INVESTIGATING THE IMPACT OF CANOPY ARCHITECTURE ON THE RADIATION USE EFFICIENCY AND YIELD OF SUGAR BEET

By

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Abstract

Current sugar beet varieties vary widely in their canopy architecture; some have a distinctively prostrate canopy angle whilst others are much more upright. Radiation use efficiency (RUE) is the amount of biomass accumulated per unit of light intercepted by the crop. In crops such as rice and wheat, where canopy architecture has been quantified, canopy angle has been shown to significantly influence light interception and RUE. This project quantifies canopy architecture and assesses its effect on RUE and yield of sugar beet.

A combination of controlled environment and field experiments were conducted to classify varieties into canopy types according to petiole angle and assess the impact of canopy angle on light interception, photosynthesis and biomass accumulation in the crop. Prostrate canopy types were demonstrated as having the greatest canopy expansion rate and to intercept more light across the season than an upright or intermediate canopy type. However, despite intercepting the most light, this did not lead to the greatest sugar yield. This research shows evidence that prostrate canopy types have lower rates of photosynthesis, and that the canopy is acclimated to shaded conditions indicative of the overlapping nature of the leaves within and between rows.

Upright canopy types had the greatest RUE of total biomass later in the season and could be suited to a later harvest due to potentially more efficient light interception at lower sun angles. Furthermore, the upright canopy angle was demonstrated as advantageous to the crop during hot and droughted weather conditions, when it retained more of its canopy.

Intermediate canopy types had the greatest photosynthetic potential under optimal conditions. This trait can be associated with high carbon assimilation throughout the summer months in the absence of significant plant stress leading to high total biomass RUE. The Intermediate 2 variety also showed favourable biomass partitioning to the roots later in the season and this also resulted in high sugar yields. However, the Intermediate 1 variety, with similar canopy architecture yielded less and had a lower RUE. This variety was from a different breeder which may indicate that genetic traits, other than canopy architecture, are also important in determining yield and RUE.

To investigate the relationship between canopy angle, RUE and yield a canopy manipulation experiment was conducted. The high yielding intermediate variety was made upright, prostrate or left as a control. Canopy manipulation had no effect on final sugar yield and the upright treatment had a higher RUE in 2022 which was a result of less proportional canopy loss and better tolerance during the drought between July and September 2022. Therefore, biomass partitioning, and high levels of photosynthesis are important traits to select for high RUE and sugar yields. However, further research is required to understand the interaction between canopy angle and RUE in winter months and water stressed conditions.

Overall, the findings from this have shown that sugar beet varieties can be classified into canopy types according to their petiole angle. Canopy angle is not as important as photosynthetic rate and biomass partitioning for high RUE and sugar yields. The impact of canopy angle on drought tolerance and harvest timing should be explored by breeders in the future.

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List of abbreviations

Abbreviation	Definition
°C	degrees Celsius
A	Carbon dioxide assimilation
Amax	Maximum rate of assimilation
ANOVA	Analysis of variance
AQY	Apparent quantum yield
BBRO	British Beet Research Organisation
C	Carbon
cm	centimetre
CO_2	Carbon dioxide
cv	cultivar
DM	dry matter
DAS	Days after sowing
DRC	Dose response curve
Eq	Equation
g	gram
GNDVI	Green normalised difference vegetation index
gs	Stomatal conductance
H_2O	Water
I	PPFD measured on a horizontal plane
Io	PPFD above the canopy
IRGA	Infrared gas analyser
Kg	kilogram
L	Leaf area index in Beers Law
L	litre
LAI	Leaf area index
LCP	Light compensation point
LiDAR	Light detection and ranging
LRC	Light response curve
LSP	Light saturation point

LL.4	Log logistic 4 curve
LSD	Least significant difference
m	meter
min	minute
MJ	megajoule
mm	millimetres
mmol	millimole
MnDBlue	Reflectance index indicating leaf chlorophyll content
mol	mole
N	Nitrogen
NDWI	Normalised difference water index
nm	nanometre
NPQ	Non-photochemical quenching
K	Extinction coefficient
PAR	Photosynthetically active radiation
PFD	Photon flux density
PPFD	Photosynthetic photon flux density
RD	Dark respiration
RH	Relative humidity
RUE	Radiation use efficiency
sec	second
SE	Standard error
SPAD	Soil Plant Analysis Development
UAV	Unmanned aerial vehicle
WUE	Water use efficiency
μmol	micromole

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Joint authorship statement

The published works contained within this thesis were jointly authored and the breakdown for authorship is as follows:

L. Tillier – Lead Author who undertook the experimentation, data analysis and drafting of all manuscripts

E. Murchie – Assisted with experimental design, interpreting photosynthesis data, feedback on all manuscripts and is final author of all chapters.

D. Sparkes – Lead for all project areas, oversaw all experimental designs, practical work, and feedback on all manuscripts and is final author of all chapters.

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Chapter 2: Does canopy angle influence radiation use efficiency of sugar beet has been accepted and published in *Field Crops Research* Journal. It is the copyright of the journal.

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Chapter 1: General introduction and literature review

1.1 General introduction

Sugar beet (*Beta vulgaris* ssp. *vulgaris*) is an important crop of temperate climates and is a source for sucrose, bioethanol and animal feed. Beet is a halophyte belonging to the Amaranthaceae, which originates from areas surrounding the Mediterranean. It is a relatively new crop, appearing in temperate regions in the nineteenth century and its popularity grew throughout the twentieth century (Draycott, 2006). Sugar beet is now grown worldwide over 4.4 million hectares and accounts for 20% of white sugar produced (FAOSTAT, 2020). In 2020, Russia (33.92MT), United States of America (30.50MT) and Germany (28.62MT) were the leading sugar beet producers worldwide (FAOSTAT, 2020). The UK is the 5th largest sugar beet producer in Europe (FAOSTAT, 2020), where the crop is cultivated across East Anglia and the East Midlands where four sugar processing factories are based. Growers grow beet contracted to British Sugar where the price is fixed each year following negotiation between the National Farmers Union and British Sugar.

Sugar beet possesses a biennial habit but is cultivated as an annual crop. It is sown in the spring and harvested in the autumn and winter months whilst in the vegetative stage of development. Throughout the growing season biomass is accumulated in the crop and sucrose formed from photosynthesis is stored in the root. In the event of a vernalisation period, sugars are remobilised from the root to the developing flower and the sugar yield is significantly reduced (Jaggard et al., 1983). Over the past few decades an average annual increase of 1.5% has been seen in sugar beet yields across Europe. Breeding progress is said to be accountable for half of this increase and improved management practices reinforced by science accounts for the other (Jaggard et al., 2010; Hoffmann and Loel, 2015). However, this increase is unlikely to be sustained without major breakthroughs from breeders. Current threats to the yield include climate change and its impact on availability of water to the crop and virus yellows which was previously well controlled by neonicotinoid seed treatments that were banned for use in the UK in 2019 (Smith and Hallsworth, 1990; Kang et al., 2009; Okom et al., 2017).

In sugar beet there is a strong linear relationship between biomass production and accumulated intercepted radiation by the canopy under optimal growing conditions (Milford, 2006). The efficiency of this conversion of light into biomass is commonly referred to as the radiation use efficiency (RUE) (Monteith, 1977). Improving crop RUE suggests one method to improve crop yield. The canopy architecture which refers to the size, shape, orientation, and angle of above ground plant organs plays a crucial role in how radiation is intercepted and may also impact RUE. Commercially grown sugar beet varieties possess visibly distinctive and varying canopy architectures, specifically in canopy angle, leaf size and leaf area Index (LAI) (Bowen, 2021). Characterizing the different canopy traits and investigating the impact on light interception and RUE could assist breeders and growers in selecting varieties for increased RUE and yields in the future.

1.2 Canopy development

The process of canopy development is determined by an ordered sequence of morphological stages and is the result of both initiation and expansion of individual leaves. The development of a canopy is genetically determined and its sustained growth has been shown to be partially determined by source (photosynthetic leaf material) – sink (root) feedback mechanisms (Rodrigues et al., 2020). Canopy development can be characterised into a set of stages: a) leaf initiation and appearance, b) leaf expansion, c) leaf angle distribution and arrangement. Each stage is key in determining the amount of light that is intercepted by the canopy across the growing season.

Seed germination and leaf initiation are induced by environmental factors such as temperature, photoperiod, soil moisture and nutrient composition. In most major crops the base temperature (threshold value below which development rate is halted) for germination and emergence have been identified (Monteith, 1984). Wheat and potato crops require a base temperature of between 0-5 °C for germination and emergence (Kirk et al., 1985; Atkinson and Porter, 1996). Canopy development and growth rate increases linearly from base up to an optimum temperature, above this the critical temperature is reached and the development rate slows.

Thermal time or accumulated growing degree days (GDD; °C days) is the daily accumulation of temperature based on average of maximum and minimum values above the base temperature and is an important factor in plant development (Bonhomme, 2000). Thermal time for the first true leaf appearance varies between crops depending on their physiology. Plant growth and development responds linearly to accumulated thermal time and is an important factor alongside radiation and water availability in modelling harvest timing and yield (Qi et al., 2005; Piekutowska et al., 2021).

In sugar beet, the base temperature for germination is 3 °C as confirmed by Gummerson (1986) and Milford et al. (1985a). After germination, a base temperature of 1 °C is required for the emergence and 3 °C for leaf expansion (Milford et al., 1985a). Following the cotyledon stage, the first true leaves unfold from the apex together. Up to 40 leaves in a growing season can be produced individually in 5:13 phyllotaxis (Clark and Loomis, 1978). Individual leaf area increases up to the 12th leaf and thereafter each leaf that emerges is slightly smaller than the previous one. Milford et al. (1985b) showed that leaf number was similar in commercial sugar beet varieties. It was also demonstrated that small differences in early phyllochron (thermal time between leaf appearance) did not influence the canopy expansion rate and final canopy size however, individual leaf size and leaf death does.

1.3 Canopy architecture

Canopy architecture is very diverse across the plant kingdom and is determined by both genetics and the environment (Duncan, 1971). Plant architectural characteristics include leaf area, angle, shape, and distribution (leaf arrangement in a 3D space) (Norman and Campbell, 1989). Plant architectural traits greatly influence the micro-environment surrounding the leaves. This in turn affects factors such as canopy humidity, radiation reflectance, air, leaf and soil temperature, wind speed and soil water balance (Nilson, 1977; Norman and Campbell, 1989).

1.3.1 Leaf area

Leaf expansion is the central process by which plants colonize space and is responsible for increasing leaf area and light interception capacity. The leaf area index (LAI) is the ratio of total projected leaf area per unit ground area. A direct relationship exists between LAI and canopy light interception (Monteith, 1977). This relationship can be described by Beer's Law which was originally used to describe the passage of light through a liquid (Equation 1) (Hirose, 2005).

$$I = I_0 e^{-KL} \qquad \text{(Equation 1)}$$

Where *I* is the photosynthetic photon flux density (PPFD) measured on a horizontal plane, *I*$_0$ is the PPFD above the canopy, *L* is the LAI and *K* is the extinction coefficient.

Beer's Law relies on even and consistent distribution of leaves in a canopy at a consistent leaf angle. In row crops such as sugar beet this is often not the case. There is a bimodal distribution of light across the canopy particularly before canopy closure and this a challenge that must be considered when measuring canopy light interception.

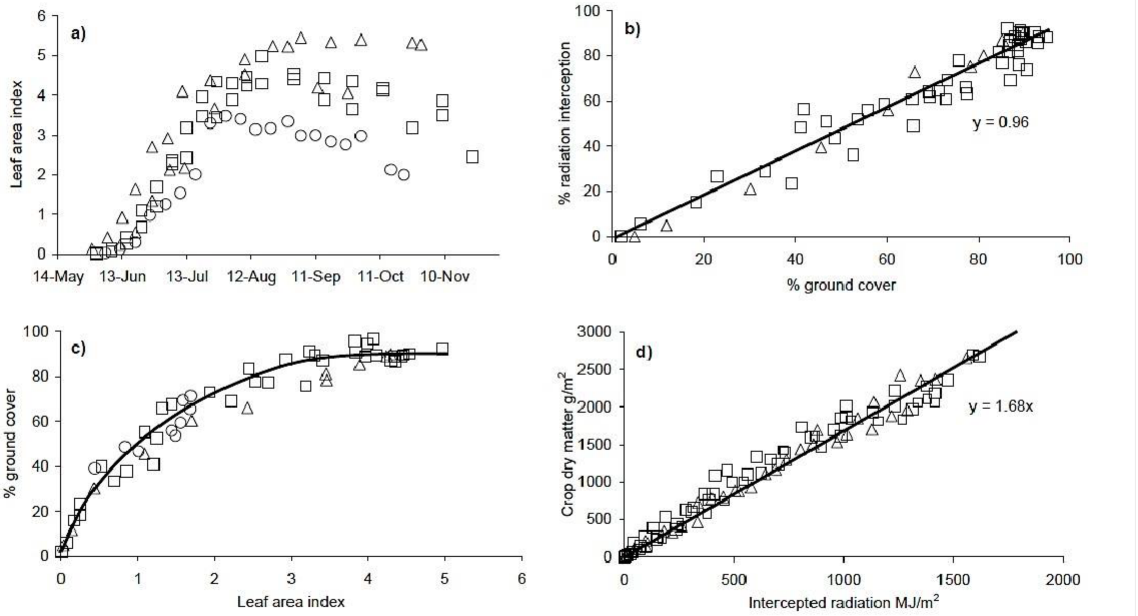

Figure 1.1 Seasonal patterns of leaf area index (a) and relationships between radiation interception and the percentage of ground covered by the foliage (b), ground cover and leaf area index (c), and the production of dry matter and radiation interception (d) on soils of low (○), average (□) and high nitrogen fertility (∆) in the UK (Milford, 2006).

For a crop to utilise light efficiently it must achieve fractional interception of light value close to 1 (intercepting near 100% of incident light) with as minimal leaf area as possible. Wheat has a larger optimum LAI of 6 compared to sugar beet of 3.5–4 to achieve equivalent radiation interception owing largely to small leaves and canopy structure (Figure 1.1). Optimal LAI also depends on canopy angle, a prostrate canopy may require a lower LAI than an upright canopy (Figure 1.2). However, the efficiency of radiation interception in upright canopies may be greater despite the cost of a greater LAI as light is able to penetrate through the canopy more effectively.

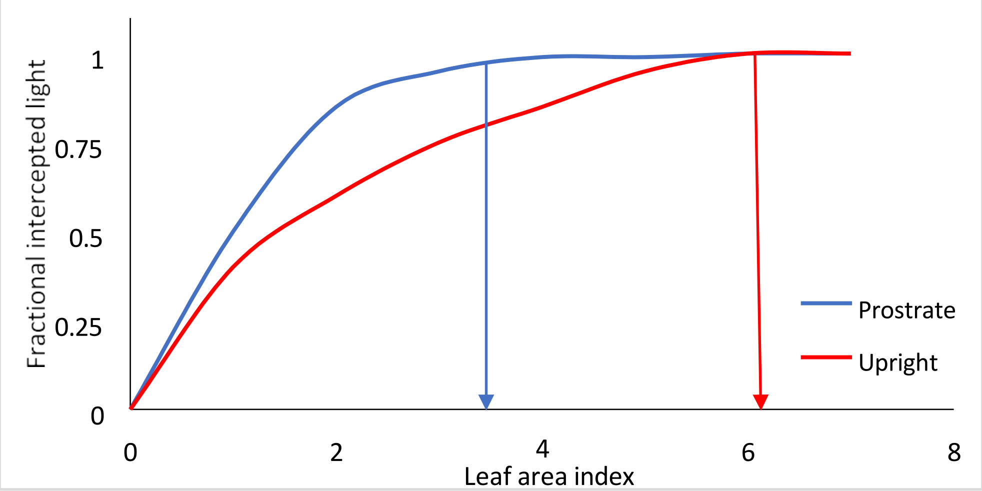

Figure 1.2 Optimal leaf area index of a prostrate and upright canopy a given crop for fractional interception close to 1.

Canopy closure is achieved at circa. 90% of canopy cover and this equates to 90% incident intercepted light by the canopy (Figure 1.1b). Commercial sugar beet crop canopies have been estimated to expand at a rate of 0.5–1.0 units of LAI per 100 GDD after sowing and require 800 GDD to reach canopy closure (Werker and Jaggard, 1998). However, this depends upon soil nitrogen and water status (Milford and Watson, 1971; Werker et al., 1999). A LAI between 3 and 4 is regarded as optimal for light interception in sugar beet after this, the energy cost of leaf production and leaf surface transpiration is greater than the benefit in terms of extra light intercepted (Figure 1.1c) (Milford et al., 1985; Jaggard et al., 2009). The LAI and hence, canopy cover, gradually declines across the season as leaves replacing older leaves are smaller in size (Figure 1.1a). In the summer the LAI can also decline due to heat, disease and drought but in most cases, after senescence regrowth ensues at a cost to yield.

High radiation receipts present in May and early June are often not fully utilised by the sugar beet canopy and during this time the LAI and % radiation intercepted is low (Figure 1.1a). Due to the strong linear relationship between accumulated intercepted light and crop biomass, a prostrate canopy would therefore benefit the crop to achieve canopy closure sooner. Early canopy closure has been shown to increase yield in sugar beet (Werker and Jaggard, 1998; Hoffmann and Kluge-Severin, 2010).

However, Hoffmann (2019) found that earlier canopy closure did not lead to increased sugar yields in commercial varieties and concluded that factors such as variety canopy architecture differences, RUE and sink strength are equally as important.

1.3.2 Canopy angle

Canopy angle is characterised by leaf and petiole angle and is a key factor of canopy architecture. Canopy angle can be defined as the inclination between the leaf blade midrib and the leaf initiation site. It can directly determine the amount of light reaching the leaf surface in turn influencing planting density and overall crop photosynthetic capacity (Ehleringer and Werk, 1986; Mantilla-Perez and Salas Fernandez, 2017).

Under optimal conditions it is beneficial for crops to intercept as much radiation as possible; therefore, a horizontal (prostrate) canopy angle, with no directly overlapping leaves is ideal. However, when the LAI is greater or there is competition for space, there is an advantage of canopies that gradually move from prostrate to more upright leaf angle distributions. This is because a high proportion of the light is intercepted at the top of the canopy in prostrate leaves whereas in more upright canopies light can penetrate through the canopy reaching a greater leaf surface area.

Steeper leaf angles of upright canopies in numerous species improve light capture when the sun is at low angles in the sky (dawn/dusk and winter) and decrease light capture at midday and summer months avoiding light saturation of upper leaves when the sun angle is higher (Falster and Westoby, 2003) (Figure 1.3). Steeper leaf angles also help to reduce heat-load on the crop, consequently increasing water use efficiency and lessening the risk of heat stress (Valladares and Niinemets, 2007). A decreased risk of photo-inhibition and increasing carbon gain can also be observed (Björkman and Demmig-Adams, 1995; Werner et al., 2001; Burgess et al., 2015).

Throughout the autumn months sugar beet biomass production slows as radiation receipts decline and the sun angle is lower in the sky. A more upright canopy should be able to intercept lower angles of light in comparison to a flatter, more prostrate, variety (Figure 1.3).

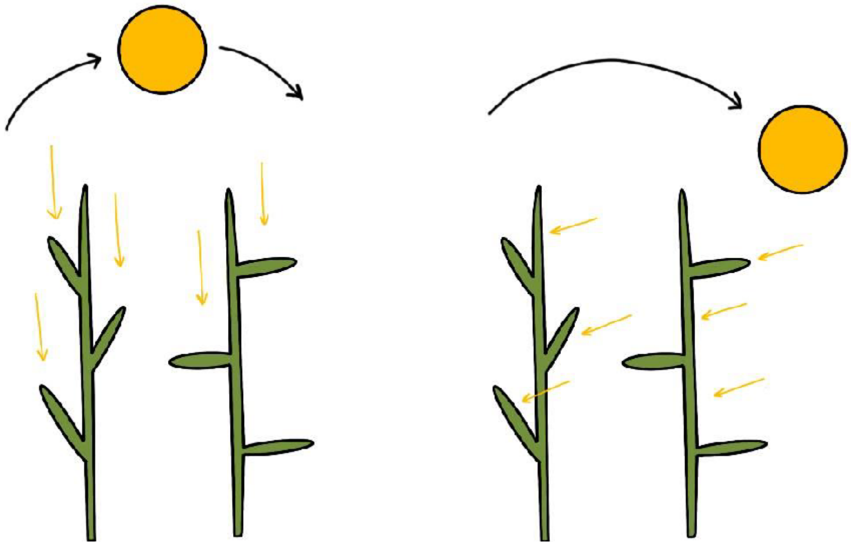

Figure 1.3 The influence of canopy angle on light interception at high sun angles (summer/mid- day) and low sun angles (afternoon/winter).

In broad-leaf canopies such as sugar beet, new leaves frequently shade older leaves. This can lessen the light availability to older leaves and thus reduce the efficiency of light interception in the crop (Niinemets, 2007). Therefore, a canopy ideotype can be proposed for sugar beet; a canopy that is mostly prostrate after emergence and then at canopy closure, new leaves are more upright and then gradually become more prostrate with age. Light is not fully absorbed by the top leaves and can reach distribute more uniformly throughout the canopy. This provides an optimal architecture for RUE whilst still enabling early weed suppression (Duncan, 1971; Niinemets, 2010; Burgess et al., 2017; Jabran and Chauhan, 2018;

Ma and Upadhyaya, 2018). Characterising and investigating the impact of canopy architectural traits and how these affect RUE and crop yield is key to underpinning future breeding strategies for high yielding sugar beet.

1.4 Radiation use efficiency

The concept of RUE was developed by Monteith (1977) from the observation of a robust, linear relationship between the accumulated crop biomass and intercepted radiation. There are a range of approaches to estimate RUE, which has led to various units and experimental methods being used. A review by Gitelson and Gamon (2015) highlighted that the most used definitions of RUE and are based on incident radiation and total absorbed light or PAR. Following on from this, the most widely used method to calculate RUE is to fit a linear regression between accumulated biomass and intercepted radiation, with the slope of this relationship representing the RUE (Sinclair and Muchow, 1999). In sugar beet accumulated intercepted radiation is strongly related to both whole plant and root biomass as well as sugar yield (Figure 1.4.) Aboveground biomass is usually used to calculate RUE. This is desirable for cereals and leaf crops; however, in root crops this is a drawback and to accurately calculate RUE the whole plant must be included. It must also be noted that the RUE value in crops can change across the season as the plant matures, this is shown in oilseed rape during the pod filling stage where RUE decreases as the energy value of the crop changes (Glauert, 1983; Sinclair and Muchow, 1999; Ober et al., 2004; Brodrick et al., 2013; Deichman and Kremer, 2019). Therefore, caution must be taken when making comparisons between crops.

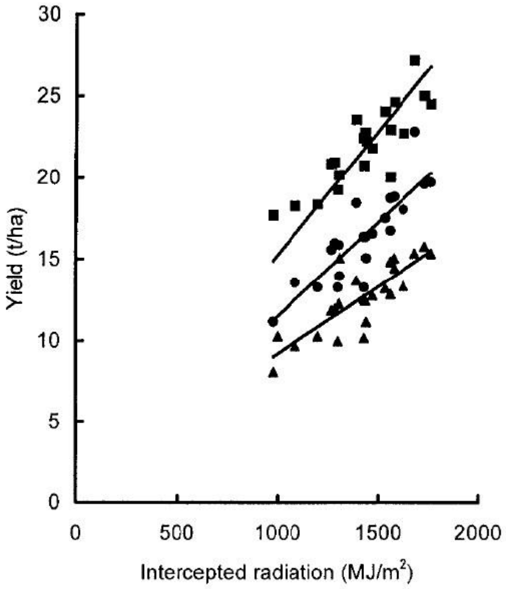

Figure 1.4 Relationship between the amount of solar radiation intercepted throughout the growing season and total dry matter (■), root dry matter (•) and sugar (▲) yields. (Jaggard and Qi, 2006).

In most C_3 crops the RUE value of total radiation is between 1.3-3 $g.MJ^{-1}$ and in C_4 crops this value is much higher and between 2.5-4 $g.MJ^{-1}$ (Deichman and Kremer, 2019). RUE is dependent on a range of factors including light quality and duration, water availability, row spacing, nutrient status and plant genetics (Sinclair and Muchow, 1999). Reported RUE values (from total radiation) in sugar beet range between 1.1-2.0 $g.MJ^{-1}$ (Hoffmann, 2019; Hoffmann and Kluge-Severin, 2010; Monteith, 1977; Werker and Jaggard, 1998). Since the 1980s in the UK and Europe, no work has demonstrated an improvement in sugar beet total biomass RUE, only seasonal variations in RUE have been shown despite increasing sugar yields during this period (Hoffmann and Kluge-Severin, 2010). Improved biomass partitioning through genetic advancements is likely to be responsible for this by increasing the root weight and marc content in beets (Hoffmann and Kenter, 2018).

Water deficit in sugar beet can reduce RUE and is accountable for up to 30% yield loss in drought years (Ober et al., 2004; Werker and Jaggard, 1998). This is because the crop freely wilts and during this period photosynthesis is limited and older leaves senesce at a greater rate (Monti et al., 2007; Jaggard et al., 2009).

Under conditions of drought stress, the advantage of upright canopies might not be an increase in RUE directly but reduced radiation interception during midday (Figure 1.3). This might delay wilting, reduce leaf scorch, and lessen water and energy expenditure lost through transpiration. A gap in knowledge exists regarding sugar beet canopy architecture and water use efficiency and its implications on RUE.

Nitrogen is also essential for RUE in sugar beet; firstly, supporting canopy development and expansion and secondly forming the basis of chlorophyll and Rubisco production in the leaf (Malnou et al., 2006; Ebmeyer and Hoffmann, 2021). Both of which are essential for light interception and photosynthesis (Loomis, 1963; Nevins and Loomis, 1970). A lack of nitrogen availability and poor reduced utilisation of nitrogen into photosynthetic components in the crop canopy has been shown to reduce RUE of sugar beet (Jaggard et al., 2009; Fei et al., 2019). Ebmeyer and Hoffmann (2021) showed differences in nitrogen utilization efficiency (yield per unit of total available nitrogen) and sugar yields between commercial varieties and hypothesised differences in biomass partitioning were responsible. However, the impact of canopy architecture on leaf nitrogen demand, photosynthesis and yield was not assessed.

1.5 Photosynthesis

Photosynthesis is a crucial step between canopy light interception and accumulated biomass in the crop. The efficiency and rate of canopy photosynthesis is dependent on individual leaf photosynthesis and can differ depending on several factors: light environment, leaf age and leaf biotic and abiotic stresses.

Leaves can become acclimated to the light environment in which they are grown (Walters, 2005). This is referred to as photoacclimilation and is a dynamic process where adjustments to the structure and function of the photosynthetic apparatus are made in response to light in order to optimize canopy photosynthesis.

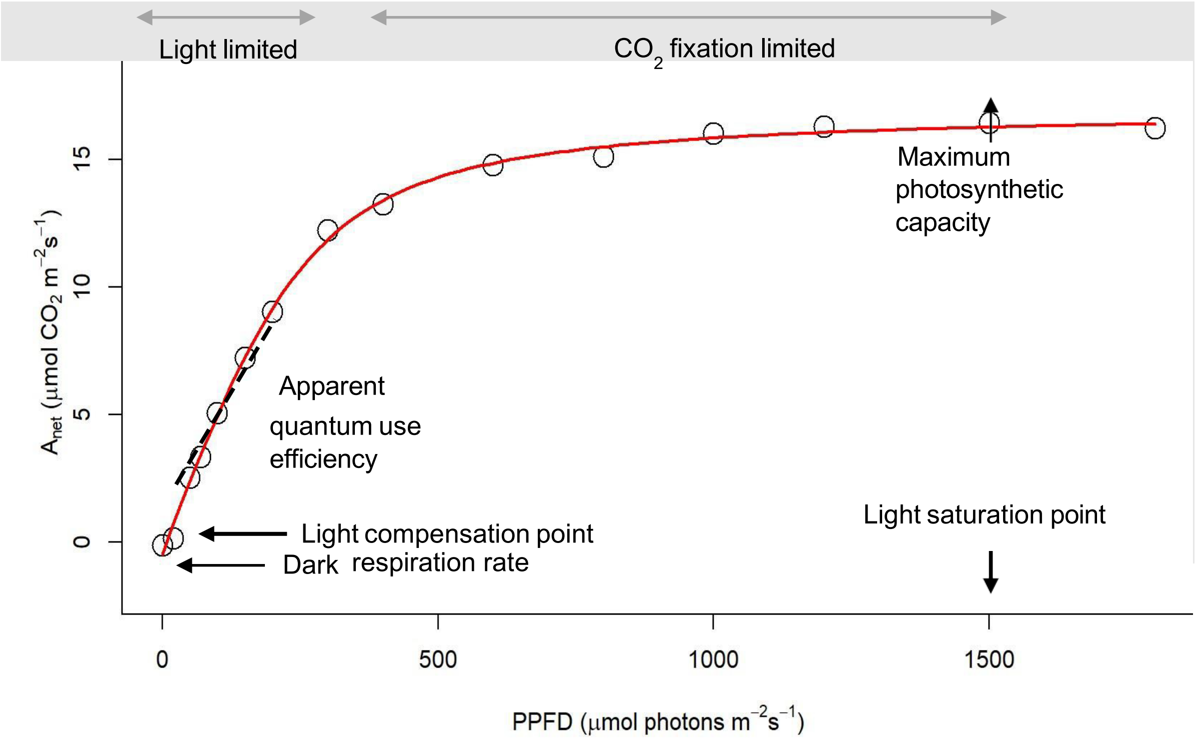

Figure 1.5 Light response curve model showing the calculated parameters: Maximum photosynthetic capacity, Light saturation point, Quantum use efficiency, Light compensation point and Dark respiration rate.

Photosynthetic light response curves (LRCs) are a useful indicator of the acclimation status of a leaf and can be used to describe how canopy (leaf) photosynthesis changes according to the intensity of incident light. LRCs are typically measured using infrared gas exchange analyser, over a period of minutes with steps of decreasing light intensity. The output can be modelled using a non-rectangular hyperbola relating net photosynthetic rate and PPFD (Sharkey et al., 2007). LRCs provide a quantitative value on the maximum photosynthetic capacity, light compensation point, dark respiration, light saturation point and can be used to assess the RUE of leaves (Figure 1.5). The acclimation state of a leaf is determined by the maximum photosynthetic capacity, light saturation point, compensation point and dark respiration rate. The light saturation point is the light intensity at which photosynthesis ceases to increase, the light compensation point is the light intensity where photosynthesis cancels out the CO_2 from respiration.

Light availability can vary significantly between the top and the bottom of a canopy (Burgess et al., 2015, 2017a). The ability to adapt a photosynthetic apparatus to changing light availability enables an overall increase in canopy productivity and hence an improvement in not only RUE but water and nutrient use. The row orientation and rosette nature of the sugar beet crop inevitability means that within the canopy there will be significant variations in light availability between leaves. The older leaves towards the bottom of the canopy would receive less light than newer leaves towards the top of the canopy. However, the inherent differences in canopy angle and LAI between varieties means that light levels within the canopy will differ between upright and prostrate canopies and in those with varying LAI. Consequently, photosynthetic capacity and RUE differences is hypothesised between different canopy angles.

In sugar beet, it has been shown that newer leaves have higher rates of photosynthesis in comparison to older leaves (Hodáňová, 1981; Monti et al., 2007). This is likely caused by leaf aging and the breakdown and remobilisation of photosynthetic components to support new leaf growth (Kudoyarova et al., 2018). Light availability could also be a significant factor in this as less light penetrates to the older leaves in the canopy and as a result the maximum photosynthetic rates in these leaves are compromised. Canopy angle could also affect leaf photosynthesis, as new leaves at the top of a prostrate canopy are subjected to higher intensities of light and are therefore adapted to utilise this light more efficiently and could become saturated at much higher light intensities compared to older leaves lower down in the canopy. It has been shown that in shaded canopies the maximum photosynthetic capacity, light compensation point, and light saturation point is considerably lower than newer leaves which receive a higher intensity of light (Li et al., 2014; Burgess et al., 2017).

The improvement of canopy photosynthesis is a significant target to improve RUE and crop yields (Long et al., 2006). This might include manipulating the canopy angle to improve light capture and photosynthetic efficiency. It has been shown that upright canopies in wheat have improved RUE (Richards et al, 2019). Several researchers have suggested that increasing the leaf angle to be more prostrate towards the bottom of the canopy and more upright towards the top can improve light distribution and provide an optimal canopy architecture for high RUE and yields (Duncan, 1971; Long et al., 2006; Zhu et al., 2010). Long et al. (2006) demonstrated that during midsummer this architecture can increase carbon uptake by 60% relative to a canopy of horizontal leaves. However, this has been established in taller canopies typically above 1 m. Whether this canopy arrangement benefits shorter, row crops such as sugar beet is undetermined.

1.6 Linking canopy architecture, photosynthesis, biomass production and yield

The yield of any crop is determined by the product of the incident light energy, fractional interception, the efficiency of the conversion of intercepted light into biomass (RUE) and the proportion of biomass partitioned into the yield components (Figure 1.6).

$$\boxed{\begin{array}{c}\text{Incident}\\ \text{light energy}\end{array}} \times \boxed{\begin{array}{c}\text{Fractional}\\ \text{interception}\end{array}} \times \boxed{\text{RUE}} \times \boxed{\begin{array}{c}\text{Biomass}\\ \text{partitioning}\end{array}} = \text{Yield ha}^{-1}$$

Figure 1.6 Components of yield equation

Canopy architecture directly influences the proportion of light intercepted by a canopy, the rate of photosynthesis, and thus biomass production (Niinemets, 2010).

Biomass production in sugar beet is proportional to the amount of light intercepted by the crop and this is determined by the LAI or canopy cover of the crop as previously described. At the beginning of the season there is a slow rate of biomass increase due to cool spring temperatures which limits canopy expansion and thus reduces light interception despite relatively high levels of incident radiation. When the crop reaches canopy closure, biomass production accelerates and is proportional to accumulated intercepted radiation. Unlike crops such as wheat that have discrete developmental stages when yield components are determined, sugar beet remains in a vegetative state throughout and hence the direct relationship between light interception and yield is consistent through the season. This would suggest that the sugar beet crop is source limited. Achieving canopy closure sooner with more prostrate canopy angles would enable higher accumulated intercepted radiation and in return increase biomass production and RUE up to canopy closure. However, recent studies have suggested that sugar beet is sink limited. The limitations have been discussed to fall at marc sugar content and phloem loading (Schnepel and Hoffmann, 2016; Hoffmann, 2019. Therefore it is not evident that simply increasing the amount of radiation intercepted result in higher sugar yields.

Near isogenic lines have been used in wheat and rice to accurately determine the connection between canopy architecture, photosynthesis and yield (Nan Su San et al., 2018; Moeller et al., 2014). Near isogenic lines are not available in sugar beet and therefore a canopy manipulation approach is required. Canopy manipulation is the process of manually manipulating the canopy to a desired angle or area and is commonly performed in viticulture (Pendleton et al., 1968). A canopy manipulation approach is advantageous as it can directly pull apart the relationship between canopy architecture and yield and occludes genetic differences between varieties. A secondary more complex approach to investigate canopy architecture and RUE can be achieved by detailed 3D canopy modelling (Burgess et al., 2017a, b; Foo et al., 2020).

1.7 3D canopy modelling

Over the past years there have been major advances in canopy phenotyping and a number of different techniques in order to capture plant structure have been developed (Gibbs et al., 2018; Guan et al., 2018; Pound et al., 2015; Xiao et al., 2020). Two-dimensional (2D) solutions provide a useful approach to phenotype whole structures such as canopy cover. However, the 2D approach does not provide detailed canopy architectural information such as leaf arrangement, leaf thickness, curvature or angle.

