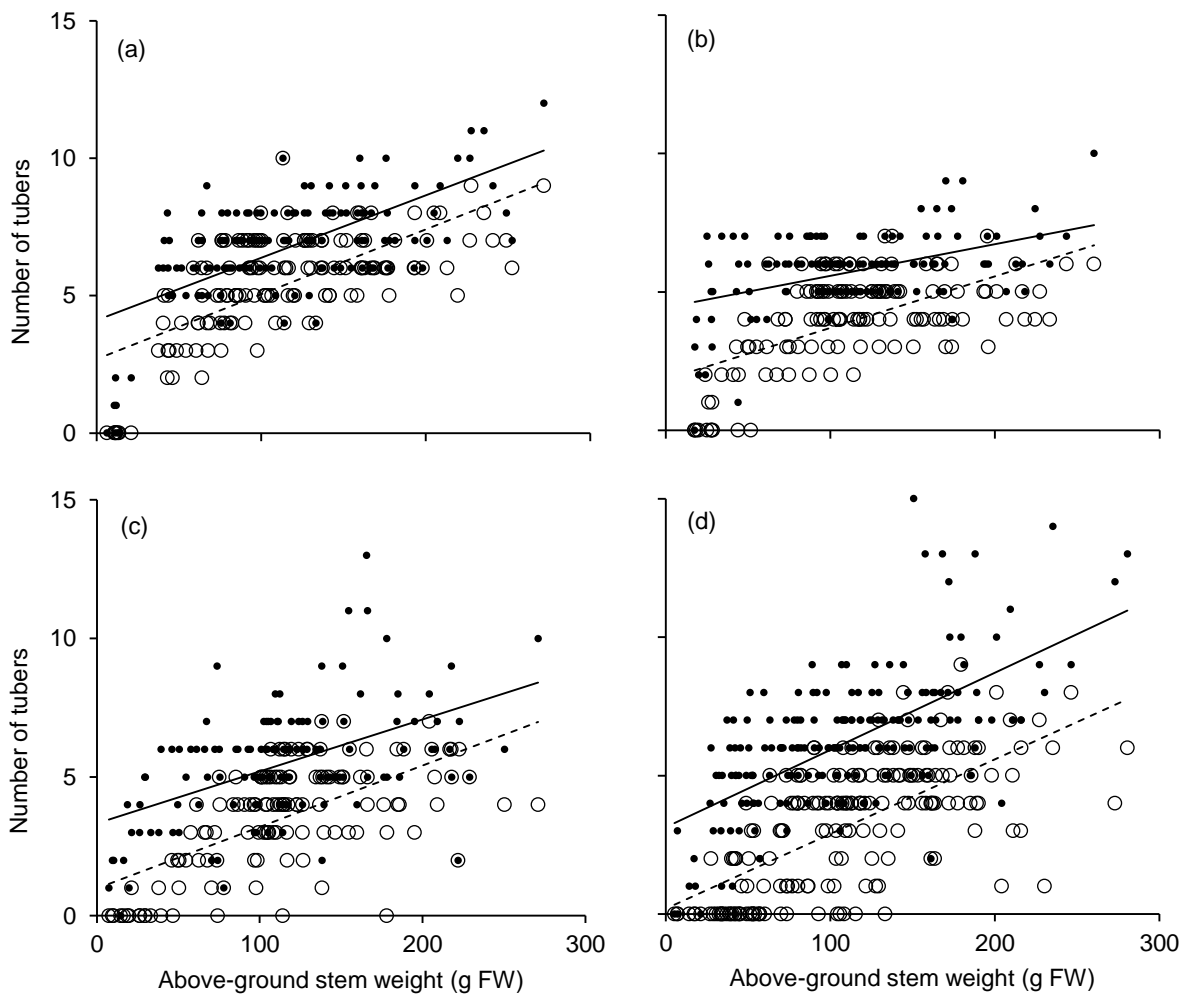
|             | Harvest | Variety     |         |                |             |
|-------------|---------|-------------|---------|----------------|-------------|
|             |         | Maris Piper | Desiree | Russet Burbank | King Edward |
| Mean (g FW) | 1       | 11.5        | 16.9    | 19.5           | 17.5        |
|             | 2       | 11.9        | 17.1    | 20.2           | 17.2        |
| COV (%)     | 1       | 46.5        | 46.5    | 47.9           | 50.6        |
|             | 2       | 47.1        | 46.4    | 48.2           | 49.4        |

### 3.12.1.5. Number of tubers per stem

The number of tubers per stem (including those < 10 mm) increased as the above-ground stem weight increased at the third harvest (c. 10 days after tuber initiation) in all varieties (Figure 79). However, relatively little of the variation in the number of tubers could be explained by above-ground stem weight, particularly for Desiree and Russet Burbank and for all varieties

there was a wide range in above-ground stem weight of stems with the same number of tubers (Figure 79). The relationships were stronger when tubers < 10 mm were excluded, but there was still considerable variation in the weight of above-ground stems with the same number of tubers (Figure 79). In King Edward, *c.* 20 % of stems did not have any tubers > 10 mm.

**Figure 79. Relationships between above-ground stem weight and the number of tubers for individual stems at the third harvest of Survey 4 in (a) Maris Piper, (b) Desiree, (c) Russet Burbank and (d) King Edward. Total number of tubers, —●—; tubers > 10 mm, - -○- -. See Table 96 for details of fitted lines.**





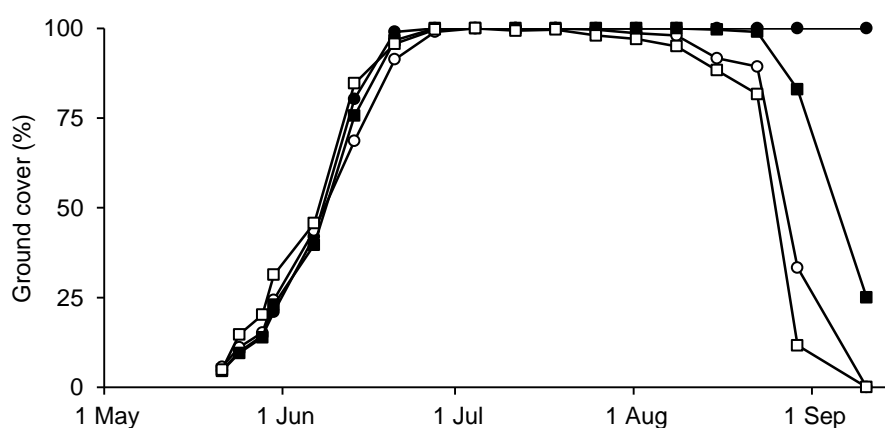
**Table 96. Details of fitted lines in Figure 79. TN = number of tubers, AG = above-ground stem weight.**  
 $TN = m \text{ AG} + c$ .

|     | Variety        |         | <i>m</i> | S.E.    | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|-----|----------------|---------|----------|---------|----------|-------|----------|-----------------------|
| (a) | Maris Piper    | Total   | 0.0227   | 0.00235 | 4.11     | 0.302 | <0.001   | 0.40                  |
|     |                | > 10 mm | 0.0236   | 0.00220 | 2.69     | 0.282 | <0.001   | 0.45                  |
| (b) | Desiree        | Total   | 0.0114   | 0.00200 | 4.44     | 0.254 | <0.001   | 0.20                  |
|     |                | > 10 mm | 0.0186   | 0.00223 | 1.85     | 0.283 | <0.001   | 0.35                  |
| (c) | Russet Burbank | Total   | 0.0188   | 0.00286 | 3.33     | 0.363 | <0.001   | 0.25                  |
|     |                | > 10 mm | 0.0221   | 0.00241 | 0.99     | 0.305 | <0.001   | 0.39                  |
| (d) | King Edward    | Total   | 0.0279   | 0.00245 | 3.14     | 0.303 | <0.001   | 0.41                  |
|     |                | > 10 mm | 0.0269   | 0.00222 | 0.20     | 0.274 | <0.001   | 0.44                  |

#### 4.13.6. Overall growth

The canopy of King Edward initially expanded more rapidly than in other varieties but *c.* 30 DAE the differences in ground cover were small and all varieties developed a complete canopy by the beginning of July (Figure 80). Ground cover started to decrease slowly in Desiree and King Edward during August and they had completely senesced by the fifth harvest (Figure 80). The canopy of Russet Burbank was more persistent but began to senesce towards the end of August and had nearly completely senesced by the fifth harvest (Figure 80). Maris Piper persisted up until the fifth harvest (Figure 80).

**Figure 80. Ground cover for Maris Piper, ●; Desiree, ○; Russet Burbank, ■; King Edward, □ for the area sampled at the fifth harvest of Survey 4.**



King Edward had the highest number of stems and tubers, followed by Maris Piper, and Desiree and Russet Burbank were similar (Table 97). The yields of all varieties were similar at the fourth and fifth harvests (Table 97). At the fifth harvest, the mean tuber size of Maris Piper, Desiree and Russet Burbank were similar despite the higher number of tubers in Maris

Piper, reflecting the less-elongated tuber shape (Table 97). The COV of tuber size was lowest in Russet Burbank and highest in King Edward at the fourth and fifth harvests (Table 97).

The COV of tuber size was substantially higher at the fifth harvest than at the fourth in Maris Piper, Desiree and Russet Burbank, but only slightly higher in King Edward (Table 97).

**Table 97. Summary of overall parameters of growth at the fourth and fifth harvests of Survey 4.**

|                                    | Harvest | Maris Piper | Desiree | Russet Burbank | King Edward |
|------------------------------------|---------|-------------|---------|----------------|-------------|
| Number of stems (000/ha)           | 4       | 105         | 87.5    | 90.4           | 131         |
|                                    | 5       | 103         | 86.0    | 83.1           | 132         |
| Number of tubers (000/ha)          | 4       | 547         | 431     | 483            | 795         |
|                                    | 5       | 543         | 415     | 410            | 844         |
| Yield (t FW/ha)                    | 4       | 24.8        | 27.7    | 23.1           | 26.8        |
|                                    | 5       | 75.5        | 71.8    | 69.3           | 74.7        |
| Mean tuber size (mm)               | 4       | 41.7        | 43.7    | 40.2           | 38.8        |
|                                    | 5       | 61.5        | 61.2    | 59.9           | 55.2        |
| COV of tuber size (%)              | 4       | 13.7        | 13.6    | 12.6           | 16.3        |
|                                    | 5       | 16.2        | 16.8    | 15.0           | 17.1        |
| Tuber shape constant (Firman 2014) | 4       | 117         | 109     | 111            | 120         |
|                                    | 5       | 119         | 110     | 108            | 124         |

The COV of the number of tubers per plant was similar at the fourth and fifth harvests in Maris Piper, Desiree and Russet Burbank, but lower in King Edward (Table 98). The COV of yield per plant was lower at the fifth harvest than at the fourth harvest in all varieties, but particularly in Russet Burbank and King Edward (Table 98). Overall however, the COV of yield per plant was similar to the COV of above-ground stem weight at the third harvest, indicating that plant-to-plant variation did not substantially change. As a consequence of these differences in the number of tubers and yield per plant, the COV of mean tuber weight also varied between harvests (Table 98).

**Table 98. Plant-to-plant variation at the fourth and fifth harvests of Survey 4.**

|  | Harvest | Maris Piper | Desiree | Russet<br>Burbank | King Edward |
|--|---------|-------------|---------|-------------------|-------------|
| COV of number of tubers per plant (%)  | 4       | 32.2        | 38.2    | 39.5              | 31.8        |
|  | 5       | 30.0        | 36.8    | 41.9              | 23.6        |
| COV of yield per plant (%)             | 4       | 24.4        | 24.6    | 33.4              | 27.0        |
|  | 5       | 21.5        | 20.6    | 24.4              | 20.9        |
| COV of mean tuber weight per plant (%) | 4       | 24.2        | 29.9    | 25.6              | 34.8        |
|  | 5       | 28.9        | 31.3    | 31.9              | 26.6        |

#### 4.13.7. Yield per plant

At the fourth harvest, differences in date of emergence between plants explained little variation in yield per plant and seed tuber weight was a better predictor, except in King Edward (Table 99). The combination of seed tuber weight and date of emergence explained *c.* 60-70 % of variation in yield per plant in each variety (Table 99). At the fifth harvest seed tuber weight explained variation in yield per plant better than date of emergence, but with the exception of Russet Burbank, the correlations were weaker than at the fourth harvest (Table 100). The difference between harvests was particularly large for Maris Piper, where only *c.* 25 % of the variation in yield per plant could be explained by variation in seed tuber weight and date of emergence at the fifth harvest (Table 100) and it is unclear why this was the case.

**Table 99. Relationships between seed tuber weight (ST, g FW), date of emergence (EM, relative to the first day that a stem emerged) and yield per plant (YD, g FW) at the fourth harvest of Survey 4.  $YD = m \text{ EM} + n \text{ ST} + c$ .**

| Variety           | EM | ST | <i>m</i> | S.E. | <i>n</i> | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|-------------------|----|----|----------|------|----------|-------|----------|------|----------|-----------------------|
| Maris<br>Piper    | ●  |    | -21.6    | 6.92 | n.a.     | n.a.  | 703      | 47.0 | <0.01    | 0.13                  |
|                   |    | ●  | n.a.     | n.a. | 14.5     | 1.53  | 157      | 44.6 | <0.001   | 0.60                  |
| Desiree           | ●  | ●  | -19.0    | 4.01 | 14.1     | 1.31  | 288      | 47.1 | <0.001   | 0.71                  |
|                   |    | ●  | n.a.     | n.a. | 11.1     | 1.02  | 239      | 38.0 | <0.001   | 0.67                  |
|                   | ●  | ●  | -21.2    | 5.79 | 10.87    | 0.935 | 391      | 53.8 | <0.001   | 0.73                  |
| Russet<br>Burbank | ●  |    | -29.9    | 8.18 | n.a.     | n.a.  | 715      | 55.1 | <0.001   | 0.17                  |
|                   |    | ●  | n.a.     | n.a. | 8.46     | 0.974 | 198      | 40.8 | <0.001   | 0.56                  |
| King<br>Edward    | ●  | ●  | -20.8    | 5.50 | 7.82     | 0.895 | 354      | 55.1 | <0.001   | 0.64                  |
|                   | ●  |    | -41.4    | 6.40 | n.a.     | n.a.  | 843      | 39.3 | <0.001   | 0.41                  |
|                   | ●  | ●  | n.a.     | n.a. | 7.3      | 1.30  | 249      | 67.2 | <0.001   | 0.34                  |
|                   | ●  | ●  | -34.3    | 5.36 | 5.7      | 1.03  | 519      | 66.7 | <0.001   | 0.61                  |

**Table 100. Relationships between seed tuber weight (ST, g FW), date of emergence (EM, relative to the first day that a stem emerged) and yield per plant (YD, g FW) at the fifth harvest of Survey 4.  $YD = m EM + n ST + c$ .**

| Variety | EM | ST | <i>m</i> | S.E. | <i>n</i> | S.E. | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----|----|----------|------|----------|------|----------|------|----------|-----------------------|
| Maris   | ●  |    | -51      | 17.2 | n.a.     | n.a. | 2074     | 126  | <0.01    | 0.12                  |
| Piper   |    | ●  | n.a.     | n.a. | 16.9     | 5.31 | 1201     | 171  | <0.01    | 0.13                  |
| Desiree | ●  | ●  | -52      | 15.8 | 17.4     | 4.91 | 1547     | 190  | <0.001   | 0.26                  |
|         | ●  |    | -43      | 20.7 | n.a.     | n.a. | 1902     | 134  | <0.05    | 0.05                  |
| Russet  |    | ●  | n.a.     | n.a. | 20.3     | 3.02 | 906      | 114  | <0.001   | 0.43                  |
|         | ●  | ●  | -36      | 15.5 | 19.9     | 2.91 | 1144     | 150  | <0.001   | 0.47                  |
| Russet  | ●  |    | -74      | 21.8 | n.a.     | n.a. | 2065     | 149  | <0.001   | 0.15                  |
| Burbank |    | ●  | n.a.     | n.a. | 21.6     | 2.20 | 763      | 89   | <0.001   | 0.62                  |
| King    | ●  | ●  | -67      | 11.9 | 21.1     | 1.79 | 1217     | 109  | <0.001   | 0.75                  |
|         | ●  |    | -79      | 21.7 | n.a.     | n.a. | 1989     | 88   | <0.001   | 0.17                  |
| Edward  |    | ●  | n.a.     | n.a. | 13.4     | 2.53 | 994      | 140  | <0.001   | 0.31                  |
|         | ●  | ●  | -82      | 16.8 | 13.6     | 2.15 | 1271     | 132  | <0.001   | 0.51                  |

Yield per plant at the fourth harvest was closely related to ground cover per plant at the date of the second harvest in all varieties (Table 101). Seed tuber weight continued to influence yield per plant after the second harvest (Table 101) despite the percentage dry matter only decreasing slightly between the second and third harvests (Table 80). The number of stems per plant also had a significant effect on yield from the second to the fourth harvest in all varieties except King Edward, and this was independent of any effect of seed tuber weight on the number of stems per plant (Table 101). Less of the variation in yield per plant at the fifth harvest could be explained from ground cover at the date of the second harvest with the exception of Russet Burbank, suggesting that the relative growth rate of individual plants varied between the fourth and fifth harvests (Table 101).

**Table 101. Correlation coefficients of relationships between the ground cover per plant at the second harvest (GC H2), seed tuber weight (ST) and the number of stems per plant (SN), and the yield per plant at the fourth (YD at H4) and fifth (YD at H5) harvests of Survey 4.**

| Variables†                  | Variety     |         |                |             |
|-----------------------------|-------------|---------|----------------|-------------|
|                             | Maris Piper | Desiree | Russet Burbank | King Edward |
| GC at H2 ~ YD at H4         | 0.71        | 0.76    | 0.73           | 0.80        |
| GC at H2 ~ YD at H5         | 0.32        | 0.41    | 0.72           | 0.53        |
| GC at H2, ST ~ YD at H4     | 0.78        | 0.82    | 0.78           | 0.82        |
| GC at H2, ST ~ YD at H5     | n.s.        | 0.50    | 0.82           | 0.62        |
| GC at H2, SN ~ YD at H4     | 0.82        | 0.79    | 0.82           | n.s.        |
| GC at H2, SN ~ YD at H5     | n.s.        | n.s.    | n.s.           | n.s.        |
| GC at H2, ST, SN ~ YD at H4 | 0.85        | 0.83    | 0.84           | n.s.        |
| GC at H2, ST, SN ~ YD at H5 | n.s.        | n.s.    | n.s.           | n.s.        |

† Variables on the left hand side of ~ are explanatory variables and the response variable is on the right hand side.

#### 4.13.8. Yield and number of tubers per stem

Variation in yield per stem at the fourth and fifth harvests was of a similar magnitude to variation in above-ground stem weight at the third harvest (Table 102). At the fifth harvest, the COV of yield per stem was similar in all varieties (Table 102).

**Table 102. Average and variation in yield per stem at the fourth and fifth harvests of Survey 4.**

|   | Harvest | Maris Piper | Desiree | Russet<br>Burbank | King Edward |
|---|---------|-------------|---------|-------------------|-------------|
| Average yield per stem (g FW)   | 4       | 236         | 317     | 255               | 204         |
|   | 5       | 742         | 834     | 841               | 563         |
| COV of yield per stem (%)   | 4       | 42.8        | 47.1    | 43.2              | 57.3        |
|   | 5       | 51.3        | 48.7    | 51.9              | 54.6        |
| Transformed and weighted average yield per stem ( $\sqrt[3]{\text{g FW}}$ ) | 4       | 6.46        | 7.17    | 6.58              | 6.38        |
|   | 5       | 9.55        | 9.90    | 10.08             | 8.80        |
| Transformed and weighted COV of yield per stem (%)                          | 4       | 12.8        | 13.1    | 12.3              | 15.6        |
|   | 5       | 14.7        | 14.5    | 14.7              | 15.4        |

Stems that emerged later or that were from plants with a higher number of stems had a lower yield in all varieties at the fourth and fifth harvests, although the influence of emergence in Desiree at the fifth harvest was weak (Tables 103-104). Overall, the individual effect of date of emergence weakened and the effect of the number of stems per plant on yield per plant strengthened compared to the relationships between these variables and above-ground stem weight per plant at the first three harvests (Tables 91-92).

**Table 103. Relationships between date of emergence (EM, relative to the first day that a stem emerged), the number of stems per plant (SN) and yield (YD, g FW) of individual stems at the fourth harvest of Survey 4.  $YD = m \text{ EM} + n \text{ SN} + c$ .**

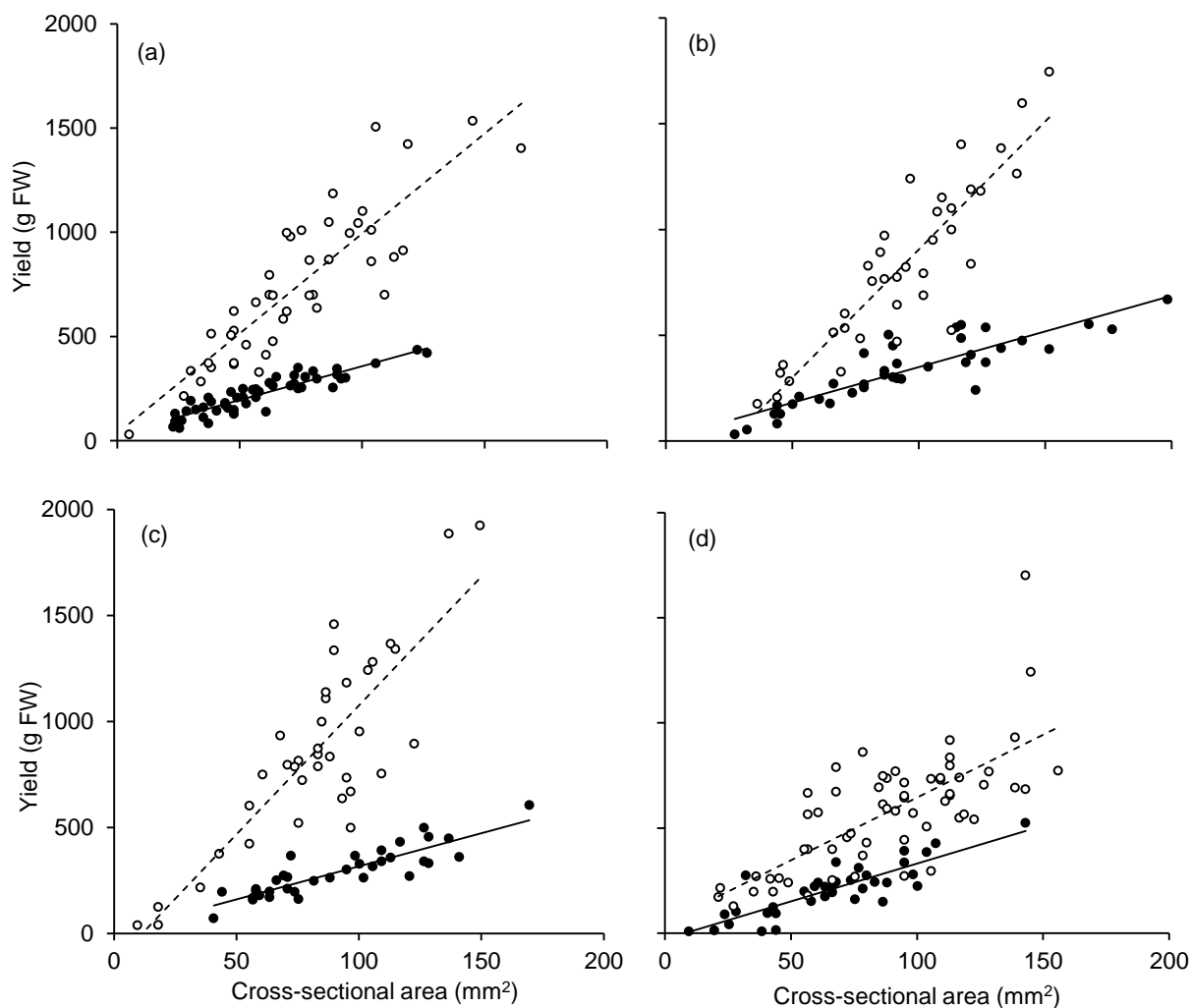
| Variety        | EM | SN | <i>m</i> | S.E. | <i>n</i> | S.E. | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|----------------|----|----|----------|------|----------|------|----------|------|----------|-----------------------|
| Maris Piper    | ●  |    | -23.5    | 2.52 | n.a.     | n.a. | 419      | 19.9 | <0.001   | 0.39                  |
|                |    | ●  | n.a.     | n.a. | -45.5    | 7.45 | 360      | 21.7 | <0.001   | 0.20                  |
| Desiree        | ●  | ●  | -21.2    | 2.29 | -34.9    | 6.00 | 497      | 22.3 | <0.001   | 0.51                  |
|                |    |    | -31.3    | 5.24 | n.a.     | n.a. | 573      | 40.8 | <0.001   | 0.25                  |
|                |    | ●  | n.a.     | n.a. | -86      | 11.7 | 523      | 30.3 | <0.001   | 0.31                  |
|                | ●  | ●  | -26.2    | 4.48 | -66.2    | 9.98 | 690      | 38.6 | <0.001   | 0.46                  |
| Russet Burbank | ●  |    | -20.3    | 2.69 | n.a.     | n.a. | 407      | 20.8 | <0.001   | 0.32                  |
|                |    | ●  | n.a.     | n.a. | -46      | 11.4 | 366      | 28.8 | <0.001   | 0.11                  |
|                | ●  | ●  | -19.3    | 2.56 | -35.1    | 9.14 | 483      | 27.9 | <0.001   | 0.40                  |
| King Edward    | ●  |    | -22.5    | 2.50 | n.a.     | n.a. | 373      | 18.6 | <0.001   | 0.36                  |
|                |    | ●  | n.a.     | n.a. | -50.0    | 6.26 | 374      | 22.8 | <0.001   | 0.28                  |
|                | ●  | ●  | -18.9    | 2.19 | -37.5    | 5.20 | 475      | 21.2 | <0.001   | 0.54                  |

**Table 104. Relationships between date of emergence (EM, relative to the first day that a stem emerged), the number of stems per plant (SN) and yield (YD, g FW) of individual stems at the fifth harvest of Survey 4.  $YD = m EM + n SN + c$ .**

| Variety | EM | SN | <i>m</i> | S.E. | <i>n</i> | S.E. | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|---------|----|----|----------|------|----------|------|----------|------|----------|-----------------------|
| Maris   | ●  |    | -58.6    | 9.72 | n.a.     | n.a. | 1232     | 82.3 | <0.001   | 0.22                  |
| Piper   |    | ●  | n.a.     | n.a. | -279     | 29.1 | 1483     | 81.3 | <0.001   | 0.40                  |
| Desiree | ●  | ●  | -44.5    | 8.00 | -234     | 27.9 | 1731     | 89.0 | <0.001   | 0.49                  |
|         | ●  |    | -39      | 16.2 | n.a.     | n.a. | 1144     | 116  | <0.05    | 0.04                  |
| Russet  |    | ●  | n.a.     | n.a. | -294     | 40.2 | 1498     | 96.0 | <0.001   | 0.31                  |
|         | ●  | ●  | -48      | 12.5 | -309     | 36.1 | 1900     | 126  | <0.001   | 0.43                  |
| Burbank | ●  |    | -86      | 12.2 | n.a.     | n.a. | 1528     | 96.7 | <0.001   | 0.32                  |
| King    |    | ●  | n.a.     | n.a. | -346     | 49.5 | 1593     | 113  | <0.001   | 0.30                  |
|         | ●  | ●  | -71      | 10.6 | -267     | 40.5 | 1993     | 108  | <0.001   | 0.52                  |
| Edward  | ●  |    | -60.4    | 6.43 | n.a.     | n.a. | 890      | 37.9 | <0.001   | 0.33                  |
| Edward  |    | ●  | n.a.     | n.a. | -158     | 19.4 | 1093     | 68.0 | <0.001   | 0.27                  |
|         | ●  | ●  | -52.9    | 5.61 | -127     | 16.0 | 1274     | 58.5 | <0.001   | 0.51                  |

Prior to the third harvest, the stem diameter of individual stems on 20 plants of each variety was measured in each remaining harvest area and the cross-sectional area of each stem was calculated. At the third harvest, the above-ground stem weight correlated strongly with the cross sectional area in all varieties ( $R^2 = c$ . 0.80-0.90, data not shown). The measurements made on stems in the fourth and fifth harvest areas therefore served as a non-destructive estimate of the size of each stem. The cross-sectional area of stems at the third harvest correlated only slightly less strongly with yield at the fourth and fifth harvests than with the above-ground stem weight at the third harvest (Figure 81; Table 105). This indicated that the relative size of stems did not substantially change between the third and fifth harvests, a period of 90 days during which the majority of yield was produced. The relationship was weaker in King Edward than in other varieties at the fifth harvest (Table 105) and this was associated with senescence being more variable in King Edward which presumably resulted in the yield of some stems not increasing up until the fifth harvest. Including the number of stems per plant in regressions did not increase the strength of the relationships (data not shown). The stronger relationships between these non-destructive measurements of stems and yield, in comparison to those between ground cover per plant and yield (Table 101) were probably due to the greater range in yield per stem than yield per plant.

