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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.

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).

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)

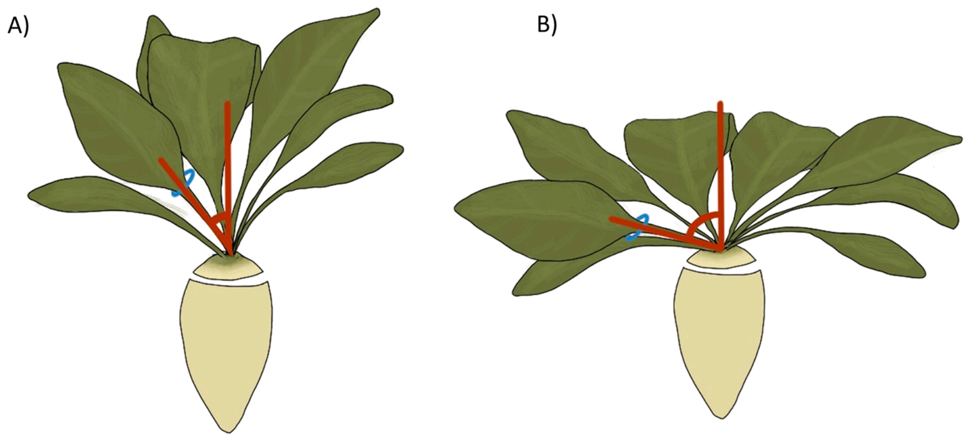

Fig. 1. Canopy angle measurements on an upright canopy type (A) and prostrate canopy type (B). Canopy angle is taken as the petiole angle from an upright insertion into the crown. Leaves of similar age were measured.

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*.

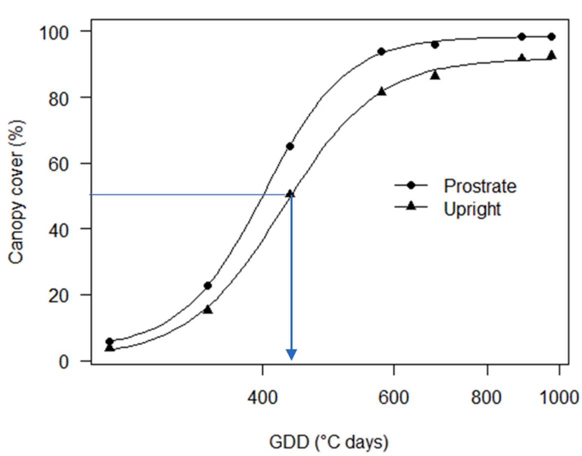

Fig. 2. Three-parameter log-logistic model used to model canopy expansion. Shown here are example data from a prostrate and upright canopy type. The inflection point of an upright canopy is indicated by the blue arrow. GDD is growing degree days or thermal time.

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)