3D canopy phenotyping approaches can provide a more detailed canopy model of the entire plant than that possible using 2D imagery. There are several sensor-based technologies available to phenotype a canopy and be classified as active or passive sensors. Each method is used to generate a point cloud of the canopy. Light detection and ranging (LiDAR) sensors fall into the active category. LiDAR emits its own light source and can detect its reflectance from surfaces such as leaves or stems. From this information, 3D canopy models can be generated and plant canopy traits such as plant height, leaf area and angle can be calculated. This approach has been used to generate high resolution point clouds in cereal crops (Omasa et al., 2007; Qin et al., 2022). However, LiDAR is expensive and models generated from sugar beet canopies are often poor quality and have absent petioles and large gaps missing in the leaves (Bömer et al., 2022).

Structure from motion (SFM) is a passive approach to 3D model canopies and is a cheaper and more accessible option. SFM has been successfully used to estimate plant canopy and root traits, and predict biomass and yield (Burgess et al., 2017b; Lu et al., 2021; Xiao et al, 2020). A previous study by Xiao et al. (2020) modelled sugar beet plant canopy in the field using the SFM approach in specialist software 3DF (Flow Science, Inc., Santa Fe, NM, USA). However, the generation of high quality models to compare canopy architecture between commercial varieties is absent from the literature. 3D canopy models have also been used to predict light interception and canopy photosynthesis (Andrieu et al., 1995; Burgess et al., 2017a,b; Retkute et al., 2018; Foo et al., 2020).

4.3.4 Modelling canopy light interception

The quantity of the light that is reflected or transmitted within the canopy varies with wavelength and is dependent on the leaf characteristics, optical properties and age. A light ray incident on a leaf surface has three possible fates: reflection, absorption, and transmission (Vos et al., 2010). Light absorption can be calculated using various methods, most of which include advanced computer graphics and depends on the solar position which can be affected by latitude, season, and the time of the day (Goudriaan and Van Laar, 1994).

Ray tracing is a theoretical technique and is used to phenotype the canopy light environment (Burgess et al., 2017a, b; Foo et al., 2020). The method can calculate the fate of light rays in a canopy. The method consists of casting light rays from a given light source in different directions and following their paths through the canopy. When the light encounters the leaf surface, it is scattered and different wavelengths can be calculated (Chelle et al., 1999). A ray tracing algorithm can be coded to a particular 3D model type or mesh. Therefore, ray tracing is not universal for all model types and is highly dependent on the quality of the model as light will pass through any gaps in the model.

The data from ray tracing can be used to calculate canopy light interception and net photosynthesis across a canopy. It can also map shaded and sun-lit areas (Retkute et al., 2018). The development of a high resolution canopy model detailing the differences in canopy architecture in sugar beet would be a major step forward as it would enable the calculation of canopy light interception and photosynthesis. As well as this partition a future for remote sensing to measure RUE at field scale from integrating a combination of high resolution models, hyperspectral measurements and gas exchange measurements (Robles-Zazueta et al., 2022)

1.8 Research questions

Several gaps in knowledge related to RUE in sugar beet requiring further investigation have been identified in this literature review. The areas that have been selected for further research are focused on identifying and defining the varietal differences in sugar beet canopy architecture, the impact of these differences on light interception, photosynthesis and RUE and whether canopy architecture has a direct effect on RUE. From this, the following research questions and hypotheses have been developed:

1. To what extent does canopy architecture (leaf and canopy angle and area) differ across modern sugar beet varieties?

Hypothesis: Modern sugar beet varieties differ significantly in canopy angle.

2. Are there differences in canopy expansion and light interception between varieties with contrasting canopy architectures?

Hypothesis: More upright varieties will intercept less light before canopy closure than prostrate varieties and take longer to reach canopy closure.

3. Does canopy architecture have a significant impact on RUE?

   Hypothesis: There will be an optimal canopy architecture for light interception. In a closed canopy, new leaves at the top of the canopy are most upright and older leaves are more prostrate and therefore light is distributed more evenly through the canopy facilitating a greater RUE.

   Upright canopy angles intercept light more efficiently at lower sun angles than prostrate canopy types and could help reduce midday heat load on the canopy.

4. To what extent are leaves at the top of the canopy more able to cope with higher light intensities and have a higher maximum photosynthesis value than those of older leaves at the bottom of the canopy? Do these values change

depending on canopy architecture?

Hypothesis: Newer leaves at the top of the canopy in prostrate varieties have a higher rate of photosynthesis under higher light intensities than in upright varieties. Older leaves in prostrate canopies become light saturated at lower intensities and are less photosynthetically active than upright varieties.

5. Is RUE determined by canopy angle or are there other genetically determined traits that affect RUE ?

   Hypothesis: Making a canopy more prostrate will increase total light interception early on however, once canopy closure is reached an upright angle canopy will have a higher RUE and subsequent yield.

1.9 Thesis layout

This thesis focuses on three studies which have been written in paper format. Each paper has been or will be submitted to a relevant journal and are included in their published format or format submitted for review.

Chapter 2: ‘Does canopy angle influence radiation use efficiency of sugar beet?’

This paper describes field experiments conducted in 2019 and 2021 which aimed to quantify the differences in canopy angle between commercial sugar beet varieties and assesses the impact of this on canopy development, light interception, RUE and sugar yield.

This paper has been published in Field Crops Research and is presented in its published format.

Chapter 3: ‘Sugar beet canopy manipulation: is radiation use efficiency and yield determined by canopy angle?’

A canopy manipulation approach was used in the field in 2021 and 2022 to manipulate a high performing intermediate canopy to be either more upright using cages or more prostrate using pegs, to help determine whether RUE and sugar yield is determined by canopy angle alone or whether varietal genetic advancements are responsible.

This paper is being prepared for submission to European Journal of Agronomy

Chapter 4: ‘Canopy architecture and photosynthesis in sugar beet’

This paper describes a controlled environment experiment where leaf and petiole angle and leaf expansion was measured on new and old leaves across three canopy types (upright, prostrate, intermediate). Light response curves were also measured on these leaves to assess the acclimation status of leaves within the canopy and their interaction with canopy architecture.

Chapter 5: 3D canopy modelling method development’

This short paper explains the development and refinement of a new technique developed to create 3D virtual models of a sugar beet plant both in the field and in pots. The method can create a high quality and detailed model of the plant which can then be used in ray tracing to simulate light in the canopy.

Chapter 6: concludes the results of all of the work conducted in a general discussion

Since the experimental chapters are written in publication format, references can be found at the end of each chapter.

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Chapter 2: Does canopy architecture influence radiation use efficiency of sugar beet?

The following chapter consists of a paper published in Field Crop Research and investigates the differences in canopy architecture in commercial sugar beet varieties and its impact on radiation use efficiency over two field seasons.

This chapter addresses the following research question and hypothesis:

1. To what extent does canopy architecture (leaf and canopy angle and area) differ across modern sugar beet varieties?

   <u>Hypothesis:</u> Modern sugar beet varieties differ significantly in canopy angle.

2. Are there differences in canopy expansion and light interception between varieties with contrasting canopy architectures?

   <u>Hypothesis:</u> More upright varieties will intercept less light before canopy closure than prostrate varieties and take longer to reach canopy closure.

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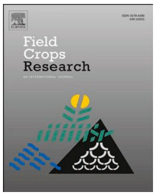

Does canopy angle influence radiation use efficiency of sugar beet?

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ABSTRACT

Sugar beet varieties differ greatly in their canopy architecture and can be classified into canopy types according to their petiole angle. Leaf angle is one of the key factors which determines the efficiency with which plant canopies utilise incident and absorbed light for photosynthesis. Sugar beet yield is strongly correlated with accumulated intercepted light but the impact of canopy angle on light interception, biomass accumulation and sugar yield has not been explored. This study aims to analyse these relationships and also to determine if varieties can be selected according to their canopy types for high radiation use efficiency (RUE) and yields. Field trials were conducted with four varieties in 2019 (one upright, one prostrate and two intermediate canopy types) and six varieties in 2021 (two each of upright, intermediate, and prostrate) as well as one alternate sowing treatment (upright and prostrate in alternate rows). Varietal differences in petiole angle were stable across the season in 2019 and consistent between canopy closure and final harvest in 2021. The upright canopy type had a lower maximum canopy cover modelled from canopy expansion curves in both years. The upright canopy type was also slower to achieve canopy closure in 2019 and had a lower LAI at canopy closure in both years. There was a linear relationship between accumulated intercepted radiation and total plant biomass across all canopy types. The intermediate canopy types had the highest RUE in 2019 and highest sugar yield in both years. The upright canopy types had the highest RUE when harvested later in 2021, possibly due to the upright canopy type being better suited to intercept and utilise sunlight during the winter months when the sun angle is lower in the sky. The root to shoot ratio was greater in the high yielding intermediate variety suggesting that, in addition to RUE, biomass partitioning is an important determinant of sugar yield. The results from this study will aid in the selection of varieties to improve sugar beet yields. Whilst canopy angle is an important contributing factor to RUE and yield in sugar beet, other factors, such as leaf level photosynthesis and biomass partitioning are also important.

1 Introduction

Radiation use efficiency (RUE) is defined as the amount of biomass accumulated per unit of light intercepted by the crop (Monteith, 1977). Values for RUE are often strongly dependent on primary processes especially photosynthesis. RUE has complex origins and can be variable depending on species, photosynthetic mechanism, environment and measurement protocol. Nonetheless, under non-limiting conditions, using consistent methodologies, there is a uniformity in RUE values between plants with similar photosynthetic mechanisms such as C3 and C4 crops (Murchie et al., 2018). Improving RUE is thought to be a target for significant yield improvement in many major crops especially where overall biomass improvement is closely linked to yield potential (Sinclair and Muchow, 1999; Robles-Zazueta et al., 2022). Erect canopies are thought to be beneficial for energy conversion because light can penetrate deeper into the canopy and the light is distributed uniformly over a larger leaf area, reducing the level of both light saturation at the top of the canopy and light limitation at the bottom of the canopy (de Wit, 1965). As a result of this, light capture and canopy net photosynthesis is improved, thus increasing the RUE. This has been demonstrated for canopies such as rice and wheat but hasn't yet been tested in the short canopies of sugar beet (Richards et al., 2019). In rice an ideotype has been created with an upright canopy angle in the upper leaves showing both high RUE and yield (Beadle and Long, 1985; Peng et al., 2008). Modelling of canopy function consistently predicts that greater penetration of light given by erect leaf angle increases the rate of canopy photosynthesis because a greater proportion of leaf area is in a less light–saturated and less light–limited state (Long et al., 2006; Song et al., 2013; Burgess et al., 2015). Empirical demonstration of potential higher productivity in erect canopies was demonstrated in wheat (Richards

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et al., 2019).

Commercial sugar beet varieties differ significantly in their canopy architecture, in particular canopy angle and leaf area index (LAI) (Wright et al., 2018; Hoffmann, 2019). Sugar beet canopy angle has not yet been quantified in field trials, despite visual differences between varieties (Bowen, 2021). Because of this, the effect of canopy angle on light capture, optimal LAI, RUE and yield is unknown. Sugar beet field trials have shown a large variation in the radiation use efficiency for the production of total biomass, values range from 1.1 to 2.0 g DM per MJ of total radiation (Monteith, 1977; Werker and Jaggard, 1998; Hoffmann and Kluge-Severin, 2010; Hoffmann, 2019). Seasonal variations in temperature and rainfall are important when accounting for these differences but canopy angle has not been investigated.

In temperate countries, sugar beet is sown once soil moisture enables a good seedbed to be prepared and soil temperatures exceed 6 °C to avoid the crop being vernalised and moving into reproductive development: in the UK this is usually in early March. In sugar beet, rapid canopy development and canopy closure is important to allow increased light interception in May and June when the level of radiation is high. A strong linear relationship is observed between light interception and accumulated sugar across the whole season which would indicate source limitation (Scott and Jaggard, 1978). However, Hoffmann (2019) concluded that the timing of canopy closure is not related to sugar yield which would suggest that factors aside from canopy expansion and total radiation intercepted are important to RUE and yield in sugar beet. The ability of the canopy to continue photosynthesising for longer in the day and more efficiently under optimal and sub optimal conditions will be vital to building biomass and sugar yield. Furthermore, other aspects of light capture and conversion could improve RUE such as pigment distribution, Calvin cycle activity and photoprotection (Long et al., 2006; Ducat and Silver, 2012; Hubbart et al., 2018). Uncoupling the significance of light interception, canopy photosynthesis and other environmental factors is essential in understanding RUE and sugar yield but this has yet to be elucidated for sugar beet crops with contrasting canopy angles.

RUE has mostly been measured in crops such as cereals by using above ground biomass only. Root biomass is rarely considered in RUE studies, and this is becoming a serious drawback (Sinclair and Muchow, 1999). This is particularly relevant for sugar beet and other root crops because the harvestable organ is mostly below ground. The partitioning of biomass to the harvested root in sugar beet is crucial in determining the sugar yield and so the root mass must be measured in RUE studies (Hoffmann and Kenter, 2018). The root to shoot ratio is the proportion of biomass in the root compared to the above ground components. In sugar beet, the root to shoot ratio increases linearly with thermal time (growing degree days; GDD °C day) above a base temperature of 3 °C as canopy closure is achieved and assimilates are stored in the root (Gummerson, 1986). After 800 GDD the first two leaves senesce and the canopy begins a gradual decline as the leaves replacing senesced leaves are smaller compared to older leaves in the canopy (Milford et al., 1985, 1988; Ehleringer and Werk, 1986). The rate of canopy decline and re-growth will vary between varieties and season due to environmental conditions, pest or disease prevalence. At the start of the season there is rapid canopy growth followed by an increase in root biomass later in the season, therefore the root to shoot ratio changes throughout the season. Varieties with high RUE resulting from higher conversion of radiation to total biomass are not always highest yielding due to their root to shoot ratio. Studies in sugar beet have demonstrated that varieties with similar total biomass production often have different sugar yields which is caused by differences in root biomass partitioning and root sugar percentage (Hoffmann, 2019; Jaggard and Qi, 2006). Assuming similar levels of light interception across the season, the greater the RUE the higher the total biomass produced. However, this doesn’t reflect yield due to biomass partitioning differences. Biomass partitioning can determine the LAI for radiation capture, photosynthesis and later it determines the root and hence sugar yield.

The aims of this study were (1) to quantify canopy angle across a range of sugar beet varieties, (2) to investigate relationships between canopy angle and canopy development, leaf chlorophyll content and leaf level photosynthesis (3) to analyse the relationship between canopy angle, RUE, root:shoot and yield of sugar beet.

2 Methods

2.1 Field and plant material

In 2019 and 2021, field experiments were established at the University Farm, Sutton Bonington, Leicestershire, UK (52°50´07′′N, 1°15´04.0′′W) on sandy loam soils (Dunnington Heath series). The experiments were arranged as randomized complete block designs with four replicates. Pelleted sugar beet (*Beta vulgaris L.*) seeds were sown at the end of March in 12 row plots, 50 cm row spacing (29/03/2019; 30/03/ 2021). The plots were then divided in two (left hand side for measurements/final harvest and right hand side for destructive biomass harvests).

In 2019, seeds were sown at 17.5 cm spacing achieving a target population density of 100,000 plants ha^{-1}. In 2021 seeds were sown at 9 cm spacing then, at the 3–4 leaf stage, the plants were manually thinned to a target population density of 100,000 plants ha^{-1}. Chemical fertilisers and plant protection products were applied according to standard agronomic practices to keep the crop free of pests, weeds, and diseases and to ensure that nutrients were not limiting (see supplementary table). Sugar beet varieties were selected from the BBRO (British Beet Research Organisation) recommended list. Different genetic backgrounds were chosen, and the varieties were categorised according to their canopy type (Table 1).

The daily incident solar radiation, rainfall and temperature were recorded by a weather station located within 200 m of the experiment each year. Thermal time as growing degree days (GDD; °C day) was calculated as the accumulation of daily mean air temperature above the base temperature from emergence up to final harvest, using a base temperature of 3 °C (Gummerson, 1986). The date of emergence was noted when over 50% of cotyledons were visible.

Table 1
Varieties used in the field trials with breeder and canopy type. * 2021 only.

Variety	Breeder	Canopy type
Degas	Strube	Intermediate (1)
BTS 1140	Beta Seed	Intermediate (2)
Cayman	SesVanderhave	Prostrate (1)
*Lacewing	SesVanderhave	Prostrate (2)
*Cayman/Sabatina	Sesvanderhave/KWS	Prostrate/Upright
Sabatina	KWS	Upright (1)
*Kortessa	KWS	Upright (2)

2.2 Plant measurements

2.2.1 Canopy angle

Canopy angle was measured after each biomass harvest to help limit edge effects. A camera (Canon Powershot sx720) was mounted on a mini tripod and positioned in the gap made by the latest harvest. Three plants per plot were selected and a tag was applied to a fully expanded leaf of a similar age in each image for reference. In the prostrate/upright plots: two upright and one prostrate plant were imaged in blocks two and three, while in blocks one and four, one upright and two prostrate plants were imaged. The images were taken at ground level at 35 cm distance from the plant. The petiole angle of the tagged leaf was measured from an upright insertion into the crown using the angle tool on Image J (Rasband, 2011) (Fig. 1). Using this technique, a small angle indicates an upright petiole (Fig. 1A), and a larger angle indicates a prostrate petiole (Fig. 1B).

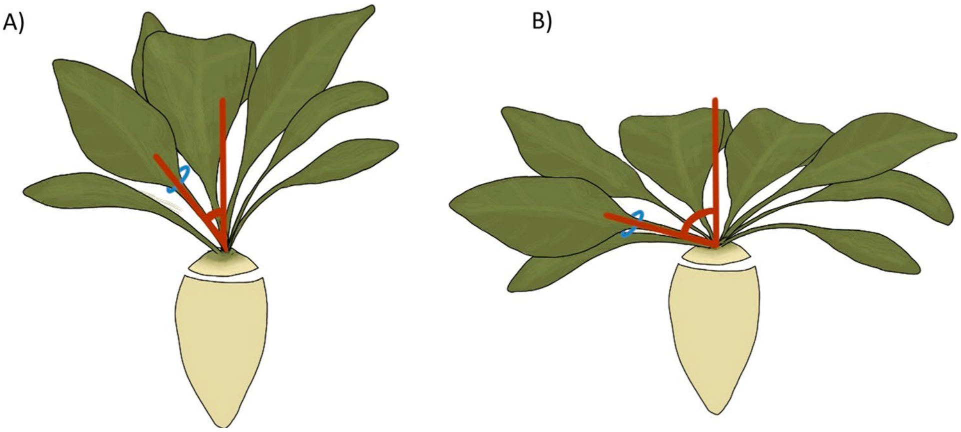

Fig. 1. Canopy angle measurements on an upright canopy type (A) and prostrate canopy type (B). Canopy angle is taken as the petiole angle from an upright insertion into the crown. Leaves of similar age were measured.

2.2.2 Establishment and canopy expansion

Establishment counts were taken at the four-leaf stage (after thinning in 2021). Plants were counted in 2 m length of row and then the number was multiplied by 10,000 to give plant population ha^{-1}. Any gaps in the plot were noted. From the six leaf stage in 2019 and eight leaf stage in 2021 canopy cover was measured each week during the canopy expansion phase, then monthly thereafter. A camera (Canon 1100D) was mounted on a frame that allowed images to be taken directly above the plots. A wide angle 10–18 mm lens was fixed at 10 mm and held above the plot at a height of 1.2 m and 2.5 m from the edge of the plot. The central three rows of sugar beet were aligned within the view of the lens. One photo was taken from the same end of the plot each time capturing 36% of the plot area. Percentage canopy green area was measured by thresholding the green area of each image in ImageJ (Rasband, 2011). Canopy expansion was modelled using a three-parameter log-logistic model in R (R Core Team, 2021) (Fig. 2). Calculated percentage canopy cover values and thermal time after emergence was plotted for each plot. Maximum canopy cover, slope, and the inflection point of the canopy in each plot was calculated. In this model, the slope is calculated between 10% and 90% of maximum canopy cover and is negative due to the equation used. The more negative the slope the faster the rate of canopy expansion. The inflection point is the thermal time value where 50% of maximum canopy cover is achieved, therefore representing the expansion rate of the canopy. A larger Inflection point value would mean that the canopy reaches canopy closure slower and *vice versa*.

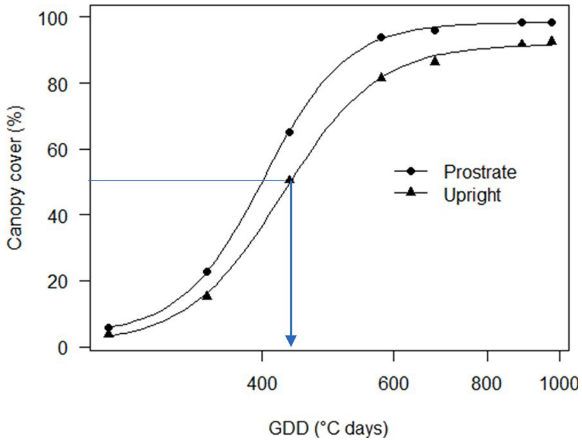

Fig. 2. Three-parameter log-logistic model used to model canopy expansion. Shown here are example data from a prostrate and upright canopy type. The inflection point of an upright canopy is indicated by the blue arrow. GDD is growing degree days or thermal time.

2.2.3 *Canopy greenness*

Canopy greenness was measured every three weeks between July and October with a Minolta SPAD-502 chlorophyll metre (Minolta Camera Co., Ltd., Japan). SPAD-502 measurements give a value for canopy greenness which is highly correlated with chlorophyll content in sugar beet (Malnou et al., 2008). Three measurements were taken per leaf and three randomly selected leaves were measured per plot. The leaves were fully expanded and clearly visible from the top of the canopy.

2.2.4 Photosynthesis

Leaf level photosynthesis was measured on 10 August on prostrate 1, intermediate 2 and upright 1 varieties. The net CO_2 assimilation rate (*A*) and stomatal conductance (*gs*) were directly measured in the field between 08:30 and 12:00. Three fully expanded leaves were selected per plot and measured using a Li-6800 portable gas exchange system (Li-COR Inc., Biosciences, Lincoln, NE, USA). The sample photosynthetic photon flux density (PPFD), CO_2 concentration, relative humidity and temperature inside the cuvette were set to 1200 μmol m^{-2} s^{-1} (light response curves taken previously indicated this was saturating), 400 μmol mol^{-1} CO_2, 50% RH and block temperature of 20 °C, respectively. The leaves had a five minute adjustment period in the cuvette before measurements were taken to allow *A* and *gs* to stabilise. The data was analysed as an average of three leaves per plot.

2.2.5 Biomass harvests

Destructive biomass harvests were taken at six points in 2019 (5/6/19, 27/6/19, 30/7/19, 3/9/19, 9/10/21 and 5/11/19) and five points in 2021 (9/6/21, 27/7/21, 23/8/21, 18/10/21 and 6/12/21). 3 m^2 of plot was harvested and washed thoroughly before total fresh weight was recorded. A 50% sub sample was taken at first harvest and 25% thereafter. The roots were separated from the tops at the lowest leaf scar. The leaf lamina were then separated from the petioles at the bottom of the leaf. Fresh weight of each component part was recorded, and leaf area measured using a LI-3100 C leaf area metre (Li-COR Inc., Biosciences, Lincoln, NE, USA) and used to calculate leaf area index. All components (leaves, petioles, roots) were then oven dried at 65 °C until a constant weight was achieved and then the dry weight was recorded. The root to shoot ratio was calculated as root dry weight divided by petiole and leaf dry weight.

2.2.6 Radiation use efficiency and yield

The radiation use efficiency (RUE) of the crops was measured in both years. Percentage canopy cover (described in Section 2.2) was assumed to be equal to the percentage of incident solar radiation intercepted by the canopy. There was no predetermined upper limit set and the maximum percentage light interception was 99% determined in both years. Canopy light reflectance was also measured across the season and no differences were seen between varieties and therefore was not used to calculate total intercepted light in this instance. This method was preferred over a ceptometer due to the bimodal nature of the canopy. Daily meteorological data was used with percentage canopy light interception to determine the amount of solar radiation intercepted throughout the season. Accumulated intercepted radiation in MJ m^{-2} (*I*)

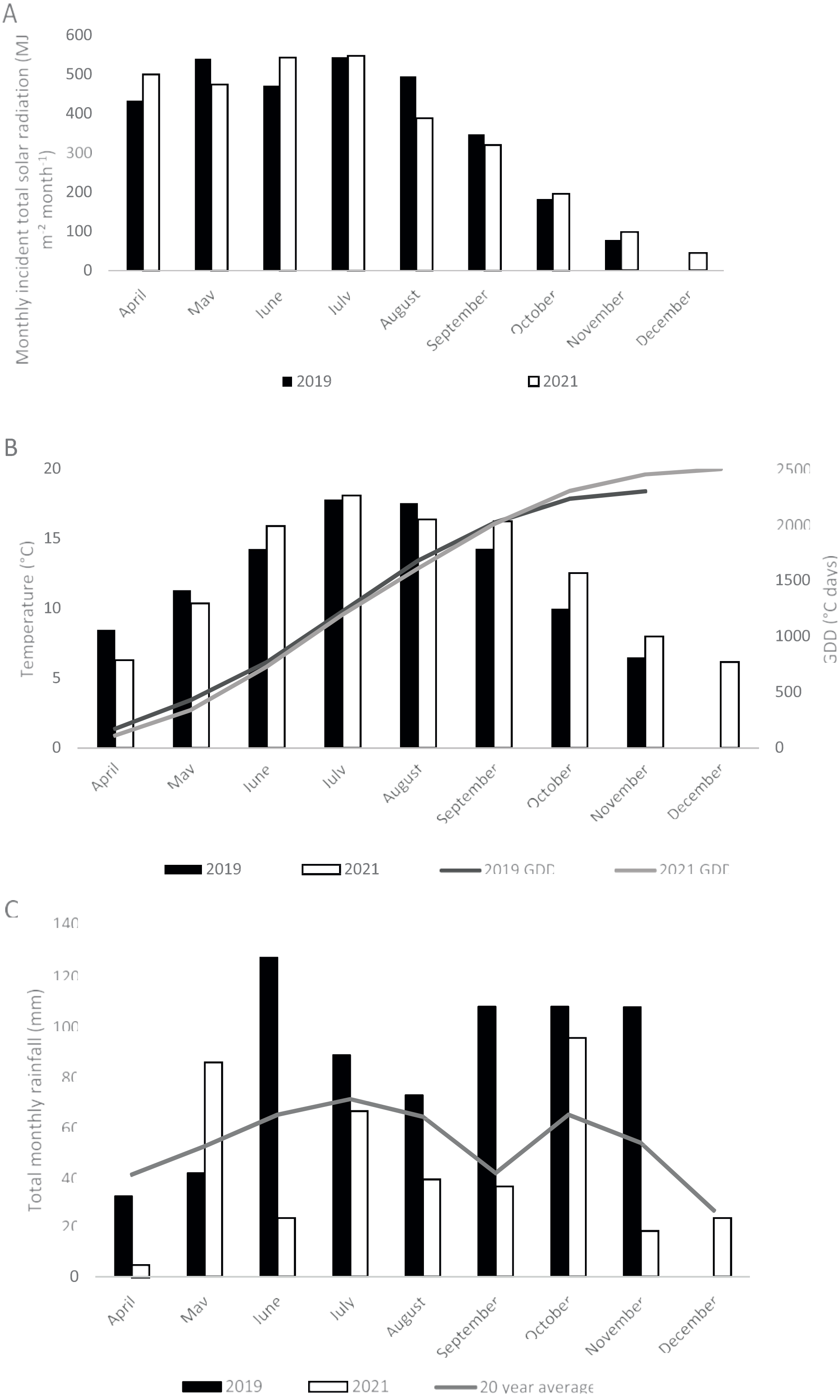

Fig. 3. Meteorological data from the Sutton Bonington weather station during the 2019 and 2021 growing season. A) Monthly total solar radiation receipts. B) monthly average temperature and growing degree days. C) monthly rainfall. GDD is growing degree days or thermal time.

was calculated as Eq. (1).

$$I = [(C_1 \times R_1) + (C_n \times R_n)] \tag{1}$$

C_1 is the percentage canopy cover assessed during week 1 and R_1 is the total incident radiation during week 1 (MJ m^{-2}). Accumulated intercepted light is calculated from daily radiation receipts and weekly percentage canopy cover assessments up until canopy closure and then fortnightly after. This approach was used due to the strong relationship that exists between percentage canopy cover calculated from canopy images taken from above the canopy and fractional canopy light interception in sugar beet (Steven et al., 1986). Percentage canopy light reflection was also measured at the same time as canopy cover measurements and no differences were seen between canopy types and was therefore not included.

RUE from total plant biomass (root and shoot) was calculated from the first percentage canopy cover assessments (18/05/19 and 27/05/2021) until the first biomass harvest and was recalculated for each subsequent harvest. For each variety, RUE was calculated as the slope of the regression of total biomass and accumulated intercepted radiation. RUE from sugar yield was calculated as sugar yield at final harvest divided by total accumulated intercepted radiation across the season.

The plots were harvested on 5 November in 2019 and 15 December in 2021. Rows 2, 3 and 4 were lifted using a three-row beet harvester and the harvested beet taken to the BBRO (British Beet Research Organisation) tare house for root weight and sugar percentage analysis. Sugar yield was calculated from the fresh clean root weight and sugar percentage.

4.3 Data analysis

Data was analysed using Genstat 20th edition (VSN International, Hemel Hempstead, UK) using one way analysis of variance (ANOVA). A repeated measures analysis was carried out on measurements taken across the season. Calculation of the least significant difference (LSD) at 5% significance was included in the ANOVA. Figures were prepared using Microsoft Excel (Microsoft Corp., Redmond, WA, USA).

3 Results

3.4 Weather data

Radiation and temperature levels were similar between the two years (Fig. 3A and B). 2019 received above average rainfall from June

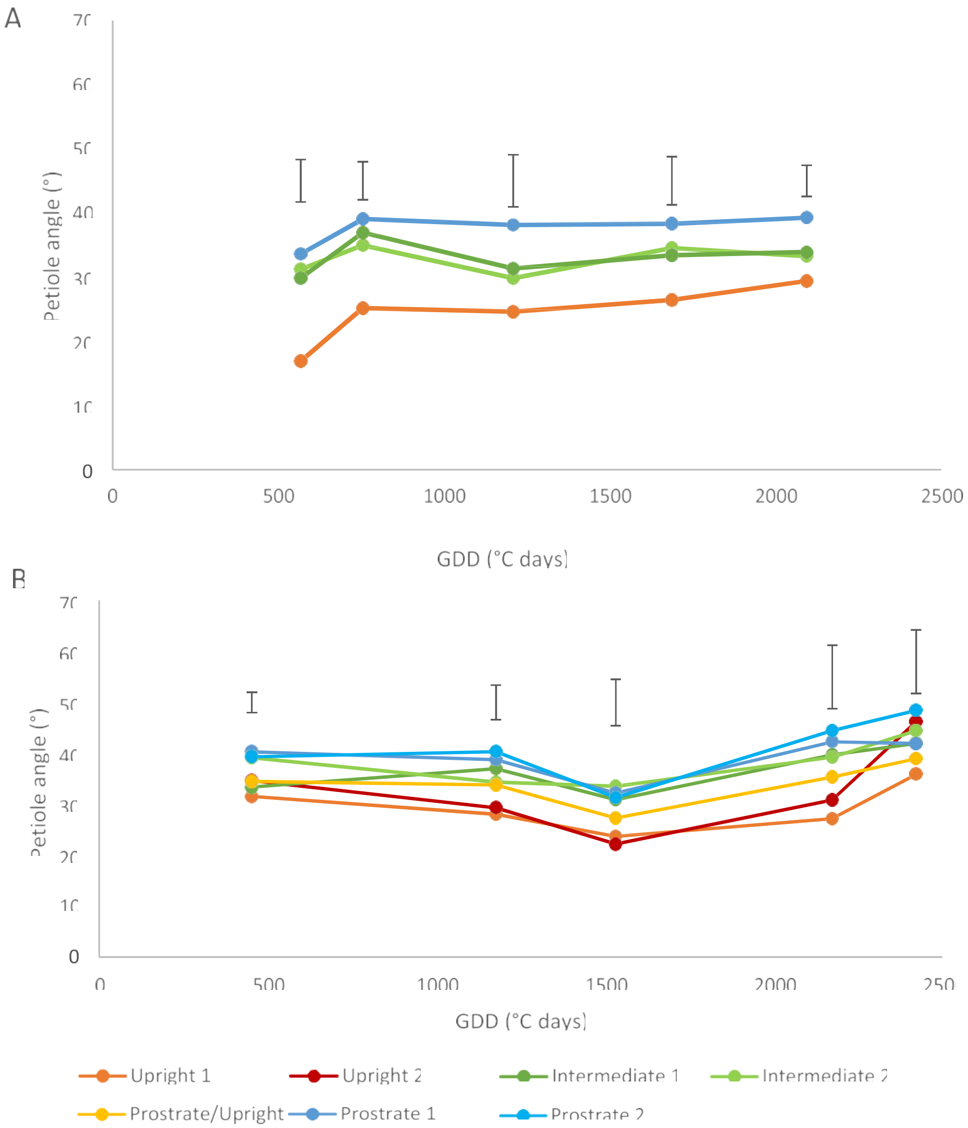

Fig. 4. Petiole angle of different canopy types measured against thermal time after emergence (GDD) in 2019 (A) and 2021 (B). Error bar shows $LSD_{5\%}$ at each interval.

onwards. June was exceptionally wet, receiving more than double the long-term mean rainfall (Fig. 3C). 2021 was considerably drier than 2019 and below the long-term mean. April 2021 was dry in comparison to the long term mean and this slowed germination and early growth before heavy rainfall at the end of May where the crop grew rapidly.

3.2 Petiole angle

In both years petiole angle differed significantly between canopy types across the season ($P < 0.05$; Fig. 4). In 2019 the petiole angle at around 500 GDD was steeper across all varieties before reaching a similar angle as 2021 at 1200 GDD. Varietal differences in petiole angle were stable across the season up to final harvest. In 2021, before canopy closure and at final harvest (450 and 2400 GDD), there were no differences in petiole angle between canopy types.

3.3 Canopy development

In 2019, the slope, inflection point, and maximum canopy cover, estimated by the log-logistic model, was significantly different between the canopy types (Table 2, Fig. 5). The prostrate canopy type expanded its canopy more rapidly but required similar GDD as the intermediate canopy types to reach 50% maximum cover. The upright canopy type reached 50% of its maximum canopy significantly later than all other canopy types ($P < 0.05$). Overall, the upright variety had a smaller canopy size than prostrate and Intermediate 1 canopy type, with the intermediate 1 canopy having a significantly larger canopy size overall. In 2021 the crop was slower to establish but grew at a faster rate than 2019, after rainfall and temperatures increased in June. There were no significant differences found in the slope and inflection point between canopy types, although a similar trend was seen with prostrate canopy types displaying a more negative slope (steeper growth curve) and less GDD required to reach 50% maximum canopy size. The upright 1 variety however, developed its canopy much faster in 2021. Overall, the modelled maximum canopy cover was higher in 2021 and the upright canopy types continued to have significantly lower canopy cover than all other canopy types ($P < 0.001$).

In both years, a negative relationship between the modelled Inflection point and petiole angle before canopy closure was found. A more prostrate angle reduced the thermal time required by the canopy to reach 50% of its maximum cover ($P < 0.001$) (Figure S1). A positive relationship between petiole angle at canopy closure and modelled maximum canopy cover was seen. Increasing the petiole angle leads to a greater maximum canopy cover achieved in both years ($P < 0.001$) (Figure S2). In 2019 this relationship was stronger with an R^2 of 0.48 in comparison to 0.24 in 2021.