**Figure 81. Relationships between the cross-sectional area of stems at the third harvest and the yield of stems at the fourth (---●---) and fifth (---○---) harvests of Survey 4 in (a) Maris Piper, (b) Desiree, (c) Russet Burbank, (d) King Edward. See Table 105 for details of fitted lines.**



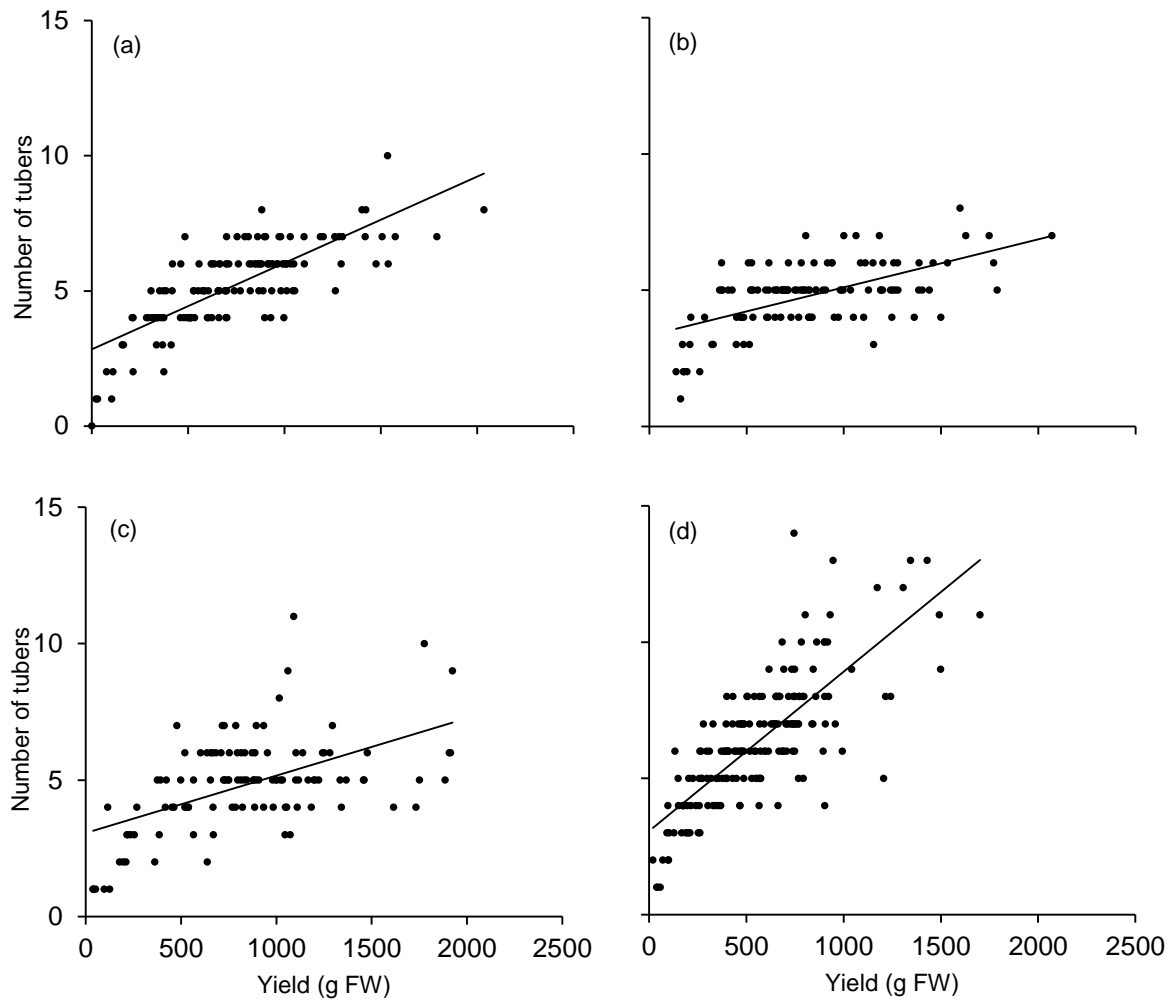
**Table 105. Fitted lines in Figure 81.  $YD = m CA + c$ . Where YD = yield and CA = stem cross-sectional area.**

|     | Variety | Harvest | <i>m</i> | S.E.  | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|-----|---------|---------|----------|-------|----------|------|----------|-----------------------|
| (a) | Maris   | 4       | 3.25     | 0.217 | 33       | 13.9 | <0.001   | 0.82                  |
|     | Piper   | 5       | 9.56     | 0.842 | 35       | 67.5 | <0.001   | 0.75                  |
| (b) | Desiree | 4       | 3.37     | 0.311 | 13       | 32.0 | <0.001   | 0.76                  |
|     |         | 5       | 12.1     | 1.08  | -304     | 106  | <0.001   | 0.78                  |
| (c) | Russet  | 4       | 3.12     | 0.301 | 5        | 29.0 | <0.001   | 0.76                  |
|     | Burbank | 5       | 12.2     | 1.31  | -140     | 115  | <0.001   | 0.70                  |
| (d) | King    | 4       | 3.60     | 0.321 | -26      | 23.0 | <0.001   | 0.71                  |
|     | Edward  | 5       | 5.98     | 0.748 | 48       | 70.5 | <0.001   | 0.51                  |

At the fifth harvest, the number of tubers per stem correlated more strongly with yield per stem in Maris Piper and King Edward than in Desiree and Russet Burbank and the slope was steepest for King Edward (Figure 82). The relationships in Maris Piper and King Edward

were stronger than those between the number of tubers > 10 mm and the above-ground stem weight at the third harvest, but were similar in Desiree and Russet Burbank (one outlier infected by *R. solani* that produced 20 tubers was excluded from the analysis of Russet Burbank).

**Figure 82. Relationships between yield per stem and the number of tubers per stem at the fifth harvest of Survey 4 in (a) Maris Piper, (b) Desiree, (c) Russet Burbank, (d) King Edward. See Table 106 for details of fitted lines.**





**Table 106. Fitted lines in Figure 82.  $TN = m YD + c$ . Where TN = number of tubers, YD = yield.**

|     | Variety        | <i>m</i> | S.E.     | <i>c</i> | S.E.  | <i>P</i> | <i>R</i> <sup>2</sup> |
|-----|----------------|----------|----------|----------|-------|----------|-----------------------|
| (a) | Maris Piper    | 0.00319  | 0.000229 | 2.84     | 0.191 | <0.001   | 0.59                  |
| (b) | Desiree        | 0.00176  | 0.000227 | 3.34     | 0.210 | <0.001   | 0.34                  |
| (c) | Russet Burbank | 0.00210  | 0.000320 | 3.07     | 0.303 | <0.001   | 0.28                  |
| (d) | King Edward    | 0.00584  | 0.000363 | 3.08     | 0.233 | <0.001   | 0.59                  |

#### 4.13.9. Mean tuber weight per plant

The mean tuber weight per plant decreased as the number of stems per plant increased in all varieties at the fifth harvest (Table 107). In isolation, yield per plant had a significant effect on mean tuber weight in Maris Piper and King Edward but not in Desiree or Russet Burbank (Table 107). However, in multiple regressions, yield had a significant effect on mean tuber weight in all varieties and the combination of the number of stems per plant and yield per plant explained c. 50-60 % of the variation in mean tuber weight per plant (Table 107).

**Table 107. Relationships between yield per plant (YD), the number of stems per plant (SN) and mean tuber weight per plant (MTW) at the fifth harvest of Survey 4.  $MTW = m SN + n YD + c$ .**

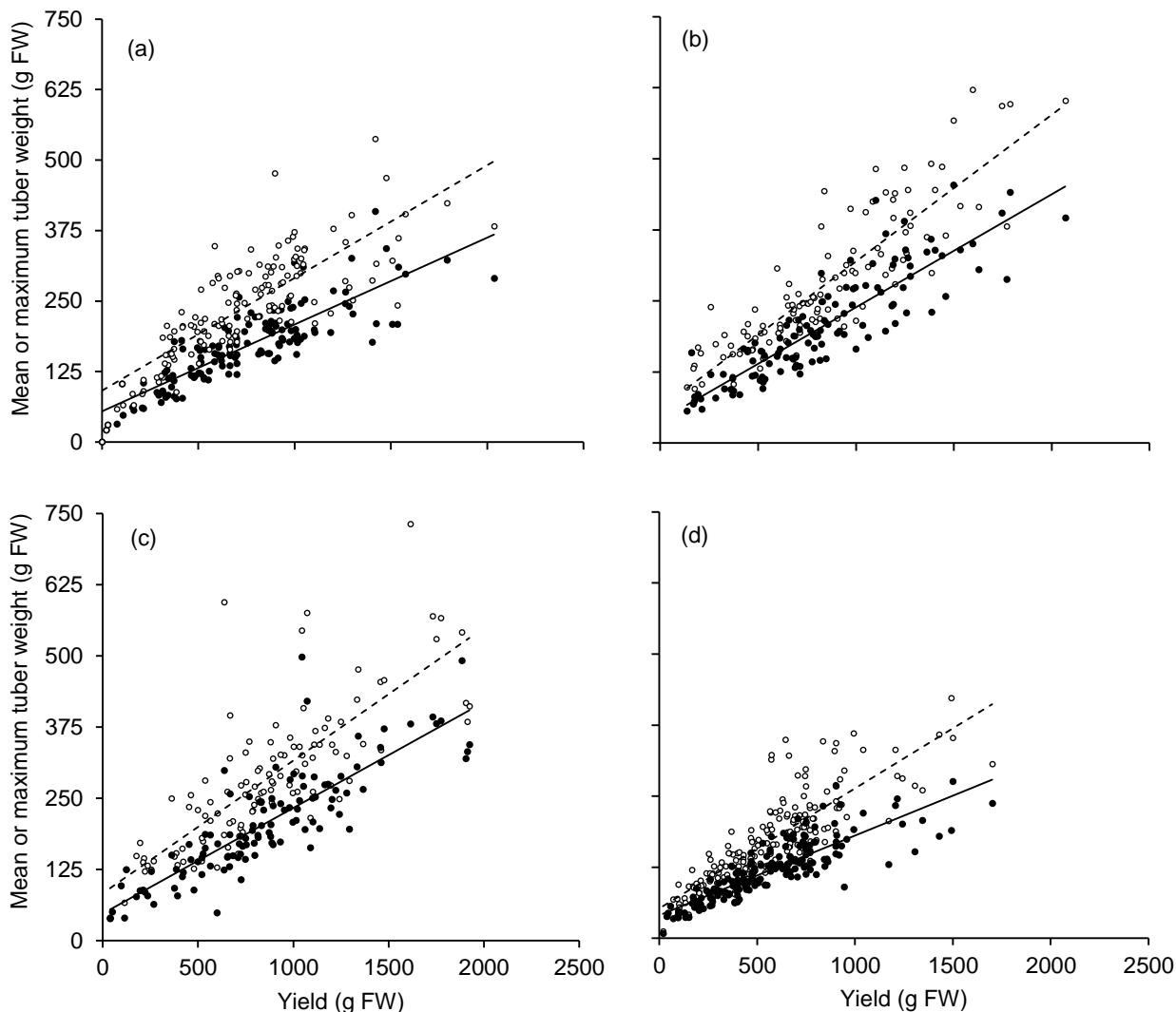
| Variety        | SN | YD | <i>m</i> | S.E. | <i>n</i> | S.E.   | <i>c</i> | S.E. | <i>P</i> | <i>R</i> <sup>2</sup> |
|----------------|----|----|----------|------|----------|--------|----------|------|----------|-----------------------|
| Maris Piper    | ●  |    | -36.1    | 7.13 | n.a.     | n.a.   | 281      | 17.8 | <0.001   | 0.30                  |
|                | ●  | ●  | n.a.     | n.a. | 0.072    | 0.0175 | 72       | 30.8 | <0.001   | 0.21                  |
| Desiree        | ●  |    | -42.7    | 5.26 | 0.089    | 0.0122 | 143      | 22.9 | <0.001   | 0.63                  |
|                | ●  | ●  | -65.7    | 9.96 | n.a.     | n.a.   | 372      | 21.0 | <0.001   | 0.42                  |
|                | ●  | ●  | n.a.     | n.a. | 0.001    | 0.0295 | 227      | 49.4 | n.s.     | 0.00                  |
|                | ●  | ●  | -91.6    | 9.53 | 0.114    | 0.0213 | 236      | 30.8 | <0.001   | 0.61                  |
| Russet Burbank | ●  |    | -58      | 11.8 | n.a.     | n.a.   | 355      | 23.9 | <0.001   | 0.28                  |
|                | ●  | ●  | n.a.     | n.a. | 0.032    | 0.0261 | 194      | 42.6 | n.s.     | 0.01                  |
|                | ●  | ●  | -82      | 11.2 | 0.102    | 0.0212 | 240      | 31.4 | <0.001   | 0.48                  |
| King Edward    | ●  |    | -19.4    | 4.05 | n.a.     | n.a.   | 200      | 12.9 | <0.001   | 0.27                  |
|                | ●  | ●  | n.a.     | n.a. | 0.038    | 0.0129 | 77       | 22.6 | <0.01    | 0.12                  |
|                | ●  | ●  | -24.3    | 3.37 | 0.056    | 0.0098 | 120      | 17.5 | <0.001   | 0.53                  |

#### 4.13.10. Yield per stem and tuber weight

Both mean and maximum tuber weight per stem correlated strongly with yield per stem at the fifth harvest (Figure 83) because although the number of tubers per stem increased as yield per stem increased, the increase was not proportional. The stronger and steeper slope of the relationships between the number of tubers and yield for Maris Piper and King Edward compared to Desiree and Russet Burbank, were associated with the relationships between the yield and mean or maximum tuber weights having shallower slopes (Figure 83). The number

of tubers had a significant effect on each of the relationships, except for the maximum tuber weight of Maris Piper, but only increased the  $R^2$  value by *c.* 0.05 (data not shown).

**Figure 83. Relationships between yield (g FW) and mean (—●—) and maximum (- -○-) tuber weight (g FW) of individual stems in (a) Maris Piper, (b) Desiree, (c) Russet Burbank, (d) King Edward at the fifth harvest of Survey 4. See Table 108 for details of fitted lines.**



**Table 108. Fitted lines in Figure 83. Mean or maximum tuber weight =  $m$  YD +  $c$ .**

|     |                |         | $m$    | S.E.    | $c$  | S.E. | $P$    | $R^2$ |
|-----|----------------|---------|--------|---------|------|------|--------|-------|
| (a) | Maris Piper    | Mean    | 0.1556 | 0.00836 | 53.0 | 6.97 | <0.001 | 0.72  |
|     |                | Maximum | 0.200  | 0.0124  | 91   | 10.3 | <0.001 | 0.66  |
| (b) | Desiree        | Mean    | 0.199  | 0.0102  | 40.2 | 9.45 | <0.001 | 0.77  |
|     |                | Maximum | 0.258  | 0.0131  | 62   | 12.1 | <0.001 | 0.77  |
| (c) | Russet Burbank | Mean    | 0.186  | 0.0108  | 47   | 10.2 | <0.001 | 0.73  |
|     |                | Maximum | 0.233  | 0.0164  | 83   | 15.5 | <0.001 | 0.64  |
| (d) | King Edward    | Mean    | 0.1405 | 0.00642 | 40.3 | 4.12 | <0.001 | 0.73  |
|     |                | Maximum | 0.211  | 0.0100  | 52.6 | 6.43 | <0.001 | 0.71  |

Variation in the size of tubers on individual stems was difficult to characterise satisfactorily due to the small number of tubers on each stem. However, the COV of tuber weight provides

a crude measure of variability and was numerically *c.* 10-20 % higher at the fourth and fifth harvests than at the third harvest in all varieties (Table 109). The extent of variation on individual stems was also highly variable; some stems produced tubers of similar weights (COV < 15 %) whilst others produced tubers of extremely different weights (COV > 100 %) (Table 109). While a crucial component of the overall variability in tuber size within the crop, the causes of this variation are obscure and the COV of tuber weight did not correlate with any of the variables measured (data not shown).

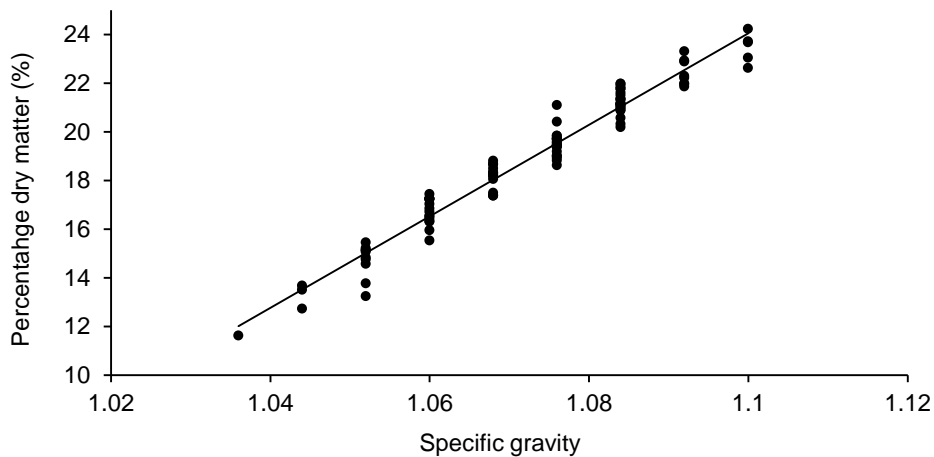
**Table 109. COV of tuber weight on individual stems and the COV of the COV of tuber weight per stem at the third, fourth and fifth harvests of Survey 4.**

|                                     | Harvest |         | Maris Piper | Desiree | Russet<br>Burbank | King Edward |
|-------------------------------------|---------|---------|-------------|---------|-------------------|-------------|
| COV of tuber weight<br>per stem (%) | 3       | Mean    | 44.5        | 49.7    | 39.3              | 44.6        |
|                                     |         | COV (%) | 37.1        | 36.4    | 46.5              | 41.8        |
|                                     | 4       | Mean    | 56.9        | 51.7    | 56.6              | 65.1        |
|                                     |         | COV (%) | 40.6        | 49.4    | 46.9              | 38.4        |
|                                     | 5       | Mean    | 64.1        | 59.0    | 61.0              | 75.5        |
|                                     |         | COV (%) | 38.6        | 42.8    | 40.0              | 32.3        |

#### 4.14. Survey 5

The specific gravity of the most dilute sucrose solution in which seed tubers floated correlated strongly with their percentage dry matter prior to planting (Figure 84). The relationship shown in Figure 84 was used to estimate the percentage dry matter of the seed tubers that were planted and in turn their dry weight and dry weight lost between planting and the harvest.

**Figure 84. Relationship between specific gravity (SG) of the most dilute sucrose solution in which seed tubers floated and the percentage dry matter of the seed tuber (DM). Fitted line:  $DM = 188.1 (\pm 3.95) \times SG - 182.9 (\pm 4.24)$ .  $R^2 = 0.96$ .**



Twenty-five seed tubers were damaged by pests prior to harvest and these were excluded from the analysis. Details of the remaining 75 plants are listed in Table 110. The amount of dry weight lost from the seed tubers was similar to the total dry weight of the above- and below-ground stem (excluding the roots and stolons) and *c.* 66 % of the dry weight of the seed tubers had been lost since planting (Table 110).

**Table 110. Summary of plant-to-plant variation in Survey 5.**

|   | Mean | COV (%) |
|---|------|---------|
| Number of stems per plant                         | 2.8  | 39.0    |
| Above-ground stem weight (g FW)                   | 36.9 | 26.9    |
| Dry weight of above- and below-ground stem (g DW) | 4.21 | n.d.    |
| Seed tuber percentage dry matter (%)              | 6.51 | 23.2    |
| Estimated dry weight lost from seed tuber (g DW)  | 3.90 | 15.0    |

The specific gravity of seed tubers did not affect the number of stems per plant and the number of stems per plant did not affect the above-ground stem weight per plant (data not shown). Seed tubers with a lower specific gravity emerged earliest, although the relationship was weak (Table 111). The number of stems per plant also had a very weak effect on emergence, with plants that had fewer stems emerging earlier (Table 111). Combined, the specific gravity and number of stems per plant explained *c.* 25 % of the variation in emergence (Table 111). Seed tubers that had a higher specific gravity at planting had a higher percentage dry matter at harvest, and date of emergence had only a weak effect on the

percentage dry matter (Table 111), which was not significant in a multiple regression when combined with the specific gravity (data not shown). The date of emergence explained c. 50 % of the variation in above-ground stem weight and while the amount of dry weight lost from the seed tuber had only a very weak effect when considered separately, along with the date of emergence, it explained a substantially greater proportion of the variation in the above-ground stem weight than the date of emergence alone (Table 111).

**Table 111. Relationships between specific gravity of seed tubers (SG), dry weight lost from seed tuber (WL, g DW), date of emergence (EM, Julian days), the number of stems per plant (SN) and date of emergence, percentage dry matter (DM) and above-ground stem weight (AG, g FW) in Survey 5.**

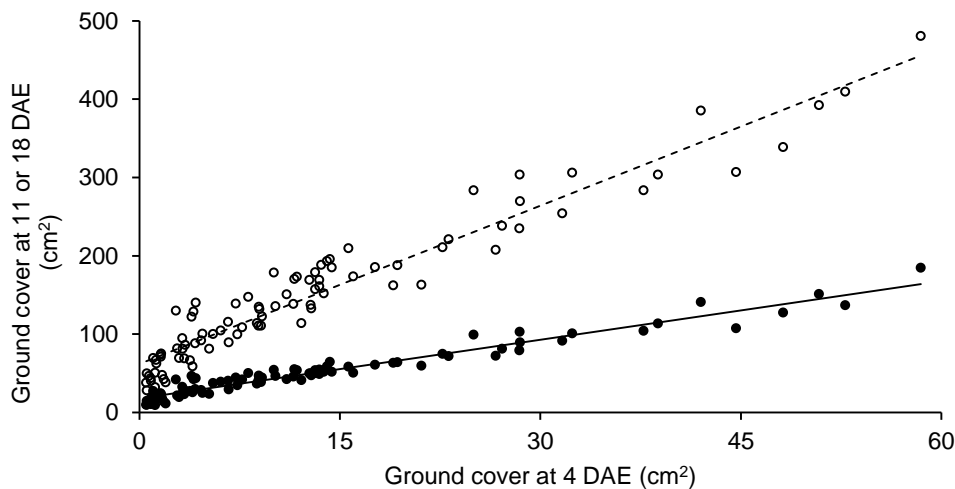
| Explanatory variable(s) |    |    |    | Response variable | Relationship  | P      | R <sup>2</sup> |
|-------------------------|----|----|----|-------------------|---|--------|----------------|
| SG                      | WL | EM | SN |                   |   |        |                |
| ●                       |    |    |    | EM                | $69 (\pm 16.6) \times SG + 75 (\pm 17.8)$                                 | <0.001 | 0.18           |
|                         |    |    | ●  | EM                | $0.60 (\pm 0.215) \times SN + 147.77 (\pm 0.646)$                         | <0.01  | 0.08           |
| ●                       |    |    | ●  | EM                | $64 (\pm 16.1) \times SG + 0.49 (\pm 0.198) \times SN + 79 (\pm 17.3)$    | <0.001 | 0.24           |
| ●                       |    |    |    | DM                | $76.0 (\pm 9.77) \times SG - 75 (\pm 10.5)$                               | <0.001 | 0.45           |
|                         |    | ●  |    | DM                | $0.221 (\pm 0.0797) \times EM - 27 (\pm 11.9)$                            | <0.01  | 0.08           |
| ●                       |    |    |    | AG                | $-134 (\pm 85.6) \times SG + 181 (\pm 91.9)$                              | n.s.   | 0.02           |
|                         | ●  |    |    | AG                | $3.9 (\pm 1.94) \times WL + 21.6 (\pm 7.64)$                              | <0.05  | 0.04           |
|                         |    | ●  |    | AG                | $-3.32 (\pm 0.392) \times EM + 533 (\pm 58.6)$                            | <0.001 | 0.49           |
|                         | ●  | ●  |    | AG                | $8.7 (\pm 1.11) \times WL - 4.09 (\pm 0.307) \times DOE + 614 (\pm 44.6)$ | <0.001 | 0.72           |

#### 4.15. Survey 6

At 4 DAE, 10 plants had not emerged and these plants were excluded from the analysis.

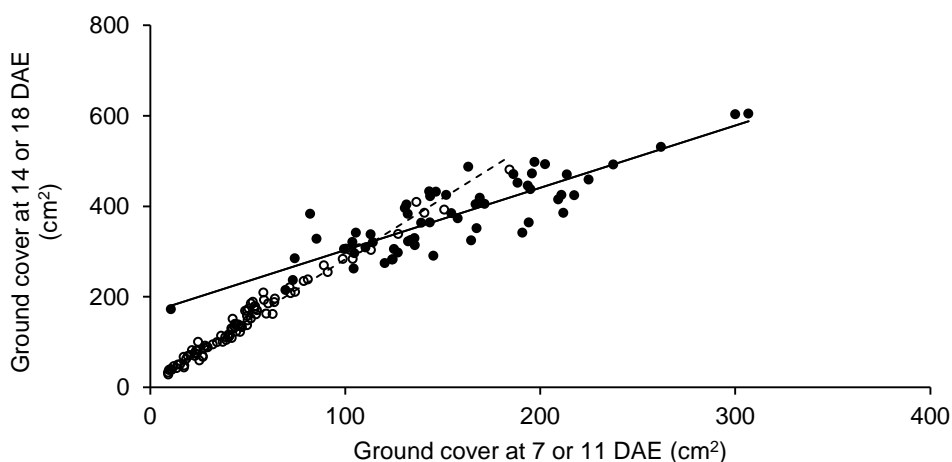
Ground cover at 4 DAE was an accurate predictor of ground cover at 11 and 18 DAE indicating that the growth rate of ground cover was determined largely by initial ground cover and not by other factors (Figure 85).

**Figure 85.** Changes in ground cover of individual plants in Survey 6 at each sampling date (GC1, GC2 and GC3, 4, 11 and 18 DAE respectively). GC1 > GC2, ●; GC1 > GC3, ○. Fitted lines GC1 ~ GC2, — GC2 =  $2.50 (\pm 0.081) \times GC1 + 18.3 (\pm 1.20)$   $R^2 = 0.93$ . GC1 ~ GC3, - - - GC3 =  $6.97 (\pm 0.257) \times GC1 + 60.2 (\pm 3.81)$ .  $R^2 = 0.91$ .



Plants grown from minitubers in Survey 6 had approximately one third of the average ground cover at 11 DAE in comparison to plants grown from seed tubers at 7 DAE in Survey 4 ( $50.8 \text{ cm}^2$  vs.  $154.6 \text{ cm}^2$ ). The largest plants grown from minitubers had a similar ground cover to the smallest plants grown from seed tubers and the ground cover of these plants increased by a similar amount during one week of growth (Figure 86). From 11 to 18 DAE the changes in ground cover of the plants grown from minitubers were uniform compared to plants grown from seed tubers from 7 to 14 DAE as evidenced by the higher correlation coefficients of the regressions (Figure 86). This would be expected if the growth of the plants from minitubers was determined only by their ground cover, whereas for plants grown from seed tubers, the weight of the seed tuber was still influencing their growth (as discussed in Section 4.13.4.2). While it is not possible to establish whether other factors influenced the changes in ground cover, it is highly probable that these differences were influenced by the difference in seed tuber weight.

**Figure 86. Changes in ground cover of individual plants grown from 30-40 mm seed tubers from 7 to 14 DAE, ● and minitubers from 11 to 18 DAE, ○. Fitted lines: Seed tubers, —  $GC2 = 1.22 (\pm 0.088) \times GC1 + 195 (\pm 12.9) R^2 = 0.72$ . Minitubers, - - -  $GC2 = 2.78 (\pm 0.048) \times GC1 + 9.4 (\pm 2.48) R^2 = 0.98$**



#### 4.16. Reanalysis of Firman & Shearman (2006b)

The original data of Firman & Shearman (2006b) was reanalysed to establish whether plant-to-plant variation may have influenced the differences in the COV of tuber size reported, as discussed in Section 2.4.2.2. The experimental treatments consisted of three seed tuber stocks of Maris Peer with increasing severities of infection by *R. solani* (Healthy Welsh, Diseased Welsh and Diseased Wiltshire, respectively) treated with and without each combination of the fungicides azoxystrobin and pencycuron. The results given in Table 112 differ slightly from those originally reported, as the COV of tuber size was calculated for the entire plot, whereas in the original analysis missing plants and their neighbours were excluded, but this did not alter the original conclusions. In the analysis of plant-to-plant variation, missing plants were treated as missing values rather than as zero values.

The COV of tuber size, number of stems per plant, yield per plant, number of tubers per plant and mean tuber size per plant all increased as the level of infection on the seed tubers increased (Table 112). Applications of azoxystrobin reduced the COV of tuber size and also the COV of number of stems per plant, COV of yield per plant and the COV of number of tubers per plant (Table 112). The differences in the COV of number of stems per plant were relatively small between the stocks in comparison to the COV of yield per plant and COV of

number of tubers per plant (Table 112). When the seed tuber stock with the highest level of infection was not treated with fungicide, the COV of yield per plant and COV of number of tubers per plant were very high (65 and 72 % respectively) and pencycuron reduced the COV of tuber size by from 20 to 16 % (Table 112).

**Table 112. Effects of seed tuber stock, azoxystrobin and pencycuron treatment on the COV of tuber size and plant-to-plant variation based on the data Firman & Shearman (2006). S.E. based on 33 D.F.**

|                                       | Seed tuber stock   | Azoxystrobin |               | No azoxystrobin |               | Mean |
|---------------------------------------|--------------------|--------------|---------------|-----------------|---------------|------|
|                                       |                    | Pencycuron   | No pencycuron | Pencycuron      | No pencycuron |      |
| COV of tuber size (%)                 | Healthy Welsh      | 15.8         | 16.7          | 16.2            | 16.9          | 16.4 |
|                                       | Diseased Welsh     | 16.4         | 16.4          | 16.6            | 17.5          | 16.7 |
|                                       | Diseased Wiltshire | 17.7         | 17.7          | 15.6            | 20.2          | 17.8 |
|                                       | S.E.               |              | 0.55          |                 |               | 0.28 |
| COV of number of stems per plant (%)  | Healthy Welsh      | 23.5         | 30.2          | 28.1            | 29.5          | 27.8 |
|                                       | Diseased Welsh     | 25.3         | 30.5          | 27.2            | 30.7          | 28.4 |
|                                       | Diseased Wiltshire | 30.5         | 32.6          | 31.4            | 42.1          | 34.2 |
|                                       | S.E.               |              | 3.21          |                 |               | 1.60 |
| COV of yield per plant (%)            | Healthy Welsh      | 29.8         | 35.6          | 25.4            | 30.8          | 30.4 |
|                                       | Diseased Welsh     | 34.2         | 39.0          | 36.8            | 37.6          | 36.9 |
|                                       | Diseased Wiltshire | 38.0         | 41.2          | 32.3            | 64.7          | 44.1 |
|                                       | S.E.               |              | 2.80          |                 |               | 5.61 |
| COV of number of tubers per plant (%) | Healthy Welsh      | 27.3         | 23.5          | 25.9            | 27.8          | 26.1 |
|                                       | Diseased Welsh     | 30.9         | 40.4          | 30.9            | 43.6          | 36.5 |
|                                       | Diseased Wiltshire | 36.7         | 38.7          | 31.7            | 54.3          | 40.4 |
|                                       | S.E.               |              | 3.85          |                 |               | 1.93 |
| COV of mean tuber size per plant (%)  | Healthy Welsh      | 8.5          | 10.0          | 8.3             | 9.9           | 9.2  |
|                                       | Diseased Welsh     | 12.4         | 11.0          | 12.6            | 11.6          | 11.9 |
|                                       | Diseased Wiltshire | 11.8         | 15.0          | 9.2             | 20.3          | 14.1 |
|                                       | S.E.               |              | 1.62          |                 |               | 0.81 |

Variation in the number of stems per plant explained *c.* 25 % of the variation in the number of tubers per plant in each stock and there was no significant difference in the correlation coefficients of the relationships between stocks or fungicide treatments (Table 113).