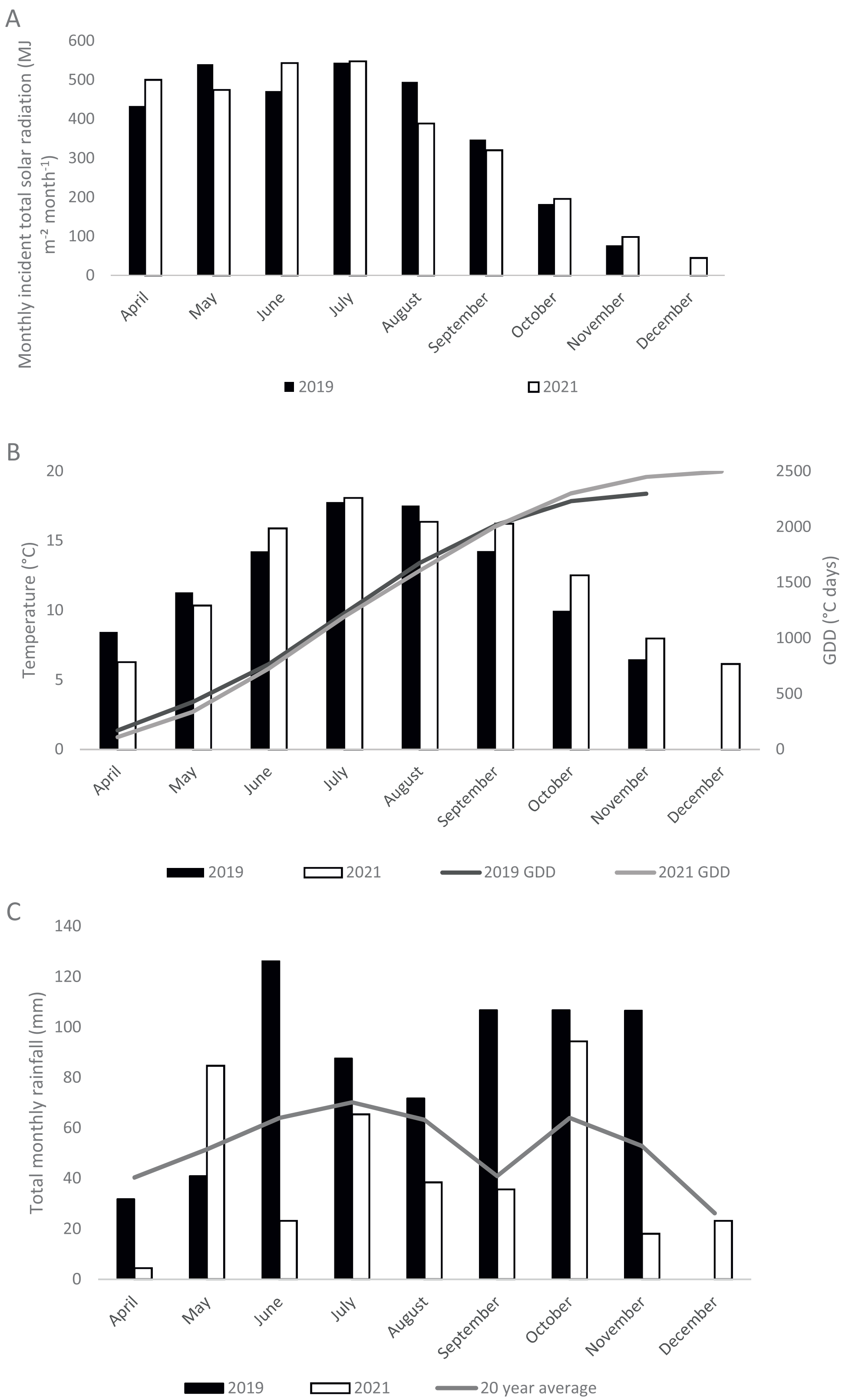

Fig. 3. Meteorological data from the Sutton Bonington weather station during the 2019 and 2021 growing season. A) Monthly total solar radiation receipts. B) monthly average temperature and growing degree days. C) monthly rainfall. GDD is growing degree days or thermal time.

was calculated as Eq. (1).

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

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.

2.3. 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

3.1. Weather data

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

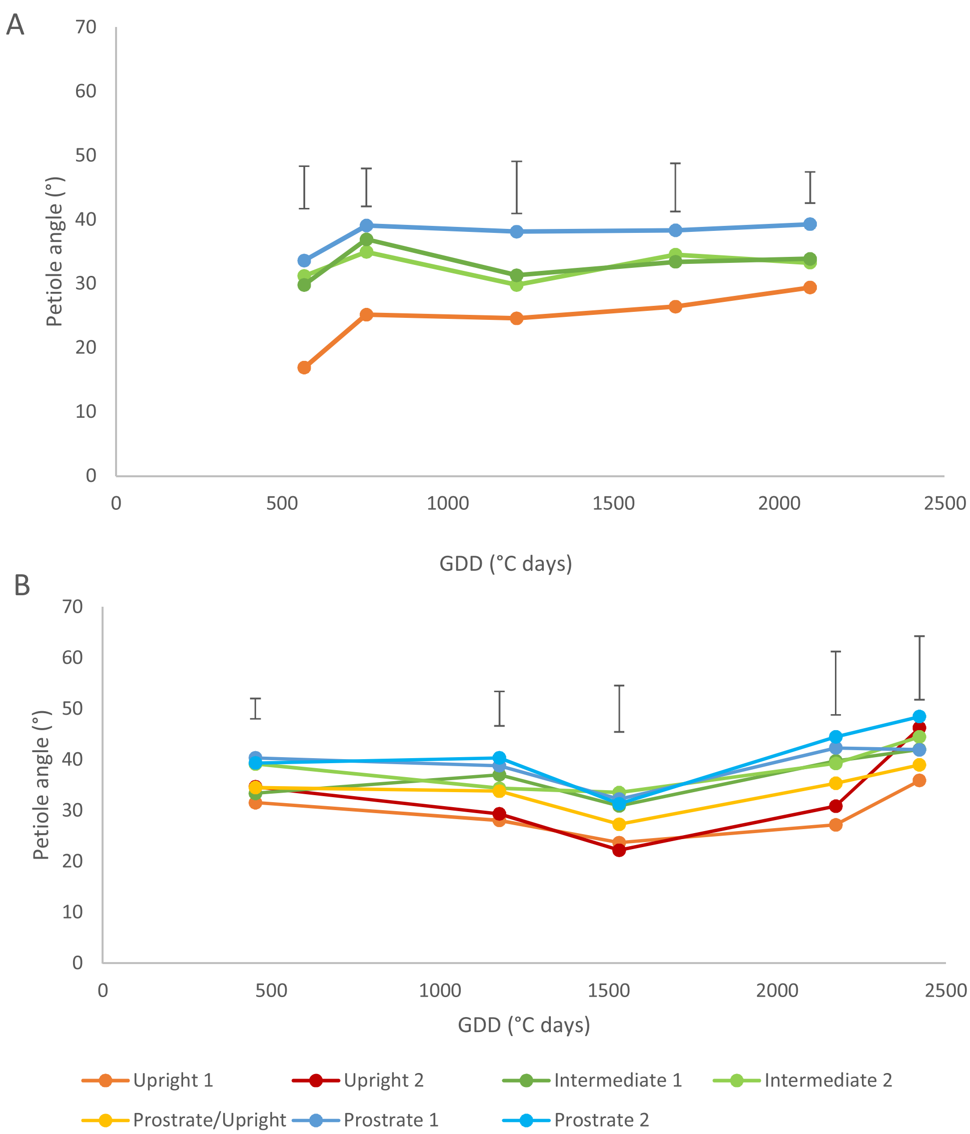

Fig. 4. Petiole angle of different canopy types measured against thermal time after emergence (GDD) in 2019 (A) and 2021 (B). Error bar shows $LSD_{5\%}$ at each interval.