In both years, petiole angle strongly influenced the total amount of radiation intercepted from the crop measured up to October (Fig. 6). A more prostrate petiole angle led to more radiation intercepted by the canopy in both years ($P < 0.001$).

In both years there were significant differences between varieties in leaf area index (LAI) through the season (Fig. 7) ($P < 0.05$). In 2019, the Intermediate 2 variety maintained a greater LAI from 1500 GDD to harvest and then, after 2050 GDD, the canopy began to decline. In 2021, a LAI of 3 was reached at 1100 GDD in all varieties except the upright canopy types. At this point, maximum canopy cover was achieved. The canopy declined more rapidly than in 2019 and the prostrate canopy types had a significantly larger LAI than the upright canopy types from 1100 GDD to harvest.

The percentage canopy cover and light interception increased asymptotically with LAI and was maximal when LAI was greater than 2.5 in all varieties. In both years the upright canopy types had a lower LAI when its maximum canopy cover was achieved (Fig. 8). Erect canopies can have higher optimal LAI than prostrate i.e. they achieve 100% canopy cover at a higher LAI. However, there were no differences between canopy types in this study (Fig. 8).

In both years there was a linear relationship between petiole angle and SPAD ($P < 0.05$). SPAD increased as the petiole angle became more upright (Fig. 9).

Measured SPAD values were higher in 2021, and this was consistent up to 32° petiole angle. As the petiole angle became more prostrate SPAD values began to reduce closer to 2019 values (Fig. 9).

Net CO_2 assimilation rate (A) and stomatal conductance (gs) were measured on 10 August 2021. Upright 1, Intermediate 2 and Prostrate 1 were measured as representatives of canopy types. This was necessary to limit time spent in the field, before weather conditions changed, which would increase variation in the data. A of the Intermediate 1 variety was 27.26 $\mu mol\ m^{-2}s^{-1}$ and was significantly higher than both Upright 1 (31.42 $\mu mol\ m^{-2}s^{-1}$) and Prostrate 1 (25.94 $\mu mol\ m^{-2}s^{-1}$) varieties ($P < 0.05$).

There was no significant difference in gs between varieties ($P = 0.075$) although a clear trend was apparent, the Intermediate 2 variety had a higher leaf conductance of 0.692 $mol\ m^{-2}s^{-1}$. Prostrate 1 had the lowest gs of 0.401 $mol\ m^{-2}s^{-1}$ and upright 1 has a gs of 0.503 $mol\ m^{-2}s^{-1}$.

3.4 Biomass accumulation and partitioning

In 2019, the intermediate canopy types accumulated more total biomass across the season from 500 to 2041 GDD than the upright canopy type ($P < 0.05$) (Fig. 10A). Between 2041 and 3030 GDD the upright canopy type continued to gain biomass and by 3030 GDD no differences were seen between canopy types.

In 2021, there were no differences in total biomass between canopy types across the season (Fig. 10B). The upright canopies gained almost 400 $g\ m^{-2}$ of biomass between 2152 and 2417 GDD (October and December). The Intermediate 2, Prostrate/Upright and Prostrate 1 variety gained much less biomass during the same period.

In 2019, the Prostrate 1 variety had a higher root to shoot ratio than the Upright 1 variety ($P < 0.05$) (Fig. 11A). From 2000 GDD to final harvest the intermediate canopy types and Prostrate 1 had a significantly higher root to shoot ratio than the Upright 1 variety ($P < 0.05$).

Table 2
Three parameter log logistic model output for modelling canopy expansion and development of different canopy types in 2019 and 2021. Lower case letter denotes significant differences.

	2019			2021		
Canopy type	Slope	Inflection point	Maximum canopy cover	Slope	Inflection point	Maximum canopy cover
Upright 1	-4.998 b	571.0 b	90.72 a	-7.929	414.7	93.33 a
Upright 2				-6.627	427.9	93.02 a
Prostrate/Upright				-6.876	429.7	97.36 b
Intermediate 1	-5.228 b	551.6 a	95.36c	-7.876	424.5	96.47 b
Intermediate 2	-5.228 b	551.1 a	91.73 ab	-7.212	422.1	96.54 b
Prostrate 1	-6.059 a	544.1 a	93.11 b	-7.901	401.1	98.4 b
Prostrate 2				-8.508	405.6	98.19 b
P	< 0.001	0.023	< 0.001	0.059	0.085	< 0.001
LSD	0.3919	16.17	1.545	1.256	22.05	1.671

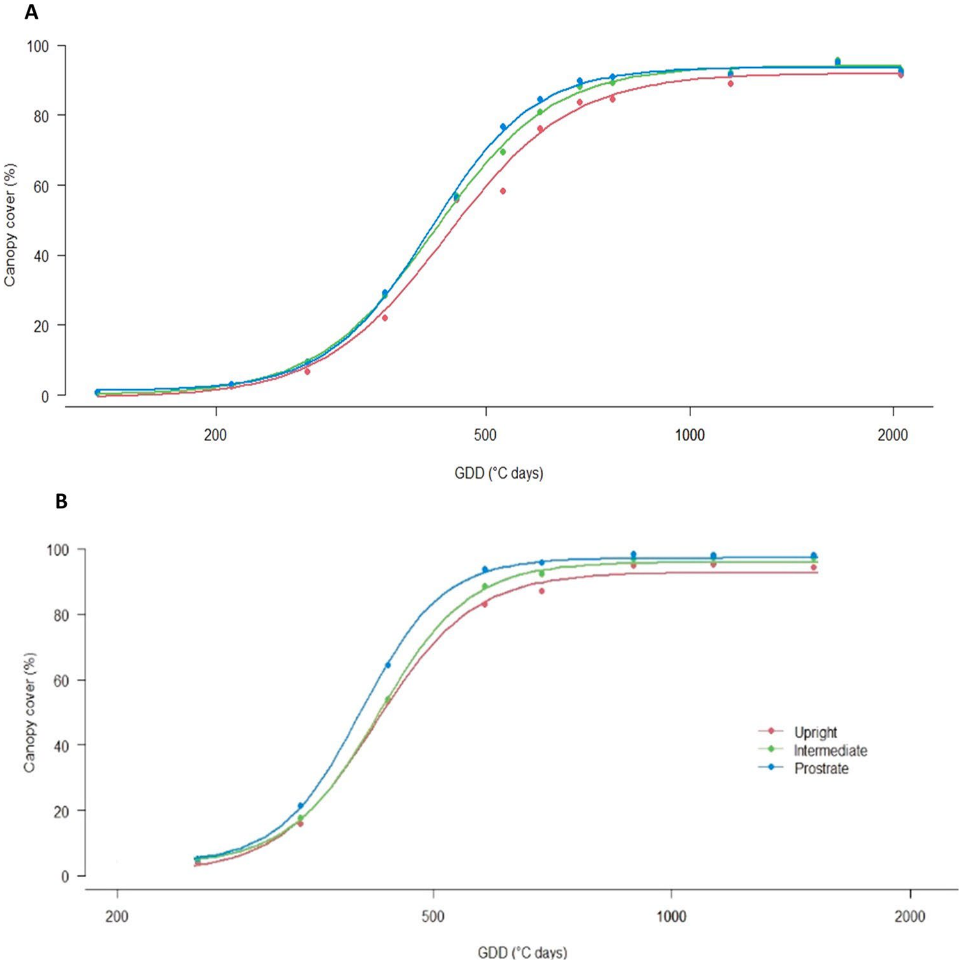

Fig. 5. Fitted curves from a three parameter log logistic model used in modelling canopy expansion and development of different canopy types in 2019 (A) and 2021 (B). The average of upright, intermediate and prostrate canopy types are show against thermal time after emergence (GDD).

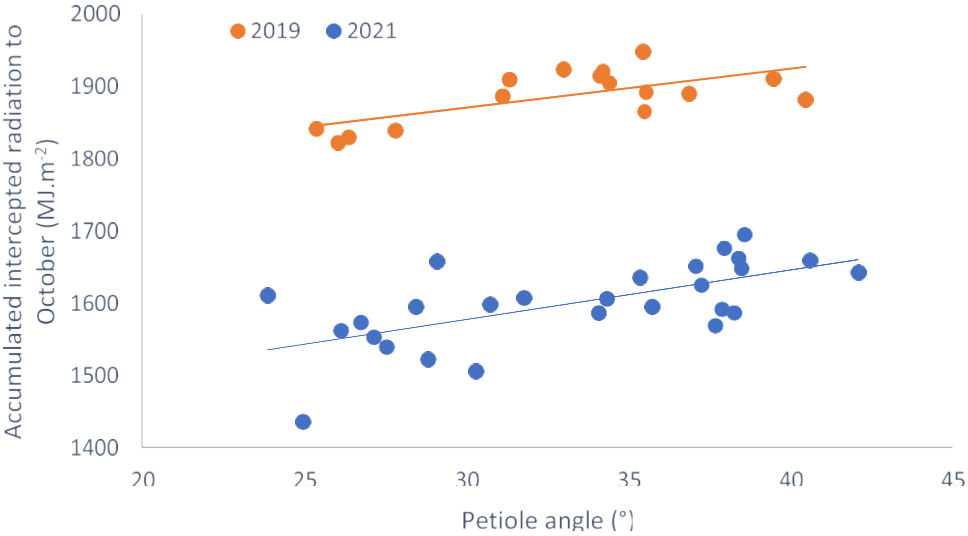

Fig. 6. The influence of petiole angle on accumulated intercepted radiation up to October. Petiole angle was calculated as an average of measurements taken from canopy closure to October in 2019 and 2021. 2019: $y = 5.395x + 1708.7$, $R^2 = 0.4501$. 2021: $y = 6.8589x + 1371.5$, $R^2 = 0.4086$.

From 1000 GDD/July in 2021, the Intermediate 2 variety consistently had the highest root to shoot ratio ($P < 0.001$) (Fig. 11B). At final harvest, the Intermediate 2 variety notably, had a much larger proportion of biomass partitioned to its roots than the other canopy types. The prostrate canopy types had consistently more biomass partitioned to its above ground portion than Intermediate 2 across the season.

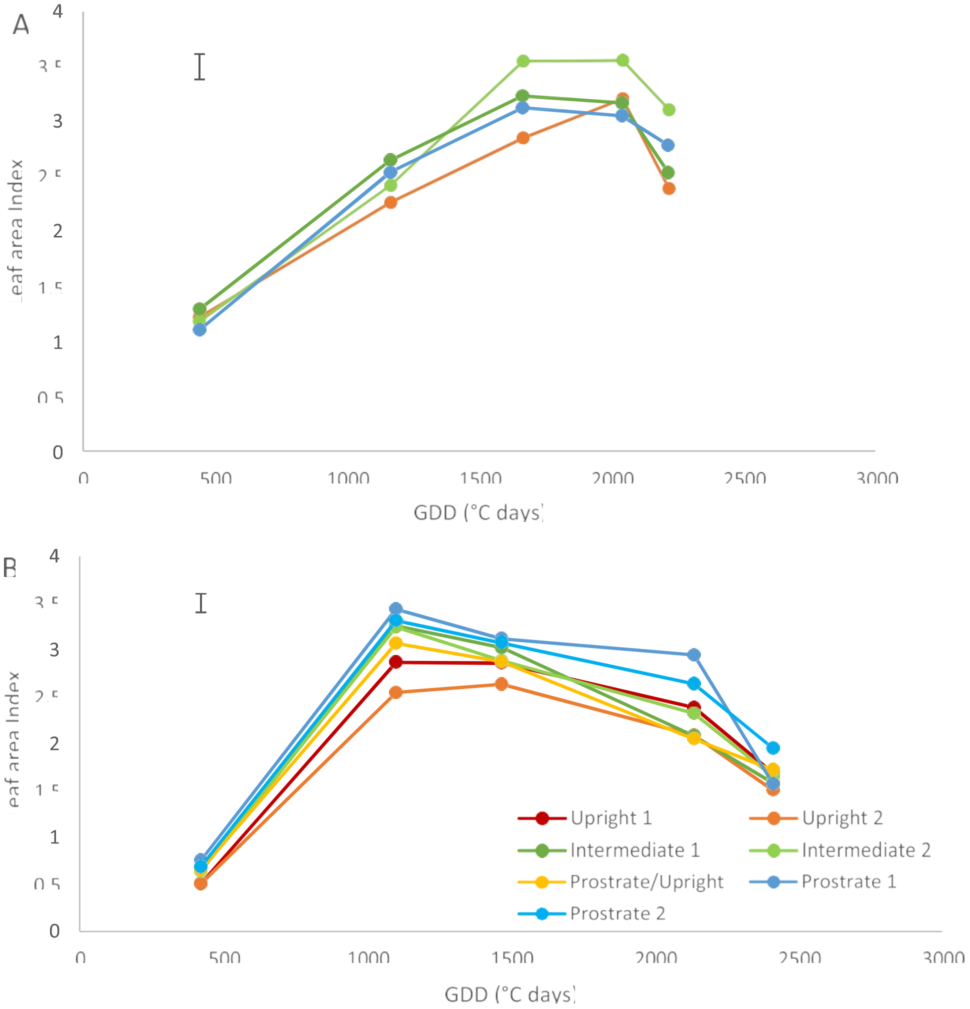

Fig. 7. Leaf area index of different sugar beet canopy types plotted against thermal time after emergence (GDD) in 2019 (A) and 2021 (B). Error bar shows variety LSD$_{5\%}$.

3.5 Radiation use efficiency and yield

Radiation use efficiency (RUE; g MJ^{-1}) was calculated as the slope of the relationship between total plant biomass (g m^{-2}) and the accumulated intercepted total solar radiation (MJ m^{-2}) in Table 3. Season long RUE from final sugar yield in Table 4 was calculated as total sugar yield (g m^{-2}) divided by accumulated total solar radiation intercepted across the season (MJ m^{-2}). RUE calculated from total plant biomass across the season was higher in 2019 than 2021 (Table 3). RUE calculated from final sugar yield was higher in 2021 than 2019 (Table 4).

Clean root yields were lower in 2021 for all varieties except prostrate 1. However, root sugar percentage measured at final harvest was over 1% higher in 2021 and consequently sugar yield in 2021 was significantly higher except for intermediate varieties ($P < 0.001$) (Table 6).

In 2019 the intermediate canopy types had the highest RUE for total plant biomass at 1.82 and 1.77 respectively. The prostrate and upright canopy types had a lower RUE of 1.66 and 1.67 ($P < 0.001$) (Table 4).

In 2021, the Prostrate/Upright and Intermediate 2 varieties had the highest RUE up to October and the prostrate canopy types had the lowest ($P < 0.001$). By final harvest in December, the upright canopy types had the highest RUE followed by the Prostrate/Upright and the intermediate canopy types. The prostrate canopy types still had the lowest RUE ($P < 0.001$) (Table 4).

The intermediate canopy types had the highest RUE for final sugar yield in 2019 ($P < 0.05$) (Table 5). In 2021 Intermediate 2 had a significantly higher RUE from sugar yield than all other varieties ($P < 0.05$).

The intermediate canopy types had the highest root yield, sugar percentage and sugar yield in 2019 and there were no differences between the prostrate and upright varieties ($P < 0.05$) (Table 5). In 2021 Intermediate 2 had the highest root yield and sugar yield and no differences in sugar percentage were seen (Table 5).

4 Discussion

Canopy architecture, notably canopy angle, varies in commercial sugar beet varieties. These varieties can be classified as upright, intermediate and prostrate according to the angle of their petiole. The objective of this study was to investigate the influence of canopy angle on photosynthesis, RUE, and yield of sugar beet from field trials in the UK. The intermediate canopy types had the highest biomass and sugar yield in both years as well as the greatest net CO_2 assimilation per unit leaf area. In 2019, the intermediate canopy types had a greater RUE from total biomass than the upright and prostrate canopy types at final harvest in November. In 2021, when RUE was calculated up to October (closest to the harvest date in 2019), the intermediate canopy again had the highest RUE. However, at a later final harvest in December, the upright canopy types had the highest RUE.

2019 and 2021 were very different years in terms of rainfall. Rainfall was higher in 2019 than in 2021, especially during April and June. 2021 experienced a dry April and June but had a period of high rainfall towards the end of May. This likely led to a greater expansion rate after a

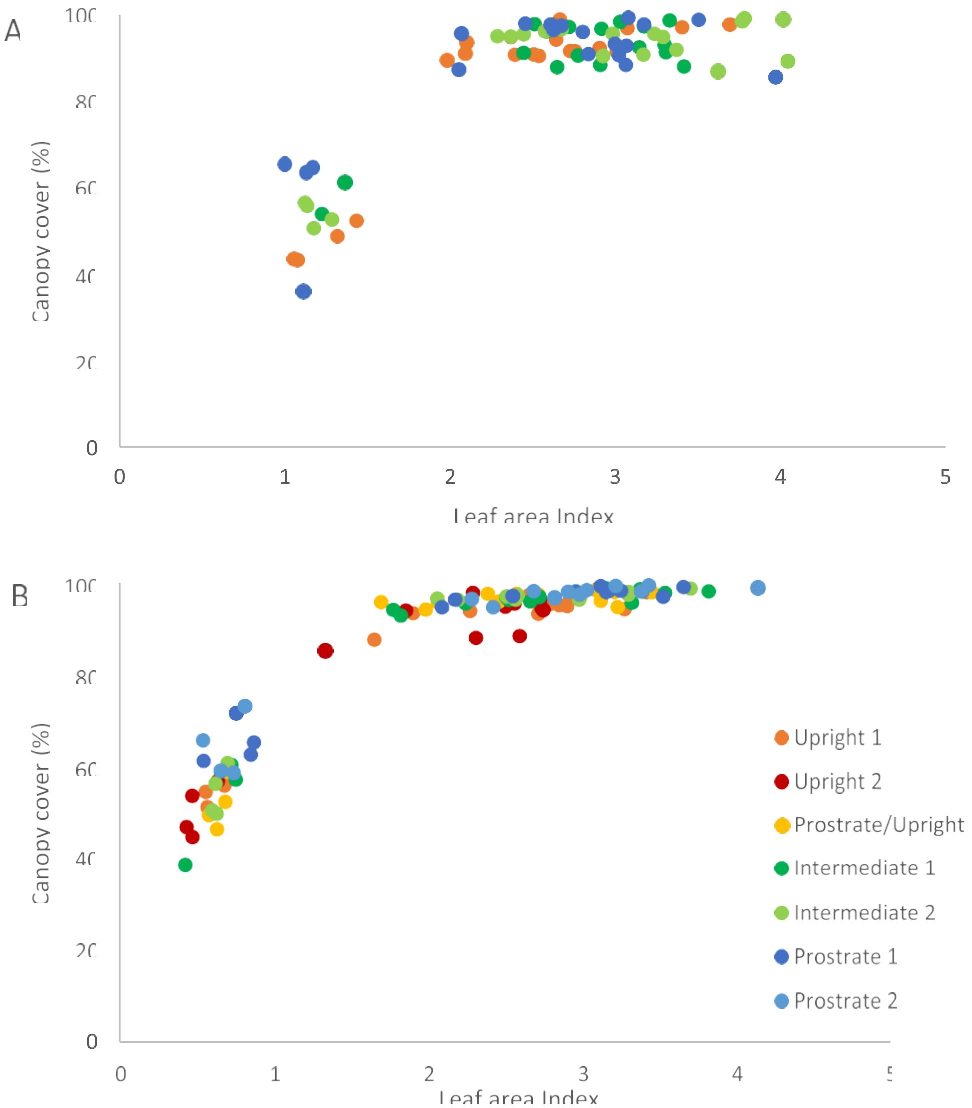

Fig. 8. The relationship between leaf area index and percentage canopy cover across the season for different sugar beet canopy types in 2019 (A) and 2021 (B).

cool and dry April and early May. Although GDD and radiation levels were similar in both years, 2019 had a higher overall RUE based on total biomass. This was likely caused by more consistent summer rainfall and the absence of mild drought seen in 2021. However, 2021 had a greater overall sugar yield, this is because in general there was a much higher sugar percentage per root fresh weight.

4.1 Canopy type and canopy development

The upright canopy types typically had petiole angles of less than 30°. The intermediate canopy types had a petiole angle between 30° and 45° and the prostrate canopy type had petiole angles of up to 50°. Petiole angle remained stable throughout the summer across varieties. However, the trials were only conducted on one soil type and the impact of soil texture on angle has not been explored. Heavier clay soils with a greater water and nutrient retention capacity have been shown to enhance canopy development and increase LAI in comparison to lighter soils, as a result the petiole angle may be also influenced by this (Richards, 2019). In 2021 the final petiole angle measurement was taken in December after the final biomass harvest, where leaf death rate had surpassed leaf appearance. This resulted in smaller secondary leaves appearing across canopy types which did not conform to the petiole angle measurements taken previously and thus more variation in angle between the measured leaves was seen despite the trend remaining the same.

The upright canopy types were slower to reach 50% canopy closure and had a lower modelled maximum canopy cover. This is because the petiole emerges out of the crown at a steeper angle than the other canopy types and as a result the leaves take longer to meet between rows. This means that the upright canopy types intercept less radiation than the intermediate and prostrate canopy types during June (pre-canopy closure) when radiation levels are high. LAI was also lower in upright canopy types and this could mean that the intercepted light may be even lower than the canopy cover indicates. Despite this, the upright variety used the intercepted light more efficiently than the prostrate varieties when measured up to December harvest.

Steeper leaf angles can increase light capture when the sun is low in the sky (morning/afternoon and winter) and can also reduce light capture at midday in the summer when the sun is directly overhead (Falster and Westoby, 2003). This can benefit the canopy by reducing midday canopy heat-load, thereby increasing water use efficiency, and decreasing the risk of photoinhibition (King, 1997; Burgess et al., 2015). Regardless of the potential increase in light use efficiency, a steeper canopy angle has a lower potential daily carbon gain by decreased light interception during the summer months which is a crucial yield building period (Scott and Jaggard, 1978). It has been hypothesised by Nobel and

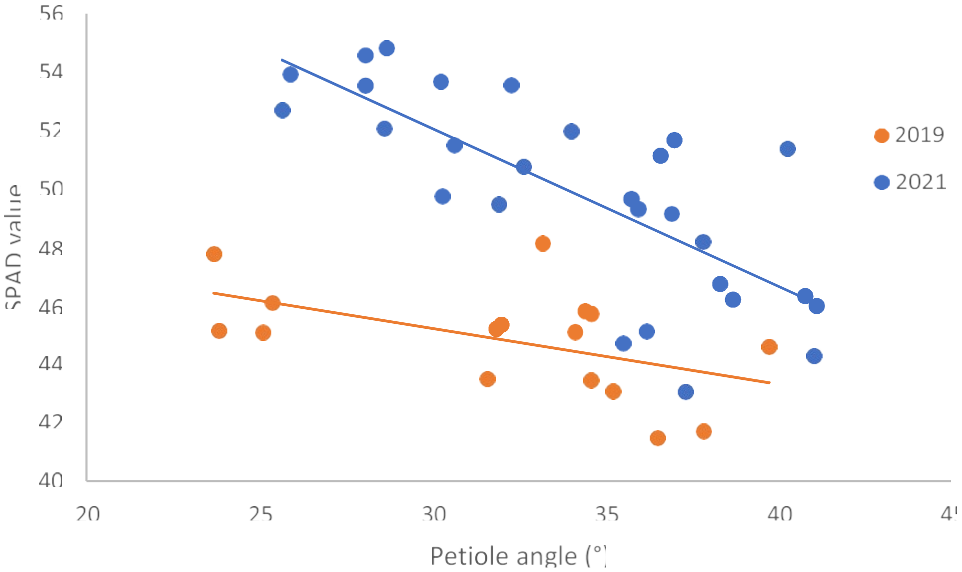

Fig. 9. The relationship between petiole angle and canopy greenness from SPAD-502 readings in 2019 and 2021. Petiole angle was calculated as an average of measurements taken from canopy closure to October in 2019 and 2021. Canopy greenness values were averaged from canopy closure to October. 2019: $y = -0.1907x + 50.942$ $R^2 = 0.27$ 2021: $y = -0.5399x + 68.259$ $R^2 = 0.56$.

Long (1985) and Huang et al. (2017) that for efficient radiation interception and photosynthesis across the season an intermediate canopy with upright new leaves and more prostrate older leaves is optimal. This is more typical of the intermediate canopy type in our study. Therefore, there is potential to further improve canopy light interception and yield by increasing the LAI and leaf angle distribution in upright varieties.

4.2 Canopy angle, chlorophyll content and photosynthesis

In both years there was a strong relationship between petiole angle and SPAD value. SPAD value gives an arbitrary value for leaf chlorophyll content considering leaf greenness. In sugar beet, SPAD and leaf chlorophyll content are highly correlated (Malnou et al., 2008). This means that in our study, a more prostrate canopy angle leads to a lower leaf chlorophyll content. In 2021, SPAD values were noticeably higher, this could be due to higher soil nitrogen availability and uptake or as a result of lower rainfall across the season leading to a higher concentration of plant pigments in the leaf (Martínez and Guiamet, 2004). The relationship between petiole angle and SPAD was stronger in 2021 as more varieties were measured. The differences in SPAD value seen across canopy types could be an adaptive trait selected by breeders. A lower concentration of chlorophyll in prostrate canopy types could form as part of an acclimation mechanism which has a photoprotective effect, minimising risk of photoinhibition in the crop (Murchie et al., 2005). Whereas the upright leaves at the top of the canopy seen in upright and intermediate canopy types have uniformly less light reaching their surface but have more chlorophyll. This could mean that the upright and intermediate canopy types can potentially absorb more of the light that reaches the leaf surface and use it more efficiently throughout the canopy. This could be an important factor contributing to a greater rate of late season biomass accumulation and higher RUE in upright canopy types.

High levels of leaf chlorophyll content seen in the upright canopy types did not lead to greater leaf photosynthesis, RUE, or yield to October harvest in this study. This concurs with Malnou et al. (2008) who also found that an increase in leaf greenness did not increase RUE in sugar beet. Ebmeyer and Hoffmann (2021) also showed no correlation between leaf nitrogen content and sugar yield. However, Loel et al. (2014), found a positive correlation between SPAD value and sugar yield when comparing old and new varieties. This could be explained by the breeding improvements seen in sugar beet over the last few decades where there has been a considerable increase in sugar yield (Jaggard et al., 2010). Chlorophyll content or high leaf greenness could also be selected for in modern varieties, but sugar yield could be influenced by a range of factors such as assimilate partitioning. In other crops with leaves which distinctly overlap, reduced leaf chlorophyll content might increase RUE and yield by improving light penetration and distribution within the canopy (Drewry et al., 2014; Slattery et al., 2017). Higher leaf chlorophyll may be beneficial towards the bottom of the canopy, in shaded conditions to improve light harvesting. Later in the season when the canopy begins to decline and incident radiation is less, increased leaf chlorophyll content could be beneficial to the crop enabling more efficient light utilization.

The Intermediate canopy type had high levels of leaf photosynthetic capacity recorded in August indicating that it is efficient at building yield during this period. However, it is unclear why this would be the case and may be due to a number of factors including leaf N and source sink dynamics (Nevins and Loomis, 1970; Paul and Foyer, 2001). These differences could be both genetic and/or an effect of the canopy angle.

4.3 Dry matter partitioning

The partitioning of biomass into the roots and tops differed significantly between canopy types and varied between years. In 2019 the upright canopy type consistently had a lower root to shoot ratio. Despite this, the upright canopy type had the smallest LAI which suggests that the leaves are fewer or smaller in size. Between August and October, the prostrate variety had the highest root to shoot ratio and by November the intermediate and prostrate canopy types had the greatest fraction of biomass partitioned to its roots.

In 2021 the intermediate 2 canopy type had a constantly higher proportion of total dry matter partitioned to root storage throughout the season. By December, the intermediate 2 canopy type had a ratio of almost double the other varieties, a greater rate of canopy senescence could explain this. The intermediate 2 canopy type was more efficient at partitioning assimilates into the storage organ and less energy was used to maintain canopy size. Across all canopy types in 2021, the leaf area index began to decline sooner than 2019 and this is likely caused by reduced new leaf formation. A smaller canopy could have benefited the crop in 2021 as below average rainfall was received. A smaller canopy

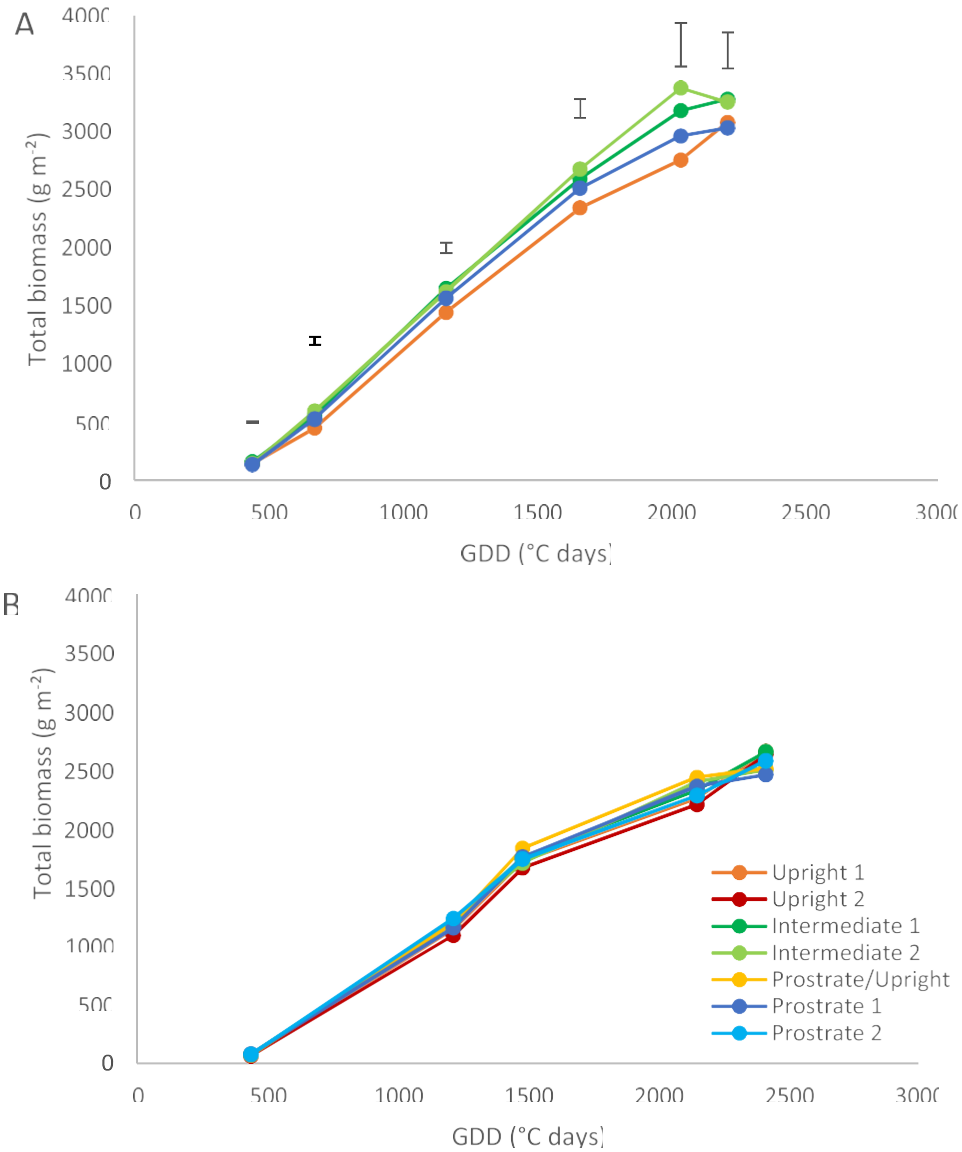

Fig. 10. Total plant biomass accumulated across the season affected by sugar beet varieties with different canopy types in 2019 (A) and 2021 (B). Error bar shows LSD$_{5\%}$.

can reduce transpiration and canopy maintenance which can be damaging to sugar yield (Hoffmann, 2014).

4.4 Canopy angle, radiation use efficiency and yield

When harvested up to November 2019 the intermediate canopy types had the highest RUE followed by the upright and prostrate canopy types. The RUE values from total plant biomass were markedly higher than 2021 but were recorded in the upper range of what has been shown previously in sugar beet (Hoffmann, 2019; Hoffmann and Kluge-Severin, 2010; Monteith, 1977; Werker and Jaggard, 1998). This is reflective of the season; the crop accumulated a lot of total biomass during the summer months where water was rarely limiting and disease incidence low. The rainfall also slowed canopy decline in 2019 in comparison to 2021 where the canopy biomass and LAI began to fall after 1500 GDD. Up to October harvest in 2021, the prostrate/upright canopy type had the highest RUE of 1.55 g DM per MJ. This is because the prostrate/upright canopy type accumulated more total biomass between July and October than the other canopy types. The alternate canopy arrangement could reduce mutual leaf shading across the canopy and as a result increase the productivity and photosynthetic potential of the canopy. This can be compared to intercropping whereby contrasting crops/canopies are often sown in alternate rows to improve radiation capture, water use and yield (Glaze-Corcoran et al., 2020).

At final harvest in December 2021, the upright canopy types had the highest RUE and the prostrate the lowest. During the period between October and December the upright canopy types continued to put on more root and canopy biomass than all other canopy types, thereby increasing the RUE value. The prostrate/upright canopy type accumulated very little biomass during this time. At final harvest in both years, the intermediate 2 variety had the highest sugar yield. The intermediate 2 variety was more efficient at intercepting and utilising light in 2019 up to final harvest and more efficient at partitioning biomass to the root in 2021. In both years, the prostrate varieties accumulated the most light however, the highest sugar yield was from the intermediate varieties indicating higher sugar yield RUE. This was supported by the higher net assimilation rate measured in the field.

