



Competition for light drives yield components in strip intercropping in the Netherlands

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ABSTRACT

Context: The partitioning of light between species in intercrops changes over time in relation to the earliness of canopy development of each species, the final plant height, and the growth duration. Seasonal patterns of light capture in crop species mixtures may be reflected in the yield components of the species.

Objective: We test the hypothesis that seasonal patterns of light capture in intercrops can explain intercropping effects on seed number, seed weight, and seed yield in different species mixture compositions, including relay and simultaneous intercrops.

Methods: We determined the seed number per unit land area, thousand-seed weight, and seed yield of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.), grown as four monocrops or as six bi-specific strip intercrops – maize/wheat, maize/faba bean, maize/pea, faba bean/wheat, faba bean/pea, and wheat/pea – in the Netherlands. Species were spring-sown and managed conventionally (i.e., non-organic). Maize was sown and harvested later than the three other species, which had approximately simultaneous growing periods. Light capture by each species before and during seed filling was estimated using a model based on strip width, plant height, and leaf area index. We then assessed the relationships between accumulated light captured per species, seed yield, and its components.

Results: Seed yields in intercrops and monocrops were strongly related to seed number for each species. In relay intercrops, both species had increased seed yield due to an increased number of seeds. Species grown in simultaneous intercrops did not have higher seed yield or seed number than the monocrop, except for faba bean intercropped with wheat or pea. Increased seed number of early-sown species in relay intercrops was related to greater light capture before seed filling compared to monocrops. Increased seed number in maize was associated with better light availability after maize overtopped the companion species. The early-sown species showed trade-offs between seed number and weight, whereas the improved light availability resulting from the early harvesting of companions allowed intercropped maize to fill all seeds to the same extent as monocropped maize did.

Conclusions: Seed yield was more strongly related to seed number than seed weight in all species in both monocrops and intercrops. In relay intercrops, seed yield increases were realised by species filling seeds to take advantage of the larger seed number.

Implications: The findings show the importance of achieving high seed number and effective seed filling for increasing seed yield in conventionally managed strip intercrops under Dutch growing conditions.

1. Introduction

Intercropping is the planned cultivation of multiple crop species on a single field for at least part of their growing cycles (Willey, 1990). For a wide range of conditions, intercrops use resources such as land, light,

water, and nutrients more efficiently than monocrops do. This holds for high-input agriculture, which aims to maximise yields (Yang et al., 2023); low-input/organic agriculture, which aims to maximise ecosystem services while minimising anthropogenic inputs (Bedoussac et al., 2015); and intermediate-input agriculture, which aims to balance

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production and environmental performance by tailoring inputs to species needs (Wang et al., 2023). Because of the potential for achieving high yields with reduced anthropogenic inputs, intercropping is viewed as an option for ecological intensification in both organic and conventional farming (Bedoussac et al., 2015; Gong et al., 2022; Li et al., 2020a, 2023; Martin-Guay et al., 2018; Stomph et al., 2020; Yu et al., 2015).

Intercropping modifies the competition for resources within the crop stand (Justes et al., 2021), leading to a yield increase or decrease as compared to monocropping (Feng et al., 2021; Gou et al., 2016; Wang et al., 2023). Yield components provide insight in impediments to yield (Grafius, 1978), and they are widely used in intercropping research to describe and interpret species responses to cultivation in mixtures (Ahmed et al., 2020; Ajal et al., 2022; Gou et al., 2016; Li et al., 2020b; Wang et al., 2020; Zhu et al., 2016). Changes in yield components are viewed as a manifestation of plastic plant responses to differences in the growth environment (Bloom et al., 1985; Sadras and Slafer, 2012) between the intercrop and monocrop. Complementary or competitive resource capture at a given growth stage is anticipated to change the yield components of the component species that are shaped at that growth phase (Gou et al., 2016; Hu et al., 2020; Monti et al., 2016; Qian et al., 2018; Wang et al., 2021a; Zhu et al., 2016).

Yield components such as seed number and seed weight are determined often in a chronological order under the influence of growing conditions and competition for resources, and each yield component has a critical phase during which it is most strongly affected by resource availability (Evans, 1975; Lake et al., 2019). Studying yield components can thus provide insight into the temporal dynamics of complementarity and competition experienced by component species in intercrops. The allocation of assimilates may also impact determination of the subsequent yield components (Patrick and Colyvas, 2014). Any intercropping effects on yield components could be indicative of the level and timing of complementary or competitive interactions between the component species. Natural differences in the timing of resource capture occur in relay intercrops in which the component species overlap only for a portion of their growth durations (Li et al., 2020a; Yu et al., 2015) due to asynchronous sowing and harvesting, i.e., temporal niche differentiation (TND; Yu et al., 2015). In simultaneous intercropping, although species are sown at the same time and mature at nearly the same time, yield components are still useful indicators of temporal variation in competition and resource capture by species.