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 μmol $m^{-2}s^{-1}$ and was significantly higher than both Upright 1 (31.42 μmol $m^{-2}s^{-1}$) and Prostrate 1 (25.94 μmol $m^{-2}s^{-1}$) 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

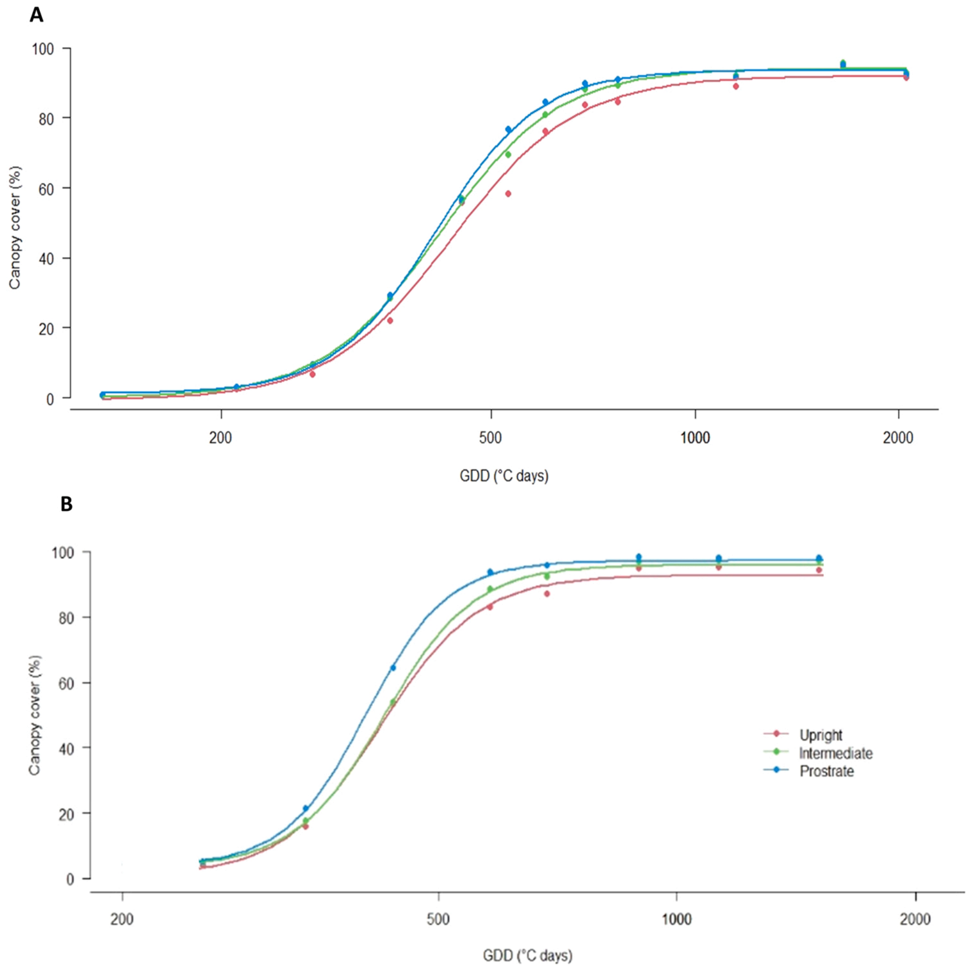

Fig. 5. Fitted curves from a three parameter log logistic model used in modelling canopy expansion and development of different canopy types in 2019 (A) and 2021 (B). The average of upright, intermediate and prostrate canopy types are show against thermal time after emergence (GDD).

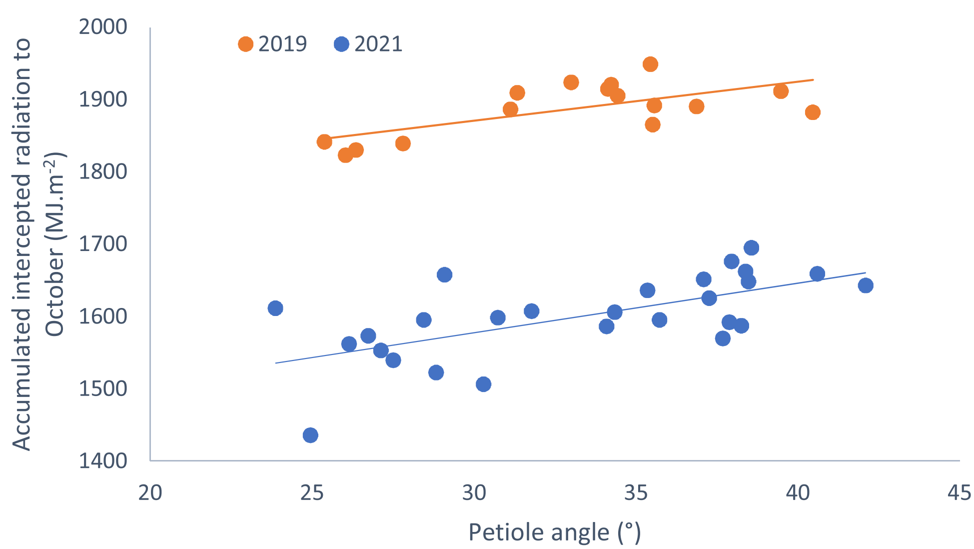

Fig. 6. The influence of petiole angle on accumulated intercepted radiation up to October. Petiole angle was calculated as an average of measurements taken from canopy closure to October in 2019 and 2021. 2019: $y = 5.395x + 1708.7$, $R^2 = 0.4501$. 2021: $y = 6.8589x + 1371.5$, $R^2 = 0.4086$.

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.