If the plots were harvested even later then perhaps the upright canopy type would have continued to build yield and therefore out yield the intermediate 2 variety. There is no published research on the relationship between canopy angle and later harvest dates in sugar beet. Studies in other crops have shown that an upright canopy angle is more

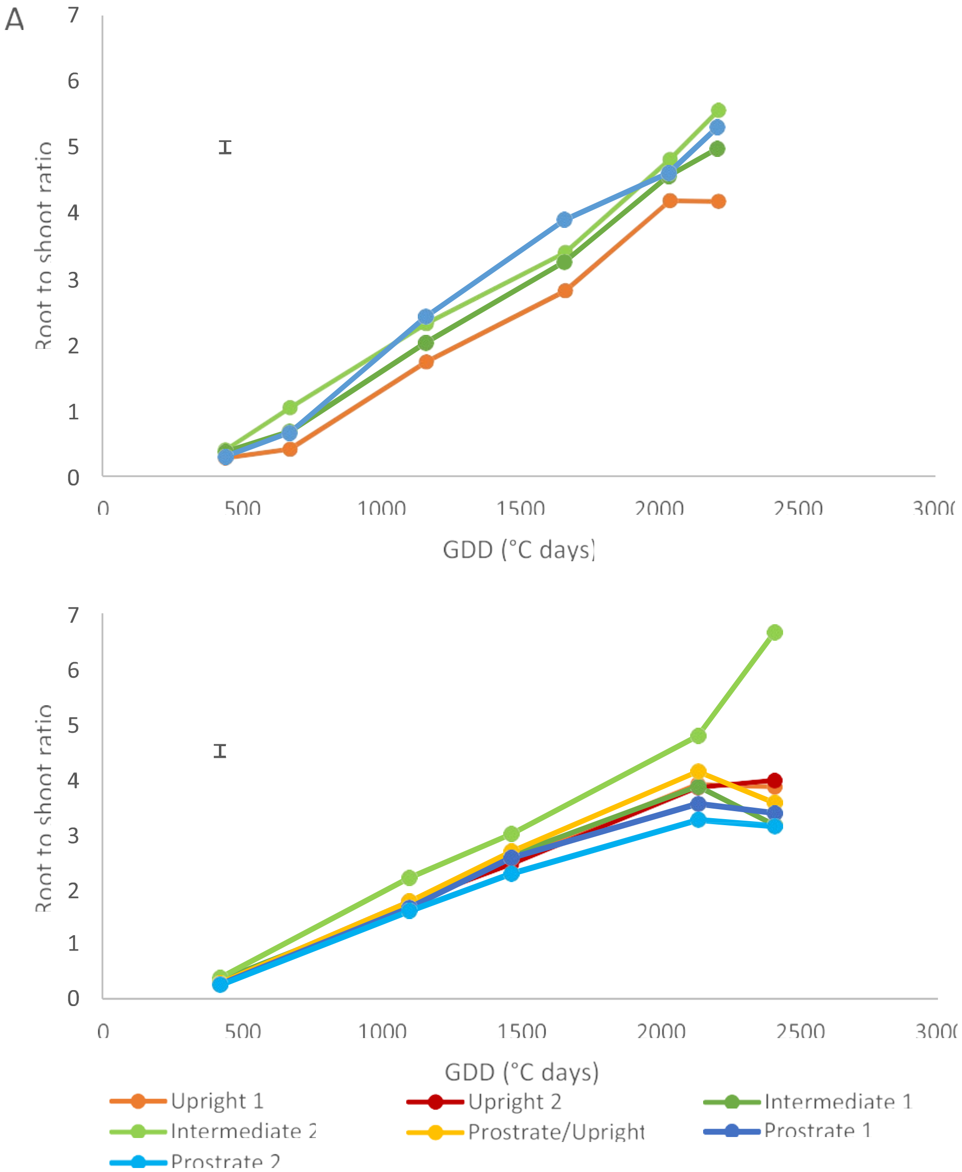

Fig. 11. Root to shoot ratio of different sugar beet canopy types against GDD (°C days) calculated as root dry weight divided by top dry weight (petioles and leaves). 5) 2019 and B) 2021. Error bar shows variety repeated measures LSD$_{5\%}$.

Table 3
Radiation use efficiency of different sugar beet canopy types calculated in 2019 and 2021 with standard error of regression (±).

Calculated radiation use efficiency (g MJ^{-1})			
Canopy type	**2019** (5/11/19)	**2021** (18/10/21)	**2021** (6/12/21)
Upright 1	1.67 ± 0.05	1.46 ± 0.06	1.49 ± 0.06
Upright 2		1.46 ± 0.06	1.51 ± 0.06
Intermediate 1	1.77 ± 0.05	1.45 ± 0.06	1.46 ± 0.06
Intermediate 2	1.82 ± 0.05	1.50 ± 0.06	1.42 ± 0.06
Prostrate/Upright		1.55 ± 0.06	1.45 ± 0.06
Prostrate 1	1.66 ± 0.05	1.44 ± 0.06	1.37 ± 0.06
Prostrate 2		1.39 ± 0.06	1.38 ± 0.06
P	< 0.001	< 0.001	< 0.001

Table 4
Season long RUE of different sugar beet canopy types calculated from final sugar yield in 2019 and 2021. Lower case letters show significant differences LSD$_{5\%}$.

Season long sugar yield RUE (g MJ^{-1})		
Canopy type	**2019**	**2021**
Upright 1	0.97 a	1.05 a
Upright 2		1.03 a
Intermediate 1	1.09 b	1.06 a
Intermediate 2	1.08 b	1.17 b
Prostrate/Upright		1.10 a
Prostrate 1	0.96 a	1.05 a
Prostrate 2		1.04 a
P	0.003	0.008
LSD	0.07	0.067

efficient at intercepting light at lower sun angles than a prostrate canopy (Gilbert et al., 2003; Sarlikioti et al., 2011). This suggests that estimations of light interception could be inaccurate when the sun angle is lower in the sky. The upright canopy types in this study could be more efficient at intercepting light in the winter months and therefore be more suited to a later harvest. The finding from a later harvest in 2021 in this study supports this.

There has been much discussion on whether sugar beet yield formation is source or sink limited (Hoffmann, 2019; Hoffmann and Kluge-Severin, 2010; Schnepel and Hoffmann, 2016). In sugar beet there

Table 5
Final clean root yield, sugar percentage and sugar yield of different sugar beet canopy types in 2019 and 2021. P value calculated for each year. Lower case letters show significant differences $LSD_{5\%}$.

Final yield ($t.ha^{-1}$)

Canopy type	2019 Root yield	2019 Sugar %	2019 Sugar yield	2021 Root yield	2021 Sugar %	2021 Sugar yield
Upright 1	107.2 a	16.7 a	17.9 a	103.8 ab	18.4	19.1 ab
Upright 2				101.6 a	18.6	18.8 a
Intermediate 1	122.2 b	17.0 b	20.8 b	106.5 ab	18.8	20.0 ab
Intermediate 2	123.5 b	16.6 a	20.5 b	117.9c	18.7	22.0c
Prostrate/ Upright				109.7 b	18.6	20.4 b
Prostrate 1	107.0 a	17.0 b	18.2 a	110.1 b	18.4	20.3 b
Prostrate 2				110 b	18.4	20.2 ab
P	0.002	0.023	0.002	0.003	0.821	0.002
LSD	8.7	0.3	1.4	7.0	0.6	1.3

is a strong linear relationship between accumulated intercepted radiation and biomass (Jaggard and Qi, 2006). This suggests that sugar beet is source limited. In our study there was a linear relationship between accumulated intercepted radiation and biomass within varieties, however, both RUE, root to shoot ratio and hence yield differed between varieties. Other studies have also found no relationship between total radiation intercepted and yield and have assumed other factors such as assimilate partitioning and root/sink storage to be limiting (Hoffmann, 2019; Hoffmann and Kenter, 2018; Schnepel and Hoffmann, 2016). In our study it is assumed that RUE is a limiting factor to yield which could be linked to canopy angle and the efficiency of radiation interception. However, the varieties used in this study differ in more than just canopy angle so it is not possible to directly attribute differences in RUE to canopy angle alone.

5 Conclusions

Sugar beet can be classified into canopy types according to their petiole angle. The impact of canopy angle on RUE and yield was investigated. A prostrate canopy type had a faster rate of canopy expansion and intercepted more light across the season. Intermediate canopy types and prostrate/upright alternate sowing treatment had the highest RUE to October/November harvest and the highest sugar yield. This was associated with a higher root to shoot ratio and may indicate a higher rate of canopy senescence as well as greater sink capacity. The upright canopy type had a lower RUE and yield (except late in season) but also had a lower LAI which may have been limiting early on in the season but potentially more efficient at utilizing available light, especially later in the sugar beet season, and thus suit a later harvest. Therefore, there is scope to further improve yield by increasing LAI and root to shoot ratio in upright canopies. The results from this study will aid in the selection of varieties to improve sugar beet yields and future breeding efforts. Whilst canopy angle is an important contributing factor to RUE and yield in sugar beet, it is likely that other factors such as leaf level photosynthesis and biomass partitioning are just as important.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2023.108841.

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Chapter 3: Sugar beet canopy manipulation: is radiation use efficiency and yield determined by canopy angle?

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3.1 Abstract

Sugar beet varieties differ greatly in their canopy architecture, radiation use efficiency (RUE) and sugar yields. Canopy or petiole angle is a key factor of sugar beet canopy architecture and is a key determinant of light interception and utilisation. Differences in RUE exist between commercial sugar beet varieties with contrasting canopy angles. It is not known whether sugar beet RUE is solely influenced by canopy angle or superior varietal genetics. This study aims to uncouple the relationship between RUE and canopy angle using a canopy manipulation approach to determine if varieties can be selected according to their canopy types for high RUE and yields. A variety with high RUE and yields was manually manipulated to be more upright using plant support cages and more prostrate using pegs alongside an untreated control. In both years (2021, 2022), the upright treatment had a lower percentage canopy cover measured up to canopy closure and in 2021 the flat treatment expanded its canopy at a greater rate and reached canopy closure sooner. This was not seen in 2022 due to warm and wet spring weather conditions leading to rapid canopy development and closure. The upright treatment coped better in the drought conditions in 2022, it lost less canopy and was less stressed which could be accounted for by the upright angle reducing the midday heat load on the canopy. The treatments had no effect on photosynthesis in both years or season long RUE in 2022. However, in 2022 the upright treatment had a higher RUE the flat treatment in July and the control treatment at final harvest. The upright treatment had a higher above ground biomass and the control treatment had a higher root to shoot ratio. Canopy angle had no effect on sugar yield in either year. Whilst canopy angle may be an important contributing factor to RUE and yield in sugar beet it is more likely that RUE and yield is genetically determined.

3.2 Introduction

Sugar beet is an economically important crop for sucrose production worldwide with Europe accounting for 60% of total sugar beet production (FAOSTAT, 2021). Sugar beet yield has steadily increased over the last few decades through the introduction of improved varieties and management practices including the use of plant protection products and early sowing dates (Märländer et al., 2003; Jaggard et al., 2010). Despite this, a yield potential of 24 tonnes of sugar per hectare hypothesised by Hoffmann and Kenter (2018) is yet to be achieved across commercially grown crops with an increasing yield gap between variety trials and commercial crops (Jaggard et al., 2012). Canopy architecture is composed of leaf area, canopy angle and leaf number and has a significant impact on canopy light interception (Duncan, 1971; Norman and Campbell, 1989). Canopy architecture is seen as an important trait for yield improvement in breeding programmes (Niinemets, 2010). In many major crops there is a strong linear relationship between accumulated intercepted radiation and biomass. The slope of this relationship is defined as the radiation use efficiency (RUE) (Monteith, 1977). The optimisation of sugar beet canopy architecture to enable more efficient light interception could help to improve RUE and increase sugar beet yields.

Early studies have suggested that leaf angle and leaf area index (LAI) are important canopy architecture targets to optimize RUE (de Wit, 1965; Duncan et al., 1967; Peng et al., 2008; Anthony and Minas, 2021). Leaves have a curvilinear photosynthetic response to increasing light intensity and therefore, more erect or upright canopies will have a higher utilization efficiency of incident light. This is due to a more even distribution of light throughout the canopy (Long et al., 2006; Zhu and Long, 2010; Burgess et al., 2017). As a result of this, an upright canopy angle has been shown to increase RUE and yields in wheat and rice (Pendleton et al., 1968; Burgess et al., 2017; Richards et al., 2019). Chapter 2 assessed the RUE of a range of sugar beet canopy types (upright, prostrate and intermediate) and found that an intermediate canopy type (classified by petiole angle) had the greatest photosynthetic rate and RUE to October and overall final sugar yield. However, due to the small number of varieties evaluated in this experiment, the extent to which the differences are it is unclear whether RUE is genetically predetermined through direct or indirect genetic effects causing increased photosynthetic capacity and sink strength.

Canopy manipulation is the process of altering a plant’s canopy architecture through manual alterations (Pendleton et al., 1968). This can include reducing leaf area or changing the angle of the leaves and/or petioles. Canopy manipulation has been successfully achieved using manual methods in many orchard and vine crops to improve RUE and reduce disease incidence through the manipulation of the canopy microclimate (Somkuwar et al., 2018; Anthony and Minas, 2021). The sugar beet canopy is very different to grape vines, the leaves are in a rosette formation and are produced consecutively from the centre of the crown (Milford et al., 1985a). Therefore, novel approaches capable of manipulating many sugar beet plants in a natural light environment are required to make the canopy angle more upright or prostrate. To be effective the manipulation treatment must be able to have a sustained impact on canopy architecture throughout the season without affecting the overall health and vigour of the crop in order to assess the effect of canopy angle on RUE and yield.

Our aim was to address the question: does canopy angle have a direct impact on radiation use efficiency of sugar beet?

3.3 Method

3.3.1 Field and plant material

In 2021 and 2022, field experiments were established at the University Farm, Sutton Bonington, Leicestershire, UK (52°50´07″N, 1°15´04.0″W) on sandy loam soils (Dunnington Heath series). The experiments were arranged as randomized complete block designs with four replicates in 2022 and blocked with four replicates in 2021. Pelleted sugar beet (*Beta vulgaris L.*) seeds, variety BTS1140 were sown at the end of March in six row plots (30/03/2021; 30/03/2022). The plots were then divided in to three sections in 2021 for each treatment and in 2022 there was one treatment per plot.

In both years, the seeds were sown 50cm apart at 9 cm spacing then, at the 3–4 leaf stage, the plants were manually thinned to a target population density of 100,000 plants ha^{-1}. Chemical fertilisers and plant protection products were applied according to standard agronomic practices to keep the crop free of pests, weeds, and diseases (see Supplementary Table S3.1).

The daily incident solar radiation, rainfall and temperature were recorded by an onsite weather station.

3.3.2 Canopy manipulation treatment

The canopy was manipulated using one upright and one prostrate method as well as an untreated control (Table 3.1). In 2021, 16 plants were treated per plot (4 rows (50 cm/row) x 75 cm length = 3 m²) and in 2022 a larger area of 6 rows (50cm/row) x 4 m length was treated. In 2021, the treatments were applied at 8 leaf stage (71 days after sowing (DAS)) and in 2022 the treatments were applied in two stages; 3 middle rows were treated at 10 leaf stage and the remaining rows treated at 14 leaf stage (59 and 78 DAS). The plants were treated at a later stage in 2022 to avoid plant stress experienced from heat and dry weather in May and June. The staggered treatment application in 2022 was due to the availability of material

Table 3.1 Canopy manipulation treatments and methods including the materials used.

Treatment	Canopy at 12 leaf stage	Method	Material
Upright		Placed over the plant at 8 leaf stage with the widest part facing up, ensuring all leaves are inside the cage	Sopafix 17/2 Es round pot supports (Soparco Ltd., Sablons-sur-Huisne, France)
Control			
Prostrate		Three fully expanded leaves were pegged down per plant at all times. No leaves were in direct contact with the soil	150 mm U-shaped Pegs

3.3.3 Plant measurements

3.3.3.1 Canopy cover and development

The plot areas were marked out after thinning and any gaps in the plot were noted. After treatments were applied, canopy cover was measured each week during the canopy expansion phase, then monthly thereafter. In 2021 the plot size was smaller than in 2022. Because of this, canopy cover was measured using a different imaging approach. In 2021, an image was taken at shoulder height above the plots using a camera (Canon Powershot sx720 (Canon Inc. Tokyo, Japan)). Care was taken to ensure all treated plants were in frame.

In 2022, a Canon 1100D camera (Canon Inc. Tokyo, Japan) was mounted on a frame that allowed images to be taken directly above the plots. A wide angle 10-18 mm lens was fixed at 10 mm and held above the plot at a height of 1.2 m and 2.5 m from the edge of the plot. The central three rows of sugar beet were aligned within the view of the lens. A photo was taken from above the treatments in the plot. Percentage canopy green area was measured by thresholding the green area on each image in ImageJ (Rasband, 2011).

Canopy expansion and development was modelled using a three-parameter loglogistic model in R (R Core Team) using the method described in Chapter 2 (Supplementary information Figure S3.1). Canopy cover measurements up to canopy closure (126 and 101 DAS) were used in 2021 and 2022 respectively. Maximum canopy cover, slope, and the inflection point of the canopy in each plot was calculated. The inflection point represents the expansion rate of the canopy and is defined as the number of days after sowing where 50% of maximum canopy cover is achieved.

In addition to canopy images, a Crop Circle DAS44X (Holland Scientific, Lincoln, NE, USA) was mounted on the same frame, at the same height, adjacent to the camera in order to measure the same area of each plot. The Crop Circle was used to measure the ambient air and canopy temperature. Canopy temperature depression (CTD) of each plot was calculated in 2022 as ambient air temperature minus canopy temperature. A high or positive CTD value in the absence of exposed soil relates to a cooler canopy from stomatal conductance during photosynthesis.

3.3.3.2 Leaf greenness

Leaf greenness was measured fortnightly from 93 DAS in 2021 and 71 DAS in 2022 to harvest with a Minolta SPAD-502 chlorophyll meter (Minolta Camera Co., Ltd., Japan). Three measurements were averaged per leaf and four randomly selected and fully expanded leaves of similar age were measured per plot.

3.3.3.3 Photosynthesis

Leaf level photosynthesis was measured on 20 September 2021 and 13 July 2022. The net CO_2 assimilation rate and stomatal conductance was directly measured in the field between 08:30 and 12:00. Three fully expanded treated leaves were selected per plot and measured using a Li-6800 portable gas exchange system (LiCOR Inc., Biosciences, Lincoln, NE, USA). The sample PPFD, CO_2 concentration, relative humidity and leaf temperature inside the cuvette were set to 1200 µmol m^{-2} s^{-1} (light responses curves indicated this was saturating), 400 µmol mol^{-1} CO_2, 50 % RH and block temperature of 20 °C, respectively. The leaves had a five minute adjustment period in the cuvette before measurements were taken to allow the leaf to stabilise. The data was analysed as an average of three leaves per plot.

3.3.4 Biomass harvest

A destructive biomass harvest was taken at 120 DAS in 2022, 2.5 m^2 of each plot was harvested and washed thoroughly before total fresh weight was recorded. A 50 % sub sample was taken, and the roots were separated from the tops at the lowest leaf scar. The leaves were then separated from the petioles at the bottom of the leaf. Fresh weight of each component part was recorded, and leaf area measured using a LI-3100C leaf area meter (Li-COR Inc., Biosciences, Lincoln, NE, USA) and used to calculate leaf area index. All components (leaves, petioles, roots) were then oven dried at 65 °C until a constant weight was achieved and dry was weight recorded.

3.3.5 Radiation use efficiency and yield

Radiation use efficiency (RUE) of the crops from total plant biomass was measured in both years. Percentage canopy cover was assumed to be equal to the percentage of incident solar radiation intercepted by the canopy and hence used, together with daily meteorological data, to determine the amount of solar radiation intercepted throughout the season (Steven et al., 1986). No differences were seen in canopy light reflectance between treatments which was measured using the Crop Circle DAS44X PAR reflectance sensor (Holland Scientific, Lincoln, NE, USA) and were therefore not used in the calculation. Accumulated intercepted global total radiation in MJ m^2 (*I*) was calculated as Equation 1.

Equation 1: $I = [(C_1 \times R_1) + (C_n \times R_n)]$

C_1 is the percentage canopy cover assessed during week 1 and R_1 is the total incident radiation during week one (MJ m^2). Accumulated intercepted light is calculated from daily radiation receipts and percentage canopy cover assessments.

RUE was calculated from the first percentage canopy cover calculations (08/06/21 (71 DAS) and 01/06/2022 (64 DAS)) until harvest. For each treatment RUE was calculated as total plant biomass divided by accumulated incident total radiation.

The plots were harvested on 9 November in 2021 and 5 October in 2022. The plots were harvested differently each year as shown in Figure 3.1. In 2021, the four middle plants of each treatment were harvested for biomass following the methods in section 2.3.4. The eight edge plants were harvested and taken to BBRO (British Beet Research Organisation) tare house for yield and sugar percentage analysis and the corner plants, roots and tops were weighed and discarded. In 2022, 6 plants were harvested each in rows 2 to 5. Rows 2 and 3 were sent to the tare house for yield analysis and rows 4 and 5 were harvested for biomass and canopy measurements. The sugar yield was calculated from the clean root weight and sugar percentage in both years. In 2021, the sample size was smaller which could have contributed to more variability in the RUE results compared to the larger sample size in 2022.

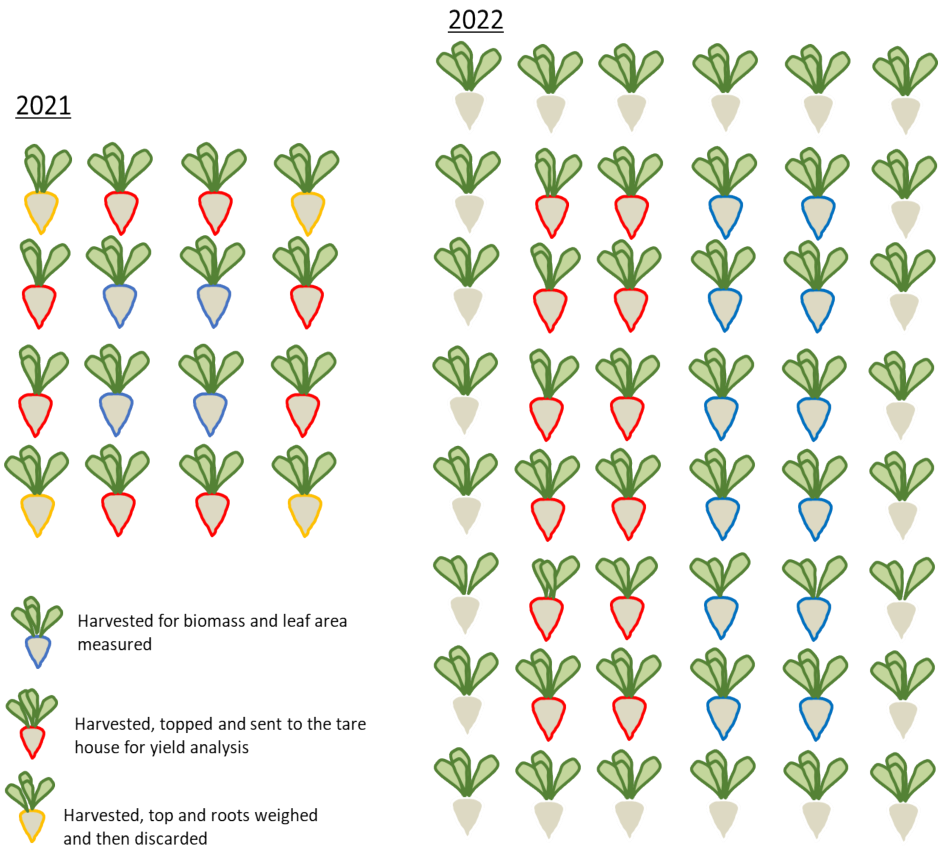


Figure 3.1 2021 and 2022 harvest plan. The destination of each harvested sugar beet is colour coded.

3.3.6 Data analysis

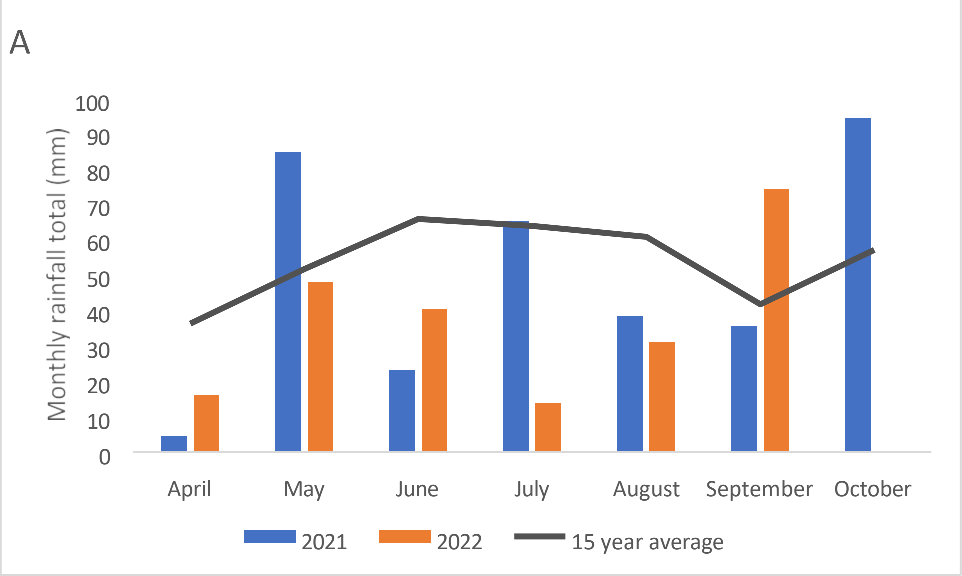
Data was analysed using Genstat 20th edition (VSN International, Hemel Hempstead, UK) using one way analysis of variance (ANOVA). A repeated measures analysis was carried out on measurements taken across the season. Calculation of the least significant difference (LSD) at 5% significance was included in the ANOVA. Figures were prepared using Microsoft Excel (Microsoft Corp., Redmond, WA, USA).

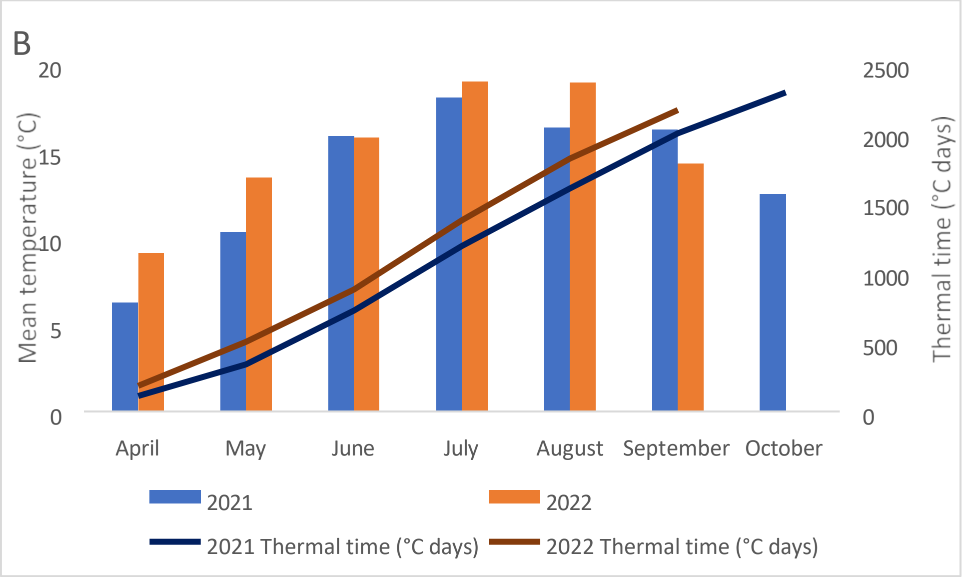
3.4 Results

3.4.1 Weather data

2021 season had a dry and cold start in April which delayed canopy growth but wetter and warmer temperatures in late May accelerated canopy expansion (Figure 3.2A, B). 2022, had a warmer and wetter start to the season and the canopy established faster and as a result the plants were ready to be treated a week earlier.

Both years were considerably drier than the long-term average. The 2022 season experienced high temperatures and low rainfall in July and August which triggered a national drought. September rainfall varied between the two years, 2022 received double the rainfall than 2021 for this period. Monthly radiation levels were generally greater across the 2022 season and particularly in August, where 180 MJ m² of more light was seen compared to 2021 (Figure 3.2C).





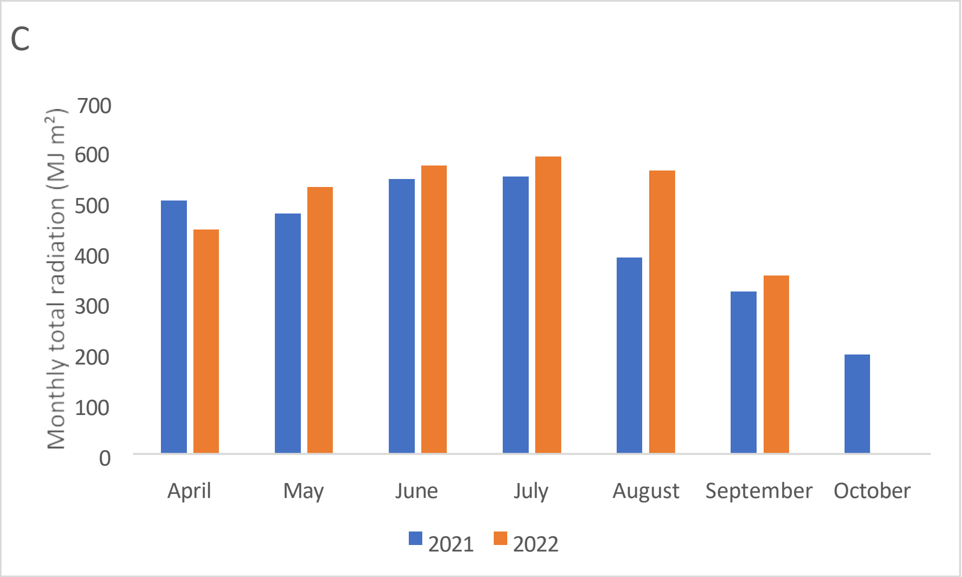


Figure 3.2 Weather data recorded at Sutton Bonington, UK across the season in 2021 and 2022. A) Total monthly rainfall across the season. B) Mean air temperature and accumulated thermal time across the season, using a base temperature of 3°C. C) Monthly total radiation.

3.4.2 Canopy development and cover

The upright treatment had a lower canopy cover than the control and flat treatments in 2021 and 2022 up to 94 DAS and 101 DAS respectively (Figure 3). In both years, there were no significant differences in canopy cover between treatments after 100 DAS until harvest (Figure 3.3A). In 2022, percentage canopy cover declined substantially across all treatments between July and August (100 to 143 DAS) when high temperatures and low rainfall was experienced (Figure 3.2A, B). The control and flat treatments saw a 20 % decrease during this period in comparison to the upright treatment which declined by 10 % (Figure 3.3B). However, despite this, all treatments recovered their canopy to pre-drought levels at similar rates during September (between 143 and 169 DAS).

In 2021, the inflection point (days after sowing required to reach 50 % maximum cover) and maximum canopy cover estimated by the log-logistic model, was significantly different between treatments (Table 3.2). A difference of 4 DAS to achieve 50 % maximum canopy cover existed between the upright and flat treatments. The upright treatment expanded its canopy at a slower rate than the control and flat treatments. The upright and control treatment also had a significantly higher modelled maximum canopy cover ($P<0.05$). The flat treatment overall required less days to reach 50 % modelled maximum canopy cover and also had the lowest modelled maximum canopy cover ($P<0.001$). Despite this, there were no differences between the slope (canopy expansion rate) between treatments.

In 2022, the treatments were applied at 20 % greater canopy cover than in 2021 (Figure 3.3). Because of this, canopy cover measurements were later and hence less data was available for the canopy development phase and the log logistic model was affected (Table 3.2). The impact of this was exaggerated in the modelled slope and maximum canopy cover whereby the upright treatment had a significantly greater modelled slope, which is the rate of canopy expansion and modelled maximum cover despite this not being seen in Figure 3.3. This value was more than double the control and flat treatments. There were no differences seen between the inflection point and maximum canopy cover. See the supplementary information, Figure S3.1 for modelled curves for 2021 and 2022.

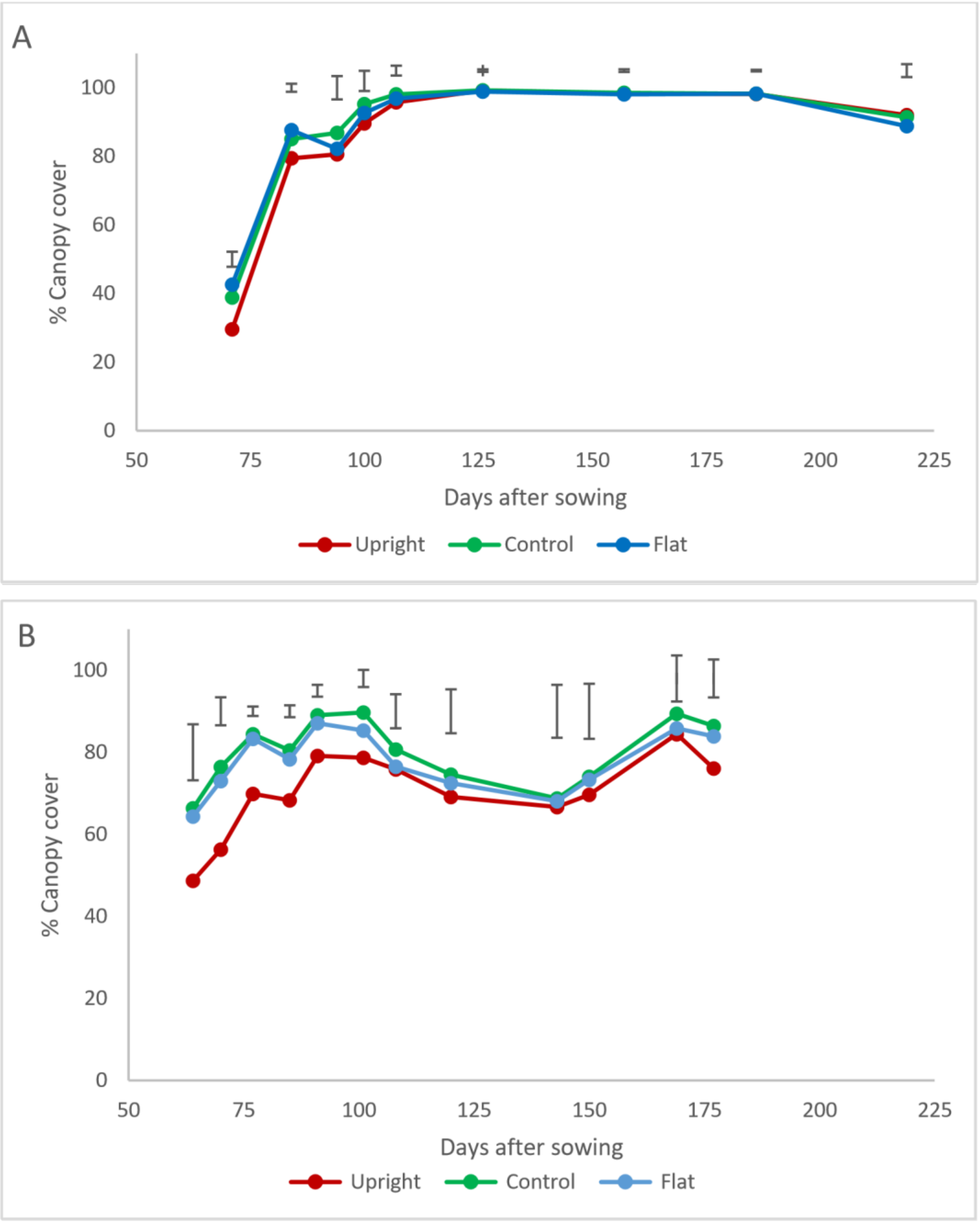


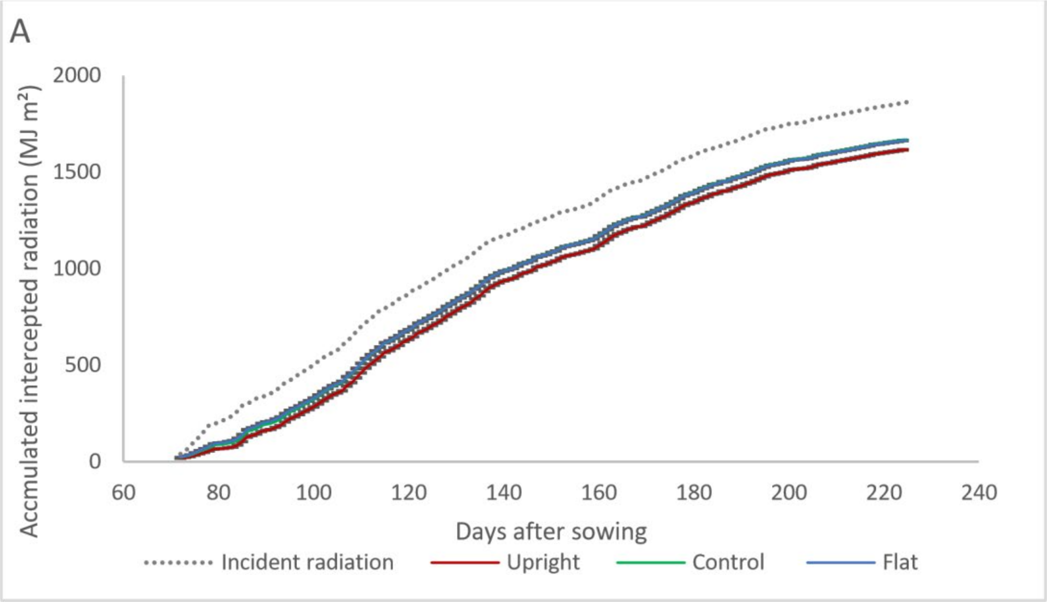
Figure 3.3 Percentage canopy cover plotted against days after sowing across the season measured from the date in which treatments were applied across Upright, control and flat treatments. A) 2021 and B) 2022. Error bars show $\mathrm{LSD}_{5\%}$.