Variation in yield per plant explained *c.* 30 % of the variation in the number of tubers per plant and treatments had no significant effect on the correlation coefficients (Table 113).

Multiple linear regressions combining yield and the number of tubers explained *c.* 50 % of the variation in mean tuber size per plant but there were no significant effects of any of treatments on the correlation coefficients (Table 113). Variation in the COV of yield per plant explained less of the variation in COV of tuber size in comparison to variation in the COV of mean tuber size per plant (Figure 87). These results are in contrast to those of Expt 4 in the current

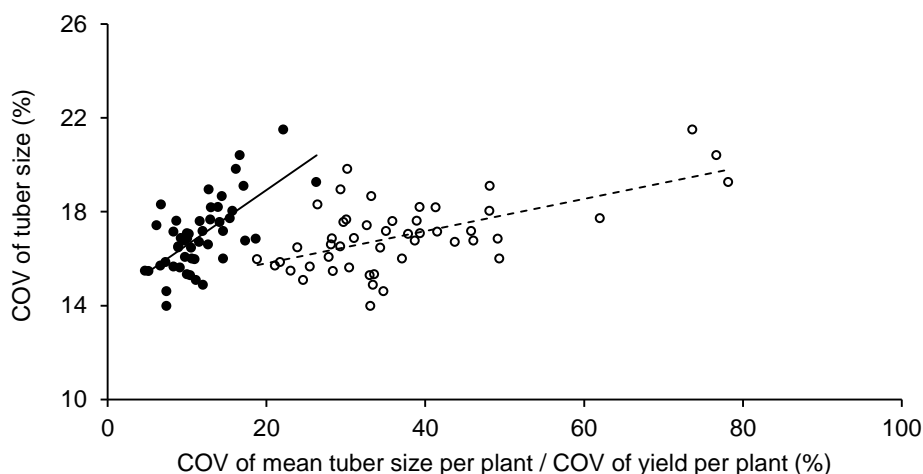


work in which increasing variation in seed tuber weight increased variation in yield per plant and the number of tubers per plant but also increased the correlation coefficient of the relationship between yield per plant and number of tubers per plant and had no effect on the COV of tuber size.

**Table 113. Effects of seed tuber stock, azoxystrobin and pencycuron treatment on average correlation coefficients of relationships between number of stems per plant (SN) and number of tubers per plant (TN), between yield per plant (YD) and TN, and between YD, TN and mean tuber size per plant (MTS) based on the data of Firman & Shearman (2006). There were no significant main effects between the treatments. S.E. based on 33 D.F.**

| Relationship | Stock              | Azoxystrobin |               | No azoxystrobin |               | Mean  |
|--------------|--------------------|--------------|---------------|-----------------|---------------|-------|
|              |                    | Pencycuron   | No pencycuron | Pencycuron      | No pencycuron |       |
| SN ~ TN      | Healthy Welsh      | 0.13         | 0.18          | 0.27            | 0.41          | 0.25  |
|              | Diseased Welsh     | 0.17         | 0.34          | 0.19            | 0.19          | 0.23  |
|              | Diseased Wiltshire | 0.44         | 0.39          | 0.24            | 0.01          | 0.27  |
|              | S.E.               |              | 0.107         |                 |               | 0.053 |
| YD ~ TN      | Healthy Welsh      | 0.34         | 0.27          | 0.20            | 0.32          | 0.28  |
|              | Diseased Welsh     | 0.28         | 0.53          | 0.22            | 0.34          | 0.34  |
|              | Diseased Wiltshire | 0.25         | 0.45          | 0.39            | 0.37          | 0.36  |
|              | S.E.               |              | 0.106         |                 |               | 0.053 |
| YD, TN ~ MTS | Healthy Welsh      | 0.40         | 0.55          | 0.69            | 0.44          | 0.52  |
|              | Diseased Welsh     | 0.59         | 0.59          | 0.56            | 0.51          | 0.56  |
|              | Diseased Wiltshire | 0.49         | 0.68          | 0.53            | 0.39          | 0.52  |
|              | S.E.               |              | 0.102         |                 |               | 0.051 |

**Figure 87. Relationships between the COV of mean tuber size per plant (MTSCOV) and the COV of tuber size (TSCOV) and the COV of yield per plant (YDCOV) and the COV of tuber size. COV of mean tuber size per plant, ●; COV of yield per plant, ○. Fitted lines: MTSCOV (—),  $TSCOV = 0.234 (\pm 0.0395) \times MTSCOV + 14.24 (\pm 0.492)$ ,  $R^2 = 0.42$ ; YDCOV (- - -),  $TSCOV = 0.068 (\pm 0.0134) \times YDCOV + 14.44 (\pm 0.528)$ ,  $R^2 = 0.35$ .**

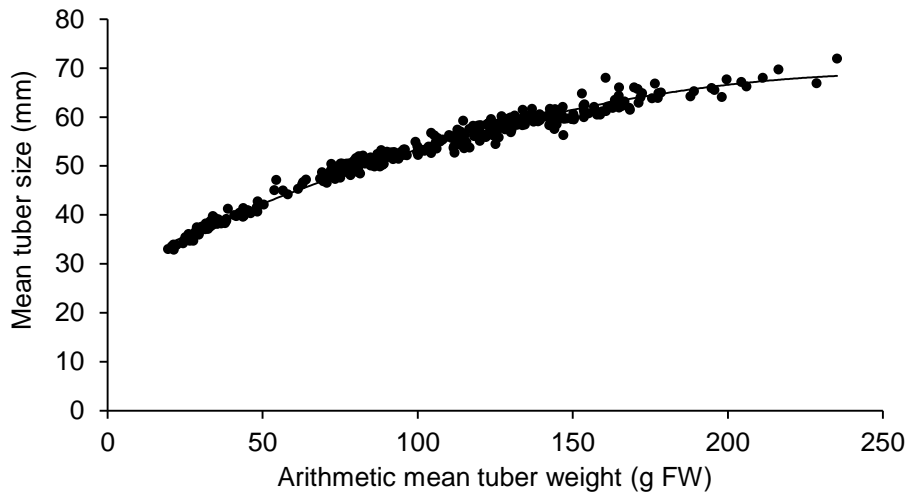


#### 4.17. Meta-analysis

##### 4.17.1. Average tuber weight and mean tuber size

The grading data for all the multiple plant samples of Maris Piper examined in this work were combined and for each sample the arithmetic mean tuber weight was calculated and the relationship between this and the mean tuber size established. A large proportion of the variation in mean tuber size was explained, but as the arithmetic mean tuber weight increased, it increased the mean tuber size by a proportionally smaller amount (Figure 88).

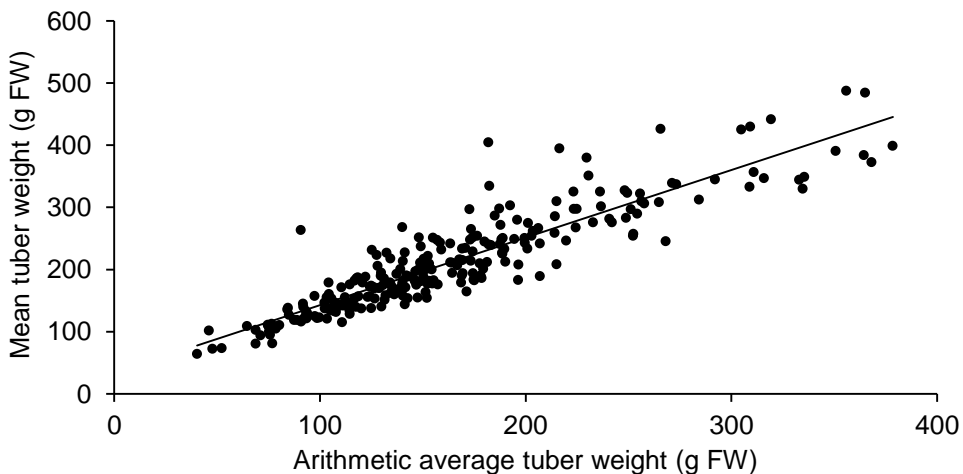
**Figure 88. Relationship between the arithmetic mean tuber weight (AMTW) and the mean tuber size (MTS) for crops of Maris Piper.  $MTS = 77.01 (\pm 0.975) + (-50.57 (\pm 0.737)) \times (0.99339 (\pm 0.000304))^{AMTW}$   $R^2 = 0.98$ .**



#### 4.17.2. Mean tuber weight

The relationship between the arithmetic mean tuber weight per plant and the mean tuber weight per plant was calculated for the final harvests of Surveys 2, 3c and Maris Piper in Survey 4. Unsurprisingly there was a strong correlation between the variables, but there was also considerable variation in the mean tuber weight amongst plants with similar arithmetic mean tuber weights (Figure 89). There were no significant differences in the relationship between the surveyed crops (data not shown).

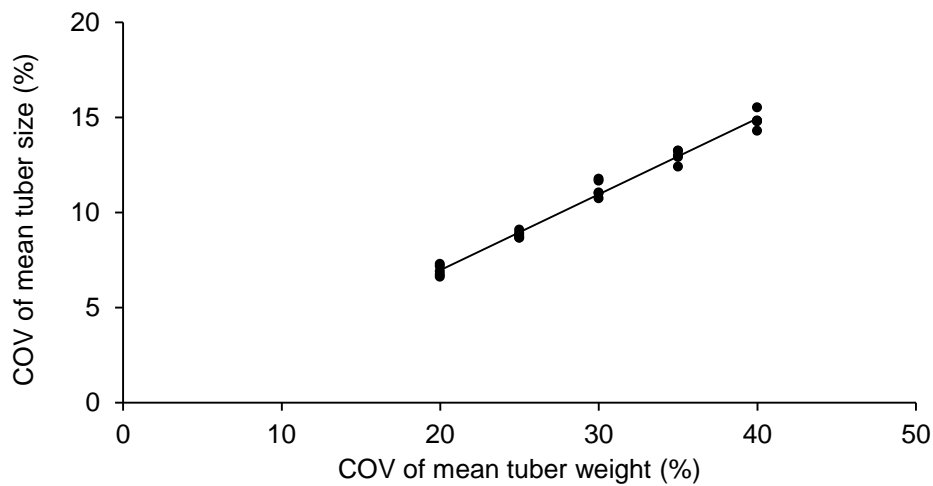
**Figure 89. Relationship between the arithmetic mean tuber weight per plant (AMTW) and the mean tuber weight per plant (MTW) at the final harvests of Surveys 2, 3c & 4.  $MTW = 1.088 (\pm 0.0325) \times AMTW + 33.9 (\pm 5.76)$   $R^2 = 0.82$ .**



#### 4.17.3. Variation in mean tuber weight and mean tuber size

Due to the non-linear relationship between tuber weight and tuber size, the COV of mean tuber weight per plant is greater than the COV of mean tuber size per plant. A simple model was used to establish the relationship between these variables across the range of mean tuber weights and COV of mean tuber weights encountered. The relationship was linear and there was a strong correlation between the variables (Figure 90). The relationship was unaffected by the mean tuber weight (data not shown).

**Figure 90. Relationship between the COV of mean tuber weight per plant (MTWCOV) and the COV of mean tuber size per plant (MTSCOV).  $MTSCOV = 0.399 (\pm 0.0103) \times MTWCOV - 1.01 (\pm 0.318)$ ,  $R^2 = 0.98$ .**



## 5. Modelling

Only a limited number of crops could be sampled in this work but modelling allows extrapolation from the results to suggest how other crops may behave. The tuber size distribution of a crop is composed of a mixture of distinct distributions, either of sections of crop, plants or stems. If the yield, mean tuber size and COV of tuber size of each part is known, then the parameters of the overall distribution can be calculated using the following equations where  $w_i$  is the proportion of the total yield,  $\mu_i$  is the mean tuber size and  $\sigma_i$  is the standard deviation of tuber size of each part (Fruhworth-Schattner 2006).

$$\mu = \sum_{i=1}^n \mu_i w_i$$

$$\sigma = \sqrt{\sum_{i=1}^n w_i (\mu_i^2 + \sigma_i^2) - \mu^2}$$

Although not applicable to all possible distributions, for tuber size distributions where there is substantial overlap between individual distributions, the resulting distribution is also normal. This modelling framework can be used to investigate how variation in tuber size at different scales contributes to the overall variation and to consider what the effect of variation in either the mean tuber size or the COV of tuber size between distinct components has on the overall distribution. One implication evident in this model is that the average COV of tuber size of each component part of the distribution must be less than the overall COV of tuber size and therefore the COV of tuber size per stem must be lower than either the COV per plant or per section of crop. By combining this approach with modelling the inter-relationships between other variables (e.g. yield, number of stems, number of tubers) it is possible to explore how the tuber size distribution may change in novel situations.

In this analysis, general properties of the tuber size distribution are discussed prior to considering the following questions:

- What effect may within-field variation have on uniformity?
- What is the average COV of tuber size per plant or stem?
- Is the COV of tuber size more sensitive to variation in yield per stem or number of stems per plant?
- What is the effect on uniformity of reducing variation in the yield per stem?
- What is the relative importance of variation in yield per stem, variation in number of tubers per stem and within-stem variation in tuber size on uniformity?

## 5.1. Properties of the tuber size distribution

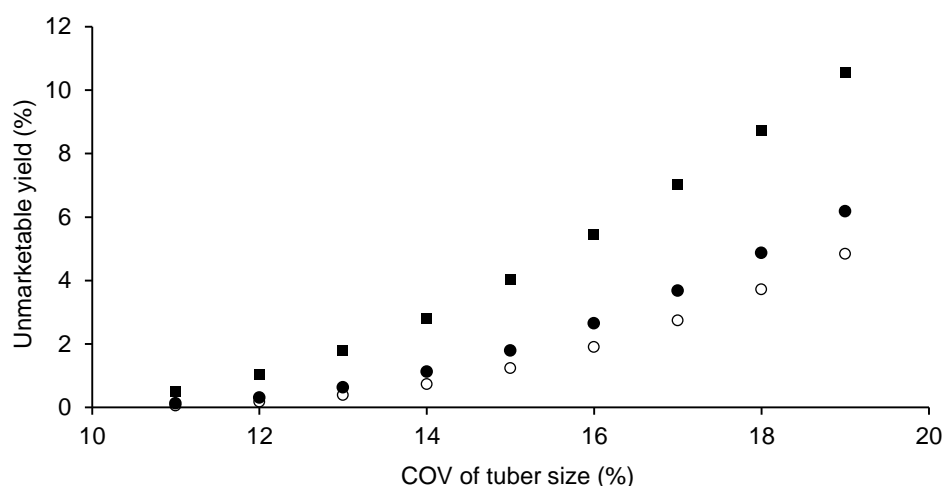
### 5.1.1. Optimal level of uniformity

Size specifications vary between markets and to achieve the optimum marketable yield, the mean tuber size should be at the centre of the specified range (Table 114). Ideally, the COV of tuber size would be sufficiently low for the entire yield to be marketable, but this is probably unrealistic. Arbitrarily, if we assume that producing 98 % of yield within specification is sufficient, the COV at which this is achieved can be calculated.

**Table 114. Example tuber size specifications for different markets.**

| Market | Lower bound (mm) | Upper bound (mm) | Optimum mean tuber size (mm) |
|--------|------------------|------------------|------------------------------|
| Salad  | 20               | 42               | 31                           |
| Seed   | 25               | 55               | 40                           |
| Ware   | 45               | 85               | 65                           |

**Figure 91. Modelled effect of the COV on the percentage of unmarketable yield for salad (●), seed (○) and ware (■) crops.**



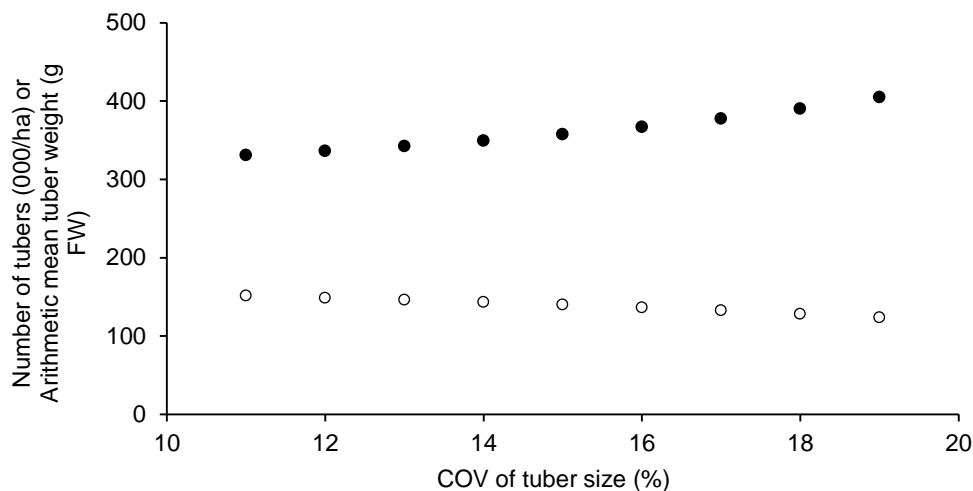
This model showed that ware crops require the lowest COV of tuber size (*c.* 13 %) to achieve optimum uniformity whereas salad and seed crops are more tolerant (*c.* 15 and 16 % respectively). For salad crops, controlling the mean tuber size is of greater importance because the relationship between the arithmetic mean tuber weight and mean tuber size results in the mean tuber size changing comparatively quickly around the optimum mean tuber size as yield develops (Figure 88).

#### 5.1.2. Uniformity and the number of tubers

A phenomenon that has not been noted previously is that more uniform crops allow for a given mean tuber size to be achieved with fewer tubers than less uniform crops. In the example given in Figure 92, a crop with a COV of tuber size of 11 % would require *c.* 70,000 fewer tubers per hectare to achieve the same mean tuber size than a crop with a COV of tuber size of 19 %. The reason for this is that non-uniform crops contain more small tubers which contribute a relatively small proportion of the total yield. Consequently, improving uniformity would not only increase the marketable yield, but also improve the efficiency of the use of seed tubers by permitting lower seed rates. This model also reveals that more uniform crops have a higher arithmetic mean tuber weight than less uniform crops with the

same mean tuber weight and this could provide a method to quantify variation in tuber size in small samples.

**Figure 92. Modelled effect of the COV of tuber size on the number of tubers per hectare (●) and the arithmetic mean tuber weight (○) for a crop with a yield of 50 t/ha and a mean tuber size of 55 mm.**



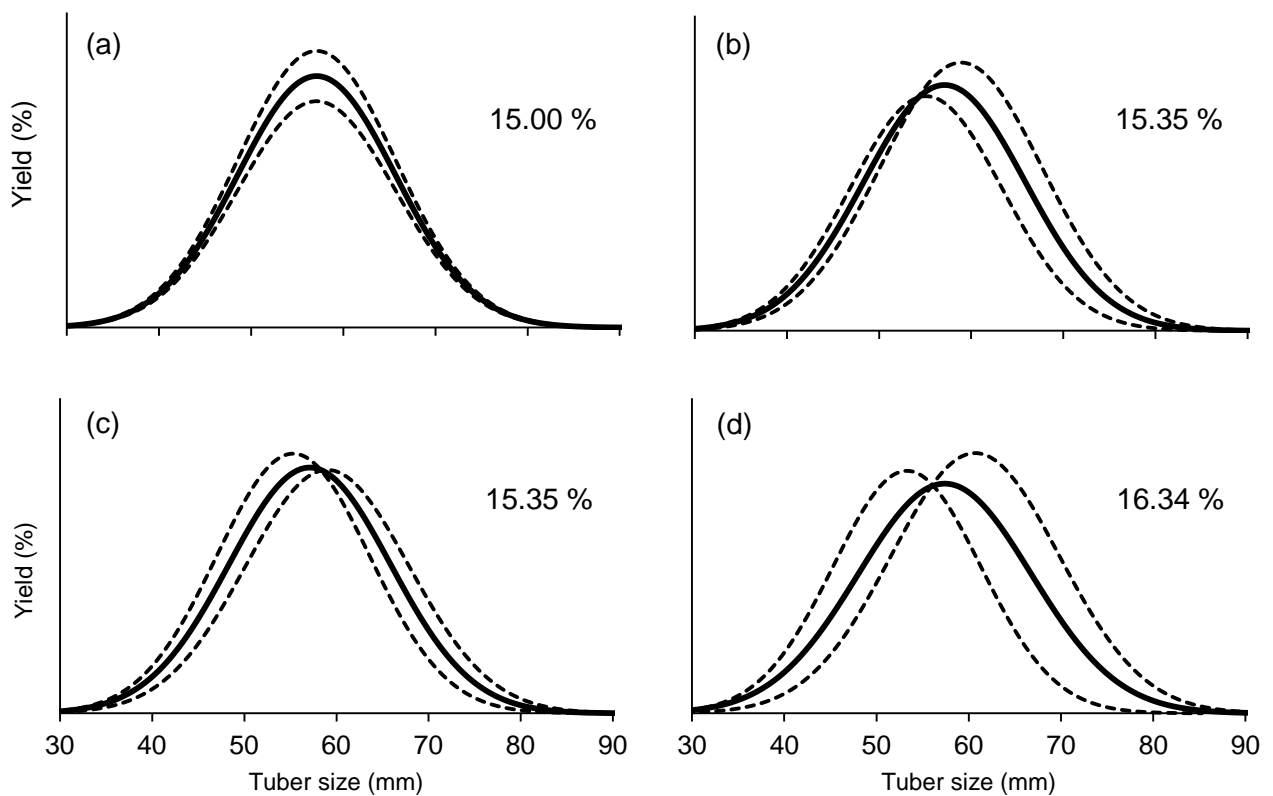
## 5.2. Within-field variation

The effect of variation in yield and number of tubers on the COV of tuber size can be modelled by combining tuber size distributions as a mixed distribution. Where yield and the number of tubers differ from the mean in two contrasting parts of a field, the effect on the COV of tuber size of the overall crop can be modelled. In this simplistic scenario, the extent of variation in both yield and number of tubers was chosen to be  $\pm 10\%$  of the mean, as this was similar to the extent of variation encountered within fields by Stalham & Allison (2014) and Stalham (2015). It is assumed that the COV of tuber size was equal in each section of the crop. If the number of tubers varies in proportion to the yield, the mean tuber size will not vary and thus the COV of tuber size will be identical to that in each section (Figure 93a). If only either the number of tubers or yield varies, while the other factor remains equal, the mean tuber size will vary between sections. However, these variations only have a small influence on the COV of tuber size, partly because  $\sigma$  varies as the mean tuber size varies. If the yield varies, the relative contribution of each location to the overall tuber size distribution varies, reducing any net effect on the tuber size distribution. Consequently, the COV of tuber



size of the overall crop is only slightly higher than in each section (Figs 93b and 93c). If the number of tubers decreases as the yield increases, then the variation in the mean tuber size is greater than in the previous scenarios and the COV of tuber size is increased to a greater extent (Figure 93d). These models are an oversimplification of the variation that occurs within crops, but they demonstrate that some variation in the yield and number of tubers within crops is tolerable and has a limited effect on uniformity.

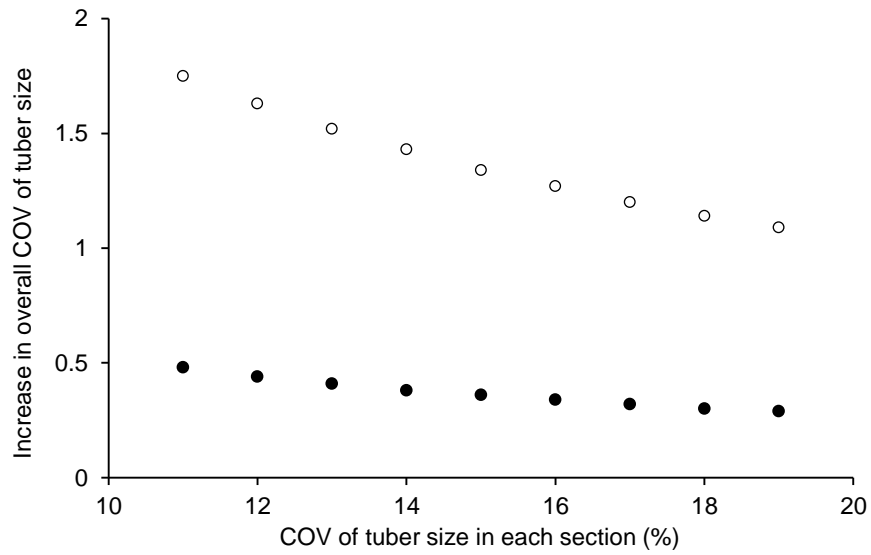
**Figure 93. Modelled effect of variations in the number of tubers (TN) and yield (YD) within a crop on the COV of tuber size. (a) TN varies in proportion to YD; (b) YD varies, TN is equal; (c) TN varies, YD is equal; (d) TN decreases as YD increases. The solid line represents the overall tuber size distribution of crops with a yield of 60 t/ha and containing 500,000 tubers/ha, resulting in a mean tuber size of *c.* 57 mm and different COVs of tuber size. The dashed lines represent the tuber size distributions of sections of crop with  $\pm 10\%$  differences in the yield and or number of tubers and each with a COV of tuber size of 15%. The overall COV of tuber size for the overall crop is shown in each panel.**



The importance of within-field variation to overall uniformity depends on the COV of tuber size in each section (i.e. that caused by variation at or below the plant level). If the COV of tuber size is low in each section, then within-field variation in the yield and number of tubers

has a relatively large effect on the overall COV of tuber size compared to if variation in each section is high (Figure 94).

**Figure 94. Modelled effect of differences in the COV of tuber size in sections of crop on the overall COV of tuber size. The models are as in Figure 93 but only presented for scenarios (c, ●) and (d, ○) as the overall COV did not change in scenario (a) and the change was identical in scenarios (b) and (c).**



### 5.3. Plant-to-plant variation

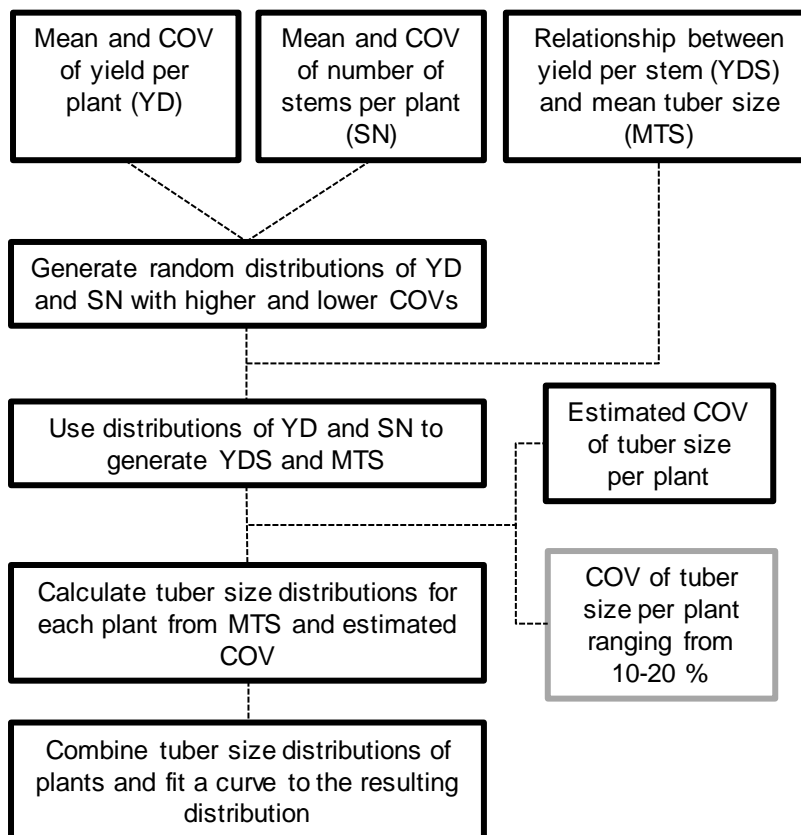
#### 5.3.1. Sensitivity of the COV of tuber size to variation in the number of stems and yield per plant

In Survey 3c there was no correlation between the number of stems and yield per plant and both of these variables were normally distributed (as determined by a Shapiro-Wilk test) so the crop was ideally suited to modelling effects of changing the COV of yield per plant and the COV of the number of stems per plant on the COV of tuber size. Random distributions of the number of stems per plant and yield per plant were generated using the observed values from the third harvest (Table 48). The yield per stem was then calculated from these random values and subsequently the mean tuber size, from the relationship in Figure 51, assuming that the mean tuber size was equal to ten times the cube root of the mean tuber weight.