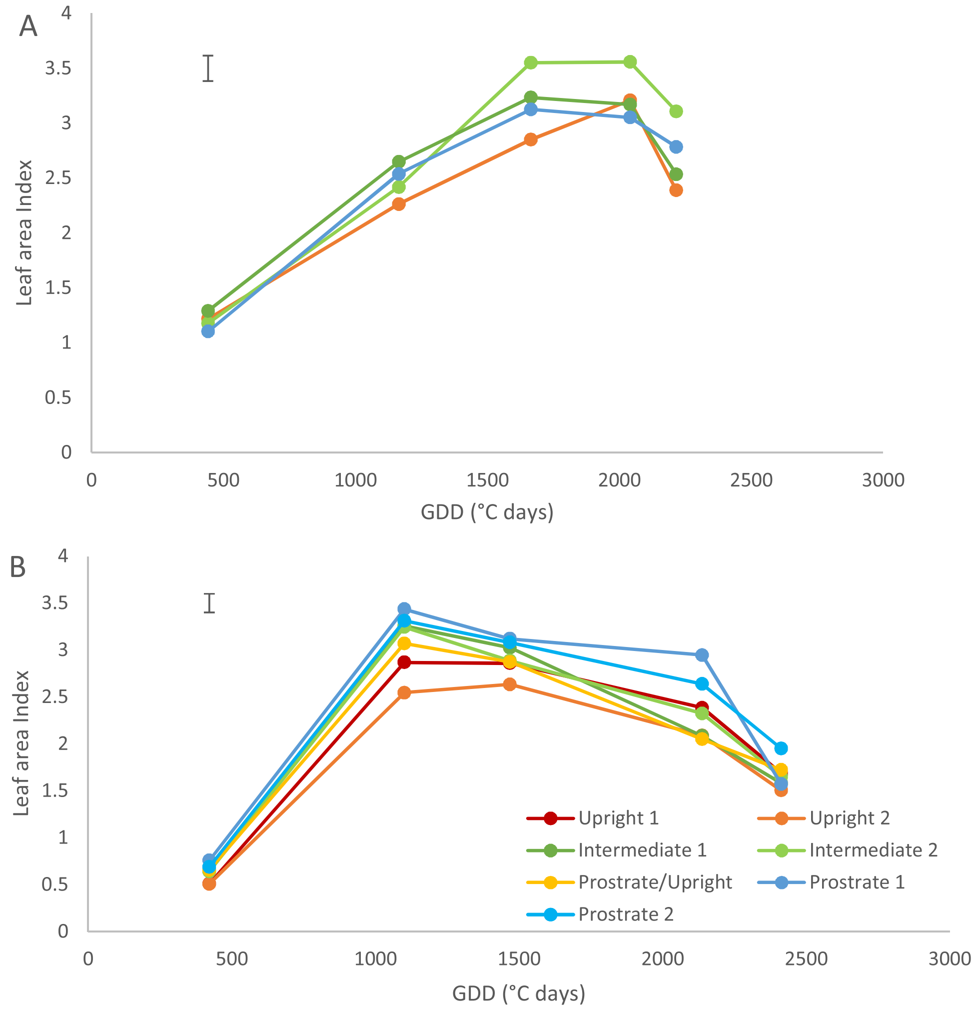

Fig. 7. Leaf area index of different sugar beet canopy types plotted against thermal time after emergence (GDD) in 2019 (A) and 2021 (B). Error bar shows variety $LSD_{5\%}$.

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

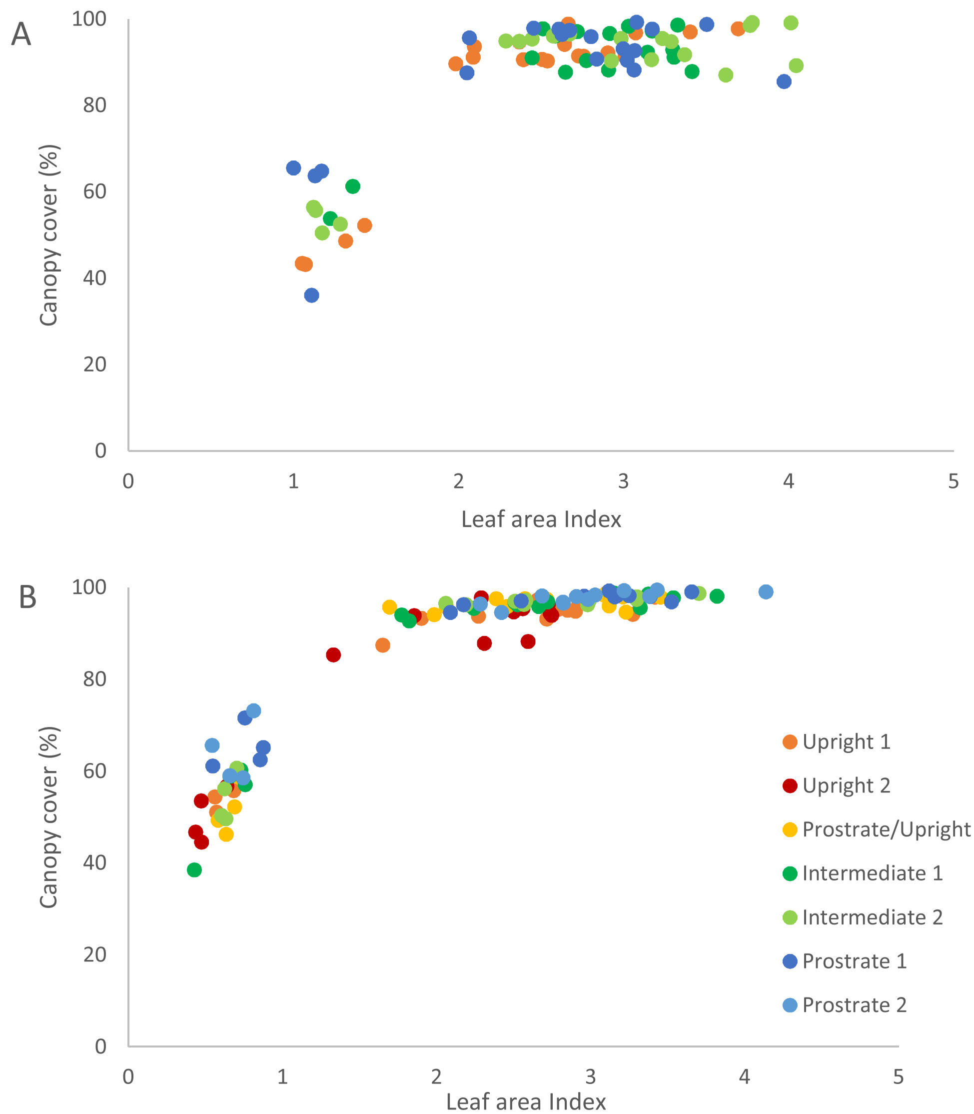

Fig. 8. The relationship between leaf area index and percentage canopy cover across the season for different sugar beet canopy types in 2019 (A) and 2021 (B).