Table 3.2 Three parameter log logistic model output for modelling canopy development between treatments in 2021 and 2022. Lower case letters show significant differences *between upright, control and flat treatments*. The modelled curves are shown in the supplementary material Figure S3.1.

2021				**2022**		
Treatment	Slope	Inflection point (Days after sowing)	Maximum canopy cover (%)	Slope	Inflection point (Days after sowing)	Maximum canopy cover
Upright	-11.47	75.8 c	96.84 b	-10.815 b	61.56	83.84
Control	-12.59	73.31 b	97.63 b	-4.445 a	55.7	95.98
Flat	-15.16	71.99 a	95.14 a	-3.89 a	53.69	100.34
P	0.299	<0.001	0.015	<0.05	0.407	0.329
LSD$_{5\%}$	5.366	0.759	1.464	4.787	13.82	25.5

3.4.3 Accumulated intercepted radiation

In both years the upright treatment intercepted less total solar radiation than the other treatments across the season (Figure 3.4). In 2021, across all treatments, the accumulated intercepted radiation was proportional to incident radiation and there were marginal differences between the flat and control treatments (Figure 3.4A). In 2022, the relationship between accumulated intercepted radiation across all treatments and incident radiation was much less proportional (Figure 3.4B). By the end of the season there was >500 MJ m^2 incident radiation that was not intercepted by the canopy in comparison to just 200 MJ m^2 in 2021. This is linked to the decline in canopy cover experienced during the drought period, as highlighted in Figure 3.3B.



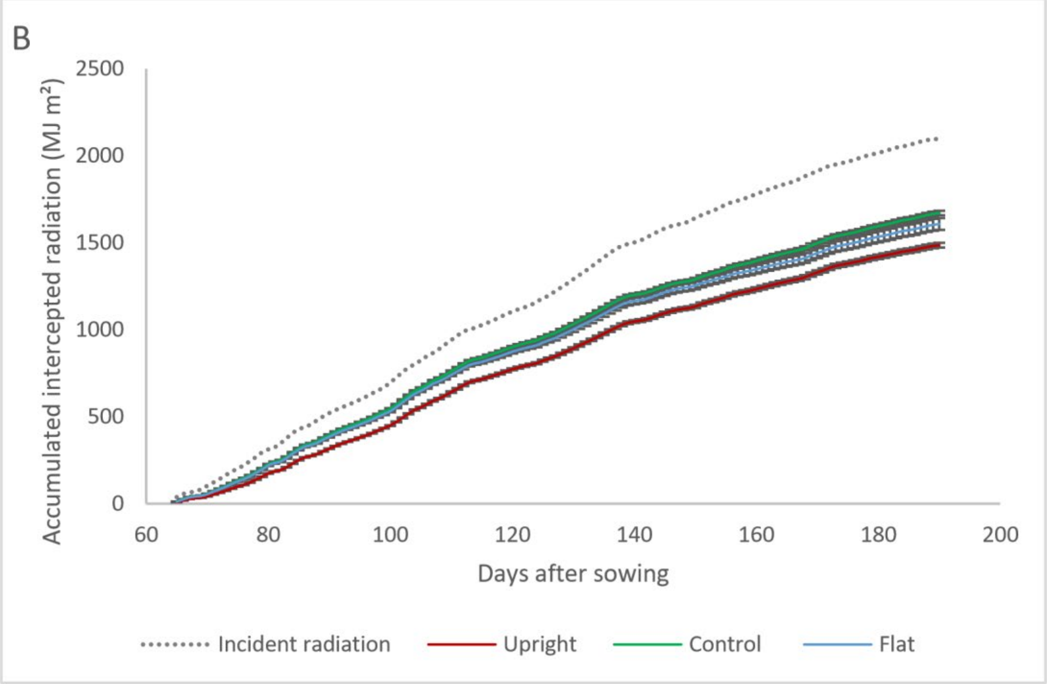


Figure 3.4 Accumulated intercepted light across the season in 2021 (A) and (B) 2022 for upright, control and flat canopy treatments. Total accumulated incident radiation is also shown for reference. Error bars show standard error (±).

3.4.4 Canopy greenness

SPAD-502 measurements give an arbitrary reading for canopy greenness which is highly correlated with chlorophyll content in sugar beet (Malnou et al., 2008). In 2021, the upright treatment had a lower SPAD across the season (P<0.05) (Figure 3.5A). There were no differences in SPAD value between the control and flat treatments in 2021. In 2022 there were no differences in SPAD between treatments (Figure 3.5B). In 2021 the recorded SPAD values across the season ranged between 45 and 55, this was also seen in 2022 up until 142 DAS where the SPAD value across all treatments increased consistently to between 62 and 66 DAS up until final harvest.

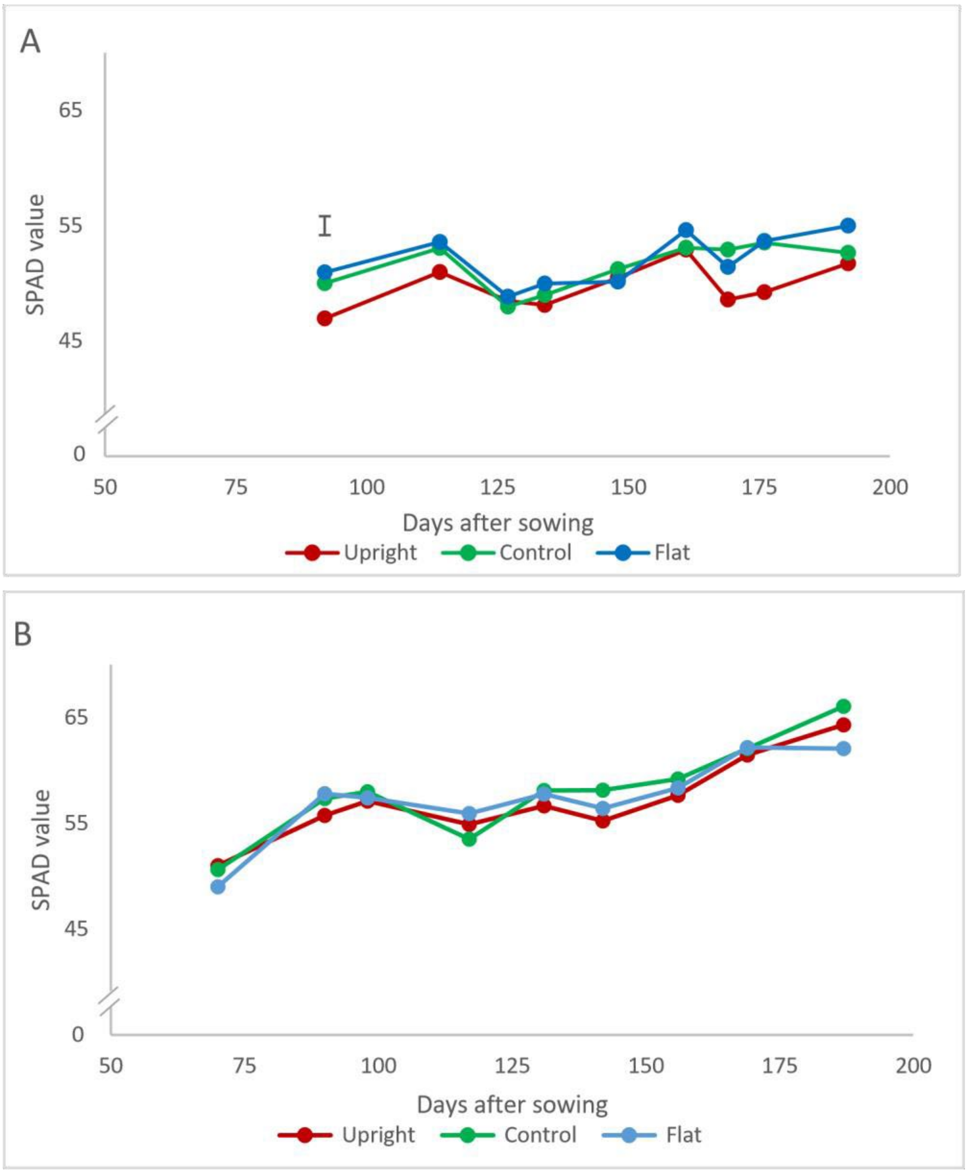


Figure 3.5 Canopy greenness measured across the season from SPAD-502 readings in A) 2021 and B) 2022 for upright, control and flat treatments. Error bar is shows treatment repeated measures LSD$_{5\%}$. Error bar is shown for 2021 only due to 2022 not being significantly different between treatments.

3.4.5 Canopy photosynthesis

Leaf net CO_2 assimilation rate and stomatal conductance were measured on 20 September 2021 and 13 July 2022 (Table 3.3). One data set is presented for each year due to the weather causing large variation in the data sets on other dates.

There were no significant differences between treatments in assimilation rate or stomatal conductance in either years (Table 3.3). However, there was a trend for the control treatment to have a higher assimilation rate and leaf conductance than the upright and flat treatments in both years.

The plants were more photosynthetically active in 2021 compared to 2022 (Table 3.3). Assimilation values were over three times higher in the upright and control treatments and 2.5 times greater in the control. Leaf conductance values were also 10 times higher in 2021. These differences between the two years were likely caused by water stress in the crop in 2022.

Table 3.3 Net CO_2 assimilation (μmol $m^{-2}s^{-1}$) and stomatal conductance (mol $m^{-2}s^{-1}$) measured on 20 September 2021 and 13 July 2022 for upright, control and flat treatments.

	20 September 2021		**13 July 2022**	
Treatment	Net CO_2 assimilation (μmol $m^{-2}s^{-1}$)	Stomatal conductance (mol $m^{-2}s^{-1}$)	Net CO_2 assimilation (μmol $m^{-2}s^{-1}$)	Stomatal conductance (mol $m^{-2}s^{-1}$)
Upright	24.13	0.58	8.77	0.06
Control	25.14	0.69	10.12	0.06
Flat	24.3	0.58	7.59	0.05
P	0.896	0.548	0.163	0.359
LSD5%	6.23	0.29	2.89	0.025

Figure 3.6 shows canopy temperature depression (CTD) measured across the season in 2022. At the start of the season, the control and flat treatments had a significantly higher CTD or canopy transpiration than the upright treatment ($P<0.05$). However, at 108 DAS the crop was considerably stressed and had limited its transpiration and as a result the canopy temperature was higher than ambient creating a negative CTD across all treatments. During this time, the upright

treatment had a significantly higher CTD and transpiration rate than the flat and control (P<0.05).

When ambient air temperature began to fall below 25 °C coupled with September rainfall the plants became more photosynthetically active and CTD was positive across all treatments. At 150 DAS the upright and control treatment had a significantly greater CTD than the flat treatment and by the end of September, 177 DAS the control treatment had the greatest CTD.

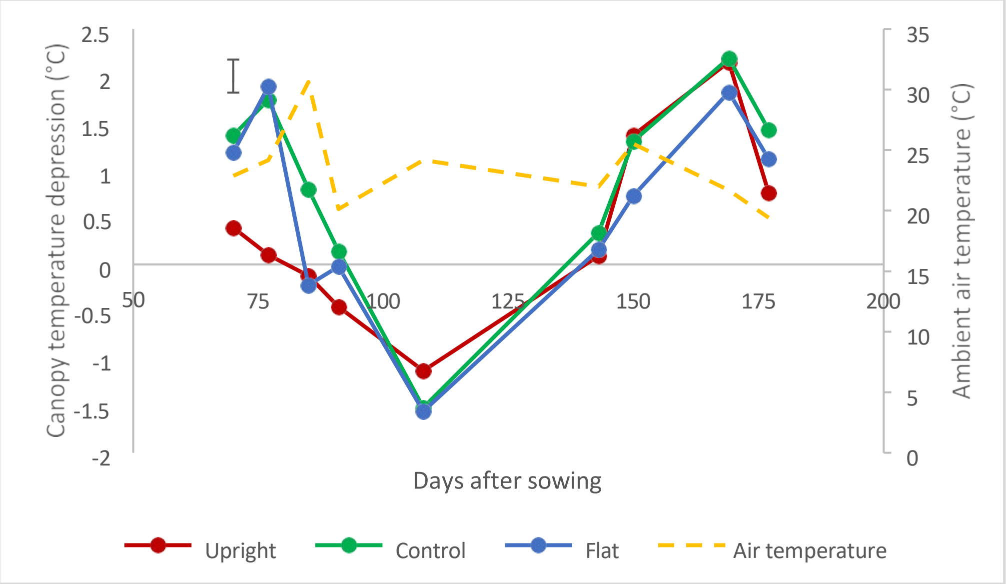


Figure 3.6 Canopy temperature depression (CTD) measured as air temperature minus canopy temperature across the season in 2022 for upright, control and flat treatments. Ambient air temperature is shown for reference. Error shows repeated measures treatment $LSD_{5\%}$.

3.4.6 Total biomass and partitioning

In 2021, there were no significant differences in total biomass per plant between treatments despite the upright treatment having 30 g less biomass than the control and flat treatments (Figure 3.7). In 2022, after canopy closure at the end of July (116 DAS), there were also no differences in total biomass between treatments. Between the end of July and start of October 2022 (186 DAS), total biomass increased markedly (Figure 3.7). There were no differences in the amount of biomass accumulated between treatments during this period or total biomass recorded at the start of October.

There were no differences in above ground biomass per plant in 2021 and end of July 2022 (Figure 3.7B). By early October 2022, the upright treatment had a significantly greater above ground biomass per plant than the control treatment (P<0.05; Figure 3.7B).

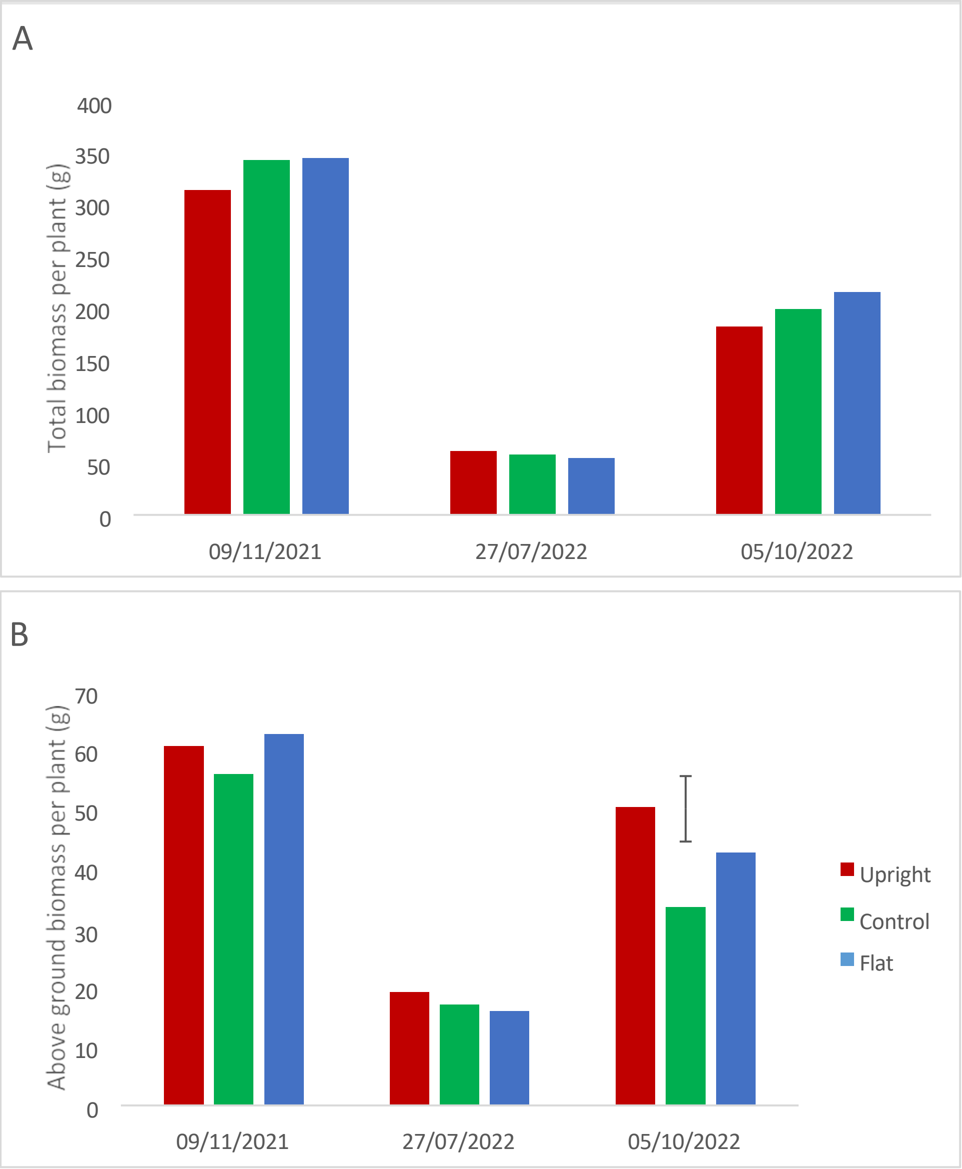


Figure 3.7 Total biomass (A) and above ground biomass per plant (B) recorded in 2021 and 2022 *for upright, control and flat treatments*. Error bar shows $LSD_{5\%}$.

In general, across both years, the upright treatment had a lower root to shoot ratio than the control and flat treatments (Table 3.4). Although in 2021 and late July 2022 this was not significantly so. In early October 2022, there were significant differences in biomass partitioning between treatments (P<0.05). The upright treatment had a significantly lower root to shoot ratio than the control treatment and a significantly greater above ground biomass weight recorded in this period (P<0.05; Table 3.4 and Figure 3.7B). Therefore, the control treatment had significantly more biomass partitioned into its root than aboveground portion.

Table 3.4 Root to shoot ratio calculated as root biomass divided by above ground biomass in 2021 and 2022 *for upright, control and flat treatments.* Lower case letters denote significant differences.

Root to shoot ratio			
Treatment	**09/11/2021**	**27/07/2022**	**05/10/2022**
Upright	4.15	2.21	3.28 a
Control	5.15	2.41	4.43 b
Flat	4.60	2.45	3.68 ab
P	>0.05	>0.05	<0.05
LSD$_{5\%}$	0.88	0.33	0.82

3.4.7 RUE and yield

Radiation use efficiency (RUE), was higher in 2021 than 2022 (Table 3.5). There were no differences in RUE between treatments in 2021. Despite this, the upright treatment had 0.12 g MJ^{-1} less than the control. The flat and control treatments had a very similar RUE value with only 0.02 g MJ^{-1} difference between the two.

In 2022, the upright treatment was the most efficient at converting light into biomass when assessed in both July and October ($P<0.05$). At late July harvest (116 DAS) the flat treatment had an RUE value of 1.34 g MJ^{-1} which was significantly lower than the upright treatment of 1.57 g MJ^{-1} ($P<0.05$). The upright treatment had a significantly greater RUE calculated to October than the control treatment ($P<0.05$). Between July and October, the upright and flat treatments became more efficient at converting light energy into biomass however, the control treatment saw a reduction in RUE value.

Table 3.5 Radiation use efficiency calculated from total biomass in 2021 and 2022 for upright, control and flat treatments. Lower case letters show significant differences.

Calculated radiation use efficiency (g MJ^{-1})			
Treatment	**09/11/2021**	**27/07/2022**	**05/10/2022**
Upright	2.22	1.57 b	1.73 b
Control	2.34	1.48 ab	1.30 a
Flat	2.36	1.34 a	1.47 ab
P	P>0.05	<0.05	<0.05
LSD5%	0.75	0.16	0.31

There were no differences in root yield, sugar percentage and sugar yield in 2021 or 2022 (Table 3.6). Overall, the plants in 2021 which were harvested later, yielded higher and had a higher sugar percentage than 2022.

Table 3.6 Final sugar yield in 2021 and 2022 for upright, control and flat treatments.

Final yield (g per plant)						
	2021			**2022**		
Treatment	Root yield	Sugar %	Sugar yield	Root yield	Sugar %	Sugar yield
Upright	1200	18.2	218.6	639.6	16.8	107.6
Control	1106.3	17.9	198.1	762.5	16.8	128.2
Flat	1240.6	18.1	224.6	660.4	16.6	110.1
P	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
LSD5%	245.25	0.55	44.05	181.60	0.26	31.14

3.5 Discussion

Over the last few decades, breeding efforts have drastically improved sugar partitioning into the root and overall sugar yield (Loel et al., 2014). Current commercial sugar beet varieties, which differ in their canopy angle, have been shown to have significantly different RUE and sugar yields (Chapter 2). The objective of this study was to investigate whether genetic advances or canopy angle are accountable for these differences in RUE and yield. A canopy manipulation approach was undertaken on a well-studied high performing sugar beet variety in field trials in the UK. In 2021, there were no differences in net photosynthesis, RUE and yield between treatments. In 2022, after a prolonged hot and dry spell, the control and flat treatments lost substantially more canopy than the upright but recovered to pre-drought levels with the upright treatment having a consistently lower percentage canopy cover. The upright treatment had a higher RUE across the season and has a greater RUE than the flat treatment in July 2022 and control treatment in October. The control treatment had the lowest RUE but the greatest root to shoot ratio.

2021 and 2022 trial seasons were very different in terms of rainfall and temperatures. Rainfall after sowing was much more consistent in 2022 than in 2021. This meant that the crop could establish and expand its canopy faster in 2022 compared to 2021. As a result of this, the canopy manipulation treatments were applied almost two weeks sooner but at a more advanced canopy development stage in 2022. The treatments were applied at 10 leaf in 2022 as opposed to 8 leaf in 2021. Temperature and rainfall differed largely between July and August in both years. 2021 experienced average rainfall for that period but in 2022 a period of prolonged high daily temperatures combined with very low rainfall led to significant crop stress and a substantial loss of canopy. Thermal time was greater in 2022 because of the summer period of high temperatures as well as this, radiation levels were higher in 2022 than 2021. The 2021 season had a higher RUE based on total biomass and sugar yield than 2022. This was almost certainly caused by a later harvest date combined with more consistent summer rainfall in the absence of drought seen in 2022.

3.5.1 Canopy expansion and percentage cover

In both years, the upright treatment had a lower percentage canopy cover up to circa 100 DAS than the control and flat treatments. This is the point where canopy closure was reached in all treatments. This canopy closed sooner in 2022 due to the warmer and wetter spring conditions. In 2021, the upright treatment was slower to reach 50% of its maximum canopy cover and overall, achieved a lower modelled maximum canopy cover than the flat treatment. The flat treatment reached 50% maximum canopy cover sooner and had a greater modelled maximum canopy cover. This was also seen in Chapter 2 where an upright canopy type required greater thermal time to reach canopy closure and achieved a lower overall maximum canopy cover.

In 2022, there were no differences in modelled maximum canopy cover and inflection point. But the upright canopy type expanded its canopy at a faster rate the other treatments shown by the slope of the model. This is due to the longer period of increase in canopy cover as more measurements could be taken before maximum canopy was achieved compared to the control and flat treatments. Because the same sugar beet variety was used across treatments, differences in the speed of canopy expansion are not expected due to the genetically determined ontogeny of leaf appearance in sugar beet which is influenced by temperature and nitrogen availability (Milford et al., 1985a, 1985b, 1985c). This was likely the effect of the manipulation treatment application timings where 2022 was applied once the plant had a greater number of leaves and therefore the model began at a higher percentage canopy cover consequently exaggerating the differences between treatments when the upright treatment was applied. As the plants grew within the cages of the upright treatment, the leaves grew against the cage and eventually out of the top once at the 14 leaf stage. At this point, the petioles became supported and ultimately the petiole angle was manipulated and maintained.

The flat peg treatment also manipulated the petiole angle. In this treatment, only three leaves at a time were manipulated to avoid any stress on the plant especially during hot and dry weather. The flat treatment did not display a greater percentage canopy cover across the season despite being more visibly prostrate. This is because the leaves were pegged down at a petiole angle greater than 50° from the crown due to the capability of the pegs. This angle is greater than prostrate canopy types measured in Chapter 2 and therefore the petioles rather than the leaves would be arching over the inter-row space. Petiole angle was not quantified in our study because the nature of the upright treatment meant that tagging and measuring leaves which overlapped was not reliable.

In this study, percentage intercepted radiation was accepted as equal to percentage canopy cover. This relationship has been described previously by Draycott (2006). However, this relationship does not consider leaf optical properties or the bimodal distribution of canopy light and should therefore be used as a proxy for comparision and not a definitive value. In both years, the upright treatment intercepted considerably less accumulated radiation across the season. This is mainly a result of being slower to reach canopy closure and having a consistently lower percentage canopy cover across the season. Despite this, in many crops it has been shown that steeper canopy angles improve the distribution of light across the canopy. A disadvantage to a steeper canopy angle is a lower potential daily carbon gain during the canopy expansion phase in May, however, could increase once optimal LAI is reached. Rapid canopy expansion seen in prostrate, flat canopy types allows for increased light absorption in May and June when irradiance is already high, and thus enhances the production of biomass (Scott and Jaggard, 1978). However, Hoffmann (2019) reported that the timing of canopy closure and hence early season light interception does not directly impact sugar beet yields.

3.5.2 Canopy photosynthesis

Photosynthesis is the central process of fixing carbon into the plant and hence is crucial for building sugar yield. Leaf photosynthesis can become acclimated to the light environment to which they are grown in and their respective photosynthetic traits such as light compensation point, light saturation point and maximum assimilation rates reflect this (Chapter 4). Canopy angle can substantially affect the amount of light each leaf in the canopy receives (Burgess et al., 2017). Because of this, it is expected that fully expanded upright leaves towards the top of the canopy measured in this study would have a lower net photosynthesis rate and leaf chlorophyll content compared to the flat canopy types. However, there were no differences seen in photosynthesis spot measurements between treatments in either years although, photosynthesis measurements in 2022 were considerably lower than

2021. Theoretically, photosynthesis values should be high in both years during this time as the plant is actively fixing carbon, building biomass and yield (Martin, 1986; Werker and Jaggard, 1998; Hoffmann and Kluge-Severin, 2010). These differences in photosynthesis are likely a result of plant stress caused by a lack of rainfall and high temperatures in 2022 which consequently reduced stomatal conductance and photosynthesis to prevent further plant stress and water loss (Ober and Luterbacher, 2002; Monti et al., 2007; Jaggard et al., 2009).

Canopy temperature depression (CTD) is defined as the temperature difference between plant canopy temperature and ambient air temperature. CTD has been shown to correlate well with the transpiration status in rice, wheat and sugar beet (Fukuoka, 2005). It is, therefore, a good indicator of plant stress and / or canopy photosynthetic activity. CTD was measured across the season in 2022, at the start of the season, up to canopy maximum canopy closure. The flat and control treatments had the greatest CTD, inferring higher transpiration rates. This is caused by the greater canopy coverage and therefore less influence of high soil temperatures in the calculation of CTD (Flerchinger and Pierson, 1991). However, during the period of low rainfall and high temperatures when the plants were considerably stressed, CTD became a negative value meaning that the canopy was in fact hotter than the air temperature. Despite this, canopy temperature of the upright canopy was cooler than the other treatments despite having similar canopy cover. This may mean that the upright treatment was actively photosynthesising and coping better under these conditions. The upright nature of the canopy could have been accountable for this as it has been shown in other crops that steeper canopy angles can reduce leaf area in contact with hot soil and decrease light capture at midday during the summer months when the sun is directly overhead (Falster and Westoby, 2003). This has likely benefitted the upright canopy during this drought period by reducing midday canopy heat-load, thereby leading to a higher water use efficiency and canopy photosynthesis (Burgess et al., 2017).

Chlorophyll represents an important pigment for photosynthesis in the leaf. Many factors can influence leaf chlorophyll concentration including nutrient availability, abiotic stresses, disease, phylogeny and the light environment. In the absence of plant stress, the light environment and phylogeny or leaf aging can influence leaf chlorophyll content and hence photosynthesis considerably. SPAD is a measurement for canopy greenness and is highly correlated with leaf chlorophyll content in sugar beet (Malnou et al., 2008). In 2021 the upright treatment had a lower SPAD value across the season. This is likely to be a result of leaf phylogeny or aging (Wild and Wolf, 1980; Milford et al., 1985b; Monti et al., 2007). The upright treatment held the leaves up for longer and effectively reduced the onset of senescence. As a result of this, older leaves were selected for SPAD than the other treatments. In 2022, leaf aging and leaf turnover was exaggerated by the drought and leaves of a closer age were measured across treatments and there were no differences in leaf chlorophyll content. The results of Chapter 2 showed that there was a positive correlation between petiole angle and leaf chlorophyll content (SPAD value) and therefore an upright canopy type had a higher chlorophyll content, and a prostrate/flat canopy type had a lower chlorophyll content. This was not seen in this study and could be indicative of lower root nitrogen uptake and in part caused by lower root partitioning seen in the upright treatment. Canopy chlorophyll content could also be influenced by plant genetics and plant hormones than canopy angle alone (Christ and Hörtensteiner, 2014; Zhu et al., 2017).

3.5.3 Biomass accumulation, RUE and yield

In 2021 there were no differences in total biomass between treatments when harvested in November. In both years the treatments displayed different rates of canopy development to canopy closure, therefore during this period between May and July the control and flat treatments intercepted more light, and it is expected these treatments would have higher biomass at canopy closure. To investigate this a biomass harvest was conducted in the final week of July in 2022 where canopy cover had reduced by up to 20% compared to maximum values. There were no differences in biomass accumulated up to July between treatments, but the upright treatment had a higher RUE than the flat treatment. This suggests that perhaps an upright canopy is more efficient at intercepting light and utilising the light during this period. There were no differences in the root to shoot ratio and therefore biomass partitioning to root yield did not improve with an upright canopy angle and could be genetically pre-determined. Due to the differences in leaf angle and therefore light interception angle, the method used to measure intercepted light using thresholded

RGB images for percentage canopy cover may need updating to account for canopy and incident light angle.

Season long total biomass RUE was higher in 2021 than 2022 and at the top of the range recorded previously in the literature where values range from 1.1-2.0 g DM per MJ (Monteith, 1977; Werker and Jaggard, 1998; Hoffmann and Kluge-Severin, 2010; Hoffmann, 2019). High RUE values above 2.0 g DM per MJ recorded in 2021 are likely the result of the combination of adequate summer rainfall, autumn temperatures, as well a smaller harvest sample size which could increase error. In 2022, sample size was larger and RUE values (1.3-1.7 g DM per MJ) were within the range reported in the literature. The lower RUE values seen in July 2022 harvest is caused by the growth sequence of sugar beet where assimilates are partitioned to building canopy cover or LAI early in the season and the drought event led to a significant loss in canopy cover across all treatments which then reduced plant total biomass and hence RUE.

At final harvest in 2022 the upright treatment had a higher season long total biomass RUE than the control treatment this could be result of reduced radiation interception during May and June. The upright treatment had a lower root to shoot ratio. This could be a result of a higher above ground biomass resulting from less leaf loss during summer drought period. The flat treatment was more efficient at partitioning biomass to the root sink and had a lower above ground biomass due to canopy loss. However, there were no differences in sugar yield between treatments in both years. This could be genetically determined in the plant, with the treatments being the same variety as well as the plants ability to store sucrose in the harvested roots (Schnepel and Hoffmann, 2016; Hoffmann, 2019).

3.6 Conclusion

The canopy manipulation treatments displayed distinctly different canopy development in 2021 and 2022. Canopy cover differences led to seasonal change in canopy temperature depression (CTD) measured in 2022 when the value became negative as canopy was lost due to drought. The upright treatment was advantaged in the drought conditions and this was seen through a lower proportion of canopy loss and higher CTD. Overall, the upright treatment was less stressed and could be a result of the upright angle reducing the midday heat load on the canopy compared to the other treatments. Season long RUE was higher in 2021 than 2022 and the more favourable summer weather conditions combined with a later harvest are the likely cause. No differences in RUE were seen between treatments in 2021 but in 2022 the upright treatment had a higher above ground biomass and RUE than the flat treatment in July due to reduced radiation interception and the control treatment at final harvest which had a higher root to shoot ratio. Canopy angle had no effect on sugar yield in either years.