An estimate of the average COV of tuber size for individual plants was calculated by examining how the overall COV of tuber size changed when COVs of tuber size from 10 to 20 % were used to generate tuber size distributions for individual plants, which were then combined. The best estimate (11 %) was considered to be the value that resulted in an overall COV of tuber size closest to that observed at the third harvest. While in practice the variation in tuber size varies between plants, this value was intended to be equivalent to the COV of tuber size if a large sample of plants with an equal yield per stem was harvested and graded.

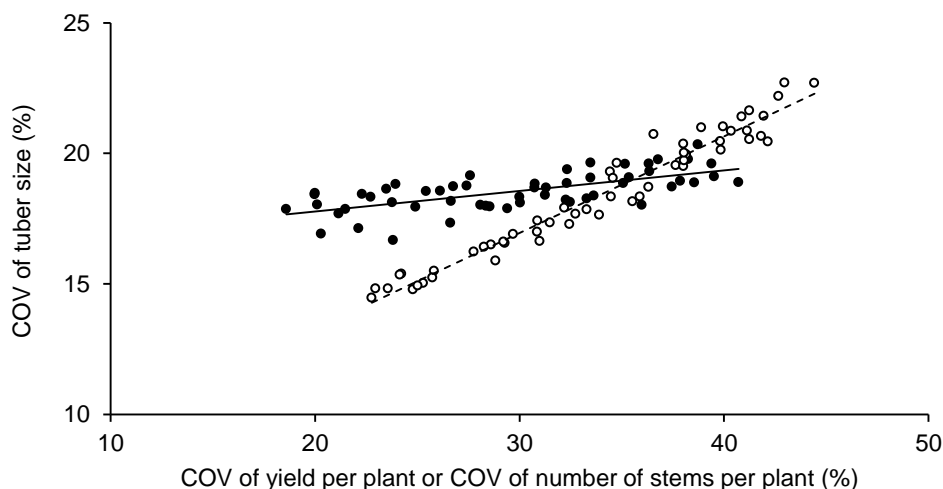
Random distributions of the number of stems per plant and yield per plant were generated with means equal to the observed values and COVs of 24-43 % for the number of stems per plant and 20-40 % for the yield per plant (i.e. 66-133 % of the observed COVs). Different levels of variation in either the number of stems per plant or yield per plant were used to calculate tuber size distributions in combination with a random distribution of the other variable with a COV equal to that observed. The variation in mean tuber size per plant was also calculated for each run of the model. A schematic of the process is shown in Figure 95.

**Figure 95. Schematic of the process used to predict the effect of changes in the COV of yield per plant and COV of the number of stems per plant in Survey 3c on the COV of tuber size. To estimate the COV of tuber size per plant, random distributions of yield per plant and number of stems per plant, equal to those observed were used, but with different values of the COV of tuber size per plant (grey box).**

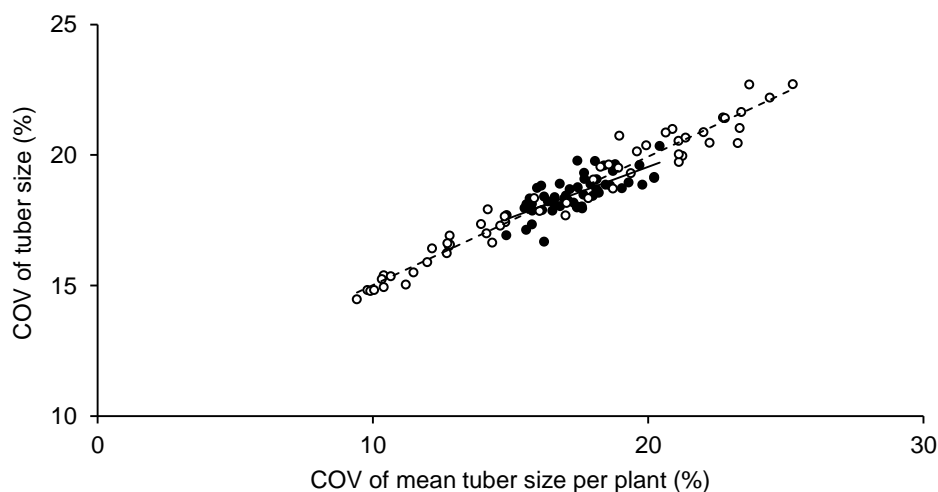


The model predicted that the COV of tuber size was more sensitive to changes in the COV of the number of stems per plant than the COV of yield per plant (Figure 96). Changing the COV of either variable resulted in changes in the COV of mean tuber size per plant and the COV of mean tuber size correlated strongly with the COV of tuber size (Figure 97). This suggests that in this crop, the variation in the number of stems per plant was a stronger cause of the variation in tuber size than variation in yield per plant and that differences in the number of stems per plant for those infected by *R. solani* probably increased the COV of tuber size.

**Figure 96. Modelled relationships between the COV of yield per plant (YDCOV) and the COV of the number of stems per plant (SNCOV) on the COV of tuber size (TSCOV). YDCOV, ●; SNCOV, ○. Fitted lines: YDCOV: —,  $TSCOV = 0.079 (\pm 0.0121) \times YDCOV + 16.20 (\pm 0.368)$ ,  $R^2 = 0.43$ . SNCOV: - - - -,  $TSCOV = 0.370 (\pm 0.0110) \times SNCOV + 5.87 (\pm 0.379)$ ,  $R^2 = 0.95$ .**



**Figure 97. Relationship between the COV of mean tuber size per plant (MTSCOV) and the COV of tuber size (TSCOV) for modelled crops with different levels of variation in yield per plant (YDCOV) or the number of stems per plant (SNCOV). YDCOV, ●; SNCOV, ○. Fitted lines: YDCOV: —,  $TSCOV = 0.389 (\pm 0.0498) \times MTSCOV + 11.77 (\pm 0.870)$ ,  $R^2 = 0.53$ . SNCOV: - - - -,  $TSCOV = 0.492 (\pm 0.0133) \times MTSCOV + 10.10 (\pm 0.233)$ ,  $R^2 = 0.96$ .**



#### 5.4. Stem-to-stem variation

##### 5.4.1. Sensitivity of the COV of tuber size to variation in the yield per stem

None of the treatments examined resulted in significant differences in the yield per stem so it was not possible to determine the influence of variation in the yield per stem on the COV of tuber size. The relationships between the yield per stem and the mean and maximum tuber

weights indicated that reducing variation in the yield per stem would reduce the COV of tuber size, but the extent of this could not be predicted.

#### 5.4.1.1. Survey 2

Although there were strong relationships between yield per stem and maximum and mean tuber weight per stem, these do not take account of the considerable variation in tuber weight that occurred on individual stems. To establish whether reducing variation in the yield of stems would reduce the COV of tuber size, stems were grouped together and the COV of tuber size was calculated for different groups. Stems were sorted by yield and split into four groups each consisting of *c.* 25 % of total yield. Tubers were assigned to size grades assuming that their size was equivalent to ten times the cubic root of their weight. Mean tuber size was calculated for each group of stems and the COV of tuber size was calculated for all stems and for stems which produced the central quartiles of the yield and also for the group containing 16-84 % of the yield.

The mean tuber size of the group of stems producing the lower quartile of the total yield was *c.* 22 % lower than that of the group of stems producing the highest quartile of yield at the seventh and ninth harvests (Table 115). The COV of tuber size obtained from allocating tubers to size grades according to their weight differed slightly from the values obtained from grading tubers (Tables 36 & 115). Excluding the tubers from the lowest and highest yielding stems within the crop reduced the COV of tuber size at the seventh and ninth harvests (Table 115). While excluding the lowest and highest 25 % of yield reduced the COV of tuber size by 2.5-3 %, excluding only the lowest and highest 16 % of yield also reduced the COV of tuber size by 1.7-2.4 % (Table 115).

**Table 115. Mean tuber size of stems producing each quartile of yield and the COV of tuber size for all stems and the central quartiles at the seventh and ninth harvests of Survey 2.**

|   | Harvest |      |
|---|---------|------|
|   | 7       | 9    |
| Mean tuber size of stems producing 1 <sup>st</sup> quartile of yield (mm)                       | 47.1    | 54.6 |
| Mean tuber size of stems producing 2 <sup>nd</sup> quartile of yield (mm)                       | 52.5    | 62.4 |
| Mean tuber size of stems producing 3 <sup>rd</sup> quartile of yield (mm)                       | 56.7    | 66.1 |
| Mean tuber size of stems producing 4 <sup>th</sup> quartile of yield (mm)                       | 60.6    | 71.6 |
| COV of tuber size of all stems (%)  | 16.2    | 17.4 |
| COV of tuber size of stems producing 16-84 % of yield (%)                                       | 14.5    | 15.0 |
| COV of tuber size of stems producing 2 <sup>nd</sup> and 3 <sup>rd</sup> quartiles of yield (%) | 13.7    | 14.4 |

#### 5.4.1.2. Survey 4

The mean tuber size of groups containing lower yielding stems was consistently lower than that of the groups containing higher yielding stems (Table 116). At the fifth harvest the difference in the mean tuber size of the lowest and highest quartiles ranged from 12-17 mm. The COV of tuber size of all stems was higher than the value obtained from grading the tubers indicating that differences in tuber shape prevented accurate description of the tuber size distribution from the tuber weight distribution (Tables 97 & 116). Decreasing variation in yield per stem by only including those that produced 25-75 % of yield reduced the COV of tuber size in all varieties at both harvests (Table 116). The reduction in the COV of tuber size was relatively small in Maris Piper and was associated with relatively small differences in the mean tuber size of the quartiles (Table 116). These results indicate that reducing variation in the yield per stem would improve uniformity, but the magnitude of the change would depend on how the number of tubers per stem varied with yield per stem.

**Table 116. Mean tuber size of stems producing each quartile of yield and the COV of tuber size for all stems and the central quartiles at the fourth and fifth harvests of Survey 4.**

|  | Harvest | Maris Piper | Desiree | Russet<br>Burbank | King Edward |
|--|---------|-------------|---------|-------------------|-------------|
| Mean tuber size of stems producing                         | 4       | 36.0        | 37.7    | 36.2              | 32.3        |
| 1 <sup>st</sup> quartile of yield (mm)                     | 5       | 56.4        | 52.7    | 53.5              | 48.2        |
| Mean tuber size of stems producing                         | 4       | 38.2        | 43.1    | 38.7              | 35.6        |
| 2 <sup>nd</sup> quartile of yield (mm)                     | 5       | 61.8        | 59.2    | 59.2              | 55.9        |
| Mean tuber size of stems producing                         | 4       | 39.8        | 45.6    | 40.9              | 38.0        |
| 3 <sup>rd</sup> quartile of yield (mm)                     | 5       | 64.2        | 63.9    | 63.5              | 58.1        |
| Mean tuber size of stems producing                         | 4       | 42.4        | 48.8    | 42.7              | 40.5        |
| 4 <sup>th</sup> quartile of yield (mm)                     | 5       | 68.9        | 69.4    | 69.4              | 62.6        |
| COV of tuber size of all stems (%)                         | 4       | 14.7        | 15.2    | 14.4              | 18.2        |
|  | 5       | 17.0        | 18.3    | 17.4              | 19.1        |
| COV of tuber size of stems                                 | 4       | 13.7        | 11.9    | 12.9              | 15.3        |
| producing 2 <sup>nd</sup> and 3 <sup>rd</sup> quartiles of | 5       | 15.9        | 14.0    | 13.7              | 15.9        |
| yield (%)  |         |             |         |                   |             |

#### 5.4.2. Within-stem variation in tuber size

##### 5.4.2.1. Survey 2

An implication of the tuber size distribution being comprised of numerous discrete distributions, for each of which the mean is known, is that the average COV of tuber size per stem can be estimated, as for plants in Section 5.3.1. As in the previous analysis, the COV of tuber size was calculated from tuber weights assuming that all tubers were the same shape. The COV of tuber size per stem was relatively stable from harvests 4 to 7 but had increased slightly by the final harvest (Table 117).

**Table 117. Estimated COV of tuber size per stem in Survey 2.**

|                                | Harvest |      |      |      |      |
|--------------------------------|---------|------|------|------|------|
|                                | 4       | 5    | 6    | 7    | 9    |
| Overall COV of tuber size (%)  | 19.0    | 16.3 | 16.3 | 16.5 | 18.0 |
| COV of tuber size per stem (%) | 11.8    | 11.5 | 11.3 | 10.9 | 12.7 |

##### 5.4.2.2. Survey 4

The estimated variation in tuber size per stem was similar in all varieties except King Edward in which it was higher and in all varieties it was higher at the fifth harvest than at the fourth harvest suggesting that the growth rates of tubers differed between harvests (Table 118).

Across the two harvests the average ratio between the arithmetic mean tuber weight and mean tuber weight and the estimated COV of tuber size per stem were strongly correlated



( $R^2 = 0.81$ ; data not shown). This was consistent with the model presented in Section 5.1.2 and suggests that this metric could be used to quantify variation in tuber size per stem in future work. In Maris Piper, the values were similar to those in Survey 2 at similar times after emergence (Table 117).

**Table 118. Estimated COV of tuber size per stem and the average ratio between the arithmetic mean tuber weight and mean tuber weight per stem at harvests 4 and 5 of Survey 4.**

|   | Harvest | Maris Piper | Desiree | Russet<br>Burbank | King Edward |
|---|---------|-------------|---------|-------------------|-------------|
| Estimated COV of tuber size per stem (%)            | 4       | 10.9        | 9.4     | 10.4              | 12.9        |
|   | 5       | 12.6        | 12.4    | 11.1              | 14.8        |
| Arithmetic mean tuber weight :<br>mean tuber weight | 4       | 0.854       | 0.879   | 0.854             | 0.811       |
|   | 5       | 0.835       | 0.857   | 0.859             | 0.751       |

To examine the effect on uniformity of the high variation in the weight of tubers on individual stems observed, the tuber size distributions were modelled for each variety in Survey 4. Each modelled stem had the same yield and number of tubers as observed, but each tuber on the stem was assumed to be of identical size and weight. The mean tuber size was reduced in each of the varieties because the mean tuber weight per stem was greater than the arithmetic mean tuber weight per stem, due to the mean tuber weight decreasing the influence of small tubers on the value compared to the arithmetic mean (Table 119). The COV of tuber size was substantially reduced in Maris Piper and King Edward, but less so in Desiree (Table 119). At the fourth harvest, the COV of tuber size was reduced in Russet Burbank, but at the fifth harvest, the decrease was modest in comparison to other varieties (Table 119).

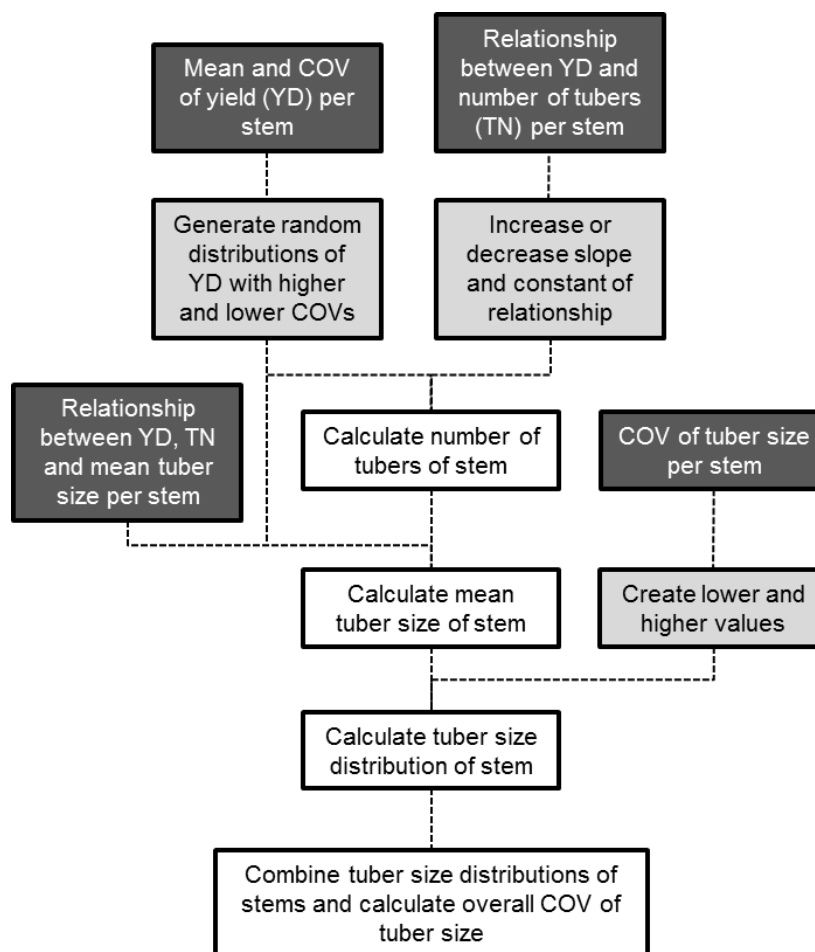
**Table 119. Observed and estimated mean tuber size and COV of tuber size assuming all tubers on each stem to be the same size at the fourth and fifth harvests of Survey 4.**

|                                 | Harvest | Maris Piper | Desiree | Russet<br>Burbank | King Edward |
|---------------------------------|---------|-------------|---------|-------------------|-------------|
| Observed mean tuber size (mm)   | 4       | 39.2        | 43.7    | 39.8              | 36.7        |
|                                 | 5       | 58.3        | 61.5    | 62.5              | 51.5        |
| Estimated mean tuber size (mm)  | 4       | 36.6        | 41.2    | 37.6              | 33.7        |
|                                 | 5       | 53.7        | 57.9    | 58.2              | 45.8        |
| Observed COV of tuber size (%)  | 4       | 14.7        | 15.2    | 14.4              | 18.2        |
|                                 | 5       | 17.0        | 18.3    | 17.4              | 19.1        |
| Estimated COV of tuber size (%) | 4       | 9.6         | 11.8    | 10.8              | 11.7        |
|                                 | 5       | 10.4        | 12.4    | 14.5              | 11.0        |

#### 5.4.3. Sensitivity of the COV of tuber size to different sources of variation

Three determinants of uniformity related to stem-to-stem variation are variation in yield per stem, the relationship between yield and number of tubers per stem, and the COV of tuber size per stem. To predict which of these may be most influential on uniformity, a model was created using data from the final harvest of Survey 4. A schematic of the process performed for each variety is shown in Figure 98. Inputs for the model were the distribution of yield per stem, the relationships between yield and number of tubers per stem and between yield, number of tubers and mean tuber size, and the within stem variation in tuber size (as estimated in Section 5.4.2.2). Different levels of the COV of yield per stem and the COV of within-stem variation in tuber size were created ranging from 66-133 % of the observed values. The slope of the relationship between yield and number of tubers per stem was altered to create a range from 50-200 % of the observed value and the constant was changed accordingly so as not to alter the mean number of tubers per stem. The tuber size distribution of 200 stems was modelled for each combination of the different sources of variation and combined to calculate the overall tuber size distribution. The model was run ten times and the average results were plotted using the ‘interp’ and ‘image.plot’ routines of the ‘fields’ package of R (Nychka *et al.* 2016).

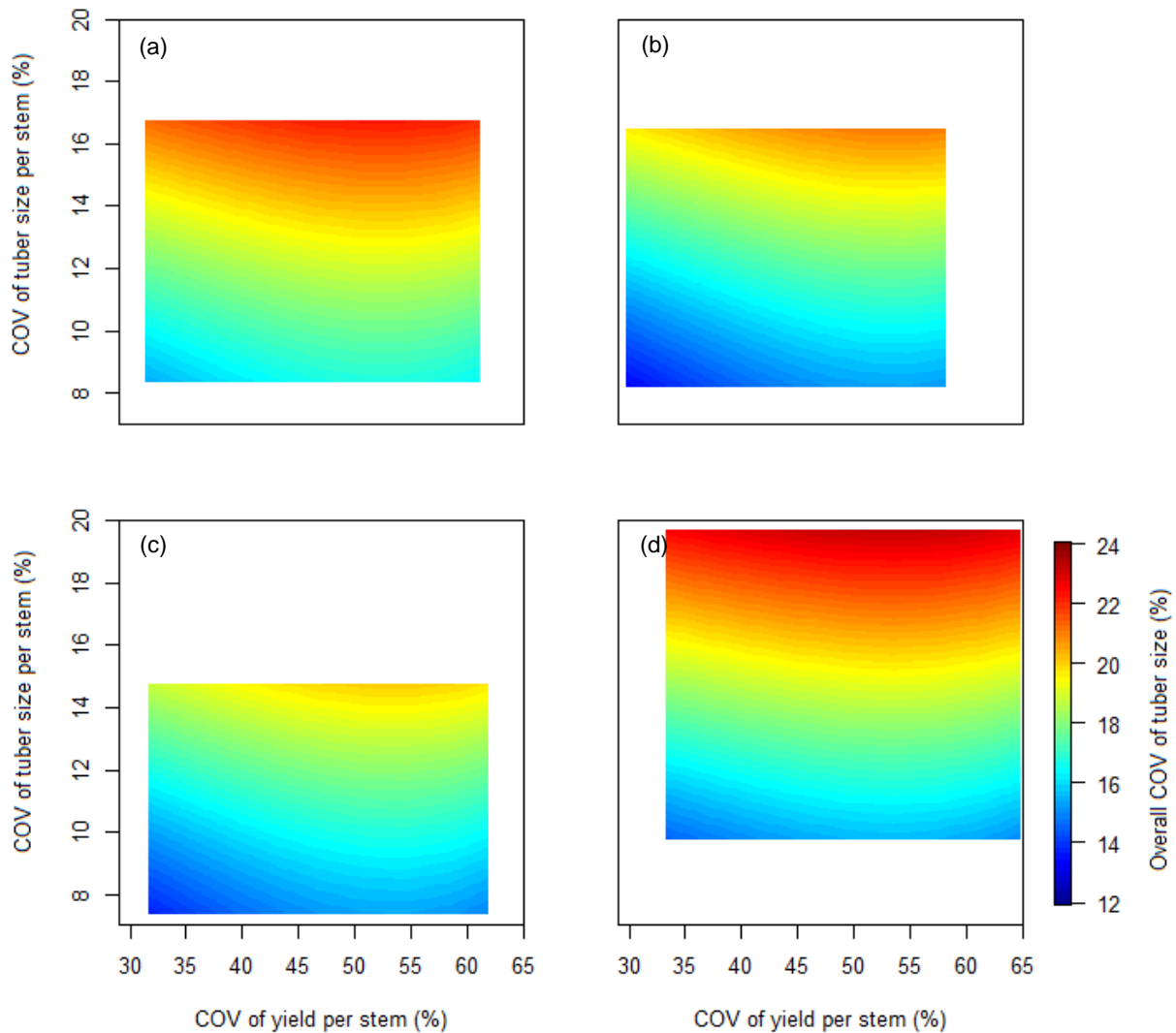
**Figure 98. Schematic of stem-to-stem COV sensitivity model. Inputs to the model are dark grey boxes, modifications to the inputs are light grey boxes and the modelled components are white boxes. See text for details of the modifications made to each input.**



In all varieties, the overall COV of tuber size was most sensitive to changes in the COV of tuber size per stem (Figure 99). Unexpectedly, the overall COV of tuber size decreased above a particular COV of yield per stem (Figure 99). This was associated with an increase in the mean tuber size as the COV of yield per stem increased due to larger stems contributing a greater proportion of the total yield (Figure 100). Consistent with the results of the simple models presented in Table 116, the overall COV of tuber size was more sensitive to variation in the yield per stem in Desiree and Russet Burbank than in Maris Piper and King Edward (Figure 100) as a result of the different relationships between yield and number of tubers per stem. For example, at the observed level of variation in within-stem variation in tuber size, changing the COV of yield per stem caused a maximum change in the overall COV of tuber size of 1.67 and 1.45 % in Desiree and Russet Burbank, but 1.18 and 0.88 % in Maris Piper

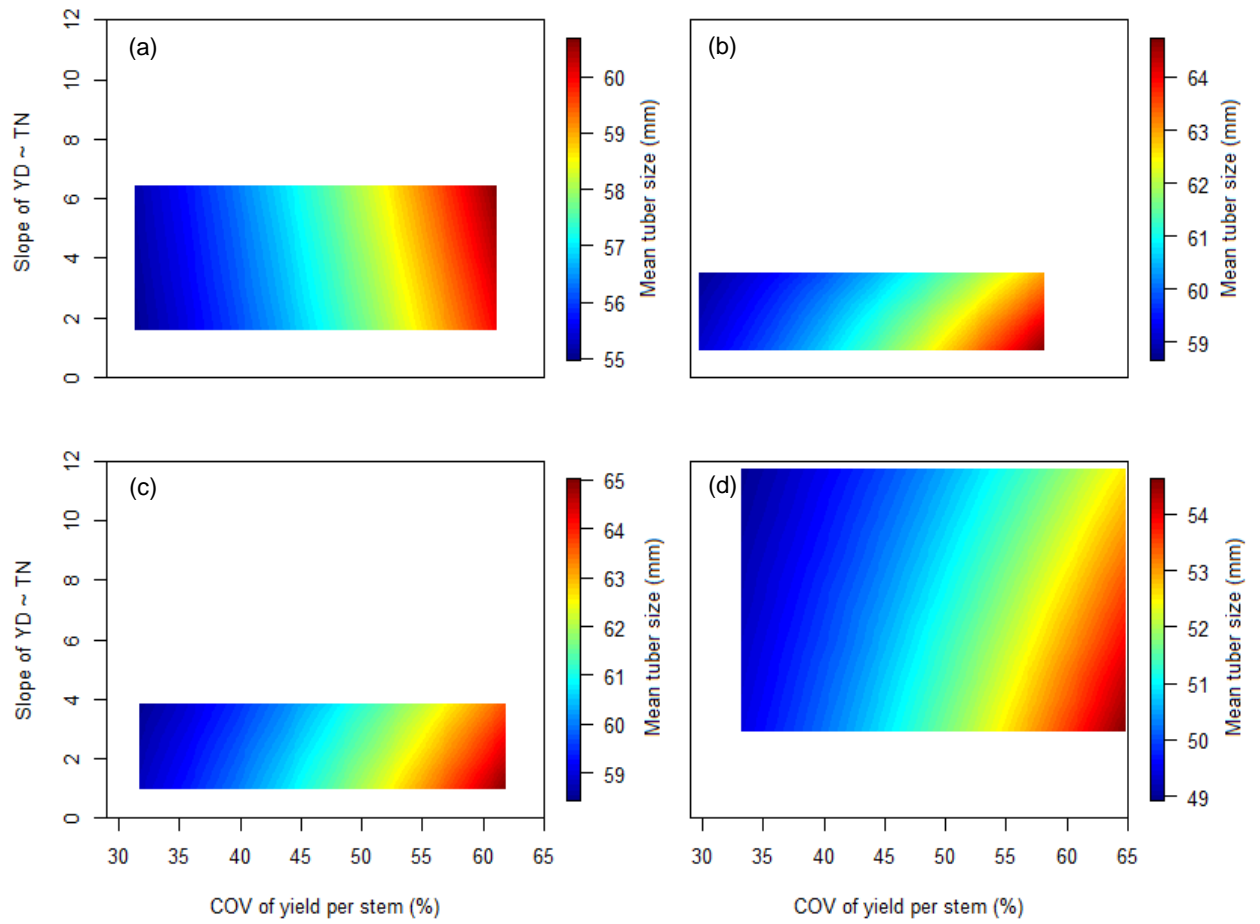
and King Edward respectively. Altering the COV of tuber size per stem had no effect on the mean tuber size (data not shown).

**Figure 99. Modelled effect of variation in the COV of tuber size per stem and the COV of yield per stem on the overall COV of tuber size for (a) Maris Piper; (b) Desiree; (c) Russet Burbank; (d) King Edward.**



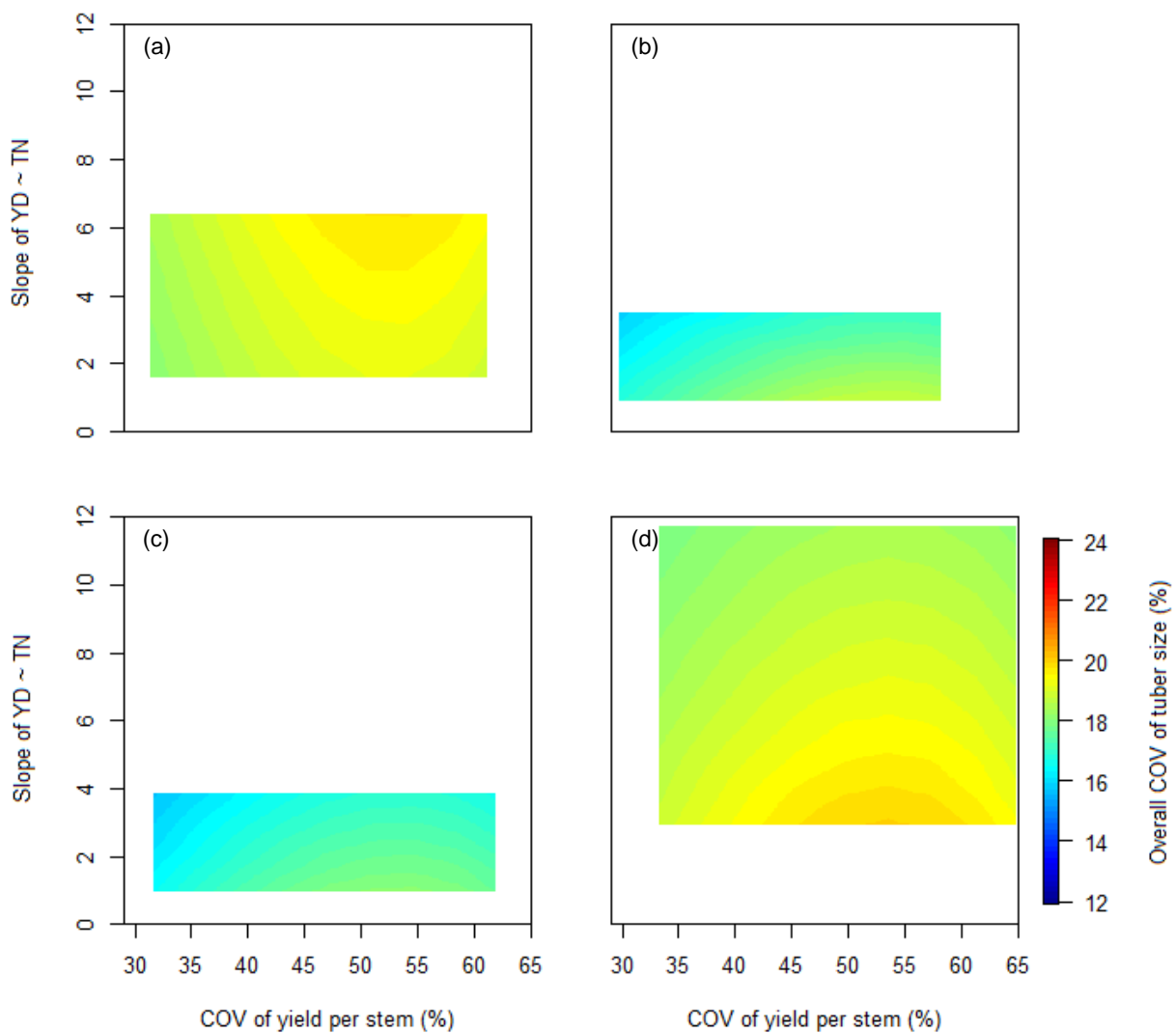
The effect of the COV of yield per stem on mean tuber size predicts that if the COV of yield per stem could be reduced, the seed rate required to achieve a given yield and mean tuber size could be reduced because fewer stems would be required to produce the same number of tubers. This is consistent with the model presented in 5.1.2 that showed that more uniform crops require fewer tubers to achieve the same mean tuber size and provides further incentives to improve uniformity.