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

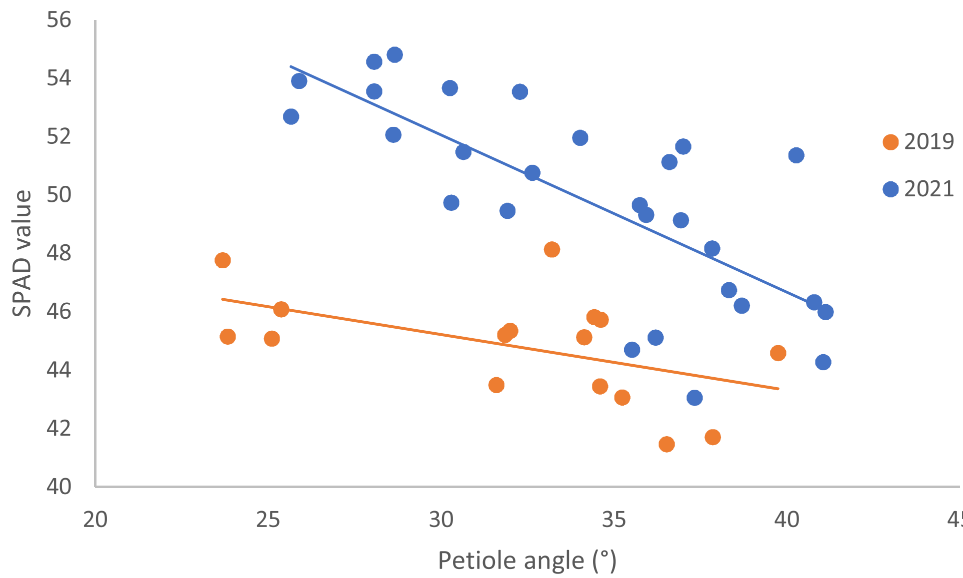

Fig. 9. The relationship between petiole angle and canopy greenness from SPAD-502 readings in 2019 and 2021. Petiole angle was calculated as an average of measurements taken from canopy closure to October in 2019 and 2021. Canopy greenness values were averaged from canopy closure to October. 2019: $y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