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3.8 Supplementary information

Table S3.1 Agronomy of trials in 2021 and 2022

2021		2022	
Previous crop	Winter Oats	Previous crop	Winter Wheat
SNS N Index	15.1 kg/ha, SNS Index 1	SNS N Index	65kg/ha, SNS Index 1
Soil indices	P:3, K:2+, Mg:4, pH:7	Soil indices	P:4, K:2+, Mg:4, pH:7.3
	Fertiliser		**Fertiliser**
29/03/2021	116 kg/ha 34.5% Nitram (40kg/ha N)	29/03/2022	116 kg/ha 34.5% Nitram (40kg/ha N)
09/05/2021	232 kg/ha 34.5% Nitram (80kg/ha N)	26/04/2022	232 kg/ha 34.5% Nitram (80kg/ha N)
09/06/2021	Opte man @ 2l/ha	13/06/2022	Opte-Man @ 2l/ha
09/07/2021	Opte man @ 2l/ha		
	Herbicide		**Herbicide**
30/03/2021	Goltix 70 SC @ 1.0 l/ha	10/11/2021	Kyleo @ 3l/ha
30/04/2021	Goltix 70 SC @ 1l/ha + Betanal Tandem @ 1l/ha	29/03/2022	Goltix @ 1.0 l/ha
07/05/2021	Goltix @ 1l/ha + Betanal Tandem @ 1l/ha + Toil @ 0.75l/ha	26/04/2022	Goltix @ 1l/ha + Betanol Tandem @ 1l/ha

		07/06/2022	Defiant @ 1l/ha + Magic Tandem @ 1.5l/ha + Toil @ 0.5l/ha
		14/06/2022	Dow Shield @ 0.3l/ha
	Fungicide		**Fungicide**
12/08/21	Escolta @ 0.35l/ha	29/07/2022	Escolta @ 0.35l/ha
07/09/21	Escolta @ 0.35l/ha		
	Insecticide		**Insecticide**
16/06/2021	Teppeki @ 0.14kg/ha	10/05/2022	Insyst @ 250g/ha
		19/05/2022	Teppeki @ 0.14kg/ha
27/05/2021	Goltix @ 1l/ha + Betanal Tandem @ 1l/ha + Toil @ 0.5l/ha	13/05/2022	Goltix @ 1l/ha + Magic Tandem @ 1.5l/ha + Toil @ 0.75l/ha

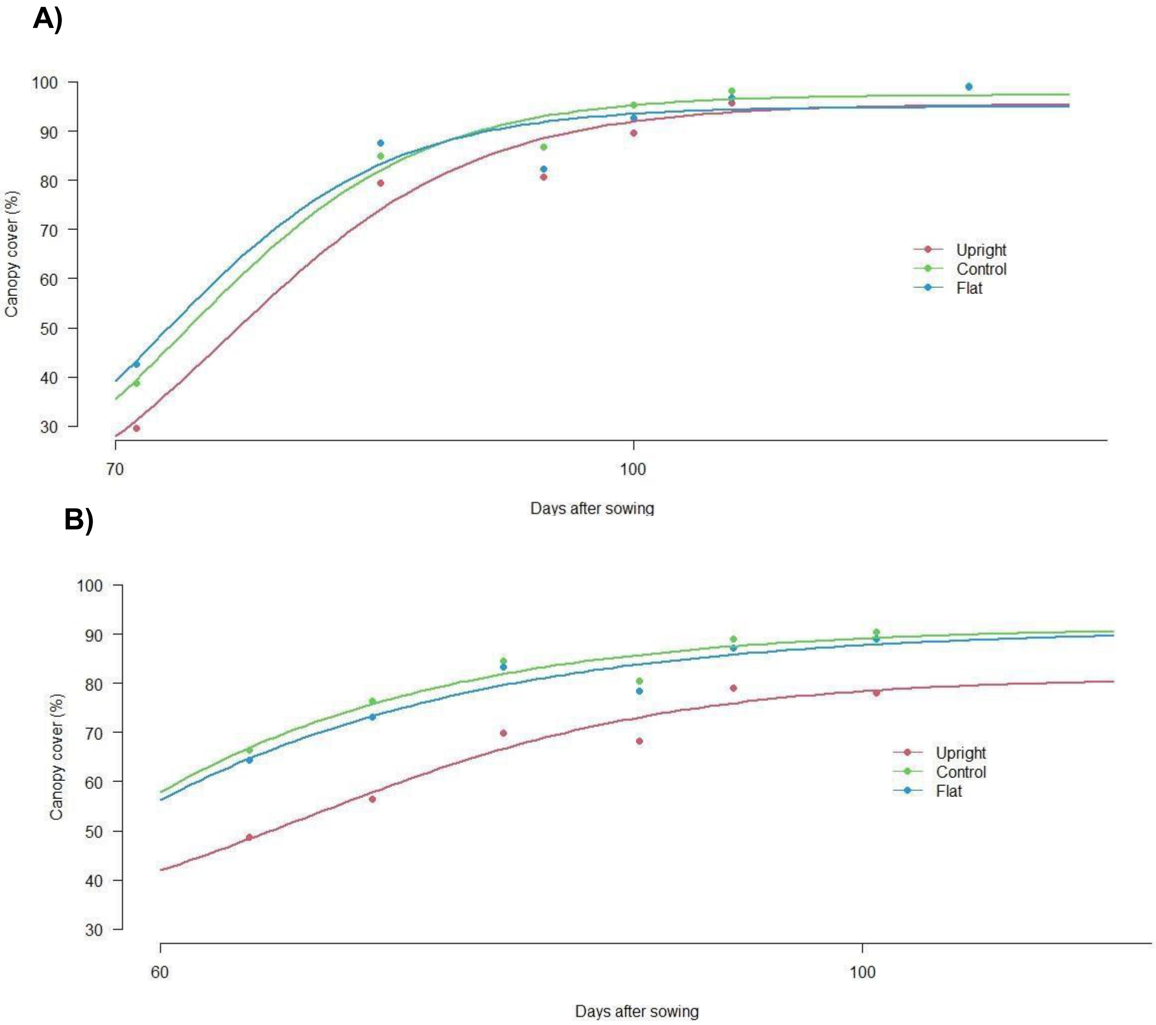

Figure S3.1 Three parameter log logistic curve model output averaged for each treatment in A) 2021 and B) 2022.

Chapter 4 Canopy architecture and photosynthesis in sugar beet

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4.1 Abstract

In sugar beet, there is a strong linear relationship between intercepted light and biomass accumulation, the slope of this relationship is the radiation use efficiency (RUE). More upright canopy angles have been shown to increase RUE in cereal crops. In the absence of limiting factors, photosynthesis is the driving force between intercepted light and biomass accumulation. Whilst the effect of leaf age on canopy photosynthesis in sugar beet has been investigated, the impact of canopy architecture on leaf photosynthesis is not known, where the canopy will consist of a population of leaves at different ages and states of sun/shade acclimation. A controlled environment experiment was conducted to investigate the impact of sugar beet canopy architecture, acclimation state and leaf age on canopy photosynthesis. An upright, intermediate and prostrate canopy type chosen from commercial varieties were investigated in this study. Canopy architecture, including petiole and leaf angle, and leaf growth were measured. An infrared gas analyser was used to measure CO_2 assimilation light response curves to assess the acclimation state of leaves 4 and 7 of each canopy type. Hyperspectral measurements were used to measure leaf absorbance and to calculate vegetative indices that might be related to photosynthetic and canopy architecture. The commercial varieties differed significantly in their canopy architecture, notably petiole angle. Leaf architecture changed with age in particular, leaf angle, which becomes flatter regardless of petiole angle. It was shown that canopy photosynthesis is correlated with canopy type, the intermediate canopy type had the greatest photosynthetic potential measured as maximum assimilation rate and is acclimated to higher light intensities. The prostrate canopy had leaves which were acclimated to shaded canopy conditions and had a lower photosynthetic potential. The upright variety used in this study does not provide evidence that an upright canopy is well adapted for high rates

of canopy photosynthesis in sugar beet. However, only one variety was measured per canopy type, and this may not be entirely representative of all varieties with these canopy types. The indices GNDVI, Water index and MnDBlue were correlated with maximum assimilation, dark respiration and petiole angle respectively. These indices have been shown to predict canopy chlorophyll and water content in other crops including sugar beet. However, these indices were only tested on a small data set and need further testing to determine their usefulness in predicting canopy and photosynthetic traits.

4.2 Introduction

Sugar beet (*Beta vulgaris* ssp. *vulgaris*) is an important crop of temperate climates and is grown worldwide over 4.4 million hectares accounting for 20 % of white sugar produced (FAOSTAT, 2020). The sugar beet plant has a rosette leaf formation and is typically sown in rows 45-50 cm apart. Sugar beet is biennial, its growth is proportional to intercepted light during its first season before entering a reproductive phase induced by vernalisation. Therefore, the crop is harvested during its vegetative phase after a season of growth. Commercial sugar beet varieties have been shown to differ significantly in their canopy expansion rate and angle (Tillier et al., 2023). Canopy expansion is composed of leaf appearance, development and expansion and is often limited by pest, disease and cool, dry springs (Milford, 1980; Milford et al., 1985a; Milford et al., 1985b). Rapid canopy expansion is advantageous to the crop by enabling high radiation interception, which is directly related to sugar yield, in addition to weed suppression in the crop (Hoffmann and Kluge-Severin, 2010; Werker and Jaggard, 1998).

Canopy angles vary widely in the sugar beet crop from being more upright with erect leaves to prostrate with flatter leaves and some are intermediate, between the two extremes. It has been shown that varieties with more upright canopy angles reach circa. 90% canopy cover or canopy closure later than more prostrate varieties despite being sown under the same conditions (Tillier et al., 2023). Because of this, less radiation is intercepted by upright canopy types especially before canopy closure. This is assuming canopy cover is proportional to the amount of radiation intercepted by the crop (Draycott, 2006). In sugar beet, a strong linear relationship exists between accumulated intercepted radiation and biomass accumulated in the crop (Monteith ,1977). However, more recently in the literature it has been shown that canopies that intercept the most radiation over the season did not necessarily accumulate the greatest amount of biomass or sugar yield (Hoffmann, 2019; Schnepel and Hoffmann, 2016). This could be explained by differences in radiation use efficiency (RUE). RUE is the conversion efficiency of intercepted light to biomass and is largely dependent on canopy photosynthesis providing there are no other limiting factors in the crop. This suggests that there are inherent differences between varieties and canopy types in terms of their photosynthetic potential.

Canopy angle influences the light environment in the canopy and as a result of this, leaves located at certain positions in the canopy will have different instantaneous photosynthetic values (Burgess et al., 2017a; Duncan, 1971; Long et al., 2006b). In many cereal crops upright canopy types, with erect leaves, have been associated with high yield potential (Richards et al., 2019). This is because more light can penetrate through the canopy leading to a more efficient and even light distribution. As a consequence of this, the erect leaves at the top of the canopy avoid light saturation and instantaneous photosynthesis of leaves towards the bottom of the canopy increases. In comparison, a larger proportion of leaves in the prostrate canopy are light limited lower in the canopy and saturated at the top *(*Zhu et al*.*, 2010; Murchie and Niyogi, 2011; Müller-Linow et al*.*, 2015).

In sugar beet, studies have shown that leaf photosynthetic capacity declines with leaf age (Hodanova, 1981; Monti et al., 2007). This could be initiated by changes to the role that the leaf plays to the overall plant physiology as it ages. This has been discussed by Joy (1964) who showed that older leaves and fully expanded leaves in the canopy export most of their photosynthates to the root and to support the growth of young leaves. The second process responsible for the reduction in leaf photosynthetic potential in older sugar beet leaves could also be caused by the canopy light gradient as less light reaches the leaf surface. This is acclimation and it reduces the leaf maximum photosynthetic rate (Amax) according to light intensity by adjusting the leaf photosynthesis machinery (Walters, 2005). It is therefore assumed that canopy angle will influence leaf photosynthesis in the sugar beet canopy which could be optimised to improve yield.

Photosynthetic light response curves (LRCs) are a useful indicator of a leaf's current acclimation state and describes how the rate of photosynthesis changes depending on the intensity of light. LRCs are usually measured using infra-red gas exchange over a period of minutes and can be modelled using a non-rectangular hyperbola relating net photosynthetic rate and photosynthetic photon flux density (PPFD) (Sharkey et al., 2007). LRCs provide a quantitative value on the maximum photosynthetic capacity, light compensation point, dark respiration, light saturation point and RUE of leaves. Combined with data on incident light in canopies they can be used to assess the rate of photosynthesis according to canopy position. Photosynthetic measurements using infrared gas analysers are traditionally time consuming and costly whilst remote sensing based approaches are very rapid and high-throughput. Vegetation indices are widely used as proxies for vegetation greenness and to estimate variables such as vegetation cover and leaf area index in sugar beet (Jay et al., 2017, 2019). Recently, it has been shown that hyperspectral leaf reflectance can remotely capture Information about photosynthesis values across many species including wheat (Fu et al., 2020; Robles-Zazueta et al., 2021, 2022). The use of spectral reflectance data to estimate the photosynthetic capacity of the sugar beet crop would be a useful tool for both breeders and growers by enabling the rapid selection of new varieties.

The main objective of this study was to assess whether sugar beet leaf photosynthesis differs with leaf age and canopy position, depending on canopy angle. It also set out to determine vegetation indices which can be used to assess leaf photosynthesis: max assimilation rate and dark respiration rate.

4.3 Materials and Methods

4.3.1 Plant material

Three commercial sugar beet varieties with contrasting canopy angles were selected for this experiment. The chosen varieties and their classified canopy type according to their canopy angle is shown in Table 4.1. Three seeds were sown per 5L pot containing Kettering loam soil (16/03/21) and thinned to a single plant at 28 days after sowing (DAS). Pots were placed at a consistent distance to the lights in two controlled environment cabinets (A2000, Conviron, UK). The pots were moved down as the plants grew to maintain a consistent distance from the lights. The pots were arranged in a completely randomized block design, with four replicate plants of each canopy type. Fluorescent tubes (LUMILUX HO 54W/840 T5, Osram, Munich, Germany) supplied 12 h of light at 400 µmol m^{-2} s^{-1} followed by 12 h of darkness, with an hour dawn and dusk light adjustment. The pots were hand-watered throughout to prevent soil drying. Humidity was set at 65% with a daytime temperature of 20°C and night-time temperature of 14 °C. This was monitored using a humidity and temperature data logger (TinyTag Ultra 2, Gemini Instruments, Chichester, UK). At 29 DAS, 1.05g of ammonium nitrate equivalent to 50kg ha^{-1} was applied to each pot in solution.

Table 4.1 Varieties used in the experiment with breeder and canopy type.

Variety	Breeder	Canopy type
BTS 1140	Beta Seed	Intermediate
Cayman	SesVanderhave	Prostrate
Sabatina	KWS	Upright

4.3.2 Canopy angle

Canopy angle was measured 60 DAS. A digital camera (PowerShot SX720 HS, Canon) was mounted on a tripod and placed at 60 cm distance from the plant which was positioned on a platform. Leaves 4, 7 and 9 (labelled in order of true leaf appearance) were measured from each plant. The angle tool in Image J was used to measure canopy angle at three points on each plant (Rasband, 2011) (Figure 4.1).

Using this technique, a small angle value indicates a more upright canopy, and a larger angle value indicates a prostrate canopy.

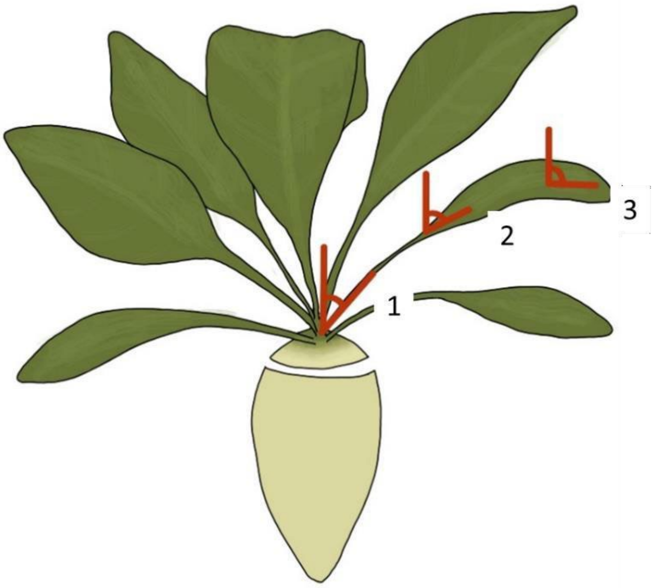


Figure 4.1 Three-part canopy angle measurement technique. Angle was measured as an upright insertion into the crown to measure petiole angle (1), the leaf to petiole attachment (2) and the leaf tip end (3). Leaves 4 and 7 were measured in this experiment.

4.3.3 Leaf expansion

Leaves 4 and 7 were tagged from emergence (classed as 4 cm in length) and their length and width measured every four to seven days at midday using a tailoring tape measure. The leaves were measured until their values became stable. Leaf length was measured from the point of petiole attachment to the leaf tip and width was measured across the widest part of the leaf (Figure 4.2). Leaf expansion was modelled using a three-parameter log-logistic model in R (R Core Team, 2021). This was used to calculate leaf width and length expansion rate, inflection point (DAS taken to achieve 50% of modelled maximum) and modelled maximum. Respective leaf area could not be calculated from these measurements due to differences in leaf shape between varieties.

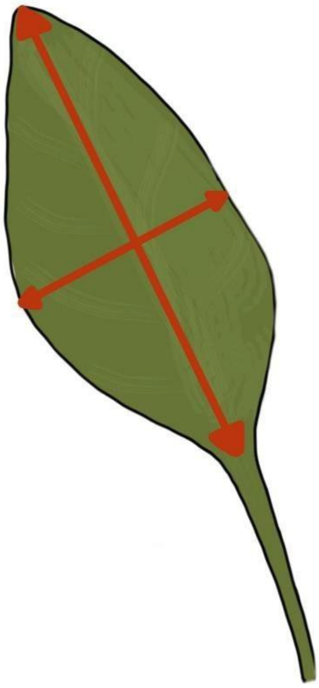


Figure 4.2 Point of leaf width and leaf length measurements. Length was measured from the point of petiole attachment to the leaf to the leaf tip and width was measured from the widest part of the leaf. Leaves 4 and 7 were measured in this experiment.

4.3.4 Projected leaf area

Projected leaf area per plant was measured at 89 DAS using images taken 70 cm above the canopy. A reference scale was set, and green pixels were thresholded and measured for each plant using Image J (Rasband, 2011).

4.3.5 Hyperspectral measurements

Leaf reflectance was measured using a field spectroradiometer with a spectral range from 350 to 2500 nm, taking a reading per nm. A leaf clip attachment was used with a halogen bulb light source (ASD Field Spec® 3, Boulder, CO, USA). Leaves 4 and 7 were clipped in the widest portion of the leaf being careful to avoid veins and secure a tight seal on the leaf. Once sampled, average reflectance from each leaf was processed using View Spec Pro software (Analytical Spectral Devices Inc., Boulder, CO, USA). These values were selected from a correlation matrix using a range of indices and used to calculate vegetation indices sourced from the literature (Table 4.2).

Table 4.2 Hyperspectral vegetation indices used in this study

Vegetation Index	Equation	Trait	Reference
mNDblue [728, 850]	(R440 − R728)/(R440 + R850)	Chlorophyll a and b Content	Sims and Gamon (2002)
Green normalised difference vegetation index (GNDVI-1)	(R800-R680)/(R800+R680)	Chlorophyll content, canopy greenness, photosynthetic capacity, energy absorption	Gitelson et al. (1996)
Water index	R900/R970	Canopy water content	Penuelas et al. (1997)

4.3.6 Leaf absorbance

Leaf absorbance was measured 94 DAS using a field spectroradiometer as in section 4.3.5. Leaves 4, 7 and 12 were measured at three points on each leaf. Firstly, the black reference clip was used (measures reflected light) before turning to the white reference (measures transmitted light) ensuring that the same area of leaf was measured each time. Once sampled, average reflectance and transmittance from each leaf was calculated.

$$A\text{bsorbance} = 1 - (\text{Transmitted} + \text{Reflected}) \qquad (4.31)$$

The absorbance values were then calculated for each leaf (Equation 4.31) and the average absorbance in the PAR region (400-700 nm) recorded. These values were then analysed to determine differences between leaf absorbance in different canopy types and leaf number. Leaf absorbance values were not used to correct photosynthesis values due to the duration of time required for each measurement.

4.3.7 Light Response Curves

Measurements were made at the 10 leaf stage, 55 DAS. For light response curves (LRCs) leaves 4 and 7 were selected which were not dark-adapted. Gas exchange measurements were taken using an infrared gas analyser (LI-6800, LI-COR, Lincoln, NE, USA). A rapid auto log light response curve programme was used with two minutes at each light level. The PPFD values descended as follows: 1800, 1500, 1200, 1000, 800, 600, 400, 300, 200, 150, 100, 70, 50, 20, 0 µmol m^{-2} s^{-1}. Reference CO_2 was set at 400 µmol mol^{-1}, RH set to 65 % and leaf temperature 20 °C, with matching at every measurement.

4.3.8 Light response curve models

Data from the light response curves were modelled using R (R core Team 2021) based on the model from Marshall and Biscoe (1980). The slope of the lightresponse curve from the point of darkness is the apparent quantum yield (AQY) and it describes the maximum efficiency with which light can be converted into fixed carbon. The net photosynthesis rate rises until it reaches a maximum, Amax. The dark respiration rate (RD) is the net rate of CO_2 exchange in darkness. The light intensity where respiration rate equals the photosynthesis rate is the light compensation point (LCP) and the light intensity where photosynthesis no longer increases is the light saturation point (LSP) (Figure 4.3).

Intrinsic water use efficiency was calculated as CO_2 Assimilation (A) /stomatal conductance (g_s) measured at each point on the LRC output.

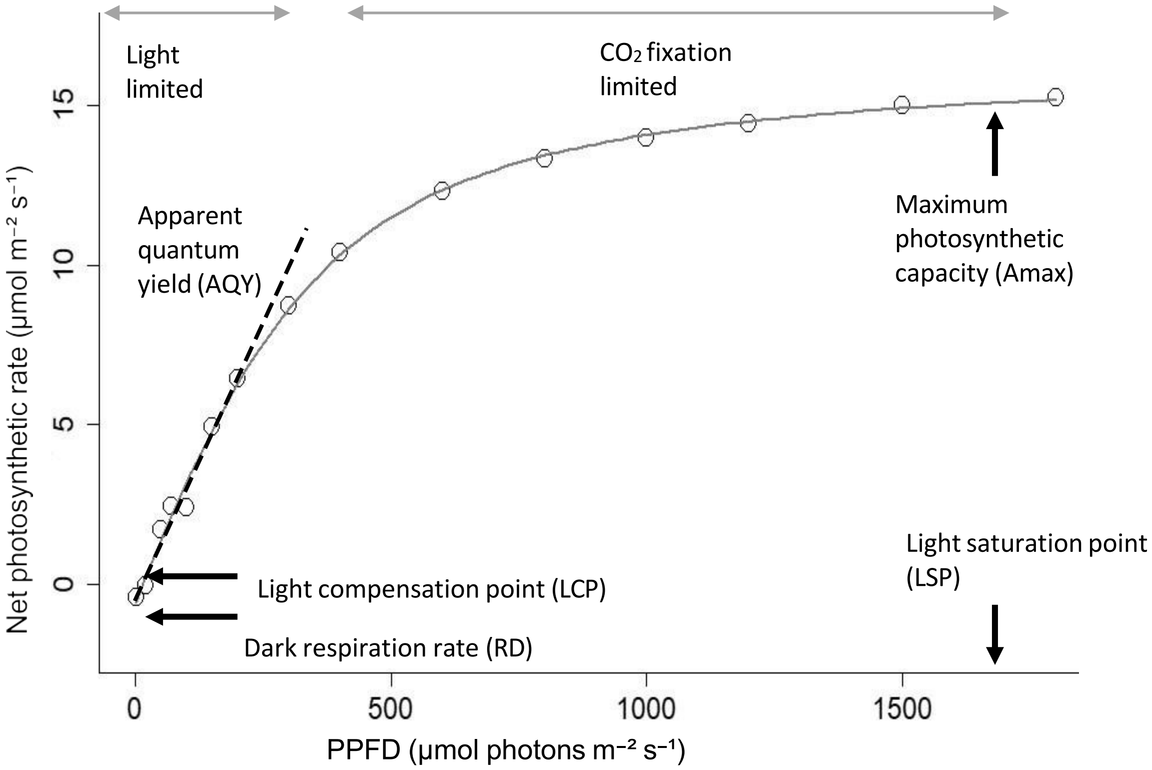


Figure 4.3 Diagram showing light response curve and the parameters modelled from it.

4.3.5 Data analysis

All statistical tests were performed using Genstat 20th edition (VSN International, Hemel Hempstead, UK). Analysis of variance (ANOVA) was used to test for significant differences between varieties, standard error and least significant deference at 5% were also calculated and used for error bars. Regression analysis was also carried out using Genstat was where the *P* value and R^2 were calculated. All graphs were made using Microsoft Excel.

4.4 Results

4.4.1 Canopy traits

The petiole angle of the upright canopy type was significantly more erect than the intermediate canopy type measured at the 12 leaf stage ($P<0.05$) (Table 4.3). The Prostrate canopy angle was not significantly different than the intermediate canopy angle. Although there were no significant differences in petiole angle with leaf age, there was a trend for petiole angle to increase (become flatter) with age. The older, leaf 4 petiole angle across all canopy types was 6.17 degrees flatter than leaf 7 and 9.74 degrees flatter than the newest leaf 9.

There were no differences in petiole to mid leaf and mid leaf to leaf tip angle between canopy types. The intermediate canopy type had a larger, flatter angle recorded at each point, but this was not significant. Across all canopy types, the oldest leaf 4 had a significantly flatter petiole to mid leaf angle and leaf tip angle than leaf 7 and 9 (*P*<0.001). Across all petiole and leaf angles there was no interaction between variety and leaf number.

Table 4.3 Components of canopy angle measured as an average across canopy types and leaf number. The top table shows average angle of measured leaves for *upright, intermediate and prostrate* and *canopy types. T*he below table shows average angle per leaf across all canopy types.

<table>
<tr><th colspan="6">Canopy type</th></tr>
<tr><td></td><td>Upright</td><td>Intermediate</td><td>Prostrate</td><td><i>P</i></td><td>LSD$_{5\%}$</td></tr>
<tr><td>Petiole angle (°)</td><td>24.0</td><td>35.2</td><td>29.5</td><td><0.05</td><td>7.90</td></tr>
<tr><td>Petiole end to mid leaf angle (°)</td><td>42.9</td><td>52.3</td><td>47.1</td><td>0.348</td><td>13.02</td></tr>
<tr><td>Mid leaf to leaf tip angle (°)</td><td>73.8</td><td>84.2</td><td>83.9</td><td>0.39</td><td>17.45</td></tr>
<tr><th colspan="6">Leaf number</th></tr>
<tr><td></td><td>4</td><td>7</td><td>9</td><td><i>P</i></td><td>LSD$_{5\%}$</td></tr>
<tr><td>Petiole angle (°)</td><td>34.9</td><td>28.7</td><td>25.1</td><td>0.054</td><td>7.90</td></tr>
<tr><td>Petiole end to mid leaf angle (°)</td><td>66.3</td><td>44.5</td><td>31.6</td><td><0.001</td><td>13.02</td></tr>
<tr><td>Mid leaf to leaf tip angle (°)</td><td>105.6</td><td>77.4</td><td>58.9</td><td><0.001</td><td>17.45</td></tr>
</table>

4.4.2 Leaves 4 and 7 expansion

There were no differences in leaf 4 leaf width and length expansion rate between canopy types (measured as inflection point). The intermediate canopy type achieved 50% of its maximum leaf 7 width sooner than the upright and prostrate canopy types (*P*<0.05) (Figure 4.4A). The maximum leaf width in leaf 7 of the prostrate canopy type was significantly greater than the intermediate and upright canopy types (*P*<0.05) (Figure 4.4B). There were no differences in leaf 7 length. Overall, there were no differences in expansion rates between leaves 4 and 7 averaged across canopy types.

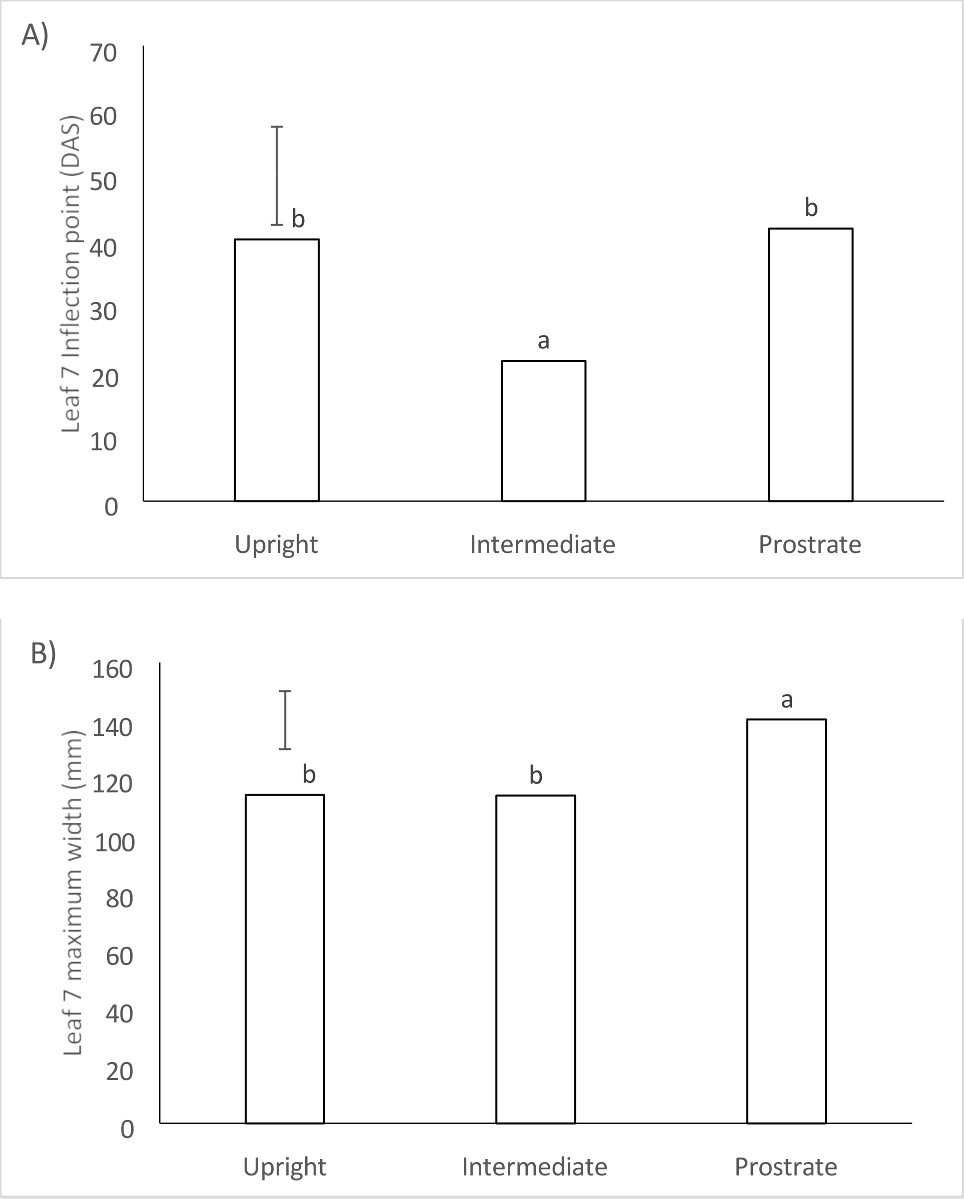


Figure 4.4 Leaf 7 (labelled in order of appearance) growth traits for upright, intermediate and control canopy types. A) Leaf seven inflection point, showing the days after sowing (DAS) taken to reach 50% of maximum leaf width. B) Leaf seven modelled maximum width. Error bar shows LSD5% and lower case letters denote significant differences.

4.4.3 Projected leaf area

The intermediate canopy type had the lowest projected leaf area when imaged from above at 89 DAS, 12 leaf stage (*P*<0.05). There were no differences in leaf area between the upright and prostrate canopy types (Figure 4.5). Upright canopies may be expected to have a lower projected leaf area; however, this method is measuring a single plant and therefore may not fully represent differences between canopies.

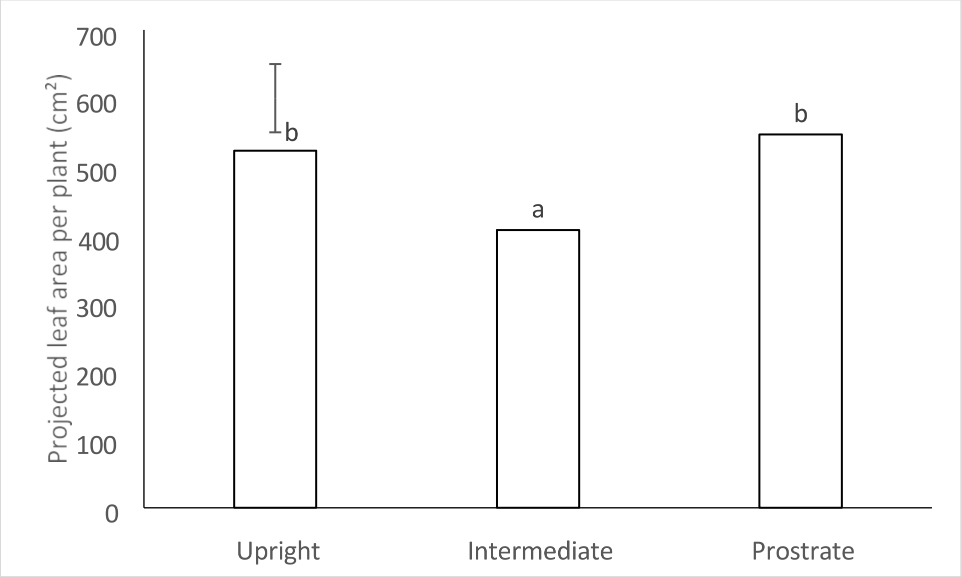


Figure 4.5 Calculated projected leaf area per plant measured across upright, intermediate and prostrate canopy types. Error bar shows LSD$_{5\%}$ and lower case letters denote significant differences.

4.4.4 Light response curves

Leaf photosynthesis at different canopy positions depends both on acclimation to light and leaf age: the ability of leaves to best exploit the variable light within the canopy can be best explored with light saturation curves. Table 4.5 shows the results from the modelled light response curve. The intermediate canopy type consistently had a higher rate of photosynthesis above 800 µmol $m^{-2}s^{-1}$ (Figure 4.6A). This led to a higher predicted Amax than all other canopy types from the fitted curve (*P*<0.001). The prostrate canopy type had an Amax of 21.48 µmol $m^{-2}s^{-1}$ in comparison to the upright canopy type with 24.72 µmol $m^{-2}s^{-1}$ and the intermediate at 28.61 µmol $m^{-2}s^{-1}$. The intermediate canopy type also had a higher LSP than all other canopy types (*P*<0.001). The intermediate canopy type had a significantly higher apparent quantum yield than the upright and prostrate canopy types (*P*<0.001).

The prostrate canopy type had the lowest LCP and dark respiration rate, this means that significantly less light is required than the other canopy types for photosynthesis to negate the CO_2 produced from respiration (*P*<0.05) (Table 4.4). Hence it was more efficient at using low light levels.

Overall, leaf 7, positioned higher up in the canopy, had a higher rate of photosynthesis (Figure 4.6B). Leaf 7 had a significantly higher Amax and LSP than leaf 4 (*P*<0.001, *P*<0.05) (Table 4.4) indicating that it was better able to cope with higher light intensities at that position in the canopy. The older leaf 4 had a significantly lower LCP and dark respiration rate than leaf 7, typical of that seen in a shaded environment (P<0.001). No differences were seen in apparent quantum yield between leaf 4 and 7. Overall, there was no significant interaction between leaf number and canopy type across all photosynthetic parameters. Stomatal conductance (g_s) and intrinsic water use efficiency was calculated and shown in Supplementary Figure S4.1, S4.2. g_s was consistently high across canopy types and therefore calculated intrinsic water use efficiency vales were variable across canopy types and leaf number.