**Figure 100. Modelled effect of the slope of the relationship between yield and number of tubers per stem and the COV of yield per stem on mean tuber size for (a) Maris Piper; (b) Desiree; (c) Russet Burbank; (d) King Edward.**



Changing the slope of the relationship between yield and number of tubers per stem had a small influence on the COV of tuber size in all varieties (Figure 101). Modelling changes to these relationships was more complex than for the other factors and the small response may be because the mean number of tubers per stem and the residual of the relationships in the model were kept equal to those observed. The direction of the change was as expected in all varieties except Maris Piper for which increases in the slope of the relationship reduced the overall COV of tuber size and the reason for this difference is unclear.

**Figure 101. Modelled effect of variation in the slope of the relationship between yield and number of tubers per stem and the COV of yield per stem on the overall COV of tuber size for (a) Maris Piper; (b) Desiree; (c) Russet Burbank; (d) King Edward.**



## 6. Discussion

A high level of uniformity has been used informally to describe potato crops with a high yield of marketable sized tubers (Wurr 1992; Wurr *et al.* 1993). While of direct importance to the grower, this does not distinguish between a high total yield, an optimal mean tuber size or low variation in tuber size. As discussed in Sections 2.1 & 2.3, the mechanisms determining the yield and mean tuber size of crops are well understood allowing these to be predicted and manipulated. This work is concerned with establishing the mechanisms that determine variation in tuber size, quantified as the COV of tuber size (Travis 1987; Wurr *et al.* 1993). The advantage of this approach is that variation in tuber size can be studied independently of the yield and mean tuber size of the crop. The distinct levels at which variation in tuber size occurs within the crop will be considered separately prior to evaluating the relative importance of each.

### 6.1. Levels of variation in tuber size

Variation in tuber size occurs at multiple levels within potato crops from variation between sections of the crop, to variation on individual stems (Figure 1). The overall variability present in a crop is the sum of the combined variation at each level and variation at each level is affected by multiple factors. Variation in mean tuber size occurs between sections of crop, individual plants and individual stems and at each level this variation is the result of variation in the yield and number of tubers. To understand the causes of variation in tuber size in the overall crop it is necessary to establish the relative extent of variation in tuber size at each of these levels and the causes of variation at each level.

### 6.2. Within-field variation

With the exception of Surveys 3a & 3b the current work did not examine the extent or causes of within-field variation in mean tuber size. Ware crops are typically only graded into

undersized, marketable and oversized tubers and consequently it is not possible to establish the COV of tuber size for these crops and compare them to hand-dug samples of the crop. Recent technological developments have allowed variation in yield to be mapped in commercial crops (see for example Clarke (2014) in the farming press) but currently data are not available to map variation in the number of tubers or tuber size which would be necessary to characterise variations in mean tuber size within the crop.

In Surveys 3a & 3b emergence occurred approximately one week later and ground cover developed more slowly on the heavy soil than on the light soil (Section 4.6.1). The combined effect of these differences was to reduce yield by *c.* 25 % on the heavy soil compared to the light soil (Table 43). Despite the plant populations not differing between the soil types, the number of stems was lower on the heavy soil at each harvest (Table 43) and across all harvests the number of stems was *c.* 15 % lower, indicating that the soil type affected the number of stems per seed tuber. The differences in the number of stems contributed to the number of tubers also being *c.* 25 % lower on the heavy soil compared to on the light soil but there was an additional effect on the number of tubers per stem, which was lower on the heavy soil (Table 43). Mean tuber size was relatively unaffected by the soil type, as the differences in yield and the number of tubers were of a similar magnitude but at the third harvest, the heavy site had a mean tuber size *c.* 2 mm larger than the light site (Table 43). Stalham & Allison (2014) conducted a pair of cultivation experiments at Hales Hospital, the crop examined in Surveys 3a & 3b. They reported that emergence was also delayed by *c.* 1 week and the yield and number of tubers reduced on the heavier soil compared to the lighter soil, but the differences were smaller than those observed in this work (*c.* 10 vs 25 %)

While it was not possible to establish the causes of the within-field variation found in Surveys 3a & 3b, the findings can be related to other work. The difference in emergence was probably the result of the heavier soil having a higher soil moisture content and thus a lower



temperature (Shukla 2008) which would be expected to delay emergence (Firman *et al.* 1992). Although Allaire *et al.* (2014) did not record emergence, they found yield increased as soil temperature one month after planting increased and this could have been due to later emergence in cooler soils. A similar difference could have been responsible for the difference in emergence and yield between Surveys 3a & 3b. Firman & Daniels (2011) observed that soil type and ped size affected both emergence and canopy development and similar effects may have slowed canopy expansion on the heavier soil, further reducing the yield.

The models presented in Section 5.2 demonstrate how the effect of variations in yield and the number of tubers within crops on their uniformity can be established. They demonstrate that small variations ( $\pm 10\%$ ) have relatively little effect on overall uniformity except where yield and the number of tubers are negatively correlated. This scenario is probably the least likely of the four scenarios presented in Figure 93 because generally, soil-related factors such as compaction or nitrogen availability that affect yield and number of tubers cause increases or decreases in both concurrently. The implication of these models is that variation that occurs at or below the plant level is of greater importance than within-field variation. While the models are a gross simplification of the variation in yield and number of tubers that occur within crops, the modelling framework presented could easily be applied to real datasets once these are available.

If consistent differences in mean tuber size were found to occur within crops, it would be possible to increase uniformity by altering the mean spacing to compensate as the technology already exists to do so (see Clarke 2014 in the farming press). Together the studies discussed in Section 2.5 demonstrate the difficulty of predicting the causes and extent of within-field variations as no consistent trends were observed between the studies and no single factor explained a substantial amount of the variation in the individual studies. It is surprising that studies of within-field variation have only quantified crop growth as the final yield and not

measured the date of emergence or canopy development despite these simple measurements being so crucial to our understanding of yield formation (Allen *et al.* 2001). It is probable that the factors that affect variation in date of emergence within different locations of the crop (as occurred in Survey 3a & 3b), will be different to those that affect canopy development, canopy persistence and allocation of photosynthate to the tubers. Consequently, it is unlikely that any single factor would explain the variation in yield within a crop. The use of unmanned aerial vehicles will expedite the collection of ground cover development within crops (Allison & Firman 2015) and assist in creating mechanistic models of within-field variation. However, at present the causes of within-field variation are too uncertain and unpredictable to be of practical use to growers and the extent of variation in the number of tubers and yield within crops is predicted to only cause small differences in the mean tuber size and not necessarily decrease uniformity.

### 6.3. Plant-to-plant variation

The plant-to-plant variation observed in this work was of a similar magnitude to that observed in the previous studies of Svensson (1966) and Silva & Andrew (1985). In crops grown from 10 mm graded seed tubers, the COVs of the number of stems per plant, yield per plant and number of tubers per plant were typically *c.* 30-40 %. Variation in seed tuber weight, date of emergence and within-row spacing were each found to affect plant-to-plant variation, but the effects were inconsistent between years and did not always result in a change in the overall uniformity of the crop. The causes of plant-to-plant variation will be considered prior to discussing how this variation affects the uniformity of the crop. The discussion will centre on the interactions between the factors and how variation in the mean tuber size per plant affects the COV of tuber size (Figure 102).



and demonstrate that the yield of individual plants is also the result of the quantity of solar radiation that the leaves intercepted.

The relationship between fresh weight of above-ground stems and yield per plant is dynamic because the overall growth of above-ground stems occurs independently of overall yield and is dependent on partitioning of dry matter between above-ground stems and tubers (Allen & Scott 1980; Allison *et al.* 2012). As the season progresses, the weight of the canopy peaks and declines as the canopy senesces, although overall yield continues to increase (Table 37; Scott & Wilcockson 1978). Thus, while it is not possible to state that a plant with any particular above-ground stem weight will have a certain yield, the plants within a section of crop with the highest above-ground stem weights are also likely to have the highest yields. The implication of these relationships is that the processes that ultimately determine plant-to-plant variation in yield begin immediately after emergence, when the above-ground stems begin to grow. Establishing the factors that affect the initial growth of plants is therefore necessary to understand why yield per plant varies.

### 6.3.2. Seed tuber weight

While seed tubers are unquestionably important to establishing the potato crop, the precise role of seed tuber substrate during the initial phases of growth is uncertain. Pre-emergence growth of sprouts is entirely dependent on seed tuber substrate and emergence marks the beginning of autotrophic growth of the plant. The uncertainty lies in determining the relative importance of the mobilisation of seed tuber substrate and photosynthesis in determining growth post-emergence.

At the vast majority of sampling dates where there was moderate variation in seed tuber weight (e.g. a 10 mm range in seed tuber size), yield per plant was positively correlated with seed tuber weight. In Expt 1 and Survey 2 (both conducted in 2013) however the relationships between seed tuber weight and yield explained only 10-20 % of the variation in

yield per plant (Tables 20 & 38) and altering the variation in seed tuber weight in Expt 1 did not have any effect on the COV of yield per plant (Table 19). In Survey 4, variation in seed tuber weight explained *c.* 60 % of the variation in yield per plant at the fourth harvest in each variety except King Edward where only 30 % of the variation could be explained, but the strength of the correlations were more variable at the final harvest (Tables 99-100). Although all varieties were grown from 10 mm ranges of seed tuber sizes, variation in seed tuber weight differed and this probably influenced the strength of the relationships, as more of the variation could be explained in Desiree and Russet Burbank, which had more variable seed tuber weights than in Maris Piper and King Edward (Table 76).

In Expt 4, where there was a greater difference in the COV of seed tuber weight between treatments than in Expt 1, increasing variation in seed tuber weight increased the COV of yield per plant from *c.* 20 to 30 % at each harvest and the effect was larger than when the variation in sprout length and within-row spacing were altered (Table 59). In the evenly spaced treatments of Expt 4, where variation in seed tuber weight was high, > 50 % of the variation in yield per plant was explained by variation in seed tuber weight (Figure 61). In Expt 5, in the evenly spaced treatments, seed tuber weight explained 34 % of the variation in yield in Markies and Marfona and 15 % in the variably-spaced treatments (Table 69). In Expt 6, seed tuber weight explained 37 % of the variation in 40-50 mm seed tubers and 64 % in ungraded seed tubers (Table 71).

The amount of variation in yield per plant explained by variation in seed tuber weight in Expt 1 and Survey 2 was similar to the average values found by Svensson (1966), where although most relationships were significant, on average only 8-15 % of the variation in yield per plant could be explained (Table 2). In Expts 4-8 & Survey 4 however, the proportion of variation in yield per plant explained by variation in seed tuber weight was substantially higher than previously reported with > 60 % of the variation accounted for at some final

harvests. Some of this is probably due to planting a wider variation in seed tuber weights, because as in Expt 4 this increased the variation in yield per plant. In this respect, the results are more similar to those of Hide *et al.* (1997) who planted approximately a five-fold range in seed tuber weights and found that in different years 22 or 41 % of variation in yield per plant was accounted for by variation in seed tuber weight.

In other instances however, even within a 10 mm grade of seed tubers, a substantial proportion of the variation in yield per plant was accounted for. A possible explanation for the greater proportion of yield per plant explained by seed tuber weight than in previous studies is that improvements in seed tuber quality have reduced the effects of other factors on plant-to-plant variation in yield and allowed the effects of seed tuber weight to be expressed more strongly. In Expt 1 and Survey 2, a small proportion of plants (*c.* 5 %) were affected by unexplained stunting and this may partially explain the weaker correlations encountered since those plants produced lower yields and their neighbours would have produced higher yields due to compensatory growth.

#### 6.3.2.1. Mobilisation of seed tuber substrate

Considering the effects that seed tuber weight had on the yield per plant it is pertinent to consider the mechanism by which larger seed tubers produced higher yields. In Surveys 2, 4 & 5 the percentage dry matter of the seed tubers was established before planting and at each harvest for which seed tubers remained intact. The percentage dry matter of the seed tubers was approximately halved 5 DAE compared to at planting in Survey 2 (Table 27) and a similar trend was observed in Survey 4 at 7 DAE (Table 80). The percentage dry matter continued to decline at subsequent harvests to 3.3 % in Survey 2 at 44 DAE (Table 27) and *c.* 4-5 % in all varieties in Survey 4 at 28 DAE (Table 80).

The percentage dry matter of seed tubers at harvests was not affected by seed tuber weight at planting indicating that the rate at which seed tuber substrate was mobilised was not related to

the fresh weight of the seed tuber (Sections 4.5.3 & 4.6.3; Table 85). Due to the variation in percentage dry matter of seed tubers, it was only possible to estimate the amount of dry weight lost from the seed tubers between planting and harvests in Surveys 2 and 4 by assuming that all seed tubers had the average percentage dry matter at planting. In Survey 5 however, the specific gravity of seed tubers was determined prior to planting allowing the dry weight to be estimated more accurately.

In Surveys 2 & 4, estimating the amount of dry weight lost from the seed tubers consistently explained a greater proportion of the variation in above-ground stem weight in the first two weeks of growth than the seed tuber weight at planting (Tables 29, 83 & 86). In combination with date of emergence, loss of dry weight from the seed tuber accounted for *c.* 70 % of the variation in the above-ground stem weight at 12 and 23 DAE in Survey 2 (Table 29) and *c.* 80 % at 7 and 14 DAE in Survey 4 (Table 89). Accounting for the specific gravity of the seed tubers prior to planting in Survey 5 did not appreciably increase the strength of the relationship between dry weight lost from the seed tuber, date of emergence and above-ground stem weight 14 DAE ( $R^2 = 0.72$ ; Table 111). This was probably due to the range in the seed tuber fresh weight being narrow (30-35 g) in Survey 5 and this was associated with less variation in the above-ground stem weight than for Maris Piper in Survey 4 at a similar interval after emergence (27 vs 37 %; Tables 80 & 110). Tubers with higher specific gravities at planting had higher percentage dry matters at 14 DAE, indicating that tubers with a lower percentage dry matter became depleted of nutrients more quickly than those with a higher percentage dry matter (Table 111).

These findings are in agreement with those of Svensson (1977) who measured the dry weight of seed tubers at regular intervals after planting and found that the percentage dry matter of seed tubers was 3-4 % 60 days after planting. Because the date of emergence was not reported, it is not possible to relate the contribution of the seed tuber substrate directly to post-

emergence growth. Bohl *et al.* 2001 excavated plants and removed seed tubers when 90 % of plants had emerged and found that the percentage dry matter of *c.* 70 g seed pieces had fallen from 21 % at planting to 16 % at emergence and 5 % 53 days after planting. That the yield was reduced by removing the seed piece at emergence, thus decreasing the seed tuber substrate to one quarter of the control, is in agreement with the findings of this work that the seed tuber substrate continued to influence the growth of plants until *c.* 14 DAE. Moorby (1967) extrapolated the results of studies investigating the growth of sprouts in storage to conclude that carbohydrates were unlikely to limit growth either pre- or post-emergence, but the validity of applying those studies to growth in the field where mineral nutrients are unlikely to be limiting is uncertain.

Although larger seed tubers tended to produce higher yielding plants, the constant of the relationship between seed tuber weight and yield per plant was consistently positive and the slope consistently shallow, such that doubling the seed tuber weight only increased the yield per plant by *c.* 40 % (Tables 38 & 99-100; Figs 61 & 66). These relationships were similar to those reported by Svensson (1966) and indicate that even though the amount of variation in yield per plant explained by seed tuber weight was higher in this work, the mechanisms that caused larger seed tubers to have higher yields may have been similar. When plants emerged, autotrophic growth began, but due to the leaf area being very small, the absolute amount of photosynthesis was minimal and the majority of growth was due to the mobilisation of seed tuber substrate. Plants growing from larger seed tubers were supplied with larger amounts of seed tuber substrate and this increased the rate of leaf expansion. Over time, the relative proportion of growth enabled by the seed tuber decreased, while the proportion of autotrophic growth increased. Plants growing from smaller seed tubers had a relatively large leaf area per gram of seed tuber compared to larger seed tubers because a greater proportion of their dry weight was derived from photosynthesis rather than from the seed tuber. Other factors probably also contributed because plants with higher above-ground stem weights grow



relatively slowly due to self-shading and allocating a greater proportion of photosynthate to structural rather than photosynthetic tissues.

While it was not possible to determine the precise role of the seed tuber substrate due to unquantified losses to respiration and root exudation, the results indicate that seed tuber substrate was a substantial source of nutrients during the first ten days of growth post-emergence. Further work is required to quantify the exact relative contributions of the seed tuber substrate and photosynthesis during the establishment of the crop.

#### 6.3.2.2. Overall growth

The findings that seed tuber weight affected the yield per plant may appear contradictory to previous findings that seed tuber substrate has only a modest effect on the growth of crops early in the season (Allen & Scott 1980) and that it is possible (and indeed advantageous) to grow high-yielding crops from small seed tubers (Allen *et al.* 1992a). The results of Expts 7 & 8 demonstrate why seed tuber substrate is unimportant in determining overall yield, but is important in determining variation in yield per plant. Expt 7 compared the early growth of two seed tuber sizes (35-45 and 45-55 mm) and thus is analogous to the situation examined by Allen & Scott (1980). Approximately doubling the seed rate increased the dry weight of the canopy by 60 % 19 DAE, but ground cover did not increase in proportion to canopy dry weight, so that ground cover was only 33 % higher (Table 72). The ground cover of the smaller seed size treatment at harvest was equal to that of the larger seed size *c.* 3 days before (Figure 70). Had the crop been allowed to grow on to maturity and had the canopies expanded at an equal rate based on their ground cover, the plants grown from the larger seed size would have formed a complete canopy *c.* 3 days earlier than those from the smaller seed size. The effect on yield that such a difference could cause would be minor and, once the extra cost of the seed tubers was accounted for, any economic benefit would be reduced even further.

There are two crucial differences between the effects of seed tuber weight on the overall growth of the crop and the growth of plants within the crop. First, the differences in seed tuber weight within a seed tuber stock can be larger than the differences between different size grades of seed tubers. In Survey 4, the difference in weight between the smallest and largest seed tubers in a 30-40 mm grade of Maris Piper was approximately three-fold and in 30-40 mm Russet Burbank the difference was eight-fold, in part due to differences in tuber shape, but potentially also due to differences in the consistency of grading. In contrast, in Expt 7, the average weight of 45-55 mm seed tubers was only *c.* twice that of 35-45 mm seed tubers. Second, the plants within a crop compete for a finite amount of space within the canopy, which determines the quantity of solar radiation they can intercept over the course of the growing season.

Whereas between crops, a difference in ground cover caused by a difference in seed size such as occurred in Expt 7 would be negated over the course of the season, when individuals compete for a finite resource, there comes a point at which the resource is exhausted (i.e. 100 % ground cover is reached), and unless the larger individuals cease growth prior to reaching that point, the smaller individuals will remain smaller. Since crops grown at wide spacings (e.g. 80 cm) can still form complete canopies (Firman & Daniels 2011), it is unlikely that the growth of larger individuals would cease and such an occurrence would cause a skewed yield distribution of individual plants which was not encountered in this work. The particularly high yields per plant achieved in Expt 8 (7.0 – 9.6 kg) demonstrated that in an indeterminate variety such as Maris Piper, the canopy can continue to grow if there is sufficient space and thus within a crop, the size of each plant is constrained by neighbouring plants. If in Expt 7, the two seed sizes were competing for an arbitrary space equivalent to 50 % ground cover, this would have been reached 14.5 DAE, at which point the large seed tubers would have occupied *c.* 60 % of the space and the small seed tubers *c.* 40 % of the space (Figure 70).

In Expt 8, the differences in seed tuber weight were greater than in Expt 7 and the plants were widely spaced, limiting competition (although they did unexpectedly begin to compete for space at *c.* 50 DAE). The weight of the seed tuber continued to affect the growth rate of plants once their ground cover had exceeded 1000 cm<sup>2</sup> (Table 74), which is substantially higher than 200-400 cm<sup>2</sup> stated by Moorby (1978). The largest seed tubers (65-70 g) achieved a ground cover equivalent to the average area per plant in the other experiments (22.86 dm<sup>2</sup>) approximately 10 days earlier than the smallest seed tubers (20-25 g; Figure 71). Had they been competing for the space equivalent to two plants, then growth of the canopies would have ceased *c.* 30 DAE, at which point the plants growing from the largest seed tubers would have had twice the ground cover of the smallest seed tubers. Some caution is required in interpreting the results from Expt 8 as the plants were growing in isolation, which probably affected their height in comparison to plants competing in a crop.

### 6.3.3. Date of emergence

As the “culmination of a large number of preceding events” (Benjamin 1990) many factors could potentially affect when a plant emerges. In potato, emergence is to some extent similar to other crops, in that it requires adequate soil moisture and temperature (Benjamin 1990; Firman *et al.* 1992), but unlike in crops grown from true seed, there is no requirement for the seed tuber to germinate, although the process of the sprout beginning to grow is to some extent analogous. Just as earlier-emerging crops may be able to intercept a greater quantity of incident radiation and produce yield more rapidly than later-emerging crops (O’Brien *et al.* 1982), plants that emerge earlier are able to produce a canopy earlier than later-emerging plants with the potential for a higher yield per plant. Thus, more protracted emergence would be expected to result in increased plant-to-plant variation in yield.

Three discrete processes determine when a sprout emerges at the soil surface: the time at which the sprout begins to elongate; the rate of elongation and the distance that the sprout

must grow to reach the surface. Each of these processes is affected by multiple factors, thus demonstrating the complexity of the overall phenomenon of emergence. When the sprout begins to elongate is partially related to dormancy, since the buds never stop growing in storage (Coleman 1987). Soil temperature will affect when a sprout of a particular physiological state begins to elongate and this will vary with planting depth (Pavek & Thornton 2009). The average rate of elongation is largely determined by temperature (Firman *et al.* 1992) but variation in the rate of elongation has not been quantified and would require non-destructive measurements. The distance is determined by planting depth, orientation of the seed tuber and the position within the ridge at which the sprout emerges.

#### 6.3.3.1. Quantification

Unlike the other variables measured in this work, it was inappropriate to quantify variation in the interval from planting to emergence as the COV as done by Svensson (1966). This was because the absolute variation is important and because the interval to 50 % emergence can vary considerably, the same absolute variation in emergence would result in a different COV. Fitting a curve to cumulative emergence counts and calculating the interval from 20 to 80 % emergence from the curve, as in this work, produces a consistent quantification of the duration of emergence.

For comparing between treatments in individual experiments, temporal variation was suitable, but it is uncertain whether equal temporal variation in emergence would always have the same effect on plant-to-plant variation. If the temperature was lower at emergence, then emergence would be expected to become more protracted temporally, but the growth rate of ground cover of plants would also be expected to be lower (Firman *et al.* 1995). Thus differences in the temporal variation in emergence would not necessarily result in the same effect on plant-to-plant variation and modelling the variation in emergence in thermal time (Forcella *et*

*al.* 2000) may be more applicable for comparing differences in the uniformity of emergence between crops.

Emergence was defined as when the sprout first became visible at the surface, but it was apparent when tagging stems in Surveys 2 & 4, that the developmental state of the sprout differed at this stage. Some stems emerged without any developed leaves, which then took several more days to develop, whereas others emerged with unfurled leaves that began to expand immediately. At the early harvests of Surveys 2 & 4, there were substantial variations in the size of plants and stems that emerged on the same day and it is unclear to what extent this was due to the developmental variations at emergence, or because plants grew at a different rate once they had emerged.

#### 6.3.3.2. Sprout length

In Expt 2, increasing variation in the sprout length of seed tubers by planting a mixture of seed tubers from cold storage and seed tubers warmed for one week at 15 °C immediately prior to planting, approximately doubled the interval for 20 to 80 % of plants to emerge (Table 21). In the course of preparing the seed tubers for Expt 2, it was observed that there was variation in the length of sprouts on the warmed seed tubers, despite being placed in a uniform environment. This was exploited in Expt 4, to create two treatments consisting of seed tubers with sprouts 2-4 mm long and a second with seed tubers with sprouts < 2 mm and > 4 mm. This also led to differences in the interval from 20 to 80 % emergence, but the interval was only 50 % greater in the more variable treatment than in the uniform treatment and thus smaller than between the control and mixed seed treatments in Expt 2 (Table 54). Planting seed tubers so that their apical ends were horizontal and warming seed tubers prior to planting did not significantly change the interval from 20 to 80 % emergence in Expt 2 (Table 21).

In Expt 2, the increased duration of emergence did not have any significant effect on the COVs of yield per plant, number of tubers per plant, or the mean tuber weight per plant (Table 22). However, in Expt 4, despite the smaller difference in the duration of emergence between treatments, increasing variation in sprout length (and consequently emergence) increased the COV of yield per plant at each harvest, the COV of the number of tubers per plant at the second and third harvests and the COV of mean tuber weight at the third harvest (Table 59). This was not associated with a significant increase in the COV of tuber size, but it is probable that if the difference in emergence had been greater, the COV of tuber size would have differed.

More of the variation in yield per plant was explained by variations in emergence in Expt 2 in the mixed treatment compared to the control at the first harvest, but at the second harvest this effect had diminished (Table 23). This was in part due to a greater proportion of the variation in yield per plant being explained by emergence at the second harvest than at the first in the control treatment, but also by less of the variation being accounted for in the mixed treatment. A similar trend was observed in Expt 4 when the sprout length was more variable, but at the second and third harvests, only *c.* 20 % of the variation in yield was accounted for by emergence (Table 61).

That reducing variation in sprout length decreased variation in emergence is consistent with our knowledge of how the physiological age of seed tubers affects emergence (O'Brien *et al.* 1983). However it is unclear why when seed tubers were stored at a uniform temperature, their sprout development differed. These findings have practical implications for growers in that they demonstrate the necessity of attempting to maintain seed tubers in as uniform an environment as possible to minimise differences in sprout growth between tubers. Further if using sprouted seed tubers, care should be taken to minimise damage during planting as this would probably lead to greater variation in emergence.

#### 6.3.3.3. Other factors

The variation in emergence that occurred in Surveys 2 & 4 was similar to that in the experiments but could not be explained by differences in planting depth, the number of stems per plant or seed tuber weight (Sections 4.5.2 and 4.13.2). Despite careful placement of seed tubers at planting, the COV of planting depth (defined as the length of un-pigmented below-ground stem) was 16 % in Survey 2 and *c.* 15 % in Survey 4 (Section 4.5.2; Table 77). This variation was similar in extent to that observed in commercial crops by Booth & Allen (1990) and Hogge (1991). With an average planting depth of 15 cm, a COV of 15 % equates to a range in planting depths of *c.* 11-19 cm, which based on the findings of Stalham *et al.* (2002) and Stalham (2003) would have been expected to result in a *c.* 2.5 day difference in emergence between the shallowest and deepest plants.

The extent of variation in emergence that occurred in Surveys 2 & 4 was relatively large (*c.* 14 days from the first to the last plant) in comparison to the differences in the interval from planting to 50 % emergence between the treatments of Stalham *et al.* (2002) and Stalham (2003). Assuming that the duration in emergence in those previous studies was similar to that found in this work, there would have been substantial overlap in the dates of emergence between different planting depths. Thus, while uneven planting depths could increase the variation in emergence, other factors would determine the majority of the variability.

It is possible that variation in planting depth in Surveys 2 & 4 was due to seed tubers being planted at the same depth, but having different effective planting depths resulting from the position on the seed tuber from which the stem grew, or the position in the ridge from which the stem emerged. Thus in the current work, the seed tubers may have experienced relatively similar temperatures and thus the sprouts would have elongated at similar rates (Firman *et al.* 1992) but if the seed tubers were planted at different depths, different soil temperatures could contribute to increasing variation in the date of emergence (Pavek & Thornton 2009).

In light of the inability to explain variation in emergence from variation in planting depth, the number of stems per plant or seed tuber weight, it was of interest to find in Survey 5 that seed tubers with a lower specific gravity and fewer stems emerged earlier than those with a higher specific gravity and more stems. Although only *c.* 25 % of the variation in emergence could be explained by these two factors the result further demonstrates that factors internal to the seed tuber contributed to variation in emergence. While it is perhaps counter-intuitive that seed tubers with lower percentage dry matter emerged earlier, as they might be expected to grow more slowly, these observations are consistent with the increased sprout growth from tubers with lower specific gravities observed in storage (Brown & Smith 1968; Silva & Andrew 1983) and suggest that tubers with lower specific gravities may have begun to sprout earlier than those with higher specific gravities.