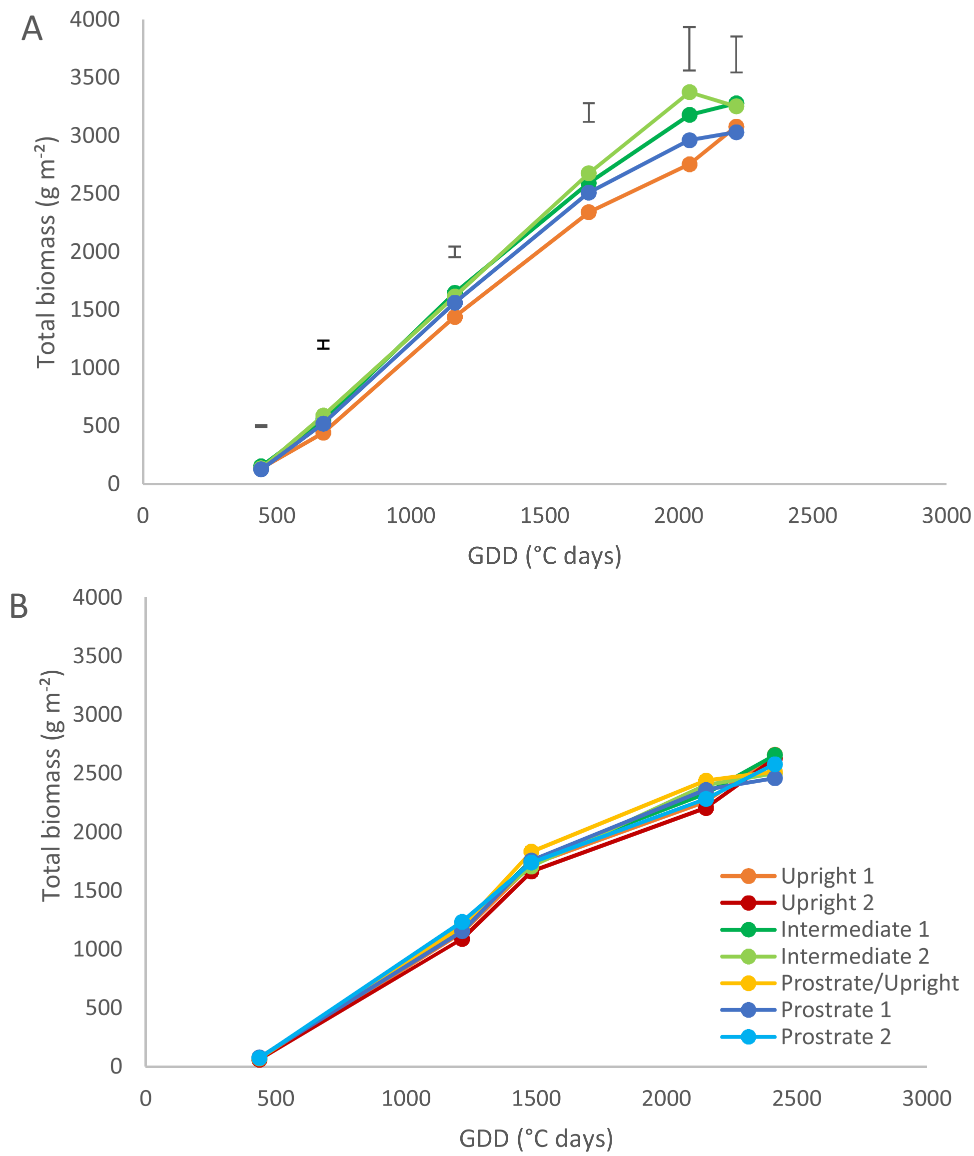

Fig. 10. Total plant biomass accumulated across the season affected by sugar beet varieties with different canopy types in 2019 (A) and 2021 (B). Error bar shows $LSD_{5\%}$.

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

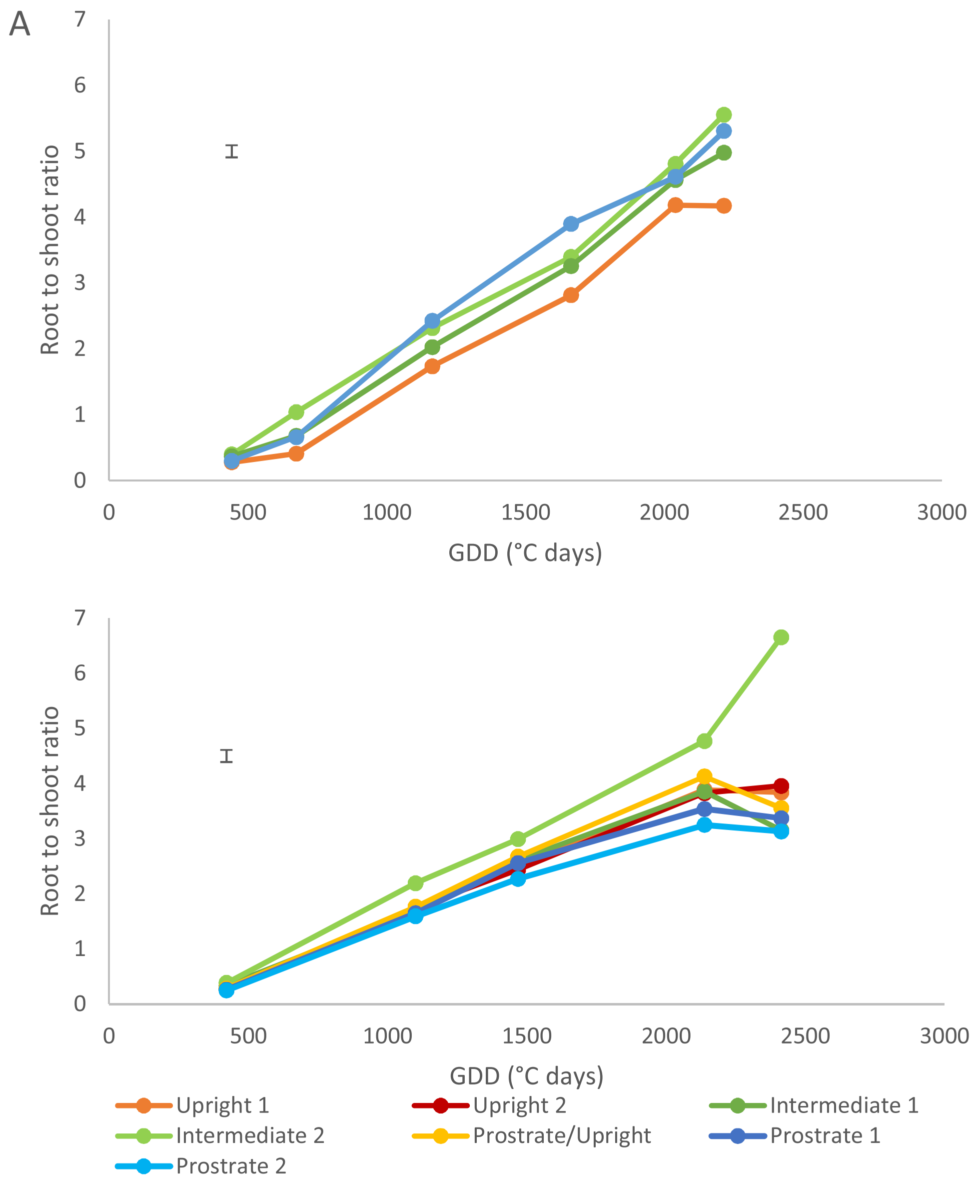

Fig. 11. Root to shoot ratio of different sugar beet canopy types against GDD (°C days) calculated as root dry weight divided by top dry weight (petioles and leaves). A) 2019 and B) 2021. Error bar shows variety repeated measures $LSD_{5\%}$.

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 ($t.ha^{-1}$)						
	2019			**2021**		
Canopy type	Root yield	Sugar %	Sugar yield	Root yield	Sugar %	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.