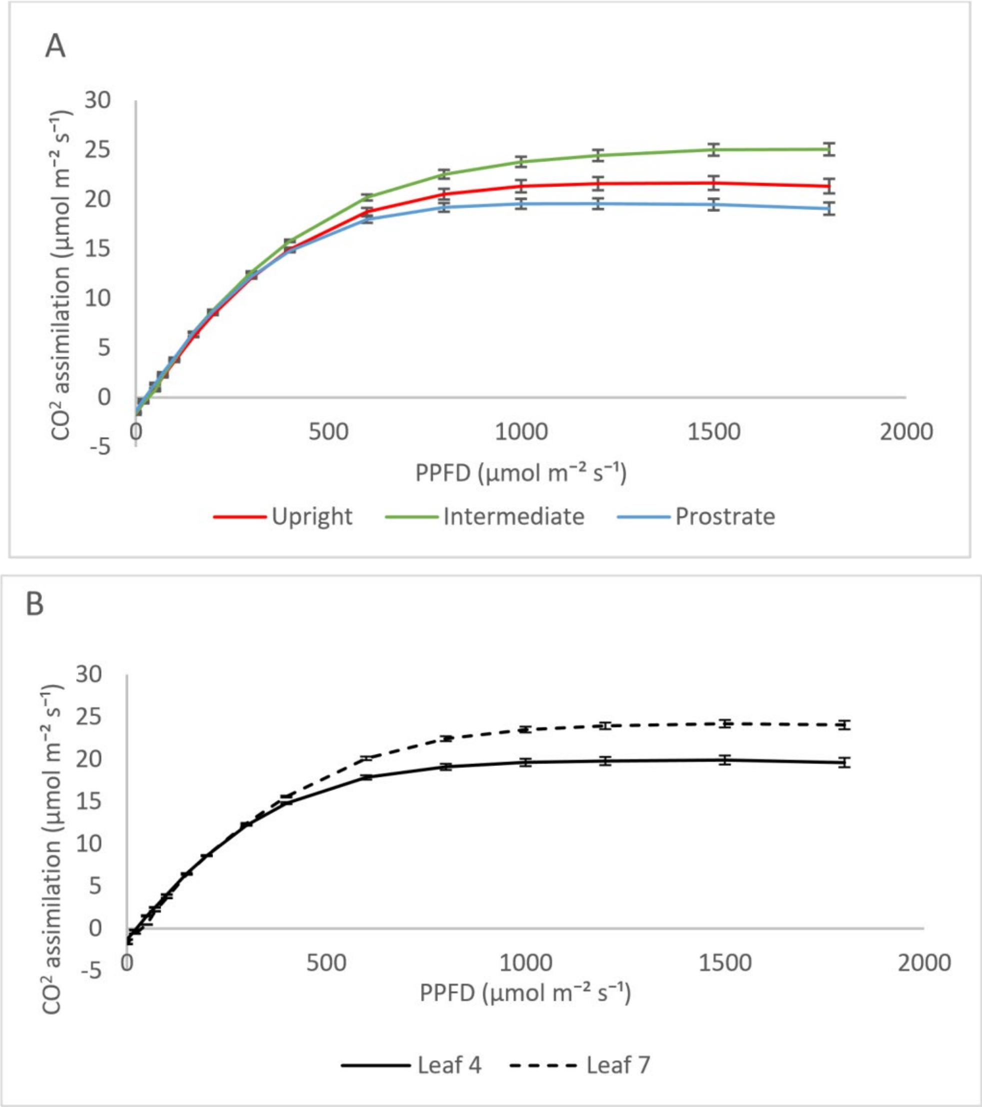


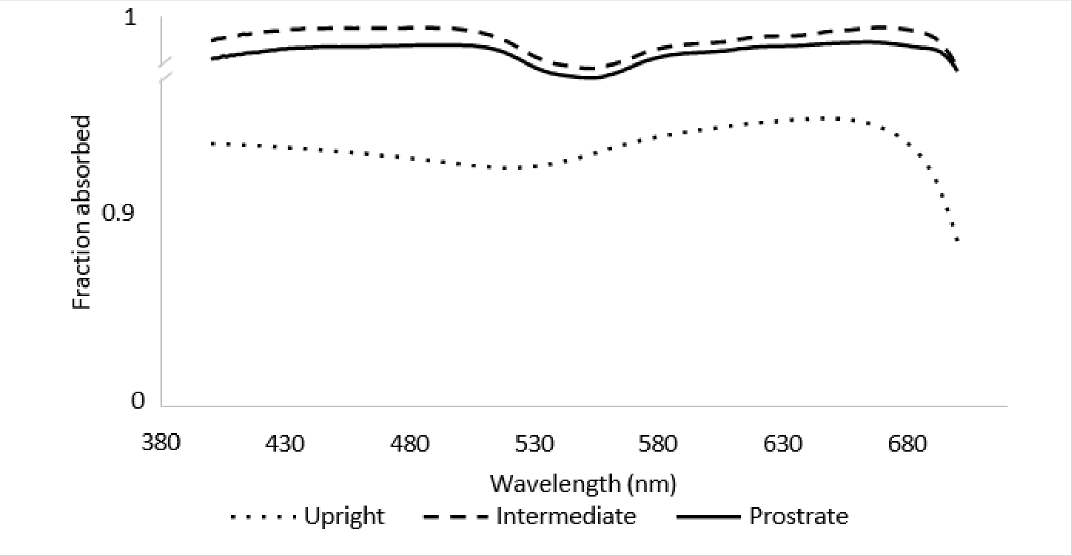
Figure 4.6 CO_2 assimilation response curves. PPFD is Photosynthetic Photon Flux Density (PPFD). A) upright, intermediate and prostrate canopy types and B) average of leaf 4 and leaf 7 across canopy types. Error bars show Standard error.

Table 4.4 Modelled light response curve output for *upright, intermediate and prostrate* canopy type and leaf number.

Canopy type					
	Upright	Intermediate	Prostrate	*P*	LSD$_{5\%}$
Amax (CO$_2$ μmol m^{-2} s^{-1})	24.72	28.61	21.48	<0.001	2.56
LSP (PPFD μmol m^{-2} s^{-1})	475	589	401	<0.001	75.80
LCP (PPFD μmol m^{-2} s^{-1})	29.33	29.58	22.26	<0.05	4.27
Dark respiration rate (CO$_2$ μmol m^{-2} s^{-1})	1.51	1.64	1.14	0.001	0.23
AQY (cm s^{-1})	0.051645	0.05593	0.051445	<0.001	0.001838
Leaf number					
	Leaf 4	Leaf 7		*P*	LSD$_{5\%}$
Amax (CO$_2$ μmol m^{-2} s^{-1})	22.13	27.45		<0.001	3.13
LSP (PPFD μmol m^{-2} s^{-1})	441.00	535.67		<0.05	61.90
LCP (PPFD μmol m^{-2} s^{-1})	21.70	32.41		<0.001	3.48
Dark respiration rate (CO$_2$ μmol m^{-2} s^{-1})	1.14	1.72		<0.001	0.19
AQY (cm s^{-1})	0.052	0.054		0.14	0.001

4.4.5 Leaf light absorption

Leaf level light absorption of leaf 7, 9 and 12 was measured 94 DAS. The upright canopy type had a significantly lower leaf light absorption in the PAR region than the intermediate and prostrate canopy types ($P<0.05$) (Figure 4.7). No differences were seen between leaf numbers. There was no interaction between leaf number and canopy type.



Leaf number				
Leaf 7	Leaf 9	Leaf 12	*P*	$LSD_{5\%}$
0.99	0.97	0.99	0.44	0.034

Figure 4.7 Average light absorption in the PAR region (400-700nm) across leaf 7, 9 and 12 for upright, intermediate and prostrate canopy types. The data table shows average absorption value in the PAR region for canopy type and leaf number.

4.4.6 Vegetation indices as a proxy for canopy angle and photosynthesis

A range of indices were tested against values across all canopy types and leaf ages for Amax, dark respiration and petiole angle using a correlation matrix and then regression. Indices with the closest relationship and greatest R^2 for each component are shown in Figure 4.8.

GNDVI-1 had a positive linear relationship with Amax across canopy types and leaf numbers. Water index had a negative linear relationship with dark respiration, the rate of dark respiration increases as water content in the leaf falls.

Petiole angle was correlated with MnDBlue which has been shown to be highly correlated with chlorophyll in sugar beet (Jay et al., 2017). The leaf chlorophyll content increases as the petiole angle becomes more upright.

Dark respiration rate was negatively regressed with water index: the water content of the leaf reduces as the dark respiration rate increases in the leaf.

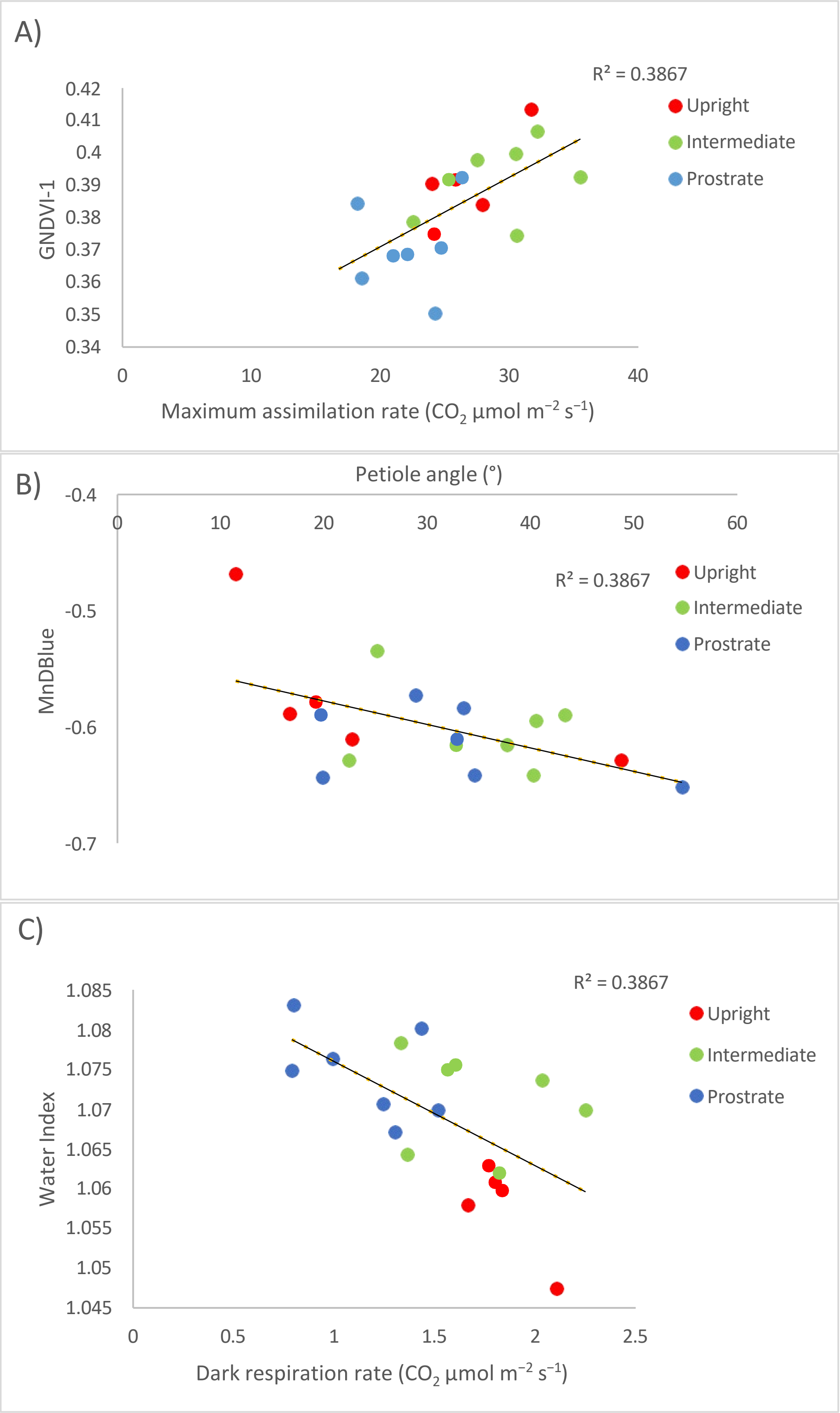


Figure 4.8 Linear regressions between selected vegetation indices and light response curve (LRC) modelled parameters and canopy angle. A) GNDVI and maximum photosynthetic rate, B) MnDBlue and petiole angle and C) Dark respiration rate and Water index. All relationships are statistically different ($P<0.05$).

4.5 Discussion

Photosynthesis of single leaves of different ages has been well documented in sugar beet (Fellows and Geiger, 1974; Monti et al., 2007). More recently the effect of leaf age as well as stress factors such as drought and nutrition and its impact on photosynthesis has been investigated (Monti et al., 2007; Fei et al., 2019). However, the ability of sugar beet to acclimate canopy photosynthesis to light conditions in the canopy has not yet been reported in the literature. In conjunction with this, it is not known whether leaf photosynthesis differs with leaf age and canopy position depending on canopy angle. The findings from this study could aid in the selection of varieties according to their canopy angle for a high radiation use efficient and high yielding crop.

4.5.1 Canopy traits

Petiole angle differed significantly between intermediate, prostrate and upright canopy types. Current results showed no difference between intermediate and prostrate canopy types. The upright canopy type had a much steeper petiole angle than the intermediate canopy type This was measured in singular plants grown outside of a typical canopy light environment which could otherwise influence these differences (Niinemets and Keenan, 2012). Petiole angle values for the upright and intermediate canopy types are within the range measured by Chapter 2 for these classified canopy types. However, the prostrate canopy type had a smaller, more upright angle than was measured in the field. This could be caused by planting density and light environment in the controlled environment, where overhead light direction and intensity is fixed, which is not typical of a canopy situation in-field. Although there were no differences in petiole angle between leaf ages, the leaf angle increased and became more prostrate with leaf age. This led to the leaf angle becoming increasingly upright in the newer leaf across all canopy types. This could be advantageous to the sugar beet crop as a steeper leaf angle in newer leaves towards the top of the canopy will enable a greater proportion of light to penetrate through to the bottom of the canopy where the leaves are more prostrate to intercept the light (Nobel and Long, 1985; Falster and Westoby, 2003).

The expansion rate of leaf 4 and 7 was modelled, the intermediate canopy reached 50% of modelled maximum leaf 7 width significantly faster than the other canopy types. This could be advantageous to the crop in achieving an optimal leaf area index for light interception. However, the prostrate canopy type had a greater leaf 7 width overall, than the other canopy types which could lead to poor distribution of light and a shaded canopy environment. The growth rate of leaf 4 did not differ between canopy types and overall, there were no differences in the size of leaf 4. This could be caused by large variation and relatively low sample number. Across all canopy types there were no differences seen between leaves 4 and 7 growth rate. In stochastic models, it has been shown that leaf 4 is the slowest expanding leaf in the sugar beet canopy and expansion rate continues to increase up to leaf 13 (Chalabi et al.,1986). Milford et al. (1985b) demonstrated that leaf size increases with each new leaf formed up to the 12 leaf stage. These differences were not detected in this study and could be caused by genetic differences or environmental factors such as water availability. The plants did not experience any mild drought events which can often be experienced in the field and can reduce leaf size and expansion (Ober and Luterbacher, 2002). When canopy projected leaf area was measured from above, the intermediate canopy had a lower projected leaf area than the other canopy types. Typically, it is expected that an upright canopy type would possess a smaller leaf area when measured from above due to the vertical arrangement of leaves. However, the intermediate canopy type had a smaller leaf width which means that the leaves could be smaller overall, contributing to a lower projected leaf area.

4.5.2 Photosynthesis

Overall, the intermediate canopy type had the greatest photosynthetic potential as measured per unit leaf area. Amax was higher than the upright and prostrate canopy types. In addition, the intermediate canopy types had a higher light saturation point, meaning that the canopy can continue photosynthesising under higher light intensities than the other canopy types but in the upright canopy type this could be ameliorated due to the angle reducing light intensity and leaf temperature. This is important for sugar beet as photosynthesis can become depressed at midday when the light intensity is highest, and the leaf slows down its photosynthetic rate, closing its stomata to conserve water (Jaggard et al., 2009; Schickling et al., 2010). The intermediate canopy type can continue photosynthesising for longer thus fix more carbon and as a consequence has a greater yield potential. However, this could come at the expense of water use efficiency.

The prostrate canopy type generally has a lower photosynthetic capacity and is adapted to a lower light intensity. This was shown by the dark respiration rate and the light compensation point for photosynthesis where CO_2 uptake matches respiration at a lower intensity of light. This trait is typical of more shaded environments where self-shading decreases the net amount of leaf area exposed to diffuse and direct light. In this case a lower dark respiration rate and light compensation point would be beneficial to the crop to enable greater plant productivity under a lower light intensity.

Leaf 7 across all canopy types had the greatest photosynthetic capacity, this could mean that newer leaves across the canopy contribute most to yield formation. It has been well discussed that newer leaves in sugar beet are more active than older leaves in the canopy (Hodanova, 1981; Monti et al., 2007). This could be a yield building mechanism, where newer leaves appear towards the top of the canopy where there is a greater light intensity and therefore can fix high amounts of CO_2 and contribute significantly to sugar storage in the root. Interestingly, there was no interaction between leaf age and canopy type. It was hypothesised that an older leaf which is positioned near the bottom of the canopy in a prostrate canopy type would be much less photosynthetically active than the same age leaf in an upright and intermediate canopy. It was also hypothesised that the newer leaf at the top of a prostrate canopy would be more active due to the over-compensation for the shaded leaves within the canopy. However, this was not seen and could be because the plants were grown out of a canopy situation, under artificial light or that photosynthetic potential of sugar beet is genetically pre-determined and not defined by the acclimation status between canopy types as affected by the leaf nitrogen distribution and photosynthetic potential..

Upright canopies have been shown to improve canopy photosynthesis and RUE (Richards et al., 2019). However, this was not assesed in the current study; the upright canopy type could have other benefits to the crop such as enabling greater canopy air flow, reducing canopy humidity and temperature. In turn, the reduced temperature and humidity could potentially lessen the risk of canopy overheating and provide a micro-climate that is less favorable to disease development (Baldocchi et al., 1983).

The controlled environment which the plants were grown in, did not fully simulate the natural canopy environment including light and humidity. This could mean that the photosynthetic values are not fully representative of the crop in the field. An upright canopy type in the field would have a more even light distribution across the leaves and abaxial and adaxial leaf surface as light is reflected off the canopy and the sun moves in the sky. Whereas, in the controlled environment, the light comes from one source positioned above the canopy. Nevertheless, this experiment provides an understanding of how canopy photosynthesis can vary between canopy types outside of an in-field canopy setting.

The upright canopy type had the lowest leaf level light absorbance values across the PAR region. Reflected light in canopy is an important factor in enabling even light distribution (Valladares and Niinemets, 2007). This could be beneficial to the upright canopy type, particularly when the sun is at Zenith angle, directly above the canopy (Falster and Westoby, 2003). In a prostrate canopy type, canopy light reflection may benefit the crop in other ways, reducing the risk of photoinhibition and limiting excessive light exposure to the new leaves at the top of the canopy, despite high levels of leaf reflectance not being seen in prostrate canopy type in this study (King, 1997; Murchie et al., 1999).

4.5.3 Indices to predict canopy photosynthetic traits

Spectral vegetation indices are widely used in crop science with modern UAV and sensor technology becoming more accessible to the wider agricultural industry (Adão et al., 2017). Using vegetation indices to assess canopy traits and photosynthetic traits could prove useful to breeders and growers in identifying high performing varieties according to their canopy angle alongside sensor technology. In this study MnDBlue was positively correlated to petiole angle. In sugar beet, MnDBlue is strongly correlated to leaf chlorophyll a and b content (Jay et al., 2017). Increasingly prostrate canopy angles had a lower chlorophyll a and b content across all leaf ages. This was also described by Chapter 2 in a field experiment testing a range of canopy types and could be linked to the reduced photosynthetic potential seen in the prostrate canopy type. In addition to this, a lower leaf chlorophyll content could form as part of an acclimation mechanism to limit damaging light exposure especially towards the top of the canopy, thus negating the need for higher levels of leaf light reflectance (Murchie et al., 1999; Walters, 2005).

G-NDVI is an indicator of canopy photosynthetic activity and nitrogen uptake (Gitelson et al., 1996). G-NDVI in this study, was positively related to Amax. This index could prove a useful tool to predict photosynthetic rate in the crop and could thereby aid in the development of higher yielding varieties, dependent on assimilate partitioning (Milford et al., 1988; Long et al., 2006).

Respiration is an important biochemical process that produces ATP from the products of photosynthesis. In annual and perennial crops, up to 60% of the carbon assimilated during photosynthesis is lost through respiration (Cannell & Thornley, 2000). Water index was negativity related to dark respiration rate across all canopy types and leaf ages. This means that small reductions in leaf water content can increase the dark respiration rate in the crop. In other crops this has been shown to have the opposite effect where a reduction in leaf water content caused by water stress decreased the dark respiration rate (González-Meler et al., 1998; Tombesi et al., 2022). The older leaves in this study had a higher rate of dark respiration and were less photosynthetically active than the newer leaves. This could mean that this relationship is more complex, and this index could be useful in conjunction with other indices to predict photosynthetic traits.

4.6 Conclusion

In conclusion, we have shown that canopy photosynthesis is influenced by canopy angle. Sugar beet is able to acclimate to canopy light conditions and an intermediate canopy type has the greatest photosynthetic potential and is acclimated to higher light intensities experienced at peak summer. Prostrate canopies are acclimated to shaded canopy conditions and overall, have a lower photosynthetic potential. An erect canopy angle is not well adapted to canopy photosynthesis in sugar beet and may have other benefits to the crop such as increasing canopy airflow, reducing humidity and lessening the risk of disease. As this study only included one variety for each canopy type, it is unclear whether photosynthesis is directly influenced by canopy angle or whether the differences between varieties are caused by other factors. It is possible to predict photosynthetic and canopy traits using vegetative indices which when used in combination with other indices could be a powerful tool in predicting sugar beet canopy photosynthesis and yield in the future.

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4.8 Supplementary information

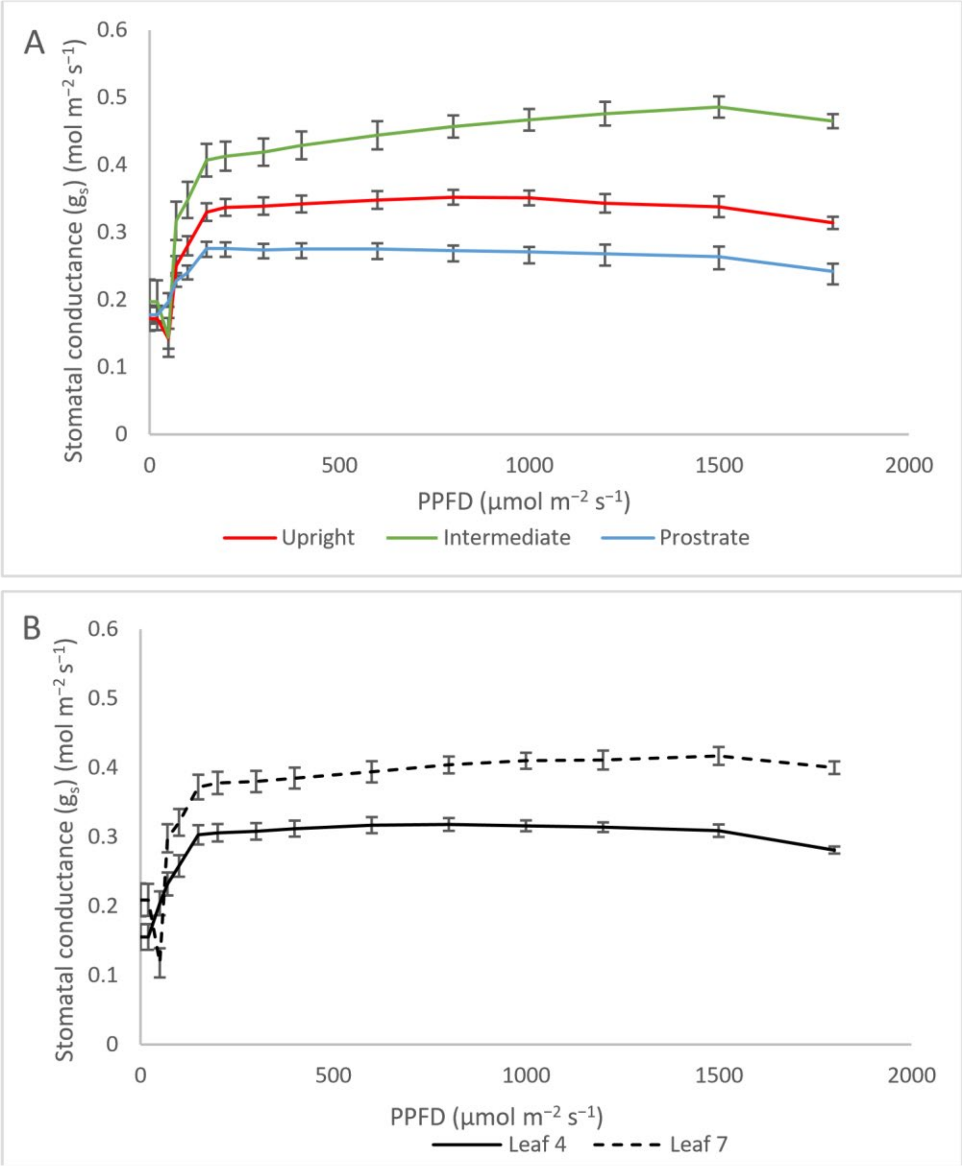

Figure S4.1 stomatal conductance (gs) measured against PPFD (Photosynthetic Photon Flux Density) of average leaves 4 and 7 (A) and average across canopy types (B). Error bar shows SE values.

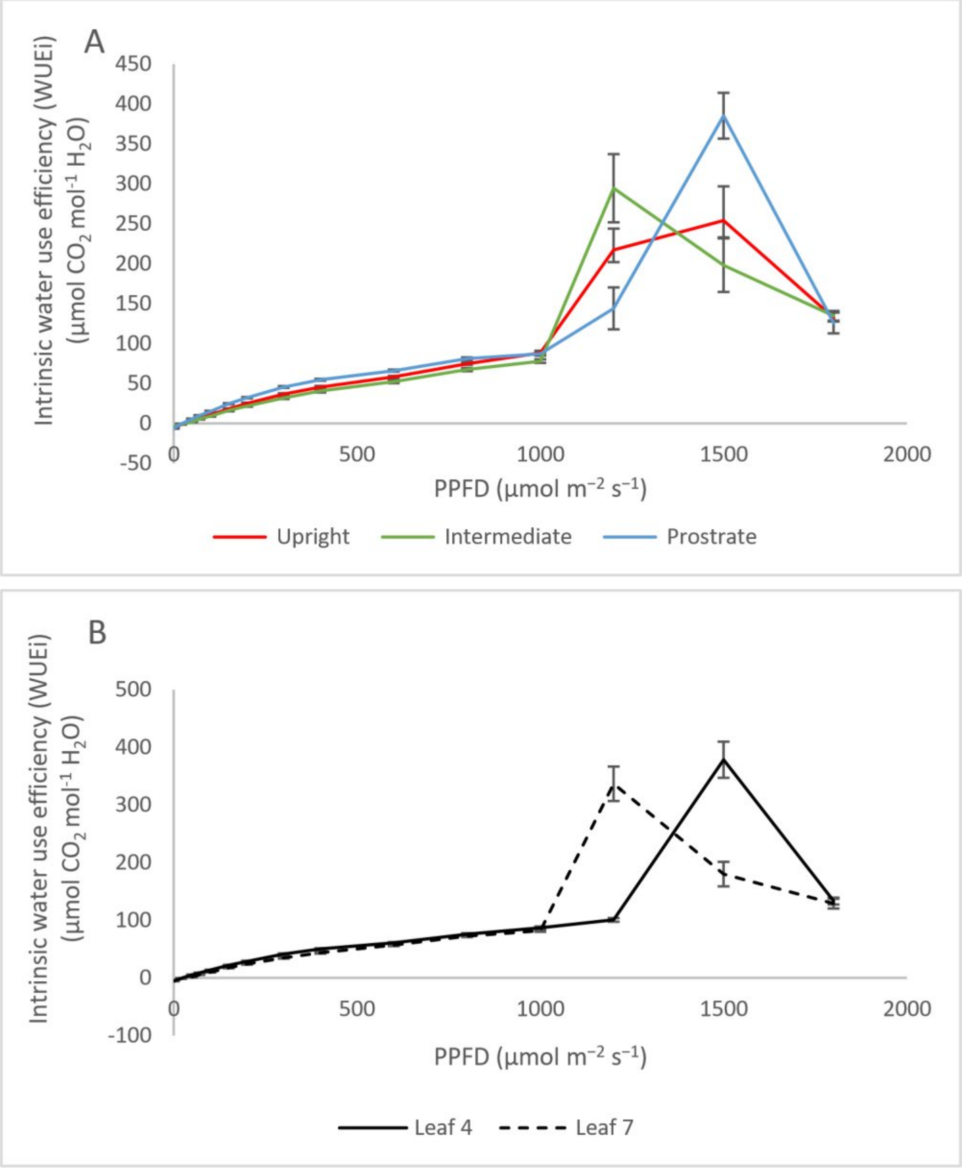

Figure S4.2 Intrinsic water use efficiency (WUEi) calculated as A/gs, of leaves 4 and 7 (A) and average across canopy types (B) measured against PPFD (Photosynthetic Photon Flux Density). Error bar shows SE values.

Chapter 5: 3D canopy modelling method development

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5.1 Abstract

Previous 3D canopy modelling approaches have been unsuccessful in capturing detailed canopy architectural traits in sugar beet. The aim of this study was to develop a method to produce high quality point clouds of sugar beet plants which can be used to evaluate the differences in canopy architecture between commercial varieties. Multiple images taken at all angles of a sugar beet plant in a pot at the 10-leaf stage formed the basis of this method. The images were used in a multi-view stereo and structure from motion algorithm in 3DF Zephyr Pro software. This method resulted in a dense high quality point cloud of a sugar beet canopy. This approach has potential to compare and categorise varieties according to their canopy architecture at field scale using drone technology. In the future it may be possible to couple this data with ray tracing technology and photosynthesis measurements to model canopy photosynthesis to predict radiation use efficiency and yield.

5.2 Introduction

The creation of 3D models in crop science is a useful method to analyse canopy architectural traits. They can be used in remote sensing to phenotype singular plants or large scale canopies. 3D canopy models can be used for a range of applications such modelling canopy light fluctuations leading to the detailed calculation of canopy photosynthesis (Burgess, et al., 2017a; Burgess, et al., 2017b). Methods typically involve the creation of point clouds representing the 3D canopy structure. The point cloud is then used to extract biologically relevant information canopy architectural information such as leaf angle, area and number.

LiDAR or Light Detection and Ranging is an active remote sensing technology which is commonly used to create 3D canopy models. LiDAR works off the basis of light reflectance from a surface. It can detect different layers within a canopy and use this data to generate a canopy model. Traits such as plant height, leaf size and area can be calculated from the resulting model (Omasa et al., 2007; Bömer et al., 2022) However, LiDAR technologies are expensive and time consuming to set up because it usually uses lasers and specialised hardware and software. The use of RGB images and their reconstruction proves a cheaper and more accessible alternative because it can be done with standard SLR cameras and, often, existing free software. This approach has been used successfully on a range of plant structures including wheat, rice and Bambara groundnut (Burgess, et al., 2017a; Burgess, et al., 2017b).

The application of computer vision has developed rapidly over the last 20 years. Structure from motion (SFM) technologies have significantly increased the speed of plant and canopy phenotyping in the field (Hui et al., 2018; Omasa et al., 2007; Xiao et al., 2020, 2021). SFM is a passive approach to canopy modeling based on an algorithm for 3D point cloud reconstruction from multiple 2D RGB images. This method, when used alongside multi-view stereo (MVS), generates a 3D dense point cloud from the detection of distinctive features from the images and stitching them together. The resolution and quality of the reconstructed point clouds depends on the number of overlapped images, a higher image number leads to better quality resolution. Despite this, the output is of similar quality to the LiDAR method.

Point clouds have been generated in a number of plant species and forms including wheat, chickpea and ground nut (Burgess et al., 2015, 2017b; Salter et al., 2021). Sugar beet canopies have a rosette leaf arrangement in a 5:13 phyllotaxis (Clark and Loomis, 1978). This makes the reconstruction process challenging because of the few distinctive features, colours and textures visible in the RGB images. The reconstructed models using both LiDAR and RGB images often have significant empty spaces in their leaves and entire petioles missing. The SFM method can improve and complete the point cloud of an individual plant by capturing images from different viewpoints in the canopy. Therefore, the more data collected from different points of view, the better quality the resulting 3D model. Xiao et al. (2020) successfully created a dense 3D point cloud or model of a sugar beet plant in the field using 3DF Zephyr Aerial software multi-view stereo and structure from motion (MVS-SFM) algorithm. These models were then used to extract plant traits including plant height and leaf area.

The aims of this chapter are to further improve on the accuracy of sugar beet canopy models and investigate their practicality in comparing canopy architecture from a range of commercial sugar beet varieties; with the scope to be further applied to assist high-throughput canopy phenotyping in the future.

5.3 Method

This method is based on the approach used by Xiao et al. (2020) using MVS-SFM algorithm but has been adjusted to obtain more detailed canopy models to be used to compare canopy architecture between commercial sugar beet varieties.

5.3.1 Imaging

The sugar beet plants can be imaged either *in situ* in the field with the nearest surrounding plants removed to avoid leaves over lapping or grown in a pot imaged in a dedicated imaging studio. The method remains the same regardless of imaging location. The method described here is based on a plant in a pot placed in an imaging studio.

The optimum time to image sugar beet plants is between the 8 to 12 leaf stage when the canopy is approaching the leaf number required for canopy closure without too many overlapping leaves impeding the reconstruction process. Sugar beet plants *var. SESVanderHave Cayman* were grown in 5 L rose pots containing Kettering loam soil and were placed at a consistent distance from the lights in two controlled environment cabinets (A2000, Conviron, UK). There were 3 replicates. The pots were moved down as the plants grew to maintain the same distance from the lights. Fluorescent tubes (LUMILUX HO 54W/840 T5, Osram, Munich, Germany) supplied 12 h of light at 400 μmol m^{-2} s^{-1} followed by 12 h of darkness, with an hour dawn and dusk light adjustment. The pots were hand-watered throughout to prevent soil drying. Humidity was set at 65 % with a daytime temperature of 20 °C and night-time temperature of 14 °C. At 29 DAS, 1.05 g of ammonium nitrate equivalent to 50 kg ha^{-1} was applied to each pot in solution. The plants reached 10 leaf stage and were ready to be imaged at 60 DAS. The plants in their pots were placed on a textured and coloured A1 target (the target is visible in all figures). The target is designed to provide distinctive features to aid in the stitching together of images in the reconstruction process. A camera, Canon Powershot sx720 (Canon, Inc., Tokyo, Japan) was used to capture multi-view images at 5184 x 3888 resolution. Images were taken in three circuits walking around the plant with camera in hand taking images from the bottom to the top in a spiral (Figure 5.1). The lighting was set up to avoid casting a shadow on the images. The images were captured with an overlap target of around 75 %. This overlap target was necessary to capture many replicates of significant plant features to enhance the reconstruction process.

Figure 5.1 Camera positions from multi-view images. Each blue rectangle represents a point of image capture.

5.4 Creating the models using 3DF software

5.4.1 Reconstructions

3DF Zephyr Pro software was used to reconstruct a point cloud from the set of images based on MVS-SFM algorithm (Figure 5.2). The image set was imported by creating a new workflow. The pre-set general settings work well with these types of images and the SFM algorithm can be set to run. The speed of the model creation depends on the computer processing power and typically takes less than five minutes with an 8GB RAM PC. The output creates a sparse point cloud (Figure 2B). By ticking the dense point cloud box under further options, a dense point cloud using the MVS algorithm can be generated (Figure 5.2C).

In order to create a clean model, the point cloud of the individual sugar beet (Figure 5.2C, D) was manually cleaned using CloudCompare, a 3D point cloud and mesh processing software (http://www.danielgm.net/). The background points in the point cloud were segmented out based on their scalar field values (colour value) which can be pre-set in CloudCompare.

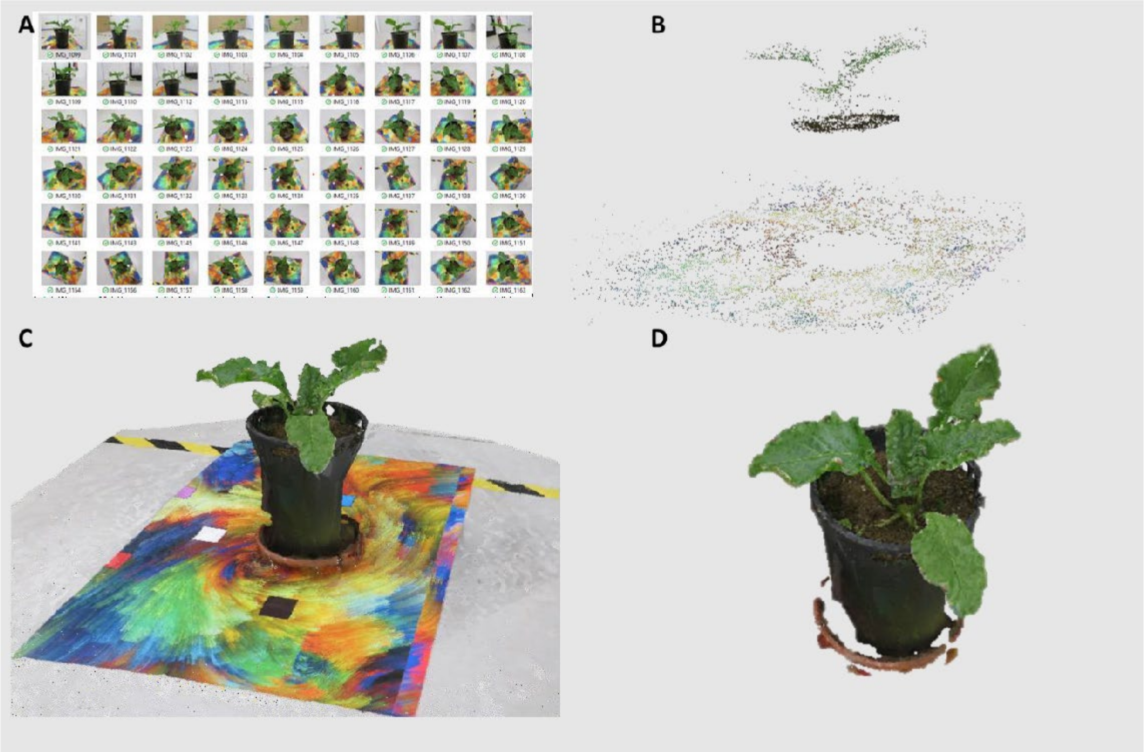

Figure 5.2 Process of creating sugar beet plant 3D model. A) Multi-view image set of sugar beet plant; B) Reconstructed sparse point cloud of sugar beet; C) Reconstructed dense point cloud of sugar beet. D) Point cloud of sugar beet after background removal in CloudCompare. The plant pictured is at the 6-leaf stage which was included in the early stages of method development.