#### 6.3.3.4. Post-emergence growth

During the *c.* two week interval after 50 % emergence, the relative growth rate of ground cover was very rapid (> 50 % per day in some instances) in Surveys 2 & 4 but declined as the plants grew larger to *c.* 10 % per day once the plants had a ground cover of *c.* 200 cm<sup>2</sup> (Figs 32 & 74). The correlation coefficients of regressions between date of emergence and above-ground stem weight per plant decreased during the initial three weeks of growth in Surveys 2 & 4 indicating that the growth rate of plants that were initially similar sizes differed during this period (Tables 28 & 81). The same trend was observed in ground cover per plant in Survey 4 with the proportion of variation explained by emergence decreasing in all varieties except King Edward between the first and second harvests (Figure 73).

These differences in growth rate were probably caused by differences in the supply of seed tuber substrate to the developing above-ground stems, but after the majority of seed tuber substrate had been mobilised, the relative growth rates were relatively similar, as indicated by ground cover per plant 14 DAE correlating strongly with above-ground stem weight 28 DAE



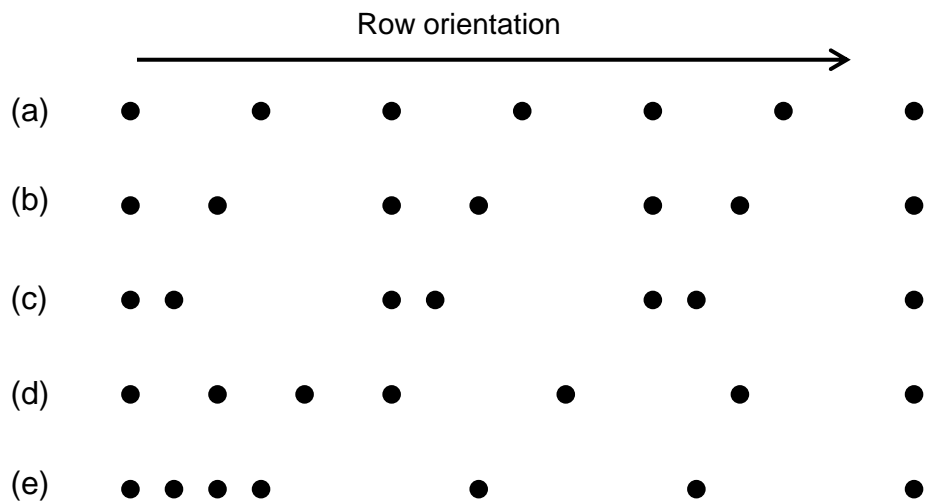
in Survey 4 (Table 88) and a similar trend was apparent in Survey 2 (Table 31). The initial growth of plants grown from microtubers in Survey 6 contrasted greatly with Surveys 2 & 4 as ground cover per plant 11 DAE correlated very strongly ( $R^2 = 0.93$ ) with the ground cover 4 DAE. The seed tuber weight of microtubers in Survey 6 was so low (1-2 g), that it would probably have been exhausted soon after emergence meaning that the growth rate would only be affected by ground cover. In crops grown from mini-tubers, emergence may therefore be more important in determining plant-to-plant variation than in crops grown from larger seed tubers.

#### 6.3.4. Within-row spacing

##### 6.3.4.1. Space per plant

Although the effects of variable within-row spacing on yield and marketable yield have been studied extensively in the past there are uncertainties as to the extent of variation that can occur within crops without affecting variation in tuber size. Previous studies have only measured the variation in the distance between plants which, while mechanically relevant, is only of limited biological significance, as each plant occupies the gaps to either side of where it emerges within the row. Quantifying the space per plant by averaging the distances to each plant's neighbours (as Martin *et al.* 2005 did for maize plants) produced a more relevant measure that could be used to evaluate the effect of variable spacing on the growth of plants. This distinction may appear abstract, but is vital to differentiate between spatial arrangements of plants within the crop (Figure 103). Previous studies would not have distinguished the arrangements of Figure 103c and Figure 103e as the COV of distance between plants is equal, but the arrangements are clearly distinct.

**Figure 103. Different spatial arrangements of plants illustrating how the distance between plants and the space per plant are distinct. (a) Uniform spacing; (b) and (c) increased variation in the distance between plants, but with equal space per plant to (a); (d) and (e) equal variation in the distance between plants to (b) and (c) respectively, but with increasing variation in the space per plant.**



#### 6.3.4.2. Commercial crops

The variation in within-row spacing encountered in the surveys of commercial crops was similar to the average values of 38 % encountered by Booth & Allen (1990) in the UK and 34 % by Pavek & Thornton (2005) in Washington, USA. In Survey 1, the spacing was comparatively uniform with a COV of 21 % (Figure 24), but in Survey 3, the COVs ranged from 33 to 36 % (Figs 44a, 52 & 56). The COV of space per plant was consistently lower than the COV of distance between plants at each site at 12 % in Survey 1 (Figure 24) and 20 to 25 % in Survey 3 (Figs 44b, 52 & 56). A more extensive dataset would be required to establish whether the variation in space per plant is similar for crops with equal variation in the distance between plants or whether these can vary independently.

In Surveys 1 & 3, the space per plant explained at most 13 % of the variation in the yield per plant (Figs 25 & 45) indicating that for the extent of variation encountered in these crops, variation in within-row spacing was relatively unimportant in determining plant-to-plant variation in yield.

#### 6.3.4.3. Experiments

The treatments in Expt 3 were chosen to create differences in both the variation in distance between plants and also variation in the amount of space per plant. It was hypothesised that variation in within-row spacing would have no effect if the space per plant remained equal (as in treatment 3) but that at some level of variation in space per plant, the treatments would increase variation in the yield and mean tuber weight per plant, adversely affecting uniformity. Considering the very large difference in the variation in space per plant between treatments 1 and 7, it was surprising that there were no detectable effects of any treatments on the COVs of yield, number of tubers or mean tuber weight per plant, nor on the COV of tuber size. The only significant overall effect was that the yield of treatment 6, which simulated doubles followed by misses, produced the lowest yield (Table 24). Ground cover was slightly slower to develop in treatment 6 than in the other treatments (Figure 29), but these differences were insufficient to account for the differences in yield. The use of single row plots may have led to neighbouring rows growing into the harvested area and compensated for the reduced yield.

Further examination of the results of Expt 3 led to the development of a method to compare the yield, number of tubers and mean tuber weight of plants with different amounts of space in treatment 7, which contained the largest differences in space per plant. Although half the plants in treatment 7 had an average of 12.5 cm space in the row and the other half had an average of 47.5 cm space in the row, the plants with less space produced similar yields and numbers of tubers at the first harvest 66 DAE (Table 26). At the second harvest, the plants with less space produced *c.* 45 % of the yield and number of tubers and this was significantly different to equivalently positioned, but evenly spaced plants in treatment 1 (Table 26). As a consequence of the yield and number of tubers decreasing by similar amounts at the second harvest, the mean tuber weight of the plants with less space did not differ from those with

more space and this may explain why there was no significant difference in the COV of tuber size between treatments (Table 24).

The results of Expt 3 showed that Maris Piper was able to tolerate large differences in the space per plant without any detectable effect on uniformity. The spatial arrangement of plants in treatment 7 of Expt 3 was repeated and compared with uniform spacing in Expts 4 and 5 to establish whether the findings of Expt 3 were reproducible and also whether different varieties responded differently to variation in within-row spacing.

In Expt 4, increasing variation in within-row spacing had no significant overall effects at the first harvest, but at subsequent harvests, the number of tubers was reduced by *c.* 10 % and yield was reduced by *c.* 5 % at the second harvest and *c.* 8 % at the third harvest (Table 58). The difference in yield could not be accounted for by differences in integrated ground cover days and full ground cover was maintained until the final harvest (Figure 57; Table 57). It is possible that the decrease in yield was due to the use of single-row plots and that the neighbouring rows compensated. At the final harvest, the COV of tuber size was increased from 15.2 to 16.1 % and this was associated with an increase in the COV of above ground stem weight (Table 58). An examination of the yields of plants with different amounts of space in the row revealed that while at the first harvest, the plants produced similar yields (47 and 53 % for plants with 12.5 and 47.5 cm space respectively), the difference in yield between plants increased between the first and second harvests and was maintained until the final harvest when plants with less space produced only 42 % of the total yield (Table 65). At the first harvest there was no significant difference in the number of tubers that plants with different amounts of space produced, but at the final harvest, plants with less space produced 47 % of the total number of tubers (Table 65). As a consequence of this difference in the relative yield and number of tubers produced by plants with different amounts of space, the mean tuber weight of plants with less space was reduced to 90 % in comparison to the plot as

a whole, meaning that the plants with more space produced substantially larger tubers (Table 65). This difference in the mean tuber weight of plants with differing amounts of space provides a mechanism by which to explain why the COV of tuber size was increased by variation in within-row spacing.

While the effects of increased variation in within-row spacing differed in Expts 3 & 4, in both experiments yield per plant was relatively insensitive to the amount of space in the row. It was surprising that yields of plants with such contrasting amounts of space were similar and this demonstrated the plasticity of the growth of the above-ground stems. The canopies of plants with less space occupied the space directly above where plants with more space emerged and those plants with more space were 'forced' into the large gap by their neighbours (Figure 104).

**Figure 104. Photograph demonstrating the plasticity in growth of plants either side of an 80 cm gap between plants at the first harvest of Expt 4. Dashed red lines highlight the position of two stems growing into the gap.**



In Expt 5, the effects of uniform and highly-variable within-row spacing were compared in Marfona and Markies. These varieties were chosen as the foliage growth of Marfona is determinate and semi-erect whereas Markies is indeterminate and erect, in contrast to the indeterminate and semi-erect foliar growth habit of Maris Piper (Potato Council 2009; Europotato 2015), which could account for the plasticity shown in Figure 104. As in Expt 4, the increased variation in within-row spacing had only a modest effect on ground cover development and treatments achieved 100 % ground cover at a similar time (Figure 63). Yield was numerically lower (55 t/ha) with higher variation in within-row spacing than with low variation (60 t/ha), but this difference was not significant ( $p = 0.06$ ; Table 66). Examining the individual effects of treatments revealed that the yield of Markies was almost identical between spacing treatments, whereas the yield of Marfona was numerically 10.8 t/ha lower with high variation in within-row spacing, although again this difference was not significant (Table 67). The number of tubers was also numerically *c.* 10 % lower when variation in within-row spacing was high, but as with the effect on yield, this was not significant (Table 66) although present in both varieties (Table 68).

In Expt 5, increasing variation in within-row spacing resulted in a substantial increase in the COV of tuber size from 14.0 to 16.8 % (Table 66) and this effect was particularly pronounced in Markies, where the COV of tuber size was increased from 13.5 to 17.3 % (Table 67). This was associated with an increase in the COV of yield per plant, but not in the COV of the number of tubers per plant (Table 66). As in Expt 4, the plants with less space produced c. 40 % of the total yield, but in contrast to Expt 4, the plants with less space produced c. 50 % of tubers and consequently the mean tuber weight of the plants with less space was c. 82 % compared to the whole plot (Table 68). The greater difference in the mean tuber weight of plants with different amounts of space accounts for the larger effect of variable within-row spacing on the COV of tuber size in Expt 5 in comparison to Expt 4.

While the results of Expts 4 & 5 are in agreement with the conclusions of Pavek & Thornton (2006) that variation in with-in row spacing is detrimental to marketable yield, the design of their experiments did not allow effects on the mean tuber size and the COV of tuber size to be distinguished. This was because the seed rate differed in the double and missing treatments compared to in the control. It was therefore unsurprising that the missing plant treatment, produced a greater proportion of oversize tubers and that the double treatment produced a greater proportion of undersized tubers, as this would be expected due to the difference in stem density altering the mean tuber size. Regardless of any changes in variation in tuber size, if the evenly spaced treatment of Pavek & Thornton (2006) resulted in an optimum mean tuber size, changing the mean tuber size would change the amount of over- and under-sized tubers. The results were extrapolated to determine the economic losses caused by irregular spacing, but it is unclear whether it is valid to do so, as within a crop, missing plants will occur at random and the plants surrounding the missing plant will compensate (Hide *et al.* 1995). While Pavek & Thornton (2006) did examine whether neighbouring rows compensated and found no response, the design did not account for the ability of second-neighbours to compensate, which Hide *et al.* (1995) found was important.

#### 6.3.4.4. Varietal differences

Although previous authors examined the effects of variable within-row spacing using different varieties (e.g. Jarvis *et al.* 1976; Pascal *et al.* 1977; Sieczka *et al.* 1986), it was not always clear why they chose to examine those particular varieties. Jarvis *et al.* (1976) noted that Pentland Crown and King Edward responded differently in some experiments but did not speculate why this was the case. Pascal *et al.* (1977) examined varieties with different shaped tubers to examine whether this affected the irregularity of spacing, but not whether varieties responded differently to variable within-row spacing. Differences in the above-ground and below-ground morphology of varieties could both potentially affect their response to variable within-row spacing. Above-ground, the development of stems needs to be sufficiently plastic for them to be able to forage for light away from where they emerge and maintain overall yield. Indeterminate varieties that continue to produce new leaves throughout the season would be expected to be less sensitive to yield losses as a result of irregular spacing since they can fill gaps in the canopy more effectively than determinate varieties. Below-ground, the effect on uniformity of any differences in the COV of yield per plant caused by variable within-row spacing depends on the response of the number of tubers per plant and if this can change depending on the amount of space per plant it would allow the crop to compensate.

The greater negative effect on uniformity in Markies as a result of high variation in within-row spacing in Expt 5, in comparison to Maris Piper in Expt 4, was due to the number of tubers per plant not responding to the space per plant in the variable treatment (Table 68) even though the total number of tubers was numerically lower (Table 67). The reduction in the number of tubers in Maris Piper in Expt 4 in response to variable spacing (both relative to the uniform spacing, but also over time) was beneficial to maintaining uniformity as tubers were more likely to be resorbed on plants with less space in the row (Table 65). This reduced the effect of the lower yield of plants with less space from influencing the mean tuber weight per plant. While the resorption of tubers could be considered wasteful since it reduces the



number of tubers and thus increases the seed rate required to achieve the target tuber population, these results indicate that the plasticity offered by resorption can be advantageous in certain situations.

#### 6.3.4.5. Remaining uncertainties

The extent of variation in within-row spacing treatments in Expts 4 & 5 was considerably higher than the variation typically encountered in commercial crops and further work is necessary to establish the practical implications of these findings. Nevertheless, they are the first experiments to demonstrate that increased variation in within-row spacing can increase variation in tuber size. The findings of this work highlight the need for further experiments on the effects of variable within-row spacing to: (a) establish the relative performance of cup and belt planters, evaluating their speed and accuracy, as well as the relative importance of misses and doubles, (which may be more frequent on cup planters), against more irregular spacing, (but potentially fewer misses and doubles) from belt planters; (b) distinguish the effect of missing plants from lower stem densities, for example by comparing equal seed rates but with even spacing and another arrangement with narrower spacing, containing gaps; (c) determine whether varieties differ consistently in their response to variable within-row spacing and if so, characterise the traits that are important.

#### 6.3.5. Number of stems

As the mean tuber weight of a seed tuber stock affects the number of stems produced (Allen & Wurr 1992), it was expected that some of the variation in the number of stems per plant would be explained by the variation in seed tuber weight within seed tuber stocks. As a component of the local stem density (the number of stems per metre of row) it was hypothesised that a more uniform distribution of stems along the row would result in more uniform growth of individual stems, consistent with the growth of crops at different stem densities.

In Expt 1, the number of stems per plant correlated very weakly with the weight of seed tubers and consequently decreasing or increasing variation in seed tuber weight had no effect on the variation in the number of stems per plant (Table 19; Figure 26). Artificially controlling the local stem density by thinning stems shortly after emergence in treatment 5 of Expt 1 did not significantly reduce variation in the weight of above-ground stems (Table 18). In Expt 4, where there was a larger difference in the variation in seed tuber weight between treatments than in Expt 1, the effect on the variation in the number of stems per plant was inconsistent between harvests. Although at the second harvest there was a significant difference in the COV of the number of stems per plant (Table 59), overall the frequency distributions were not substantially different (Figure 58). In Expt 6, which compared 40-50 mm seed tubers and ungraded seed tubers with the same mean weight, there was no significant effect of variation in seed tuber weight on the COV of the number of stems per plant (Table 70; Figure 64). Although the relationships between seed tuber weight and the number of stems per plant were almost identical (Figure 65), the greater range in seed tuber weight in the ungraded treatment meant that 50 % of the variation in the number of stems per plant was explained, compared to only 14 % in the graded treatment (Table 71).

In Surveys 2 & 4, the number of stems per plant was also poorly explained by variation in seed tuber weight within 30-40 mm Maris Piper ( $R^2 = 0.02$  &  $0.14$  respectively; Figs 30 & 72). Variation in seed tuber weight explained *c.* 25 % of the variation in the number of stems per plant in Desiree and Russet Burbank in Survey 4, but this was partly caused by the fact there was greater variation in seed tuber weight in those varieties due to differences in tuber shape (Figure 72). These correlations were similar to those reported by Svensson (1966) who found that an average of 15 % of the variation in the number of stems per plant was explained by variation in seed tuber weight (Table 2). The implication of these results is that variation in the number of stems per plant is relatively insensitive to variation in seed tuber weight.

In Expt 7, 45-55 mm seed tubers had lower variation in seed tuber weight and the number of stems per plant than 35-45 mm seed tubers, (Table 72) but the early harvest prevented establishing whether this would have affected uniformity. The difference in the number of stems between seed tubers grown from the contrasting soil types of Surveys 3a & 3b was greater than that between seed tuber stocks that were *c.* 5 weeks different in chronological age reported by Firman & Shearman (2007) (20 *cf.* 8 %; Table 72). While some of the difference can be explained by the seed tubers grown on the heavy soil emerging *c.* 1 week later than on the light soil (and thus also initiating tubers *c.* 1 week later; Section 4.6.1) this cannot explain the entire difference and thus other, as yet unidentified factors affected the average number of stems per seed tuber. Effects of soil type on seed tuber attributes have been noted previously, although typically in terms of the yield of the daughter crop (Wurr 1978) rather than the number of stems produced. Were similar differences in crop growth to occur in a seed tuber crop as between Surveys 3a & 3b then the variation in the number of stems per plant in the resultant crop would be increased.

It is counterintuitive that whilst the average number of stems per plant increases as seed tuber weight increases, changing the variation in seed tuber weight had minimal effects on the variation in the number of stems per plant. The relationships between seed tuber weight and the number of stems per plant were not atypical (Figs 26 & 65) of those between the average seed tuber weight and the average number of stems (e.g. Firman & Daniels 2011), but the large amount of scatter demonstrates that the true determinants of the number of stems per plant are yet to be established. Further research is required to establish the physiological and or biochemical changes that occur during chronological aging to establish why it increases the number of stems per plant. It would also be of interest to establish whether the changes that occur are also able to explain variation in the number of stems produced by each seed tuber.

The reanalysis of Firman & Shearman (2006) revealed that the seed tubers heavily infested with *R. solani* (96 % had symptoms and 44 % had > 12.5 % surface area infected) had more variable numbers of stems per plant than healthy seed tubers (42 vs 30 %) and the effect was negated by applications of fungicides (Table 112). In this study, plants severely infected by *R. solani* were only encountered in Survey 3c and those plants produced *c.* 40 % fewer stems and more variable numbers of stems per plant than healthy plants (Section 4.6.2). The results of the model described in Section 5.3.1 indicate that by affecting the number of stems per plant, *R. solani* probably decreased the uniformity of the crop. Previous investigations of the effects of *R. solani* on the tuber size distribution have ascribed changes to stolon pruning (Cother & Cullis 1985; Hide *et al.* 1985a, 1985b), this analysis suggests that increasing variation in the number of stems per plant can also have negative consequences.

Although the number of stems per plant is an easily distinguishable difference that occurs between plants, the results of this work show that it is a crude classification, since there is tremendous within-plant variation in the size of stems, such that there can be very little difference between some plants with different numbers of stems, and substantial differences between plants with the same number of stems (Figure 76). At the level of individual plants, the production of stems is better considered as a continuum rather than discrete classes, beginning with single-stemmed plants, followed by two-stemmed plants with one very large stem and one very small stem and ranging to plants with multiple stems, but where each is a similar size.

This pattern of variation in the size of stems within crops is analogous to the process that occurs between seed tuber stocks as the chronological age of seed tubers increases and is considered to be caused by differences in apical dominance, which gradually diminishes as seed tubers age and more sprouts are able to grow (Coleman 2000). The extent of variation

within each seed tuber stock is so large however that it is difficult to conceive that this same mechanism can account for all of the variation.

The cause of the variation in the number of stems per plant is therefore uncertain and given the fundamental importance of the stem as the unit of population within the potato crop, undoubtedly merits further attention. Considering the effect of chronological age on the average number of stems per plant, it is possible that the variation in the number of stems per plant represents differences in the chronological age of seed tubers. However, the extremes that occur within a crop represent considerably larger differences in the number of stems per plant than would be expected if the differences were the result of tubers initiating over a period only *c.* 1-2 weeks long (O'Brien *et al.* 1998). It is curious that despite the importance of the number of stems per plant (both on average and in the variation) little is known about the genetic variations that determine differences between varieties, or the physiological and biochemical changes that occur as the chronological age of seed tubers changes.

#### 6.3.5.1. Effect on yield

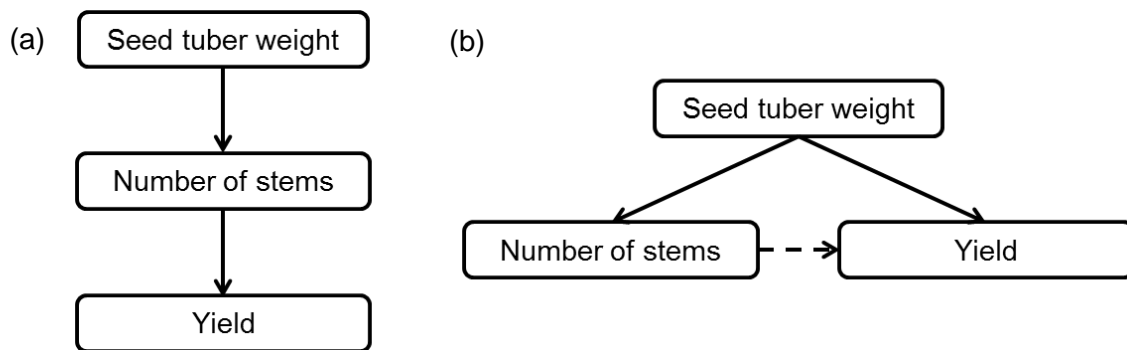
Svensson (1966), Silva & Andrew (1985) and Firman & Shearman (2007) reported that the yield per plant increased as the number of stems per plant increased but this study found little evidence that the number of stems per plant directly affected the yield of individual plants. Plants with more stems did at times produce higher yields than those with fewer stems (e.g. Tables 17, 46 & 51 ), but where seed tuber weight was also recorded, the effect of the number of stems was not significant in multiple regressions. At the final harvest of Expt 4, yield per plant increased as the number of stems per plant increased in the treatment with a high level of variation in seed tuber weight, but not when there was little variation in seed tuber weight (Figure 59), despite the variation in the number of stems not differing (Table 59). The same trends occurred in Expt 6, where the number of stems per plant correlated moderately with yield in the ungraded seed treatment, but very weakly in the graded seed tuber treatment

(Table 69), when there were no significant differences in the average or COV of the number of stems per plant (Table 70). In Expt 7, although there were differences in the number of stems produced by seed tubers from different soil types, the ground cover and above-ground dry weight did not differ 19 DAE (Table 72). In Expt 8, the number of stems correlated significantly with the ground cover of individual plants from 8-45 DAE, but in multiple regressions where the weight of the seed tuber was included, the number of stems only had a significant effect at one sampling date (Table 75).

Surveys 3c and 3d were contrasting crops in terms of the relationships between the number of stems and yield per plant. In Survey 3c, the use of large, tightly graded seed tubers (50-55 mm) contributed to a high number of stems per plant (on average 6.6) and with a COV of *c.* 35 % meant that the number of stems per plant ranged from 1-13 (Figure 46). At each harvest there was either no correlation, or a very weak correlation, between the number of stems per plant and yield per plant (above-ground stem weight at the first harvest; Table 47). In Survey 3d however, the use of ungraded seed tubers contributed to yield per plant increasing as the number of stems per plant increased at each harvest (Table 51).

Overall, the results indicate that rather than the number of stems directly affecting yield (Figure 105a) the weight of the seed tuber affected both the number of stems and the yield per plant (Figure 105b), which may also account for the correlations between the number of stems and yield per plant previously reported by Svensson (1966) and Firman & Shearman (2007).

**Figure 105. Possible interactions between seed tuber weight, the number of stems per plant and yield per plant. (a) seed tuber weight influences the number of stems which influences yield; (b) Seed tuber weight affects both yield and the number of stems, but there is no direct effect of the number of stems on yield.**



These findings are difficult to reconcile with the well-established knowledge that overall yield increases as stem populations increase (Sharpe & Dent 1968; Allen & Wurr 1992; Firman & Daniels 2011) which simplistically, could be expected to result in plants with more stems being inherently more productive. There are several factors that may explain this apparent contradiction. The yield of individual plants is best considered in terms of relative yield per plant, and the factors that determine this (e.g. seed tuber weight) are relatively unimportant in determining overall yield.

Distinguishing between the effects of the plant population, stem population and seed rate on yield is difficult, since these factors are inter-related. For a given variety and a specific weight and chronological age of seed tubers, increasing the stem population also increases the plant population and seed rate (Allen & Wurr 1992). Practically, the inter-relatedness of these factors is of little importance and while many experiments have compared different seed sizes planted at different densities, none have been conducted with large differences in either the seed rate or plant population while controlling for the stem population. This is partly due to the difficulty of precisely predicting stem populations prior to planting, but comparisons could be made between small, chronologically old seed tubers (producing many stems) and large, chronologically young seed tubers (producing few stems) or between chronologically young tubers of different sizes (all producing few stems).

Evidence from experiments with minitubers may help to untangle these inter-related factors from each other. Firman (2015) examined the effect of seed tuber chronological age and size on the number of stems and yield of Jelly and Venezia. In Jelly, the two smallest seed sizes (*c.* < 15 and 15-20 mm) of both ages produced almost entirely single-stemmed plants and the stem populations were indistinguishable. Larger seed tubers produced ground cover more rapidly than smaller seed tubers, but the difference mainly occurred during the initial phase of growth from 0 to 20 % ground cover and subsequently the rate of ground cover expansion was similar. Consistent with the differences in ground cover, yield increased as seed tuber weight increased, with the smallest seed size (1.1 g) yielding 40 t/ha whereas the largest (4.4 g) yielded 59 t/ha.

#### 6.3.6. Number of tubers

In Maris Piper, the number of tubers per plant consistently increased as the number of stems per plant and the yield per plant increased (Tables 17, 46 & 49). These findings are in agreement with Svensson (1966) and also with knowledge of how the number of tubers within a crop changes as the plant population is altered (Allen & Wurr 1992; Firman & Daniels 2011). As the plant population decreases, assuming that a complete canopy still forms, each plant occupies a larger area and intercepts a greater proportion of the total incident radiation. This is associated with the number of tubers per plant increasing as the plant population is decreased, although the net effect is that the total number of tubers decreases (Allen & Wurr 1992; Firman & Daniels 2011). Due to the variation in the number of stems and yield per plant, the crop is composed of plants that are equivalent to the average plants within crops grown at different densities but having similar yields. The relationships found in this work are not unexpected, and an implication of these similarities between different scales is that the relationships established between stem populations and tuber populations for different



varieties (Firman & Daniels 2011; Firman 2014) may inform us of how the variation in the number of tubers changes as the variation in yield per plant changes.

There are distinct differences in this trait between varieties and these were quantified by Firman (2014) as the variable cTPSd, describing how the number of tubers per stem changed as the stem density was increased from 75,000 to 125,000 stems/ha. The relevance to uniformity is that if the number of tubers per stem changes with changes in stem density, the number of tubers per plant will also change as the yield per plant changes and will buffer changes in the variation in yield per plant from affecting the variation in the mean tuber weight per plant and thus the overall variation in tuber size. Maris Piper is an intermediate variety in this respect (Figure 8) whereas King Edward is relatively plastic and Russet Burbank is relatively stable (Figure 7). These varietal differences will be discussed further in Section 6.4.2.

In Expts 4 and 6, although the variation in the number of stems per plant was not consistently significantly increased by increasing variation in seed tuber weight, the variation in the number of tubers per plant was increased (Tables 59 & 70). In Expt 4, there was still considerable variation in the number of tubers per plant amongst plants growing from seed tubers of a similar weight (Figure 62), but the reduced variation compared to 25-45 mm seed tubers suggests that there may be some limits on the number of tubers produced by seed tubers of identical weights. Growing plants at wide spacings (as in Expt 8, but with earlier harvest dates) would allow this to be investigated further and differentiate between the role of the seed tuber and plant size.

It is important to note that the relationship between the yield and number of tubers per plant is not directly causative, since tubers are initiated 2-3 weeks after emergence (O'Brien *et al.* 1998), prior to any substantial yield formation. Rather, it is an indication that for plants with a certain number of stems, those with higher above-ground stem weights at tuber initiation

produced more tubers and remained larger throughout the growing season so that they intercepted more solar radiation and produced higher yields.

#### 6.3.6.1. Resorption

As noted in Section 6.3.4.3, the resorption of tubers > 10 mm in diameter by plants with less space in the row in Expt 4 reduced the influence of the lower yield per plant on the variation in the mean tuber weight per plant. Despite resorption being recognised as important for determining the final number of tubers within the crop (Ewing & Struik 1992; O'Brien *et al.* 1998; Celis-Gamboa *et al.* 2003a) little is known about how the process occurs. Viola *et al.* (2001) is the only molecular-based work to mention the process (referring to it as tuber abortion, rather than resorption). While it could be considered detrimental, due to reducing the total number of tubers (and thus increasing the optimum seed rate) the findings presented here demonstrate that the resorption of tubers by low-yielding stems may act to improve uniformity by diverting assimilates away from tubers that would not be marketable to those that are.