References

Beadle, C.L., Long, S.P., 1985. Photosynthesis — is it limiting to biomass production? Biomass 8 (2), 119–168. https://doi.org/10.1016/0144-4565(85)90022-8.
Bowen, S., 2021. Variety tactics for 2022. Br. Sugar Beet Rev. 89 (2), 21–22 (Available at). ⟨https://edition.pagesuite-professional.co.uk/html5/reader/production/default.aspx?pubname=andedid=216f9ad4-5df1-4a2c-b159-583d1514c7b0⟩.
Burgess, A.J., Retkute, R., Pound, M.P., Foulkes, J., Preston, S.P., Jensen, O.E., Pridmore, T.P., Murchie, E.H., 2015. High-resolution three-dimensional structural data quantify the impact of photoinhibition on long-term carbon gain in wheat canopies in the field. Plant Physiol. 169 (2), 1192–1204. https://doi.org/10.1104/pp.15.00722.
Drewry, D.T., Kumar, P., Long, S.P., 2014. Simultaneous improvement in productivity, water use, and albedo through crop structural modification. Glob. Change Biol. 20 (6), 1955–1967. https://doi.org/10.1111/GCB.12567.
Ducat, D.C., Silver, P.A., 2012. Improving carbon fixation pathways. Curr. Opin. Chem. Biol. 16 (3–4), 337–344. https://doi.org/10.1016/J.CBPA.2012.05.002.
Ebmeyer, H., Hoffmann, C.M., 2021. Efficiency of nitrogen uptake and utilization in sugar beet genotypes. Field Crops Res. 274. https://doi.org/10.1016/j.fcr.2021.108334.
Ehleringer, J.R. and Werk, K.S., 1986, Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level, On the economy of plant form and function: proceedings of the Sixth Maria Moors Cabot Symposium, Evolutionary Constraints on Primary Productivity, Adaptive Patterns of Energy Capture in Plants, Harvard Forest, August 1983 [Preprint]. Available at: ⟨https://www.ehleringer.net/uploads/3/1/8/3/31835701/071.pdf⟩ (Accessed: April 14, 2021).
Falster, D.S., Westoby, M., 2003. Leaf size and angle vary widely across species: what consequences for light interception? N. Phytol. 158 (3), 509–525. https://doi.org/10.1046/j.1469-8137.2003.00765.x.
Gilbert, R.A., Heilman, J.L., Juo, A.S.R., 2003. Diurnal and Seasonal Light Transmission to Cowpea in Sorghum–Cowpea Intercrops in Mali. J. Agron. Crop Sci. 189 (1), 21–29. https://doi.org/10.1046/J.1439-037X.2003.00005.X.
Glaze-Corcoran, S., Hashemi, M., Sadeghpour, A., Jahanzad, E., Keshavarz Afshar, R., Liu, X., Herbert, S., 2020. Understanding intercropping to improve agricultural resiliency and environmental sustainability. Adv. Agron. 162, 199–256. https://doi.org/10.1016/BS.AGRON.2020.02.004.
Gummerson, R., 1986. The effect of constant temperatures and osmotic potentials on the germination of sugar beet. J. Exp. Bot. 37 (179), 729–741.
Hoffmann, C.M., 2014. Adaptive Responses of Beta vulgaris L. and Cichorium intybus L. Root and Leaf Forms to Drought Stress. J. Agron. Crop Sci. 200 (2), 108–118. https://doi.org/10.1111/JAC.12051.
Hoffmann, C.M., 2019. Importance of canopy closure and dry matter partitioning for yield formation of sugar beet varieties. Field Crops Res. 236, 75–84. https://doi.org/10.1016/J.FCR.2019.03.013.
Hoffmann, C.M., Kenter, C., 2018. Yield potential of sugar beet – have we hit the ceiling? Front. Plant Sci. 9, 289. https://doi.org/10.3389/fpls.2018.00289.
Hoffmann, C.M., Kluge-Severin, S., 2010. Light absorption and radiation use efficiency of autumn and spring sown sugar beets. Field Crops Res. 119 (2–3), 238–244. https://doi.org/10.1016/J.FCR.2010.07.014.
Huang, S., Gao, Y., Li, Y., Xu, L., Tao, H., Wang, P., 2017. Influence of plant architecture on maize physiology and yield in the Heilonggang River valley. Crop J. 5 (1), 52–62. https://doi.org/10.1016/j.cj.2016.06.018.
Hubbart, S., Smillie, I., Heatley, M., Swarup, R., Foo, C., Zhao, L., Murchie, E., 2018. Enhanced thylakoid photoprotection can increase yield and canopy radiation use efficiency in rice. *Commun. Biol.* 1 (1), 1–12. https://doi.org/10.1038/s42003-018-0026-6.
Jaggard, K.W., Qi, A., 2006. Agronomy. Sugar Beet. Blackwell Publishing Ltd,, Oxford, UK, pp. 134–168. https://doi.org/10.1002/9780470751114.ch7.
Jaggard, K.W., Qi, A., Ober, E.S., 2010. Possible changes to arable crop yields by 2050. Philos. Trans. R. Soc. B: Biol. Sci. 365 (1554), 2835–2851. https://doi.org/10.1098/rstb.2010.0153.
King, D.A., 1997. The functional significance of leaf angle in eucalyptus. Aust. J. Bot. 45 (4), 619–639. https://doi.org/10.1071/BT96063.
Loel, J., Kenter, C., Märländer, B., Hoffmann, C.M., 2014. Assessment of breeding progress in sugar beet by testing old and new varieties under greenhouse and field