5.5 Future developments for this method

This method is an efficient and easy way of modelling a sugar beet plant. It uses RGB images taken free hand which are then used to generate a 3D model using an MVS-SFM algorithm in the 3DF software. The resulting models are very high quality and overcome the missing leaves and petioles which was an issue when using previous approaches (Figure 5.3A).The output is more complete and captures more detailed canopy traits than models created of single sugar beet plants using Li-DAR technology or previous approaches (Figure 5.3) (Bömer et al., 2022).

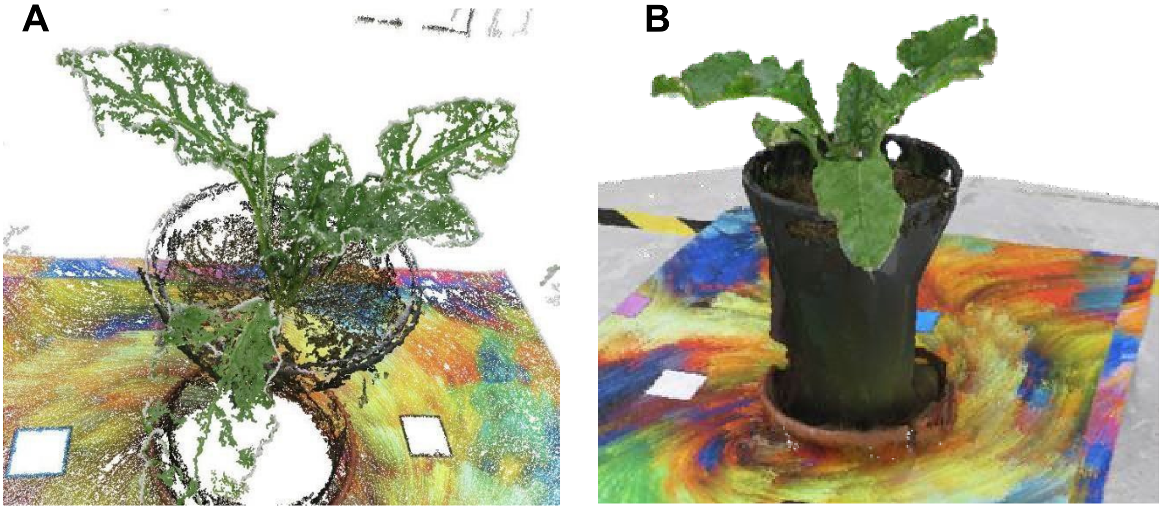

Figure 5.3 Comparison between previous approach based on Pound et al. (2014) and Burgess et al. (2015) (A) and the new method using MVS-SFM and 3DF software (B) to model the sugar beet canopy.

The 3DF canopy modelling method has potential to further evolve. Currently, the method described does not use a scale and therefore, quantitative length, angle or area measurements have not been taken as these have previously been obtained manually. Scaling the model would be possible and could lead to detailed sugar beet canopy trait analysis detailing leaf angle, area and length which will be useful once compared to the physical measurements. The scope of this approach could help tackle the phenotyping bottleneck faced by sugar beet breeders. Canopy architectural traits of interest have the potential to be detected non-invasively *in-situ,* rapidly and cheaply. This method could be scaled to UAV mounted cameras to identify canopy traits at in the field.

In the future, this method could be applied to a ray tracing algorithm to simulate light (specifically photon flux density) distribution within a plant canopy across the duration of a day in a pre-set location and season (Song et al., 2013). The canopy light distribution data can be coupled with photosynthesis light response data to predict whole canopy photosynthesis and radiation use efficiency (Burgess et al., 2017a). This would be a useful tool when scaled up to an entire sugar beet canopy as seen in Figure 5.4, demonstrating canopy photosynthesis in a range of species. The 3D model could be used for contrasting architectures which would enable a prediction of light distribution. Coupled with photosynthesis data the model could be used to predict optimal architecture for high radiation use efficiency and yield potential which could then be validated in the field. The model could also assist in the categorisation of varieties for early or late harvest according to their light interception efficiency across the season as the sun angle becomes lower in the sky. Ray tracing was not completed in this project due to the existing ray tracing algorithm being incompatible with the 3D output from this canopy model. Rewriting and adapting the ray tracing algorithm to this model requires specialist programming knowledge and therefore fell outside the scope of this project.

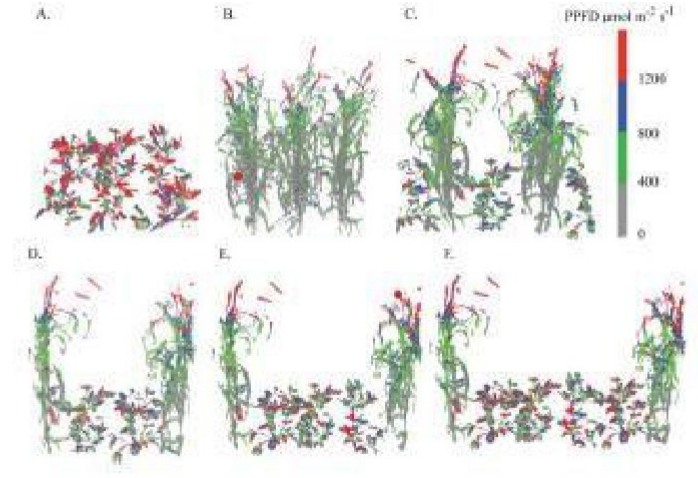

Figure 5.4 Example reconstructed canopies with the maximum PPFD shown on a colour scale at midday. Sourced from Burgess et al. (2017b).

5.6 Conclusion

After a long period of development and refinement, this method can successfully generate detailed 3D models of a sugar beet plant whilst avoiding significant holes in the leaf and petioles. Small gaps can be seen in the plant due to the occlusion of leaves and may only be overcome by destructively removing leaves and imaging. The model can demonstrate differences in canopy architecture and be applied to both field and pot grown plants. To my knowledge, high quality 3D plant models, such as those described above, have not previously been applied to assess sugar beet canopy architecture. This method provides a basis for further development to enable large scale canopy phenotyping or predictive light modelling *in-situ* to allow for varieties to be selected according to their canopy traits to improve radiation use efficiency and yield.

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Chapter 6 General discussion and conclusions

6.1 Introduction

This thesis has investigated the impact of sugar beet canopy architecture on radiation use efficiency (RUE) and sugar yield. This work aimed to gain a greater understanding of sugar beet canopy architecture traits and its effect on RUE by addressing the research questions and hypotheses identified in Chapter One, which are restated below.

1. To what extent does canopy architecture (leaf and canopy angle and area) differ across modern sugar beet varieties?

Hypothesis: Modern sugar beet varieties differ significantly in canopy angle, with prostrate and upright extremes.

2. Are there differences in canopy expansion and light interception between varieties with contrasting canopy architectures?

Hypothesis: More upright varieties will intercept less light before canopy closure than prostrate varieties and take longer to reach canopy closure.

3. Does canopy architecture have a significant impact on RUE?

Hypothesis: There will be an optimal canopy architecture for light interception. In a closed canopy, new leaves at the top of the canopy are most upright and older leaves are more prostrate and therefore light is distributed more evenly through the canopy facilitating a greater RUE.

Upright canopy angles intercept light more efficiently at lower sun angles than prostrate canopy types and could help reduce midday heat load on the canopy.

4. To what extent are leaves at the top of the canopy more able to cope with higher light intensities and have a higher maximum photosynthesis value than those older leaves at the bottom of the canopy? Do these values change depending on canopy architecture?

Hypothesis: Newer leaves at the top of the canopy in prostrate varieties can cope with higher light intensities than in upright varieties. Older leaves in prostrate varieties become light saturated at lower intensities and are less photosynthetically active than upright varieties.

5. Is RUE determined by canopy angle or are there other genetically determined traits that affect RUE ?

Hypothesis: Making a canopy more prostrate will increase total light interception early on however, once canopy closure is reached an upright angle canopy will have a higher RUE and subsequent yield.

The findings are now summarised and discussed in terms of canopy architecture in commercial sugar beet varieties, photosynthesis and RUE and the clarification of whether RUE and yield is subjected by canopy angle or genetics. Finally, take home messages for sugar beet industry stakeholders are stated and future research priorities are recognised.

6.2 Sugar beet canopy architecture

Much of the research undertaken has been to identify and quantify the differences in canopy architecture between commercial sugar beet varieties and to investigate the impact of this on RUE and sugar yield. Previous studies have shown that commercial sugar beet varieties differ significantly in their canopy architecture, in particular canopy development and leaf area index (LAI) (Hoffmann, 2019; Wright et al., 2018). Sugar beet canopy architecture in relation to angle, has not yet been investigated despite being a significant factor influencing canopy light interception and RUE (Duncan, 1971; Burgess et al., 2017a). This research has quantified sugar beet canopy architecture focussing on petiole angle, LAI and percentage canopy cover at field scale (Chapter 2) and assessed the influence of leaf aging on petiole and leaf angle and leaf expansion in a controlled environment (Chapter 4).

6.2.1 Canopy angle

We aimed to test Hypothesis 1 by quantifying the canopy architecture of commercial sugar beet varieties. It was found in Chapters 2 and 4 that modern sugar beet varieties differ significantly in their canopy architecture. It was demonstrated that varieties can be classified into canopy types according to their petiole angle. Petiole angles measured in the field and controlled environment varied slightly but had a similar trend and this was likely caused by the differences in their environment:

notably whether they were grown individually in pots, or in a canopy in the field and the light environment that they were growing in.

A meticulous method was devised that measured petiole angle as an upright insertion into the crown. The upright canopy types typically had a petiole angle below 30°, intermediate canopy types between 30-45° and up to 50° for prostrate canopy types. These values were measured across the season in Chapter 2 and at the 10-leaf stage in Chapter 4. A range of factors can influence canopy angle including plant genetics and abiotic stresses such as water and nitrogen availability. Numerous studies have been conducted to investigate the natural variation in canopy angle in cereal crops (Li et al., 1999; Chen et al., 2005; Nakamura et al., 2009; Dong et al., 2016; Yang et al., 2016; Huang et al., 2022). These studies have indicated that canopy angle is complex and determined by plant hormones including brassinosteroids and auxins controlled by multiple genetic loci with variable effects. The genetic and hormonal control of canopy angle in major crops, including sugar beet, is poorly understood, and their elucidation could enable targeted breeding programmes for optimal canopy architecture and development of smart canopies as seen in wheat and rice (Ort et al., 2015).

Leaf angle distribution influences canopy spectral reflectance and transmission properties, and hence interception, absorption and photosynthesis (Hikosaka and Hirose, 1997; Hirose, 2005). Chapter 3 has shown that petiole and leaf angle become more prostrate with age across all canopy types. This is due to the arrangement of leaves in the sugar beet canopy, older leaves are typically positioned towards the bottom of the canopy as new leaves emerge from the centre of the crown (Milford et al., 1985a). Therefore, the increasing canopy angle towards the bottom of the canopy in sugar beet could be a result of leaf senescence and remobilization of nutrients and water to newer leaves resulting in a more turgid upright petiole and leaves in the upper canopy (Fellows and Geiger, 1974).

Several researchers have suggested that increasing the leaf angle to be more prostrate towards the bottom of the canopy and more upright towards the top can improve light distribution and provide an optimal canopy architecture for high RUE and yields (Duncan, 1971; Long et al., 2006; Zhu et al., 2010). Long et al. (2006) demonstrated that during mid-summer this architecture can increase carbon uptake by 60 % relative to a canopy of horizontal leaves. However, this has been established in taller canopies, above 1 m. Sugar beet typically follow this arrangement with more prostrate older leaves, yet it is undetermined whether this benefits the crop during mid-summer.

The quantification of leaf angle is problematic in the field. The overlapping nature and rosette formation of sugar beet grown in rows means that measuring leaf angle without manually moving the leaves is near impossible. Hence in this project, leaf angle was assessed using singular plants grown in a pot. Petiole angle measurements can be undertaken in the field and in pots. It is higher throughput and more accurate and was detected as a defining canopy architectural trait in our study and used to define canopy angle. The method of quantifying canopy angle could be improved to enable a larger number of plots to be analysed at field scale and to be implemented in breeding programmes. A remote sensing approach would be ideal for this using high-definition canopy reconstruction approaches (Burgess et al., 2017).

6.2.2 Leaf area

Leaf area can be defined as the area of the leaf which has the potential to be actively photosynthesising. Leaf area per unit ground area is termed the leaf area index (LAI). When the LAI increases, light or photon flux density (PFD) captured by the canopy increases until canopy closure is achieved, leading to higher photosynthetic production in the canopy. However, when leaves at the bottom of the canopy receive a lower PFD required for the compensation point of photosynthesis, an increase in LAI decreases canopy photosynthesis. Therefore, there is an optimal LAI that maximizes rates of photosynthesis (Monsi,1953).

An optimal LAI of between 3 and 4 has been suggested for sugar beet for maximal canopy cover and light interception (Jaggard and Qi, 2006; Milford, 2006). It is advantageous to achieve canopy cover of >85 % with minimal leaf area as possible to prioritise carbon allocation into the root and conserve water (Milford, 2006). However, the suggested optimal LAI for sugar beet does not consider canopy angle. In general, a larger LAI is required for an upright canopy compared to a prostrate canopy to achieve equivalent fractional light interception. This is because in prostrate canopies, the leaves are essentially flat and directly intercepting light and therefore a larger proportion of the canopy is overlapping and shaded, and hence extra LAI is wasted resources compared to an upright canopy where a larger LAI is required to utilise incident light (Duncan, 1971).

Nitrogen, water availability and temperature have been closely associated with leaf expansion and canopy growth in sugar beet (Milford and Watson, 1971; Milford, 1980; Milford et al., 1985a; Milford et al., 1985b; Malnou et al., 2006; Laufer and Koch, 2017). The prostrate canopy in Chapter 2 had a higher LAI in 2021 and individual leaf width measured under controlled environment conditions in Chapter 4. In 2019, the Intermediate 2 variety had the highest LAI, this means that LAI could vary between seasons depending on variety. There could be differences between varieties in the ability to develop and maintain canopy depending on the season. This was seen in 2021, it was a drier autumn and the intermediate canopy type lost more canopy area to in theory conserve more water. Despite this, LAI values ranged between 3-3.5 during the summer months and declined into the winter as leaf death surpassed new growth. Loel et al. (2014) found that LAI had not significantly changed between new and old sugar beet varieties. This suggests that due to the rosette nature of the canopy, LAI may not need to alter between canopy types and other factors such as leaf chlorophyll content and photosynthesis rate may be more important.

6.2.3 Canopy development and light interception

Rapid emergence and canopy development in sugar beet is vital for optimal light interception. In sugar beet there is a strong linear relationship between accumulated intercepted radiation, total biomass and sugar yield in the crop (Scott, 1964; Scott and Jaggard, 1978; Tillier et al., 2023). In spring, canopy formation is largely affected by temperature and by the summer months, water availability is usually limiting (Ober et al., 2004). Early sowing has been shown to increase final sugar beet yield by facilitating increased light interception during May and June and therefore greater biomass production (Jaggard et al., 1983; Wood and Scott, 1975; Hoffmann and Kluge-Severin, 2010). However, sugar beet can become vernalised at temperatures between 1 and 12 °C and transition into a reproductive phase or ‘bolt’ which leads to significant loss of taproot sugar and biomass (Jaggard et al., 1983). Therefore, in the UK, the earliest safe sowing date recommended for sugar beet is the first week of March. Because of this, rapid canopy expansion and development is essential for high light interception during May and June and sugar yields at harvest.

Hypothesis 2 was confirmed by Tillier et al. (2023) which demonstrated that upright canopy types have a slower rate of canopy expansion and overall lower percentage canopy cover. A strong linear relationship was seen between petiole angle and light interception across the season. The prostrate canopies intercepted the most light across the season seen in both Chapter 2 and 3. This can be explained by a higher quantity of light intercepted during May and June.

Canopy expansion, leaf initiation and turnover is affected by a range of biotic and abiotic factors such as temperature, nitrogen and water availability and plant diseases (Ebmeyer and Hoffmann, 2022; Laufer and Koch, 2017; Milford and Watson, 1971). Chapter 2 and 3 demonstrated that canopy development is dependent on spring temperature and rainfall. Each field trial year was very different in terms of rainfall and temperature, and this was reflected in the canopy development and canopy cover across the seasons. Those years with low rainfall and cooler spring temperatures reached canopy closure considerably later and intercepted less light during this period compared to warmer wetter spring as seen in 2019 and 2022 where the canopy expanded at a much greater rate. The sugar beet canopy expands as individual leaf area increases with each leaf up to the 12-leaf stage. At this point canopy cover is near maximum (Milford et al., 1985b). After canopy closure, new leaves replacing older leaves are smaller and as a result of this the canopy begins to decline as replacement rate slows.

The canopy manipulation 2022 trial season experienced drought conditions during the summer months and all treatments lost canopy cover. However, the upright treatment where the leaves were suspended above the ground, lost proportionally less cover than the flat and control treatments but had a similar resulting canopy cover.

In sugar beet it is well established that percentage canopy cover is proportional to percentage of intercepted light in the canopy (Steven et al., 1986; Milford, 2006). Therefore, thresholded images taken above of the canopy were used to calculate percentage canopy cover and thus accumulated intercepted light (reflectance of 8% had been used in other studies but no difference in canopy light reflection was seen and was therefore not included (Hoffmann, 2019)). This method of calculating accumulated intercepted light may not be adequate to account for differences in canopy angle as it assumes that light is intercepted at the top of the canopy and does not consider incident light angle, canopy angle, light transmission and absorbance.

Leaf level light absorbance calculations in Chapter 4 showed that the upright canopy type absorbed less light in the PAR region than the intermediate and prostrate canopy types. In future, this factor should also be included in light interception calculations. A raytracing canopy modelling approach method maybe more accurate at calculating light interception but would require detailed canopy models and leaf optical properties despite being tedious and time consuming to create (Burgess et al., 2017).

6.3 Photosynthesis

Crop photosynthesis is the driving force between canopy light interception, carbon capture and biomass production in the plant. The productivity and efficiency of photosynthesis is a key determinant of RUE (Monteith and Moss, 1977). Leaf nitrogen is an important factor for canopy photosynthesis as photosynthetic proteins contain around half of total leaf nitrogen (Evans, 1989). As a consequence of this, there is a strong correlation between leaf nitrogen content and photosynthesis capacity across many major crops (Evans, 1989; Mu and Chen, 2021). This was not seen In Chapter 2 and 4. The intermediate canopy type had the greatest photosynthetic capacity (Maximum CO_2 assimilation rate) despite not having the greatest leaf nitrogen content.

MnDBlue and SPAD are both indicators of leaf chlorophyll and nitrogen content in sugar beet (Jay et al., 2017; Malnou et al., 2006). MnDBlue and SPAD were strongly correlated with petiole angle in Chapter 2 and 4. This means that prostrate canopy types had the lowest leaf chlorophyll content and upright canopy types the highest. Low leaf chlorophyll content in prostrate canopy types could be a result of large thin leaves and thus photosynthetic apparatus is spread out over a wider area compared to the upright canopy type. High levels of chlorophyll in the upright canopy type could be excessive and actually cause the leaf to become saturated at low light intensities due to large quantity of light harvesting complexes (Beadle and Long, 1985). The intermediate canopy type may contain optimal levels of leaf chlorophyll to facilitate high rates of photosynthesis under higher light intensities.

Photo-acclimation is the process where plants adjust their photosynthetic machinery according to incident light levels (Walters, 2005). In sugar beet and other crops, it is well reported that leaf photosynthetic capacity declines with age (Hodanova, 1981; Monti et al., 2007). This was also seen in Chapter 4, where across all canopy types, the newer leaf 7 had a higher maximum photosynthetic rate compared to the older leaf 4. This partially supports hypothesis 4 that photosynthesis of leaves declines with age but there were no differences between the decrease and canopy type.

In the sugar beet crop, new leaves could contribute most to yield formation. This is advantageous for the crop as these leaves appear towards the top of the canopy where incident light is greatest. Chapter 4 confirms that across all canopy types, newer leaves are more acclimated to higher light intensities and therefore can fix high amounts of CO_2 and contribute significantly to sugar storage in the root.

Hypothesis 4 is based on the theory behind previous studies that have shown canopy angle influences the canopy light environment and therefore, leaves located at certain positions in the canopy will have different instantaneous photosynthetic values depending on canopy angle (Duncan, 1971; Long et al., 2006; Burgess et al., 2017b). These studies have shown that erect leaves at the top of the canopy avoid light saturation and instantaneous photosynthesis of leaves towards the bottom of the canopy increases. In contrast, a larger proportion of leaves in the prostrate canopy are light limited lower in the canopy and saturated at the top. Hypothesis 4 states that newer leaves at the top of the canopy in prostrate varieties can cope with higher light intensities than in upright varieties. Older leaves in prostrate varieties become light saturated at lower intensities and are less photosynthetically active than upright varieties.

Chapter 3 did not support hypothesis 4. It reported that leaves at the top of prostrate sugar beet canopies did not have a higher light saturation point than upright canopies and there was no interaction between leaf number and canopy type. As well as this, older leaves towards the bottom of the canopy in upright varieties do not show higher rates of photosynthesis compared to the prostrate canopy. However, Chapter 4 demonstrated that the prostrate canopy type overall had a lower dark respiration rate and light compensation point. This trait is typical of more shaded environments where self-shading decreases the net amount of leaf area exposed to diffuse and direct light. In this case a lower dark respiration rate and light compensation point would be beneficial to the crop to enable greater plant productivity under a lower light intensity.

It was inferred in hypothesis 4 that an upright canopy type would have a consistent rate of photosynthesis across all leaves. This was not supported by the results in Chapter 4 which showed that the older leaves had a lower photosynthetic potential then the newer leaves. This could mean that the nature of the sugar beet canopy: plants arranged in rows 50 cm apart, with a rosette of overlapping leaves: means that the difference in light distribution between the canopy types is not significant.

However, an upright canopy type may have other advantages to the crop which may improve photosynthesis under certain conditions. The upright canopy manipulation treatment in Chapter 4 demonstrated that during the drought period in the summer months, the upright canopy treatment had a higher canopy temperature depression (CTD). CTD is an indicator of canopy photosynthesis and is caused by the latent cooling effect from canopy transpiration (Fukuoka, 2005). An upright canopy angle could reduce midday heat load on the canopy thus enabling more efficient photosynthesis and help reduce canopy water loss (King, 1997). As well as this, the upright canopy could intercept light more efficiently at lower sun angles at dawn and dusk and later in the season. This is particularly relevant for sugar beet as the harvest campaign can extend over the winter months. To fully determine the impact of an upright canopy angle on light interception at varying solar zenith angles, a canopy modelling ray tracing approach is required to simulate canopy light transmission.

The intermediate canopy type had the greatest photosynthetic rate in the controlled environment and in the field (Chapter 2 and 4). Additionally, the intermediate canopy type had a higher light saturation point. This means that photosynthesis becomes saturated at higher light intensity than all other canopy types which could be advantageous to the crop enabling photosynthesis to continue for longer in the day. This is important for sugar beet as photosynthesis can become depressed at midday when the light intensity is highest, and the leaf slows down its photosynthetic rate, closing its stomata to conserve water (Jaggard et al., 2009; Schickling et al., 2010).

The intermediate canopy type can subsequently fix more carbon over a longer period and therefore has a greater yield potential. However, as the stomata remain open actively taking in CO_2, this can come at an expense of water loss. Ebmeyer and Hoffmann (2022) found higher WUE in sugar beet is related to high sugar yield and thus photosynthesis. This is likely due the crop's anisohydric nature keeping stomata open and photosynthesising, building yield, even under water stress conditions, therefore this trait may not excessively disadvantage the intermediate canopy (Ober et al., 2004; Jaggard, et al., 2009; Barratt et al., 2021).

6.4 Radiation use efficiency and yield

Hypothesis 3 stated that there is an optimal canopy architecture for light interception facilitating a greater RUE. A sugar beet canopy composed of upright leaves towards the top and prostrate towards the bottom represents the theoretical optimal structure as it enables incident radiation to be uniformly distributed throughout the canopy. This canopy architecture has been shown to improve RUE in other crops (Duncan, 1971; Peng et al., 2008; Song et al., 2013). We investigated whether this was also the case in sugar beet. Chapter 2 confirmed hypothesis 3 and found that the intermediate canopy types closest to this canopy arrangement had the highest RUE from total plant DM in 2019 and highest sugar yield in both years. The upright canopy types had the highest RUE from total DM when harvested later in 2021. The RUE values were lower in 2021 compared to 2019 across all canopy types and this is likely a result of rainfall differences across the season (Jaggard et al., 2009).

Upright and prostrate canopy types were sown in alternate rows as a treatment in 2021 to determine whether this could improve RUE by providing an optimal canopy angle through upright and prostrate canopy angle interaction. Up to October harvest in 2021, the prostrate/upright canopy type had the highest RUE of 1.55 g DM per MJ. This was because the prostrate/upright canopy type accumulated more total biomass between July and October than the other canopy types. In our study, the alternate canopy arrangement could reduce mutual leaf shading across the canopy and as a result increase the productivity and photosynthetic potential of the canopy. Sowing alternate varieties may also improve disease resistance as varieties with different susceptibility can be selected (BBRO, 2019). As a result of this, the alternate sowing treatment can be compared to intercropping whereby contrasting crops/canopies are often sown in alternate rows to improve radiation capture, water use, disease resistance and yield (Glaze-Corcoran et al., 2020). However, choosing an alternate sowing treatment may need careful consideration by growers. Firstly, in the drill set up to enable seed placement for each row and secondly at harvest; it has been discussed that sugar beet varieties differ in crown height and therefore the grower could lose potential yield through crown loss (Milford and Houghton, 1999) However, the UK has now transitioned to whole beet delivery where there is an allowance for more crown and green leaf material.

Biomass partitioning is vital to yield formation in sugar beet. Loomis (1979) described an ideotype for high sugar yields in sugar beet as having minimal canopy biomass compared to root biomass. Therefore, a distinction must be drawn between RUE (calculated using total biomass) and sugar yield. Varieties with a high RUE do not necessarily equate to high yields. This was seen in the upright canopy type in both Chapter 2 and 4. In both experiments each had the greatest RUE at final harvest, but this did not equate to a higher sugar yield. In Chapter 2, during the period between October and December the upright canopy types continued to put on more root and significantly more canopy biomass than all other canopy types therefore increasing the RUE value. However, the Intermediate 2 variety had the highest sugar yield as it was more efficient at intercepting and utilising light and more efficient at partitioning biomass to the root. If the plots were harvested even later then perhaps the upright canopy type would have continued to build yield and out yield the Intermediate 2 variety. There is no published research on the relationship between canopy angle and later harvest dates in sugar beet. Studies in other crops have shown that an upright canopy angle is more efficient at intercepting light at lower sun angles than a prostrate canopy (Gilbert et al., 2003; Sarlikioti et al., 2011). The upright canopy types in this study could be more efficient at intercepting light in the winter months and therefore be more suited to a later harvest. The findings in Chapter 2 support this.

Only two varieties per canopy type were used in Chapter 2 and one per canopy type in Chapter 4. The two intermediate varieties were from different breeders and hence different genetic backgrounds. The upright and prostrate canopy types had varieties from the same breeders for each type. There was a significant sugar yield difference between the two intermediate varieties. This means that differences in RUE and yield may be genetic and not solely caused by canopy angle.

6.5 The distinction between canopy angle and genetics

To pull apart whether RUE and yield is determined by canopy angle; a canopy manipulation experiment was carried out in the field across two years (Chapter 3). Hypothesis 5 stated that manipulating the high yielding intermediate canopy to be more prostrate will increase pre-canopy closure light interception and once canopy closure is reached an upright canopy angle will have a higher RUE and subsequent yield. In our study, the prostrate canopy manipulation increased early season light interception but this had no effect on photosynthesis or final sugar yield. The upright manipulation improved RUE from total plant dry matter in 2022 due to a higher canopy biomass. Whilst canopy angle may be an important contributing factor to RUE and yield in sugar beet it is likely that RUE and yield is genetically determined and may be limited by the plant's ability to store sucrose in the harvested roots (Hoffmann and Kenter, 2018).

In other crops, genes have been discovered which improve biomass accumulation and partitioning (Molero et al., 2019; Sierra-Gonzalez et al., 2021). Although care must be taken when comparing sugar beet to crops with distinct pre and post anthesis differences in RUE. Loel et al. (2014) found that new varieties have a decreased proportion of biomass partitioned into the canopy compared to old varieties. Specific genes controlling this have not been published but have been a source of significant yield improvement and have seemingly been selected for by breeders. Assimilate partitioning in sugar beet could be regulated by a negative feedback system controlled by the sink (roots) which regulate source activity and the partitioning of assimilates in the plant (Ho,1988). It is likely that this, alongside photosynthesis improvements in the leaf, are responsible for high RUE and yield.

As manipulating canopy angle had no effect on sugar yield, this implies that the differences in RUE between varieties is not explained by canopy angle. However, canopy manipulation was not able to completely replicate differences in canopy architecture between varieties, hence further work is required to confirm this. Additional studies using near-isogenic lines with different canopy angles across a range of soil types over more seasons would be an ideal approach to test this hypothesis more rigorously.

6.6 Take home messages for sugar beet industry stakeholders

6.6.1 Growers:

Sugar beet growers should consider canopy architecture when they are selecting varieties. Canopy angle has been established as a key architectural trait in in sugar beet and is classified by petiole angle. Intermediate canopy types with petiole angles ranging between 30-45° are highest yielding as demonstrated in Chapter 2. These canopy types have demonstrated high levels of photosynthesis and are acclimated to high light intensity experienced during peak summer.

Prostrate canopy types have larger, wider leaves and have rapid canopy expansion reaching canopy closure faster. These canopy types could be sown where weed pressure is high to achieve canopy closure sooner and hence outcompete weeds.

Upright canopy types have slower canopy expansion but may be a good option for later harvests if their higher RUE later in the season proves to be consistent. On lighter soils, upright canopy types could be sown to limit canopy loss during drought as fewer leaves would be in direct contact with the soil.

6.6.2 Breeders:

From this study the key factors or crop ideotype determining high yield are high leaf photosynthetic activity and increased biomass partitioning into the root without compromising canopy for light interception. Chapter 2 demonstrated that the Intermediate variety had the highest photosynthetic rate and greatest root to shoot ratio. The canopy manipulation study determined that this is not exclusively an effect of canopy angle but is underpinned by other factors.

For breeders to identify varieties with high sugar yield potential, lines with a high root to shoot ratio (without compromising canopy cover) and high photosynthetic rate should be selected for. The use of CTD measurements from UAVs could aid in the selection of varieties with high photosynthetic rates post canopy closure and for pre canopy closure, LRCs taken in controlled environments could indicate canopy photosynthetic potential. In order to determine biomass partitioning, destructive biomass harvests should be undertaken.

Canopy angle ought to be assessed in relation to drought and disease tolerance and harvest timing as this study has shown that in particular, the upright canopy coped well under drought conditions and continued to build biomass into December.

The current method to quantify canopy angle in the field is very accurate but time intensive. The development of a high throughput remote method of measuring canopy angle will be very beneficial in classifying new varieties.

6.7 Future research

The findings from this study have identified a range of new research ideas which could help to further understand sugar beet canopy architecture and its impact on RUE and yield as well as the wider influence of canopy architecture on plant disease and environmental stress.

Assessing RUE using near isogenic lines with varying canopy architecture would be beneficial to determine the influence of architecture on RUE. However, as previously outlined, near isogenic lines are not available in sugar beet. Therefore, modelling sugar beet canopies and performing ray tracing to ascertain canopy light interception would be beneficial to establish the impact of sugar beet and other row crops on light interception and RUE. As well as this, combining photosynthesis data from Chapter 4 with the output from the ray tracing models could help to determine the photosynthetic productivity of the canopy, following work that has been previously demonstrated in cereal crops.

Leading on from this, the assessment of canopy light interception using raytracing would also support the future research relating to canopy angle and harvest timing by evaluating RUE at varying zenith angles. This would follow up findings from Chapter 2 where it was demonstrated that upright canopy types continue to build biomass more readily during the winter months.

This thesis demonstrated that canopy angle may have other benefits to the crop such as drought or disease tolerance. It would be useful to investigate this further by monitoring the microclimates (e.g. humidity, temperature, air flow) of different canopy types and the impact of this on disease Incidence and the impact of drought. Finally, the development of a remote and high throughput method to quantify canopy angle in the field is essential to further explore the effect of canopy architecture on RUE and other factors discussed above. The development of this method will enable experiments to be undertaken over a number of seasons and soil types for varietal screening and classification of angle which in the future could be a useful addition to the sugar beet recommended list.

6.8 Conclusions

The major conclusions from the works reported in this thesis can be summarised as follows:

1. Commercial sugar beet varieties can be classified into canopy types, upright, intermediate or prostrate, according to their canopy (petiole) angle.

2. Canopy angle strongly influences light interception across the season; an upright canopy has a slower rate of canopy expansion and a lower percentage maximum canopy cover and thus intercepts less light than an intermediate or prostrate canopy. A prostrate canopy has a faster rate of canopy expansion and reaches canopy closure sooner and a higher maximum canopy size. Therefore, the prostrate canopy intercepts more light across the season.

3. Optimal LAI does not change according to canopy angle. An upright canopy type does not have a higher optimal LAI compared to prostrate canopy types at a similar percentage canopy cover.

4. Intermediate canopy types have a higher rate of photosynthesis under optimal conditions and are well primed for high levels of photosynthesis in the summer months, under a high intensity of light. Photosynthesis in prostrate canopy types is acclimated to shaded conditions. High photosynthetic activity leads to greater carbon gain across the season and final sugar yield.

5. Individual leaf photosynthesis decreases with age and they become more prostrate regardless of canopy type. Newer leaves in the canopy are most photosynthetically active and could contribute the most to sugar yield.

6. An upright canopy type had a higher RUE later in the season. An upright canopy angle could be more efficient at intercepting and utilizing light at a lower sun angle and therefore suit a later harvest.
7. An upright canopy type is not well adapted for high levels of photosynthesis under optimal conditions but could be beneficial for sub optimal weather conditions such as drought by reducing the midday heat load on the canopy and reducing leaf senesce.

8. Canopy angle does not influence RUE and sugar yield in sugar beet. Other factors such as canopy photosynthesis, biomass partitioning and sink strength may be more important for high sugar yields.

6.9 References

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