#### 6.3.7. Mean tuber weight and size

Svensson (1966) described the mean tuber weight per plant as the arithmetic mean (i.e. yield ÷ number of tubers). A disadvantage of this method is that it does not account for the distribution of yield between tubers and consequently in some situations can be a poor descriptor of the size of tubers. The methods of Sands & Regel (1983) and Travis (1987) accounted for the distribution of yield between different sized tubers for entire crops, providing a more economically relevant description of the mean tuber weight or size. These methods were unsuitable for describing the mean tuber weight or size of individual plants where the relatively small number of tubers meant that yield was not normally distributed between weights or size grades. The method described in Section 3.1.3.2 was advantageous as small tubers (e.g. 1-10 g at final harvests) which are a small fraction of the total yield were

given less influence on the mean tuber weight than if the arithmetic mean was calculated. Unsurprisingly the arithmetic mean tuber weight correlated with the mean tuber weight but there were occasionally substantial differences for some plants and the mean tuber weight was on average *c.* 9 % higher than the arithmetic mean (Figure 89).

In Survey 1, tubers from each plant were graded, the total yield in each grade was recorded and the mean tuber size calculated. The process of grading was laborious and the variable shapes of tubers meant that the same tuber weight distribution would not necessarily have the same mean tuber size as there is substantial overlap in the weight of tubers between size grades (MacKerron *et al.* 1988). Since the shape of tubers did not appear to consistently vary between plants, weighing individual tubers was considered to provide a more consistent description of the distribution of yield between individual tubers than size grading of tubers and so this method was used in the other surveys and in the experiments. Where necessary, a conversion between tuber size and weight was made, assuming that the diameter of a tuber in mm is approximately ten times the cubic root of its weight in g (Hide *et al.* 1997; Marshall 2000).

The mean tuber weight (and thus size) of individual plants was consistently related to the yield and number of stems and tubers per plant. These findings are in agreement with the processes that determine the mean tuber size of individual crops (Travis 1987; Allen & Wurr 1992; Firman & Daniels 2011). For a given crop, as the yield increases the average yield per stem increases and the mean tuber size increases. Conversely, for a given yield and variety, crops grown at higher densities have a lower average yield per stem and a lower mean tuber size. This principle applied in all commercial crops sampled in this study (Figure 22; Tables 46, 49 & 53) and also in Survey 4 (Table 107) so that plants with the lowest mean tuber weight had the lowest average yield per stem. At both scales, this occurs because the number of tubers per stem does not increase in proportion to the yield per stem.

In Survey 1, the COV of mean tuber size per plant was 6.8 % (Table 16) and, with a mean tuber size of 55.5 mm, the mean tuber size of plants ranged from *c.* 45-65 mm (Figure 23). Similar variation in the mean tuber weight was encountered in Survey 3 (Tables 44, 48 & 52). The variation in the mean tuber weight was of a similar magnitude to the COV of the arithmetic mean tuber weight reported by Svensson (1966) across a range of crops (Table 1). The variations in mean tuber weight per plant equated to variations in the mean tuber size per plant at least as great as those encountered in Survey 1 (Figure 90). Consequently, the mean tuber size per plant typically varied by *c.* 20 mm between plants within crops when the mean tuber size was *c.* 60 mm.

In Expts 1-3, the COV of mean tuber weight per plant ranged from 23-40 % but was not affected by treatments (Tables 19, 22 & 25). In Expt 4, increasing variation in seed tuber weight increased the variation in the mean tuber weight from 17 to 21 % at the first harvest, but there was no significant effect at later harvests (Table 59). Increasing variation in sprout length and within-row spacing had no effect at the first two harvests but at the final harvest, both increased the variation in mean tuber weight per plant from 23 to 27 % (Table 59). In the variable within-row spacing treatment, but not in the sprouting treatment, this was associated with a significant increase in the COV of tuber size (Table 58). In Expt 5, increasing the variation in within-row spacing increased the COV of mean tuber weight per plant from 27 to 39 % and as in Expt 4, this was associated with an increase in the COV of tuber size from 14.0 to 16.8 % (Table 66). In Expt 6, increasing variation in seed tuber weight did not affect the COV of mean tuber weight per plant, but did increase the COV of tuber size from 14.5 to 15.3 % (Table 70).

While in the experiments, higher COVs of mean tuber weight per plant were not consistently associated with increases in the COV of tuber size, the model presented in Section 5.3.1 and the reanalysis of data from Firman & Shearman (2006b) support the general trend that these

two variables were related (Figs 97 & 87). One reason for the lack of consistency is that there was variable within-plant variation in tuber size and thus, within samples of 10 to 20 plants, the variation in the mean tuber weight per plant did not always correspond to the overall variation in tuber size. A further reason is that the yield per plant varied, determining the relative contribution of each plant to the overall tuber size distribution. A low-yielding plant that produced small tubers would increase the variation in the mean tuber weight per plant, but contribute little to the overall yield and so not adversely affect the COV of tuber size. Conversely, a high-yielding plant that produced small tubers would increase the COV of tuber size.

#### 6.3.8. Effects on uniformity

The effect of plant-to-plant variation on the overall variation in tuber size operates through the same mechanism as within-field variation, discussed previously. Individual plants have different yields and numbers of tubers and this causes variation in their mean tuber size and weight. In the same manner that differences in the mean tuber size at different locations within a crop can decrease uniformity, the different mean tuber sizes between plants contribute to the lack of uniformity. To understand how the factors investigated in this study affect uniformity, it is necessary to consider not only whether they affected the variation in the number of tubers per plant or yield per plant, but also whether these changes affected variation in mean tuber weight.

##### 6.3.8.1. Plasticity and compensation

A consistent difficulty encountered in this work was that the standard error of the COV of tuber size was large, making it difficult to detect small, yet economically relevant changes in the tuber size distribution. In the experiments the standard error of the COV of tuber size was a similar size to the standard error of the mean tuber size, even when the absolute value of the mean tuber size was 3-4 times larger. A similar trend in the size of standard errors was

encountered by Firman & Shearman (2006b; 2007) and Firman (2008). One possible reason for this is that variation in the seed tuber weight, date of emergence and number of stems per plant occurred independently of each other and consequently, even if the overall distributions of each factor were identical between plots, the population of plants differed. If a large seed tuber produced few stems and emerged early, it would probably produce large tubers and if a small seed tuber produced many stems and emerged late, it would probably produce small tubers. Conversely, if a large seed tuber emerged late and a small seed tuber emerged early, they would both produce similar sized tubers. If by chance, a plot contained plants in which the variables combined to create larger differences in the mean tuber size per plant, then the COV of tuber size would be higher than if the variables combined to minimise the differences. Larger plots than are typically used in potato experiments were used in Expts 1-3 in an attempt to reduce these chance variations, but it did not improve the sensitivity of the analyses. The multifactorial designs of Expt 4 & 5 were more successful in distinguishing effects of treatments on uniformity due to the increased replication of main effects.

#### 6.3.8.2. Variation in mean tuber size

The main conclusion of this work on the effects of plant-to-plant variation on uniformity is that variations in the mean tuber size (or weight) per plant affect the overall variation in tuber size within the crop. This mechanism is analogous to the examples of within-field variations in Figure 93, but the extent of variation in mean tuber size between plants was greater than in the hypothetical scenarios of within-field variation. In Survey 1, the mean tuber size per plant ranged from 45-65 mm (Figure 23) and similar ranges were encountered in Surveys 2-4 and in the experiments as discussed in Section 6.3.7. These differences were equivalent to a three-fold difference in either the yield or numbers of tubers and thus considerably larger than the within-field variation encountered in Surveys 3a & 3b and by Stalham & Allison (2014).

A consequence of the variation in the mean tuber weight per plant affecting uniformity is that plant-to-plant variations in yield and the number of tubers are not inherently detrimental. If, as in the high variation in seed tuber weight treatment of Expt 4, plant-to-plant variation in yield is increased, but higher yielding plants also produce more tubers, then there may be no difference in the variation in the mean tuber weight per plant between treatments and consequently no effect on uniformity. This was not appreciated by Svensson (1966) or Silva & Andrew (1985), and as they did not report the correlations between these variables, it is not possible to determine whether the crops with more variable numbers of tubers and yield per plant would have been less uniform than crops with lower plant-to-plant variation.

Although in this work, variation in seed tuber weight was only found to affect uniformity in Expt 6 in which there was a large difference in variation in seed tuber weight between treatments, in other situations smaller differences could potentially affect uniformity. The influence of seed tuber weight on the yield per plant would not be expected to differ substantially between varieties and between years, but the number of stems (and thus the number of tubers) varies both between varieties and between seed tuber stocks. If the slope of the relationship between seed tuber weight and the number of stems per plant was very shallow (e.g. as Firman 2014 found for Sapphire), then the number of tubers per plant may be insufficient to compensate for the effect of seed tuber weight on yield and, if this were the case, larger seed tubers could produce plants with a larger mean tuber size than small seed tubers consequently decreasing uniformity. Conversely, if the slope of the relationship was very steep (e.g. as Firman 2014 found for Perline) then larger seed tubers could produce plants with a smaller mean tuber size than small seed tubers and similarly decrease uniformity. The relationship between the yield per plant and the number of tubers per plant would also influence these relationships, with a less plastic variety such as Russet Burbank being more susceptible to changes in uniformity than a more plastic variety such as King Edward.

Understanding the mechanism by which plant-to-plant variations can affect uniformity allows the factors investigated to be differentiated. As previously discussed, changes in the variation in seed tuber weight affected plant-to-plant variation, but there was no effect on uniformity as larger seed tubers tended to produce higher yields, but also more tubers. Changes in the variation in emergence and within-row spacing were distinct from changes in the variation in seed tuber weight, as they affected variation in the yield per plant but without any corresponding change in the number of stems per plant. While there were compensatory effects of the number of tubers per stem varying, these were not sufficiently large to prevent the variation in mean tuber weight increasing.

#### 6.3.8.3. Pathology

The principles established in this work of how plant-to-plant variation affected uniformity can be related to previous findings of how some diseases decrease uniformity. The reanalysis of the data of Firman & Shearman (2006b) revealed that the decrease in uniformity caused by *R. solani* was associated with increased variation in the number of stems, number of tubers, yield and mean tuber weight per plant (Table 112). The pruning of shoots by *R. solani* (Hide *et al.* 1985a) can increase the variation in the number of stems per plant either by completely killing sprouts or by causing them to branch prior to emerging. This can increase the variation in the number of tubers per plant and, unless a proportional change in yield occurs, increase variation in the mean tuber size per plant and decrease uniformity.

Unlike typical infestations of *R. solani*, blackleg and gangrene can kill some plants within a crop prematurely. If this occurs early in the season, the plant produces no yield and thus cannot directly affect the tuber size distribution. However, the gap in the canopy left by the dead plant may be compensated for by neighbouring plants which produce higher yields and unless the number of tubers increases, larger tubers (Hide *et al.* 1995, 1996). If infection occurs later in the season, the plant would have a lower yield and consequently smaller tubers



which will contribute to decreasing uniformity and in addition the neighbouring plants may also compensate and produce larger tubers. Such a mechanism may explain the effects found by Firman (2004) where increasing levels of blackleg inoculum progressively increased the COV of tuber size.

#### 6.3.8.4. Commercial implications

Relating these findings to current commercial practice is challenging. While they suggest that growers should strive to space plants as evenly as possible and that prolonged emergence is detrimental, the extent of variation that can be tolerated remains unclear. The relatively small difference in emergence between treatments in Expt 4 had a similar effect on the variation in mean tuber weight to the much larger difference between the within-row spacing treatments. This suggests that variation in emergence may be of greater importance than moderate variation in within-row spacing. An important consideration however is that while the causes of variation in emergence are poorly understood and thus uncontrollable, variation in within-row spacing is easily quantified and manageable.

There remains a great deal of uncertainty over how different varieties respond to the factors investigated and further work is required to determine this. Ideally, a mechanistic approach would be taken to characterise varietal traits that affect uniformity and these could be used to advise growers on how to manage different varieties. For example, if the different responses to variable within-row spacing between Maris Piper and Markies were shown to be consistent, it would be worthwhile for growers to concentrate on achieving uniform spacing in Markies, but it would be less important in Maris Piper.

While variation in emergence caused relatively small differences in the COV of yield per plant in comparison to variation in seed tuber weight, because there was no compensatory effect of the number of stems, the changes in yield were detrimental to uniformity. Although emergence is frequently recorded in experiments, variation in emergence has rarely been

reported and it is therefore difficult to place the results of this work into context. Currently growers estimate the date at which emergence began, and when 50 % of plants have emerged, to schedule irrigation to control common scab, but the uniformity of emergence is not accurately determined. Mechanised planting probably leads to emergence being more protracted in commercial crops than in the experiments conducted in this work, but the extent of this difference must be determined to establish the importance of variation in emergence in affecting variation in tuber size. In the future, the use of unmanned aerial vehicles and automated image analysis may assist in quantifying the duration of emergence in commercial crops. It is important to distinguish plant-to-plant variations in emergence from within-field variations in emergence as was encountered between Surveys 3a & 3b. The factors that caused those differences were not determined in this work but probably differ, both in their cause and their effect on uniformity.

#### 6.4. Stem-to-stem variation

Although stems are the true individuals that compose the potato crop (Allen & Wurr 1992), the variation between stems has not previously been described. Investigating the growth of individual stems is severely complicated by entanglement of the roots, stolons and tubers growing from each of the stems of the plant within the soil (Figure 4), which has probably contributed to this variation not being quantified previously. For the same reason, in this study, the yield of individual stems was only recorded in Surveys 2 and 4 (and at the second harvest of Surveys 3a & 3b) as it was not practically feasible to harvest individual stems in replicated experiments. However, above-ground stems were harvested individually in the majority of the experiments, which as discussed in Section 6.3.1 provided an indication of the relative yield of individual stems within the experiments.

While insights have been gained from studying plant-to-plant variation, each value obtained for a plant is either the sum or the average of the individual stems. In some instances, this

probably increased the variability of relationships since plants with identical yields and numbers of stems could be composed of very different individual stems. For example a plant with two stems of similar yields and another with two stems of very different yields, would be unlikely to have the same number of tubers or mean tuber weight. Thus, although studying stem-to-stem variation is challenging, it is essential to understand the true nature of the processes that affect variation within the potato crop.

#### 6.4.1. Yield

A consistent finding of this work was that the yield of stems was substantially more variable than the yield of plants. Whereas the COV of yield per plant was *c.* 20-30 % in Surveys 2 & 4 (Tables 37 & 98) the COV of yield per stem was *c.* 50-60 % (Tables 39 & 102). Similar levels of variation in the above-ground stem weight were encountered in Expts 1, 3 & 4 (Tables 18, 24 & 58) and Surveys 3a-d (Tables 44, 48 & 50). None of the treatments significantly affected the COV of above-ground stem weight except for the high variation in within-row spacing treatment in Expt 4 (Table 58).

The populations of stems within the crops studied were therefore highly variable but the minimal effects of treatments on stem-to-stem variation, (even, as in Expt 4, where there were large differences in plant-to-plant variation) indicated that stem-to-stem variation occurred independently of plant-to-plant variation. For this to be the case, there must have been sources of variation influencing the growth of stems that were greater than those that influenced plants, and that were relatively unaffected by changes in plant-to-plant variation.

Fundamentally, the processes determining stem-to-stem variation in yield must have been similar to those that caused plant-to-plant variation in yield, since each plant was composed of a group of stems, and as discussed in Section 6.3.1, the mechanism of yield formation for individual plants was similar to that for crops. It is therefore possible to infer the causes of

stem-to-stem variation from the effects of the experimental treatments on plant-to-plant variation.

#### 6.4.1.1. Quantification

The largest stems produced the greatest proportion of the total yield, whereas there were many small stems which together only contributed a small proportion of the total yield (e.g. Figure 19). This distribution was analogous to that of the tuber weight distribution, and a method was required to account for the combined yield of the stems, rather than their frequency, as when the yield of tubers in each grade is measured and the variation quantified by the method of Travis (1987). Stems were grouped into classes as discussed in Section 3.1.3.3 and this method had the advantage of giving less influence to the smallest stems, which could potentially have distorted the COV of above-ground stem weights. Despite this different method of analysis, differences in the transformed and weighted COV of above-ground stem weight were only observed where there were also differences in the untransformed and unweighted COV of above-ground stem weight.

#### 6.4.1.2. Emergence

As with the date of emergence of individual plants, the date of emergence of individual stems could not be explained by any of the factors examined in this work. In Survey 2, the interval from 20 to 80 % emergence was *c.* 1 day longer for stems than plants (Section 4.5.2) and in Survey 4, the interval was < 1 day longer for stems than plants in any varieties except King Edward, for which the interval was 1.3 days longer (Table 77). These findings suggest that while the slightly more protracted emergence of stems may have contributed to the higher COV of yield per stem than the COV of yield per plant, it is unlikely that this accounts for such a substantial difference, considering the modest increases in the COV of yield per plant caused by greater differences in the duration of emergence in Expts 2 & 4.

Earlier-emerging stems produced higher yields in both Surveys 2 & 4, but the date of emergence only explained 22-33 % of the variation at the final harvest (Table 40, Table 104) except in the case of Desiree, where only 4 % of the variation in yield was accounted for. In Survey 2, this was similar to the proportion of variation in yield per plant explained by emergence (Table 38) but higher than in Survey 4, where the date of emergence only explained 5-17 % of the final yield per plant (Table 100).

#### 6.4.1.3. Number of stems per plant

That the yield per plant was relatively insensitive to the amount of space in the row in Expts 3-5 indicates that the local stem density (essentially the number of stems per plant) was also unlikely to have substantially affected the relative growth rate of stems, since the development of stems was similarly as plastic as that of plants. In Survey 4, it was observed in all four varieties that during the initial phases of growth, in which stems from the same plant were competing, the leaves of each stem were orientated such that the entire leaf area was unshaded (Figure 106). In view of the general shade-avoidance strategies that plants have evolved to increase their fitness by maximising opportunities to forage for light (Ballare *et al.* 1997) it was not surprising to observe that stems developed in this way. Late-emerging stems may have been at some disadvantage as they probably allocated a greater proportion of their weight to the main-stem for it to elongate and position their leaves in full sunlight.

**Figure 106. Photographs demonstrating that late-emerging stems were not shaded by their neighbouring stems. The photographs were taken nine days after the first stem emerged and four days after the smallest stem emerged.**



#### 6.4.1.4. Changes over time

In Surveys 2 & 4, the COV of the above-ground stem weight decreased between the first and second harvests taken approximately 7 and 14 DAE from 84 to 64 % in Survey 2 (Table 32) and from an average of 69 to 56 % in Survey 4 (Table 90). This would be unlikely to occur if growth was determined entirely by the leaf area of the stems and indicated that the relative growth rate of the smallest stems was higher than that of the largest stems between these harvests, thus reducing the overall variation. In Survey 2, from 33 to 131 DAE, the COV of the above-ground stem weight increased from *c.* 60 to 70 % but the COV of yield per stem remained at *c.* 60 % from 44-131 DAE (Table 39). As the harvests were unreplicated it was not possible to distinguish temporal changes from chance variations between the sampled areas, but there was no consistent trend between harvests.

In Survey 4, from 28 to 120 DAE, the relative size of stems was stable in all varieties except King Edward, as indicated by their cross-sectional area at the third harvest correlating strongly with their yield at the fourth and fifth harvests (Figure 81). This finding is helpful to understand how the final yield of each stem was reached, since this period was when the majority of yield was formed and indicates that the variation in yield was largely determined

prior to 28 DAE, rather than being due to differences in growth after the canopy had closed. Although the canopies of the crops lodged between the fourth and fifth harvests, this did not substantially alter the size hierarchy that existed previously. The weaker relationship in King Edward was associated with variable senescence of stems with some having ceased growth one month prior to the final harvest.

#### 6.4.1.5. Seed tuber substrate

Given that the mobilisation of dry weight from the seed tuber was found to affect the growth of plants (Section 6.3.2), it was sensible to establish the role of the seed tuber on the growth of individual stems. There is a fundamental difficulty in doing so, since the stems of each plant are competing for a single resource (Moorby 1967) and no method was used by which definitive conclusions could be reached (e.g.  $^{14}\text{C}$  labelled seed tubers). However, the following analysis is consistent with the previously discussed findings for the growth of entire crops and individual plants. Two relationships will be considered: that between seed tuber weight and the total proxy diameter of below-ground stems, and that between the proxy diameter of each below-ground stem and the weight of each above-ground stem.

For the seed tuber substrate to affect the growth rate of plants after emergence, nutrients must be mobilised and transported from the seed tuber to the developing leaves and a thicker sprout should allow for a greater rate of transport from the seed tuber. In Surveys 2 & 4, the weight and planting depth of each below-ground stem was established (after removing roots and stolons). From these measurements, a proxy measure of the stem diameter was calculated – a below-ground stem that was heavier, but of the same length (planting depth) must also have had a larger average diameter. This method was advantageous over measuring the stem diameter directly, since the below-ground stems were not uniform cylinders and measurements of weight and length were considered less subjective and error-prone.

In both Surveys 2 & 4, the proxy below-ground stem diameter per plant increased in proportion to the seed tuber weight *c.* 7 and 14 DAE (Table 30; Table 84). The proxy below-ground stem diameter per plant also increased as the number of stems per plant increased and increased the correlation coefficients of the relationships from *c.* 0.45 to 0.65 in Survey 2 (Table 30) and from *c.* 0.60 to 0.75 in Survey 4 (Table 84). The implication of these relationships is that while the number of stems per seed tuber varied widely for seed tubers of the same weight (as discussed in Section 6.3.3), the total diameter of the stems was relatively similar and the average below-ground stem diameter of plants decreased as the number of stems per plant increased.

Although these allometric relationships between the seed tuber weight and the diameter of the below-ground stems have not previously been established for conventionally sized seed tubers grown in the field, other evidence corroborates these findings. Headford (1962) found the weight of the seed tuber piece affected the dry weight of the sprouts that it produced and that the total weight of sprouts was unaffected by the number of sprouts (i.e. the average weight and therefore diameter decreased as the number of sprouts increased). Working with minitubers (187-3000 mg), Lommen (1994) found that the diameter of stems at emergence increased as the weight of the minitubers increased.

The correlation between the proxy below-ground stem diameter and the above-ground stem weight strengthened between *c.* 7 and 14 DAE and the slope of the relationship increased (Figs 33 & 77). That the slope of the relationships increased suggests that the correlations were not the result of the above-ground stem weight increasing the proxy below-ground stem diameter since, if this were the case, stems with an equal above-ground stem weight would have been expected to have equal below-ground stem diameters at each harvest. When the date of emergence of each stem was considered along with the proxy below-ground stem diameter, *c.* 80 % of the variation in above-ground stem weight could be explained at the first



three harvests of Survey 2 (Table 34) and *c.* 90 % in Survey 4 (Table 94). Such strong relationships in two years in Maris Piper and in each of the varieties in Survey 4 suggest that these two factors were important determinants of the early size of stems.

Given the relationships that existed between the seed tuber weight and the total proxy diameter of the below-ground stems, and between the below-ground stem diameter and the above-ground stem weight, it is logical that the proxy below-ground stem diameter provided an estimate of the relative amount of seed tuber substrate that each stem of a plant received from the seed tuber. Svensson (1966) estimated the seed tuber substrate per stem and assumed that each stem on the same plant shared the seed tuber substrate equally, but since stems growing from the same seed tuber were of different sizes shortly after emergence (Figure 76), this was an invalid assumption. At the first three harvests of Survey 2, the COV of seed tuber substrate per stem was *c.* 55 % (Table 35) and at the first two harvests of Survey 4 it was 46-50 % in each of the varieties. Despite the seed tuber weight varying substantially in Survey 3d, the COV of seed tuber substrate was 38 % and thus lower than in Surveys 2 and 4 (Figure 55). Interestingly, these differences in the COV of seed tuber substrate per stem were also associated with differences in the COV of yield per stem (above ground stem weight in Survey 3d) at the final harvests (Tables 39, 50 & 102).

The high variation in seed tuber substrate per stem is crucial to understanding its importance in determining the relative yield of stems. The seed tuber substrate per stem could only be estimated through destructive harvesting and so it was not possible to determine directly its influence on the final yield of stems. However, the results of Expts 1, 4 & 6 in which there were differences in variation in seed tuber weight between treatments provide evidence that can be applied to stem-to-stem variation, if we consider that the processes that determine the growth of the plants were equivalent to those that determined the growth of stems. The trend from these experiments was that, as the variation in seed tuber weight increased, seed tuber

weight explained a greater proportion of the variation in the yield per plant (Tables 20 & 71; Figure 61). The implication for stem-to-stem variation is that the wide variation in seed tuber substrate per stem, made it a more substantial cause of variation in the yield per stem than variation in seed tuber weight as a cause of variation in the yield per plant.

Further experimental work is required to establish conclusively the importance of variation in the seed tuber substrate per stem in determining variation in the yield per stem. Planting minitubers of different weights, but which are predicted to produce only single stems (as found by Firman 2015), close together to simulate a plant would be the most controllable way by which to manipulate seed tuber substrate per stem, but would be of limited practical applicability. The COV of seed tuber substrate in Desiree was 38 % in Survey 3d (Figure 55) and 46 % in Survey 4 (Table 95) and in Maris Piper was 55 % in Survey 2 (Figure 41) and 47 % in Survey 4 (Table 95) demonstrating that the seed tuber substrate per stem is not fixed within a variety. It would be useful to quantify how the COV of seed tuber substrate changes as the chronological age of seed tubers increases, since the distribution of seed tuber substrate per stem could conceivably change as the average number of stems per seed tuber changes.

#### 6.4.1.6. Overview

In Survey 2, the yield per stem decreased as the interval from planting to emergence increased and as the number of stems per plant increased (Table 40). The amount of variation that could be explained by these factors varied between harvests, but typically each factor explained *c.* 25-40 % of the variation and in multiple regressions they consistently explained *c.* 50-60 % of the variation (Table 40). Both of these factors also affected the yield per stem in Survey 4 and as in Survey 2 explained *c.* 50 % of the variation (Table 104). Later emerging stems would have produced lower yields for the same reason as plants did (Section 6.3.3), but they may have been at an additional disadvantage if they emerged later than stems growing from the same seed tuber, since the percentage dry matter of the seed tuber would

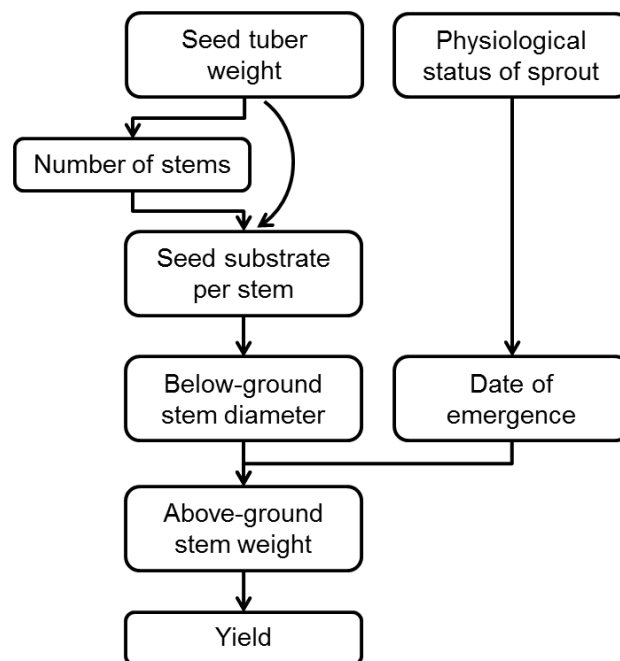
have been lower by the time they emerged, decreasing the quantity of seed tuber substrate available to them.

It is difficult to establish whether the number of stems per plant affected the yield per stem due to the seed tuber substrate per stem decreasing as the number of stems increased, or due to the increased number of stems reducing the space available for them to grow in. The number of stems per plant only explained *c.* 10 % of the variation in the above-ground stem weight at the first two harvests of Survey 2 (Table 33) and at that date emergence was the predominant factor determining stem size. Similar relationships were found in each of the varieties in Survey 4 (Table 92). Density must play some role in determining the yield of each stem since, if two stems were of identical sizes, but one had neighbours shading its leaves and the other was growing in isolation, the growth rate of the isolated plant would be higher. However, the extent of the difference is unclear as is the relative importance of this competition between stems within plants in determining the variation in the yield per stem in comparison to the influence of their initial size. It was anticipated that the relationships between the cross-sectional area of stems 28 DAE (prior to canopy closure) and their yield 120 DAE (Figure 81) would be strengthened by accounting for the number of stems per plant, but this was not found.

Whilst Allen & Scott (1980) concluded that seed tuber substrate was not an important factor in the growth of the potato crop, the crucial difference with this analysis is that while the average seed tuber substrate per stem is of little importance to overall yield, the variation in seed tuber substrate within a seed tuber stock is so large that it represents a substantial source of variability that is present prior to any competitive interactions caused by differences in emergence or the space per plant. The same principles apply as in the previous discussion (Section 6.3.2) of the influence of seed tuber weight on the yield of plants, except that the variation in seed tuber substrate per stem was estimated to be considerably higher than that of

the variation in seed tuber weight within a 10 mm size grade of seed tubers and so it is even more important in determining the relative yields of stems. This analysis has led to the formulation of the model shown in Figure 107. That plant-to-plant variation was reduced to c. 15 % in Expt 4 when the seed tuber weight and emergence were as uniform as possible suggests that there could be substantial decreases in stem-to-stem variation in yield if the seed substrate per stem and emergence of stems were less variable.