conditions. Eur. J. Agron. 52, 146–156. https://doi.org/10.1016/J.EJA.2013.09.016.
Long, S.P., Zhu, X.G., Naidu, S.L., Ort, D.R., 2006. Can improvement in photosynthesis increase crop yields? Plant, Cell and Environment. John Wiley and Sons, Ltd,, pp. 315–330. https://doi.org/10.1111/j.1365-3040.2005.01493.x.
Malnou, C.S., Jaggard, K.W., Sparkes, D.L., 2008. Nitrogen fertilizer and the efficiency of the sugar beet crop in late summer. Eur. J. Agron. 28 (1), 47–56. https://doi.org/10.1016/J.EJA.2007.05.001.
Martínez, D.E., Guiamet, J.J., 2004. Distortion of the SPAD 502 chlorophyll meter readings by changes in irradiance and leaf water status. Agronomie 24 (1), 41–46. https://doi.org/10.1051/AGRO:2003060.
Milford, G.F.J., Pocock, T.O., Riley, J., 1985. An analysis of leaf growth in sugar beet. II. Leaf appearance in field crops. Ann. Appl. Biol. 106, 173–185.
Milford, G.F.J., Travis, K.Z., Pocock, T.O., Day, W., Jaggard, K.W., 1988. Growth and dry-matter partitioning in sugar beet. J. Agric. Sci. 110 (2), 301–308. https://doi.org/10.1017/S0021859600081326.
Monteith, J.L. (1977) Climate and the efficiency of crop production in Britain, Trans. R. Soc. Lond. B.
Murchie, E.H., Townsend, A., Reynolds, M., 2018. Crop radiation capture and use efficiency. Encycl. Sustain. Sci. Technol. 1–34. https://doi.org/10.1007/978-1-4939-2493-6_171-3.
Nevins, D.J., Loomis, R.S., 1970. Nitrogen Nutrition and Photosynthesis in Sugar Beet (Beta vulgaris L.) 1. Crop Sci. 10 (1), 21–25. https://doi.org/10.2135/CROPSCI1970.0011183×001000010009X.
Paul, M.J., Foyer, C.H., 2001. Sink regulation of photosynthesis. J. Exp. Bot. 52 (360), 1383–1400. https://doi.org/10.1093/JEXBOT/52.360.1383.
Peng, S., Khush, G., Virk, P., Tan, Q., Zou, Y., 2008. Progress in ideotype breeding to increase rice yield potential. Field Crops Res. 108 (1), 32–38. https://doi.org/10.1016/J.FCR.2008.04.001.
R Core Team, 2021, R Core Team, R Development Core Team. R A Lang. Environ. Stat. Comput (2016). https://doi.org/http://www.R-project.org.
Rasband, 2011, W. Rasband, ImageJ, U. S. Natl. Institutes Heal, Bethesda, Maryland, USA.
Richards, J.P. (2019) The effect of cover crops on soil structure and the subsequent yield of sugar beet. Thesis. p.203.
Richards, R.A., Cavanagh, C.R., Riffkin, P., 2019. Selection for erect canopy architecture can increase yield and biomass of spring wheat. Field Crops Res. 244, 107649 https://doi.org/10.1016/J.FCR.2019.107649.
Robles-Zazueta, C.A., Pinto, F., Molero, G., Foulkes, M.J., Reynolds, M.P., Murchie, E.H., 2022. Prediction of photosynthetic, biophysical, and biochemical traits in wheat canopies to reduce the phenotyping bottleneck. Front. Plant Sci. 0, 287. https://doi.org/10.3389/FPLS.2022.828451.
Sarlikioti, V., De Visser, P.H.B., Marcelis, L.F.M., 2011. How plant architecture affects light absorption and photosynthesis in tomato: towards an ideotype for plant architecture using a functional–structural plant model. Ann. Bot. 108 (6), 1065–1073. https://doi.org/10.1093/aob/mcr221.
Schnepel, K., Hoffmann, C.M., 2016. Effect of extending the growing period on yield formation of sugar beet. J. Agron. Crop Sci. 202 (6), 530–541. https://doi.org/10.1111/jac.12153.
Scott, R.K.; Jaggard, K.W. (1978), Theoretical criteria for maximum yield, in Proceedings of the 41st Winter Congress of the International Institute for Sugar Beet Research, Brussels, pp. 179–198.
Sinclair, T.R., Muchow, R.C., 1999. Radiation use efficiency. Adv. Agron. 65, 215–265. https://doi.org/10.1016/S0065-2113(08)60914-1.
Slattery, R.A., Vanloocke, A., Bernacchi, C.J., Zhu, X.G., Ort, D.R., 2017. Photosynthesis, light use efficiency, and yield of reduced-chlorophyll soybean mutants in field conditions. Front. Plant Sci. 8, 549. https://doi.org/10.3389/FPLS.2017.00549/BIBTEX.
Song, Q., Zhang, G., Zhu, X.-G., 2013. Optimal crop canopy architecture to maximise canopy photosynthetic CO_2 uptake under elevated CO_2 – a theoretical study using a mechanistic model of canopy photosynthesis. Funct. Plant Biol. 40 (2), 108. https://doi.org/10.1071/FP12056.
Steven, M.D., Biscoe, P.V., Jaggard, K.W., Paruntu, J., 1986. Foliage cover and radiation interception. Field Crops Res. 13 (C), 75–87. https://doi.org/10.1016/0378-4290(86)90012-2.
Werker, A.R., Jaggard, K.W., 1998. Dependence of sugar beet yield on light interception and evapotranspiration. Agric. For. Meteorol. 89 (3–4), 229–240. https://doi.org/10.1016/S0168-1923(97)00081-6.
de Wit, C.T. (1965). Photosynthesis of leaf canopies. Agricultural research reports, No. 663. Wageningen. Pudoc. ⟨https://edepot.wur.nl/187115⟩.
Wright, A.J.D., Bussell, J.S., Stevens, M., Back, M.A., Sparkes, D.L., 2018. Physiological differences between sugar beet varieties susceptible, tolerant or resistant to the beet cyst nematode, Heterodera schachtii (Schmidt) under uninfested conditions. Eur. J. Agron. 98, 37–45. https://doi.org/10.1016/J.EJA.2018.05.005.