**Figure 107. Processes that determine the relative yield of stems within the crop.**



#### 6.4.2. Number of tubers

The quantity of incident radiation during tuber initiation can affect the average number of tubers per stem within crops (Gray & Holmes 1970; Sale 1976; O'Brien *et al.* 1998; Firman & Daniels 2011). It was therefore anticipated that the number of tubers per stem would increase as above-ground stem weight increased as, this correlated with the leaf area of the stem and therefore the amount of radiation intercepted during tuber initiation. Such relationships were found c. 30 DAE in Surveys 2 & 4 and explained c. 30-50 % of the variation in the number of tubers per stem (Table 41; Figure 79). Yield per stem was a proxy measurement of the total quantity of radiation intercepted over the season, and assuming the

non-destructive measurements of stems in Survey 4 were typical, reflected the size of the stem shortly after tuber initiation (Figure 81). The proportion of variation in the number of tubers per stem explained by yield per stem at the final harvest of Survey 2 was similar to the proportion explained by the weight of the above-ground stem at *c.* 30 DAE although the correlations strengthened at successive harvests (Table 41). In Survey 4, the strength of the correlations between the number of tubers per stem and above-ground stem weight 28 DAE were similar to those between the number of tubers per stem and yield per stem 120 DAE in Desiree and Russet Burbank, but the correlation coefficients increased from *c.* 0.45 to 0.59 in Maris Piper and King Edward (Tables 96 & 106). As the relative size of stems did not change substantially from 28-120 DAE (Figure 81) and tubers would not have initiated after 28 DAE, this may indicate that in Maris Piper and King Edward, stems with a relatively high number of tubers for a given yield may have been more likely to resorb tubers which could account for the stronger correlation at 120 DAE.

At the final harvest of Survey 4, the slope of the relationships between the yield and number of tubers per stem for different varieties was consistent with how the varieties respond to changes in stem density. In King Edward, the number of tubers per stem increased steeply as the yield per stem increased; whereas in Russet Burbank, the slope of the relationship was shallower and there was a five-fold range in the yield of stems with five tubers (Figure 82). These relationships were similar to what would be predicted from relationships between stem population and tuber population previously established for entire crops of King Edward and Russet Burbank (Firman & Daniels 2011; Figure 7).

At 28 DAE, tuber initiation would have been complete (O'Brien *et al.* 1998) and stems with higher above-ground stem weights would have intercepted more solar radiation, and it was surprising that the correlation between above-ground stem weight and the number of tubers per stem was not stronger. The analysis of factors affecting yield per stem in this work

showed that at tuber initiation, stems with higher above-ground stem weights were those supplied with greater quantities of seed tuber substrate. From this perspective, it is impossible to distinguish between the influences of seed tuber substrate and the quantity of solar radiation intercepted. It is therefore uncertain what determines the number of tubers per stem but it may be relevant that the process of tuber formation begins with stolon growth that starts shortly after emergence (Struik *et al.* 1991). While incident radiation can influence the average number of tubers per stem, other factors appear to be responsible for causing the variation between stems.

#### 6.4.3. Tuber size

Of the many relationships examined in this work, the most important finding was that the mean and maximum tuber weight per stem correlated strongly with yield per stem as the increase in the number of tubers per stem as yield per stem increased was insufficient to counter the effect of yield on tuber size (Table 41; Figs 41 & 83). This occurred at each sampling date throughout the season in Surveys 2 & 4 and also at the second harvest (*c.* 40 DAE) in Surveys 3a & 3b (Figure 41). Although there was high variation in tuber size within stems (Tables 42 & 109), these relationships indicate that the higher yielding stems within the crops produced the largest tubers. This is consistent with the findings from individual plants and with existing knowledge of mean tuber size between crops as discussed in Section 6.3.7. The extent of variation in yield between stems and the relationship between the yield and mean tuber weight of stems meant that the extent of variation in mean tuber size between stems was greater than that between individual plants.

Although the mean tuber weight correlated strongly with the yield per stem in Surveys 2 & 4, predicting the effect of reducing variation in the yield per stem on the COV of tuber size was complicated by the variation in the number and relative size of tubers on each stem. A simple method to simulate reducing variation in the yield per stem was to sort the stems by their

yield and split the crop into four groups each containing 25 % of the total yield and calculate the mean tuber size of each group and the COV of tuber size for the group containing 25-75 % of the yield. In Survey 2, the COV of tuber size was *c.* 3 % lower for the group of stems containing 25-75 % than for all stems at the seventh and ninth harvests (Table 115). In Survey 4, the reduction in the COV of tuber size was less in Maris Piper (*c.* 1 %; Table 116). In Desiree and Russet Burbank, the effect of reducing variation in the yield per stem on the COV of tuber size was greater, decreasing it by 3-4 % and in King Edward the effect was intermediate, reducing it by 2-3 % (Table 116). The extent of these reductions in the COV of tuber size were linked to the difference in the mean tuber size between each of the groups, and in turn to the relationships between the yield per stem and the number of tubers per stem. The implication of this analysis is that changes in the variation in the yield per stem will impact on the COV of tuber size, but the extent of the effect will vary between varieties. Consequently, the framework for studying plant-to-plant variation set out by Benjamin & Hardwick (1986) is relevant to the uniformity of potato crops despite there being an extra level of variation below that of the individual stems.

The cause of the considerable variation in tuber size on individual stems remains obscure. It was conceivable that greater competition between tubers on stems with more tubers would increase the variation; but no such trend was apparent in Surveys 2 & 4. While it would improve the uniformity of the crop if this variation could be reduced (Table 119; Figure 99) it is uncertain what determines this variation and whether it can be decreased. Struik *et al.* (1991) discussed possible physiological causes of this variation, but only presented data for individual plants rather than stems. It is likely that the factors affecting this variation are distinct from those examined in this work and could be studied separately from stem-to-stem variation. The high degree of variation in the COV of tuber weight between stems (Figure 38; Tables 42 & 109) would make finding significant differences difficult, and the ratio between

the arithmetic mean tuber weight and mean tuber weight may provide an alternative quantitative measure (Section 5.4.2).

## 6.5. Physiological and genetic perspectives

This work has concentrated on macroscopic physiological descriptions of the potato crop but relating the findings to current microscopic physiological and genetic understanding of the potato crop is also of interest. Their relation to uniformity is speculative, since variation in tuber size has not been studied from these perspectives.

### 6.5.1. Potential physiological causes of variation in tuber size

#### 6.5.1.1. Branching

The production of stems by the seed tuber, and stolons by the stem are both instances of shoot branching, a topic of fundamental importance in plant development (Domagalska & Leyser, 2011). Considerable progress has been made in elucidating the regulation of shoot branching and it involves multiple factors including light, sugars, nitrogen, auxin, strigolactones and cytokinins (Rameau *et al.* 2015). While there are probably similarities with above-ground shoot branching in model plants, the production of stems and stolons is distinct in that their development is not directed to maximise the interception of light. An exhaustive description of the molecular physiology of branching is outside the scope of this work, but recent and relevant findings which may have a bearing on uniformity will be discussed.

Working with a diploid backcross population Celis-Gamboa *et al.* (2003a) concluded that stolon branching was important for determining the number of tubers. The study focussed on understanding the temporal variation in tuber development between varieties and did not state the number of tubers formed either per plant or per stem, but in a sister publication Celis-Gamboa *et al.* (2003b) reported there were on average *c.* 10 tubers per stem meaning that the findings are of little relevance to commercialised tetraploid varieties that typically



produce *c.* 3-5 tubers per stem (Firman 2014). In this work, although not quantified, stolon branching was rarely observed and probably did not account for the variation in the number of tubers per stem either within or between genotypes. Tuber position in relation to stem architecture was not quantified in this work, and distinguishing whether tubers formed on primary, lateral or branched stolons (as done by Brierley & Firman 2000) would provide further insights. For example, the number of primary tubers could be consistent, with plasticity in the number of tubers due to the formation of tubers on lateral and branched stolons. Similarly, it is uncertain whether varieties that produce more tubers per stem do so because they produce more stolons, or because a greater proportion of stolons tuberise.

Pasare *et al.* (2013) silenced *CCD8*, a gene involved in the biosynthesis of strigolactones, a family of plant hormones that regulate branching. Silencing of *CCD8* had numerous effects on plant development but of most relevance to this work, it increased the number of tubers per stem cutting by up to 3.9 times compared to wild-type Desiree and increased the number of stems per plant although this was not quantified and plants were not propagated from seed tubers. Nicholas *et al.* (2015) established that there is an alternative splice site in the *BRANCHED1a* gene of *Solanum* that results in two forms being produced. The long form is a transcription factor that inhibits shoot and stolon branching whereas the short form is inactive as a transcription factor and interacts with the long form preventing it from acting as a transcription factor. Silencing *BRANCHED1a* resulted in excessive stolon growth and increased the frequency of branched stolons in comparison to the wild type. The authors suggested that the ratio of these two forms of *BRANCHED1a* could be influenced by the environment and fine tune the extent of branching.

Pasare *et al.* (2013) and Nicholas *et al.* (2015) reported substantial effects on both above- and below-ground development by modifying the expression of single genes but without relating these findings to variation between varieties it is unclear how important these genes are in

determining phenotypic variation in practice. Varietal characterisation has shown that the number of stems per seed tuber and the number of tubers per stem vary independently (Firman 2014). In crops, major determinants of above-ground branching are stem density and nitrogen supply (Vos 1995) but stem density may only have limited effects on the number of tubers per stem depending on the variety (Firman & Daniels 2011) and nitrogen generally has no consistent effect beyond any that can be accounted for by increased radiation interception as a result of faster canopy development (Firman *et al.* 2007). These agronomic experiments indicate that branching of the seed tuber, above-ground stem and below-ground stem occur independently and it is difficult to reconcile this with the current molecular understanding.

The response of the number of tubers to the yield per stem is potentially most simply explained by sucrose stimulating the initiation and retention of tubers. Sucrose alone is sufficient to induce tuberisation during *in-vitro* microtuber production (Garner & Blake, 1989) and the production of more propagules when resources are more available would be consistent with the relationships between plant size and seed number in cereal crops (Sadras 2007) and with shading experiments in potato (O'Brien *et al.* 1998). This cannot explain the different responses between varieties however and the physiological differences between varieties with different responses of tuber population to stem population (e.g. King Edward and Russet Burbank) are undetermined.

#### 6.5.1.2. Tuberisation

An area that has received considerable attention is the identity of mobile tuberisation signals first demonstrated to exist in the 1950s (Gregory 1956), that move from the leaves to the stolons (Jackson 1999). Navarro *et al.* (2011) found evidence that two paralogues of the mobile FLOWERING LOCUS T protein can induce tuberisation, even in varieties that tuberise under long-day conditions. A simple mechanism to explain variation in tuber size on stems is that it is a consequence of differential timing of tuber initiation, with those that

initiate first remaining largest throughout the season. That stolons on the same stem initiate tubers at different times, indicates that stolon tips differ in their sensitivity to the signal produced by the leaves and the reason for this is uncertain.

Although there is extensive knowledge of the role of hormones and genes involved in tuberisation (Ewing & Struik 1992; Kloosterman *et al.* 2008), the relevance of this to improving uniformity is uncertain as investigations have focussed on understanding the formation of tubers in general (and primarily only tuber initiation), rather than on either the causes of differential timing of tuber initiation or competition between tubers. In an analogous manner to how variation in emergence and number of stems per plant could not be explained by the same factors which explain the mean, understanding the precise sequence of events that lead to the development of single tubers may not provide any insights into the causes of variation between tubers. Vreugdenhil & Struik (1989) suggested potential causes of variation between tubers developing differently including that: groups of stolons are influenced by different leaves on the stem that in turn affects when they initiate; the distance of a stolon to either the leaves or the seed tuber causes differences in the supply of hormones; mechanical stress as stolons extend causes ethylene to be produced; stolons differ in the sensitivity to hormone levels. Struik *et al.* (1999) recognised the importance of studying tuber formation at the level of whole plants and in relation to the whole crop, but this has seemingly not prompted any further developments and the hypotheses of Vreugdenhil & Struik (1989) remain untested.

The results of this work demonstrate that an even broader approach than studying tuberisation within plants, as suggested by Struik *et al.* (1999), is required to improve the crop because it is a population of individual stems of different sizes, and the processes that lead to variation in tuber size begin with the production of sprouts by the seed tuber. The sprouting behaviour of seed tubers has been studied extensively but primarily in relation to limiting sprout growth

in storage (e.g. Burton *et al.* 1992; Sonnewald & Sonnewald 2014) rather than understanding the factors that affect the growth of individual sprouts in the field and how their relative size and date of emergence is determined. Beyond the number of stems that a seed tuber stock produces and when 50 % emergence will occur, our knowledge of how seed tubers sprout under field conditions is limited. Bradshaw *et al.* (2008) reported that there was a negative correlation between sprouting of tubers in storage and emergence between clones in a breeding population and interpreted this as being caused by genetically determined differences in dormancy. Varieties also differ in the duration over which tubers break dormancy when sprouted in controlled environments (van Ittersum 1992; Firman *et al.* 1999), but it is unclear whether this translates into differences in uniformity of emergence. Darsow (2014) reported that uniformity of emergence differed in a breeding population but did not establish the consistency of this between years which would be necessary to demonstrate that the differences were genetic rather than physiological.

#### 6.5.1.3. Resource allocation

Under optimal environmental conditions, overall growth of the potato crop is determined by the capacity of the canopy to intercept light (i.e. source driven; Allen & Scott, 1980). Allocation of assimilate between the canopy and the tubers is genetically determined but also influenced by the environment, particularly by nitrogen supply (Allison *et al.* 2012). The pattern of allocation between stems in the crop is similar to that of the whole crop as evidenced by the strong correlations between above-ground stem weight and tuber yield (Section 6.3.1). Engels & Marschner (1986) noted that unlike the development of tomato fruits where sink strength decreases as fruits develop, in potato tubers, sink strength increases as their fresh weight increases. Further, in fruit, as well as cereals grains, cell division occurs during initial development and is followed by cell expansion (Engels & Marschner 1986), whereas in potato tubers, cell division and expansion occur simultaneously (Plaisted 1957).

These differences may be related to tubers initiating earlier in crop development compared to other storage organs and because tuber growth is indeterminate.

Gray and Smith (1973) suggested that tubers are supplied with assimilate preferentially from particular leaves, suggesting a source influence on the growth of individual tubers. However, this has not been examined critically in the field, for example by establishing whether leaf removal increases variation in tuber size. Oparka (1985) found that in a field-grown crop, the amount of assimilate transported to tubers correlated with their fresh weight when samples were taken at different times during the season, indicating that allocation between tubers was sink-driven. Since no direct measurements of individual tuber growth were made in this work, no indication of the importance of source-sink relationships to uniformity could be ascertained. The slight increases in the estimated COV of tuber size per stem over the course of the season (Tables 117-118) suggests assimilate is partitioned differentially between tubers as they grow, but this could be either source or sink determined. That the change was relatively small indicates that these changes during tuber bulking are relatively unimportant in comparison to those which occur as a result of differential timing of tuber initiation.

#### 6.5.2. Improving existing varieties

Due to the consumer preference for established varieties such as Maris Piper and King Edward, it is worth considering whether there are methods by which existing varieties could be manipulated to produce a more uniform crop. Previous attempts to improve uniformity investigated how external factors influenced variation in tuber size (e.g. drought, fertiliser rates and pathology) but less attention has been given to how factors internal to the seed tuber affect uniformity. The mechanistic approach taken in this work has shown that the processes that determine variation in tuber size begin prior to planting. Establishing the factors affecting the COV of seed tuber substrate per stem may lead to improvements in uniformity by reducing variation in yield per stem. Potential factors which could affect this include the

management of the seed tuber crop and the chronological and or physiological age of seed tubers.

John Green, a founding grower member of Cambridge University Potato Growers Research Association, proposed that the ideotype of a potato population would consist of evenly spaced, small seed tubers, producing single stems. Such populations are achievable (e.g. Firman 2015) but a disadvantage is that it requires higher numbers of seed tubers than when multiple stems are produced and would therefore be less economical. The findings of this work suggest that this ideotype may be unnecessary however, since the final size of stems was influenced more by their initial weight than by their amount of space in the row or the number of stems per plant. Consequently, the ideotype would be for a physiological state where the number of stems per plant correlates more strongly with seed tuber weight and crucially, where the stems produced by each seed tuber are of relatively similar sizes at emergence so as to produce an even stand.

### 6.5.3. Breeding for uniformity

Breeding of new potato varieties remains relatively empirical and genetically unsophisticated due to the difficulty of understanding the genetic basis of economically important traits in tetraploids (Bradshaw *et al.* 2008). While the potato genome has been sequenced (The Potato Genome Sequencing Consortium 2011), there are currently few genetic markers that are routinely used during breeding (Jansky *et al.* 2016). Due to the physiological complexity of uniformity, any directed attempts to improve uniformity through breeding would require splitting the trait into underlying component traits (Yin *et al.* 2004). Although uniformity is a desirable trait, no specific attempts to improve uniformity have been reported, but with the ever-increasing demand for uniform produce combined with the need to reduce food wastage, the trait will probably become more important in the future. Given the ability to add pest and disease resistance traits to potato varieties through genetic modification (e.g. Green *et al.*

2012; Jones *et al.* 2014), the aims of breeding programs may shift away from the current objectives of improving disease resistance in existing varieties, towards improving more complex polygenic traits such as yield and uniformity, to which monogenic traits could be added through genetic modification.

Without detailed phenotypic descriptions such as those made in this work, attempts to breed more uniform varieties can only assess it as an individual trait, with no appreciation of the underlying sub-traits. The ideotype for producing a uniform tuber size distribution would have evenly-sized and uniformly-emerging sprouts, plasticity in the number of tubers per stem and canopy development, and initiate tubers over a short period of time. Innumerable genes must be involved at different stages of development relating to dormancy, sprout development of seed tubers, competition between sprouts for reserves of the mother tuber, stolon development, tuber initiation and allocation between tubers. There are multiple ways in which these traits could be adapted to improve uniformity because identical tuber size distributions could be achieved through different combinations of traits.

The relationships between the number of tubers per stem and the yield per stem identified in Survey 4 differed between varieties and were consistent with density experiments (Firman & Shearman 2006a; Firman & Daniels 2011) demonstrating that there are differences between varieties in traits that influence uniformity. If the number of tubers per stem increased in proportion to yield, then variation in yield per stem would be unimportant since there would be little variation in mean tuber weight per stem. A disadvantage of this ideotype however is that the tuber population would be constant and stem density could not be altered to manipulate mean tuber size. Seed tubers that produced more evenly-sized sprouts would reduce variation in yield per stem and improve uniformity in varieties where the relationship between yield and number of tubers per stem was similar to in this work. While collecting data on the yield and number of tubers per stem is arduous, this work has shown that the

characteristics can be determined from simpler measurements. When a full canopy is present, the above-ground stem weight is closely related to the yield per stem and so measuring variation in above-ground stem weights can provide an estimate of the variation in yield per stem. Similarly, relationships between the yield and number of tubers per stem can be inferred from the relationship between the average yield per stem and average number of tubers per stem, calculated per plant. Thus, recording the yield, number of stems and number of tubers per plant provides an estimate of the slope of the relationship between the yield per stem and number of tubers per stem. Reducing variation in tuber size on individual stems would also improve uniformity, but it is unclear how feasible this would be, since quantifying the variation in size in a small sample is challenging. However, without optimising the variation in yield per stem and number of tubers per stem, reducing variation in tuber size on individual stems could only result in modest improvements in uniformity (Table 119).

It is unsurprising that previous attempts to assess uniformity in breeding programs concluded that the trait was inconsistent and has low heritability given the crude methods of assessment (Love *et al.* 1997; da Silva *et al.* 2006; Darsow 2014). Establishing better screening methods would probably improve the success of breeding programs, but a major obstacle is that breeders initially select individual plants whereas uniformity is a property of the population. Typically, it is not until the fourth year that 24 plant plots are grown from which the first representative (but still unreplicated) assessment of a guarded area of crop can be made (Slater *et al.* 2014). By this stage many clones will have been discarded that potentially had useful traits. Further, as shown by the high standard errors of the COV of tuber size in this work, the uniformity of a variety can vary considerably in an identical environment, so even in the fourth year of selection, assessments may provide a poor estimate of uniformity.

The majority of research on tuberisation has relied on reverse genetics to establish the role of single genes on development. The resultant phenotypic differences (e.g. of Pasare *et al.* 2013;



Nicholas *et al.* 2015) are extreme in comparison to those between varieties suggesting that more subtle genetic differences are responsible for the variation that occurs through breeding. To produce improved varieties, a forward genetics approach that sought to characterise differences between existing varieties would be more successful. After identifying varieties that display consistent differences in uniformity and determining the associated sub-traits, quantitative trait loci (QTLs) could be identified in their genomes (Collard & Mackill 2008). Once determined, QTLs would expedite the production of improved varieties since marker-assisted selection could be performed on seedlings and so new clones would not need to be grown for several years before uniformity could be assessed. These techniques have been successfully applied to identify sources of pest and disease resistance as well as some tuber quality attributes but they have generally been restricted to use in diploid varieties (Bryan 2011). Although Bryan (2011) noted the importance of uniformity of tuber size as a quantitative trait, no reports of attempts to identify QTLs were given, demonstrating the lack of progress in this area. An alternative approach to determine parts of the genome that influence polygenic traits is association mapping which has been successfully applied in tetraploid populations (D'hoop *et al.* 2008). Gebhardt (2011) noted that accurate phenotyping is crucial to the success of association mapping however and at present such data are not available and would require considerable resources to acquire.

There are probably evolutionary trade-offs that are at least partially responsible for variation in tuber size in potato crops. Wild genotypes in which all stems emerged uniformly would be more susceptible to frost and pest damage. Natural selection would favour genotypes that emerged over a range of time to reduce the chance of single events leading to extirpation. Trade-offs exist between the number of seeds produced and their size (Westoby *et al.* 1992) and although there are probably different evolutionary pressures on tuber size in comparison to true seed size (e.g. tubers are not dispersed), there must be similarities. Within a genotype there could be advantages to producing numerous small tubers (with fewer reserves but less

susceptible to predation) as well as fewer large tubers (with many reserves but more susceptible to predation) so as to optimise fitness in a range of conditions.

As well as morphological traits, pathology and management are major determinants of uniformity and a purely morphological approach to breeding uniform varieties would not necessarily result in more uniform crops in practice. In commercial production, disease pressure from *Rhizoctonia solani* and *Phoma foveata* may be higher than in breeding programs. In addition, within-row spacing is variable and yield varies spatially. To achieve optimal uniformity, varieties must therefore also be resistant to these diseases and display plasticity in the growth of the canopy so that variation in mean tuber size is reduced when variation in yield occurs within crops or when within-row spacing is variable. While there are almost certainly opportunities to improve uniformity through breeding, the role of the grower will remain crucial in ensuring that the potential uniformity of a variety is achieved through precise crop management.

#### 6.6. Further research

This work has revealed that our current understanding of the basic development of the potato crop is incomplete and opened up many areas for further research encompassing breeding, physiology and agronomy. Researchers across these disciplines should work together more closely, integrating genetic and physiological understanding of the potato crop with agronomic principles and relaying the needs of the potato grower to all disciplines of potato research.

Two fundamental areas where our knowledge is lacking are the genetic causes of differences in the number of stems per seed tuber and the number of tubers per stem. These traits are not only relevant to uniformity but also to optimising the mean tuber size of crops for different markets. As well as influencing the inherent uniformity of a variety, these relationships also affect how they respond to the environmental factors investigated in this work. In varieties

where the slope of the relationship between seed tuber weight and number of stems is relatively small and where the number of tubers per stem is relatively constant at different densities, seed tuber weight will correlate with mean tuber size per plant and the use of tightly graded seed tubers (e.g. 5 mm) could improve uniformity. Varieties where the number of tubers per stem is responsive to changes in density should be less susceptible to variation in within-row spacing causing decreases in uniformity since any increase in the variation in yield per stem would have less of an effect on variation in mean tuber weight per stem. If these principles could be established for a limited set of extreme varieties, it would allow predictions to be made about how other varieties will respond, from the same simply quantified relationships used to determine optimum seed rates. Comparing varieties with similar relationships between stem population and tuber population would allow the relative importance of plasticity in canopy growth on the response to variation in within-row spacing to be determined.

Intimately linked to the number of stems per plant is the variation in seed tuber substrate per stem. Although this work established that it is an important cause of stem-to-stem variation it could not be manipulated and establishing how variable this factor is between varieties and whether it varies with seed tuber physiology should be a priority for future research. If it could be reliably manipulated, it would allow the relative importance of seed substrate on the final distribution of yield per stem to be determined and indicate whether or not it is a factor that should be manipulated through breeding in order to improve uniformity.

The relative importance of variation in emergence to uniformity remains uncertain since the duration of emergence in commercial crops has not been widely quantified. While it is apparently simple to collect such data, predicting when emergence begins and the necessity of regular visits to crops makes this practically challenging. Time lapse photography or the use of unmanned aerial vehicles may improve the ability to collect such data. The genetic and

physiological characteristics that determine variation in emergence are also uncertain and it would be of great interest to improve our understanding of this trait by quantifying the relative importance of soil conditions, seed tuber physiology and genetics. Development of x-ray tomography could allow the development of sprouts in soil to be measured non-destructively and establish whether differences in the date of emergence of stems are primarily a consequence of differences in when sprouts begin to elongate or the rate at which they extend.

The lack of any relationship between the number of stems per plant and yield per plant, once seed tuber weight was accounted for, suggests that the relationship between stem density and crop yield confounds the effects of stem density and seed rate. Given that contemporary studies (e.g. Bussan *et al.* 2007) continue to investigate the effect of stem density on yield, it would be prudent to unravel this inter-relationship. This could be achieved by comparing conventional seed tubers with groups of minitubers that produce single stems or by comparing seed sizes in varieties where the number of stems increases relatively little as seed tuber weight increases.

At present there is little information on the extent of variation in uniformity between varieties and which sub-traits are responsible for any differences. Before any directed attempts to breed more uniform varieties is possible, experiments need to be conducted to establish whether varieties differ consistently and likewise to critically evaluate the relative importance of genetics and the environment on influencing uniformity. Once differences between varieties are established, further research could reveal the genetic basis of sub-traits associated with uniformity and allow marker-assisted selection of seedlings instead of the imprecise visual selection methods currently used.

## 6.7. Conclusions

Many factors affect variation in tuber size and it occurs at distinct levels within the crop. Previous studies (Travis 1987; MacKerron *et al.* 1988; Wurr *et al.* 1993; Firman & Shearman 2006b, 2007; Firman 2008) have not established any mechanisms to explain how tuber size varies or from where the variation originates. The tuber size distribution was described as a normal distribution using the methods of Travis (1987) and Wurr *et al.* (1993) with the benefit of being able to quantify variation in tuber size in relative terms as the COV, independently of the yield and mean tuber size. The standard error of the COV of tuber size was consistently large, which meant that detecting small changes in uniformity was difficult, particularly with relatively small sample sizes. The overall tuber size distribution is composed of numerous distinct tuber size distributions with different mean tuber sizes. As for overall mean tuber size, variation in the mean tuber size is caused by differences in the yield and number of tubers. The variation in the means of these distributions contributes to the overall variation in tuber size of the crop. Models can be used to establish the influence of variation at different levels of the crop on the overall crop and to estimate the COV of tuber size per stem for varieties.

Although only limited data are available, within-field variation in yield and the number of tubers was found to have minimal effects on uniformity. Plant-to-plant variation in mean tuber size was substantially larger than within-field variation and increase in the variation in the mean tuber size per plant was associated with decreased uniformity. Generally, a greater proportion of plant-to-plant variation in yield could be accounted for by the factors of seed tuber weight and the date of emergence than in previous studies (Svensson 1966; Silva & Andrew 1985). Variation in emergence explained a large proportion of variation in plant size early in the season but this effect diminished as the weight of the seed tuber began to affect the growth rate of plants and also later due to competitive interactions between plants.

Consistent with previous studies, the cause of variation in the number of stems per plant (and

in turn the number of tubers per plant) was only weakly affected by seed tuber weight, despite the average seed tuber weight determining the average number of stems per plant.

Decreasing variation in seed tuber weight compared to current commercial practice did not improve uniformity despite decreasing plant-to-plant variation as larger seed tubers tended to produce higher yields but also more tubers. Plants emerged asynchronously over two weeks and some of this variation was explained by differences in sprout length at planting, but not by variation in planting depth. Although emergence did not explain a large proportion of the variation in yield at final harvests, the differences in the duration of emergence affected the variation in mean tuber size per plant as variation in yield increased but there was less of a compensatory effect on the number of tubers compared to that observed when variation in seed tuber weight was altered. More work is necessary to relate these findings to commercial crops for which the duration of emergence has rarely been recorded. Plant yields were shown to be relatively insensitive to the amount of space per plant in the row due to the plasticity of canopy development. In Maris Piper, large differences in the variation in within-row spacing had only a small effect on uniformity as plants with less space produced fewer tubers as well as lower yields. Varieties responded differently to uneven within-row spacing and further work is required to characterise these responses and allow general inferences to be drawn about novel varieties.

Varieties are known to differ in the extent to which the number of tubers per stem changes as the stem density is altered (Allen & Wurr 1992; Firman 2014). These differences were apparent in the relationships between the yield per stem and the number of tubers per stem for individual plants and stems within crops. Varieties in which the number of tubers per stem is more sensitive to changes in the stem density should theoretically be more uniform as variation in the mean tuber weight per stem is reduced. For varieties in which the number of tubers per stem is relatively stable at different stem densities, variation in the yield per stem is

more important in determining uniformity. However, variation in tuber size on each stem also influences the inherent uniformity of a variety and similar uniformity could be achieved through different mechanisms. It is uncertain whether varieties consistently differ in their uniformity and what the relative importance of any such differences may be in comparison to the way that agronomic practices affect uniformity also remains to be established.

Stem-to-stem variation, for which there is no previously published data, was found to be considerably more variable than plant-to-plant variation but was affected relatively little by the experimental treatments. Higher yielding stems produced larger tubers than low yielding stems and reducing variation in the yield per stem was predicted to improve uniformity and reduce mean tuber size, permitting lower seed rates. The causes of variation in the yield per stem could not be definitively investigated, but it is proposed that variation in the seed tuber substrate per stem was a substantial cause of the variation encountered despite the average seed tuber substrate per stem having only modest influence on the overall growth of the crop. There was considerable variation in tuber size on individual stems and reducing this would improve uniformity substantially, but it is arduous to quantify the variation and the causes of this variation remain to be determined.

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