Crop species differ in traits that affect resource capture and thus yield components, such as growth cycle (e.g., sown and harvested early vs. sown and harvested late) (Yu et al., 2015), developmental pattern (e.g., determinate vs. indeterminate) (Ye et al., 2023), shoot and root architecture (e.g., tall vs. short; deep rooting vs. shallow rooting) (Homulle et al., 2021; MacLaren et al., 2023), and physiology (e.g., C3 vs. C4; nitrogen-fixing vs. non-nitrogen-fixing) (Dong et al., 2024; Rodriguez et al., 2020). These differences suggest that various species may interact uniquely in terms of resource capture. Thus, studying yield component determination in diverse species combinations helps assess their suitability for specific production situations. Yield components offer insight into how species interactions (e.g., shading, nitrogen complementarity) during different growth phases contribute to final yield, helping with the identification of advantageous species combinations and configurations for intercropping.

Conventional farming aims to lift constraints on crop growth by nutrients, leaving only water and light as key limiting resources (Gallagher and Biscoe, 1978). Light is a crucial resource in conventionally managed intercrops (Gou et al., 2017; Li et al., 2021; Mao et al., 2014; van Oort et al., 2020; Wang et al., 2021b; Zhang et al., 2008a; Zhu et al., 2015).

While the relationship between seed yield (or biomass) and light capture in intercrops has been explored (Gou et al., 2017, 2016; Raza et al., 2019; Umesh et al., 2023; van Oort et al., 2020), the effects of light capture dynamics during different growth phases on yield components have not been analysed in previous studies. Here we aim to provide

insight into how light capture over time affects the two most important yield components – seed number per unit land area and individual seed weight – across intercrops. This can help identify the main limiting yield component and its associated critical growth phase, offering guidance on optimising species combinations and configuration to improve light capture for the limiting yield component. Ultimately, this approach can help increase yields in intercropping systems.

We conducted a two-year field experiment to investigate seed number per unit land area, seed weight, and seed yield of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.) in six bi-specific strip intercrops, and in the four corresponding monocrops. The intercrops included relay intercrops with maize (i.e., maize/wheat, maize/faba bean, and maize/pea) due to its later sowing and harvesting. In contrast, combinations without maize (i.e., faba bean/wheat, faba bean/pea, and wheat/pea) were nearly simultaneous, as wheat, faba bean, and pea were sown on the same date while differences in maturity were less than three weeks.

Because of the temporal complementarity in relay intercrops and related dynamics in plant stature (Gou et al., 2016; Yu et al., 2015), we expected that the early-sown and shorter species would capture more light during early growth, whereas the late-sown and taller maize would capture more light during later growth. Consequently, we expected that the early-sown species would show an intercropping advantage in seed number but a disadvantage in seed weight, due to shading by maize during seed filling, whereas the late-sown but taller species (i.e., maize) would show an intercropping disadvantage in seed number due to shading during seed formation but a compensatory advantage in seed weight due to improved light capture after maize overtops companion species. In simultaneous intercrops, the effects of light capture on yield components are related to the height dynamics of the species but not to a difference in sowing date (Li et al., 2021). Here, we expected that taller species would benefit from intercropping due to greater light capture, both with respect to seed number and seed weight, whereas shorter species were expected to have both components reduced due to shading by the companion species (Fig. 1). We also expected that a greater seed number of early-sown species in relay intercrops would result in intensified within-plant competition for assimilates (Patrick and Colyvas, 2014), aggravating the seed-weight-reducing effect of light competition from maize during the seed filling of the early-sown species.

2. Materials and methods

2.1. Experimental design

A two-year field experiment was conducted at Droeendaal Experimental Farm of Wageningen University & Research, Wageningen, the Netherlands (51° 59' 20" N, 5° 39' 16" E) in 2018 and 2019. The growing seasons ran from March 21 to September 10 in 2018 and from April 1 to September 18 in 2019. The two seasons had average air temperatures of 16 and 15 °C, accumulated photosynthetically active radiation (PAR) of 1537 and 1514 MJ m⁻², and accumulated precipitation of 300 and 252 mm. The minimum and maximum temperatures for the two seasons were -3 °C and 35 °C in 2018, and -4 °C and 38 °C in 2019. The farm has sandy soil with a pH of 5.7, an organic matter content of 3.4 %, and a C/N ratio of 11 in the top 30 cm. Different but adjacent fields were used for the two seasons; see Wang et al. (2023) for further details.

Six strip intercrops – maize/wheat, maize/faba bean, maize/pea, faba bean/wheat, faba bean/pea, and wheat/pea – were cultivated using four crop species: maize (*Zea mays* L., cv. 'LG30.223'), wheat (*Triticum aestivum* L., cv. 'Nobless'), faba bean (*Vicia faba* L., var. 'Fanfare'), and pea (*Pisum sativum* L., var. 'Astronaute'). A monocrop of each species was also cultivated. The intercrops involving maize were relay intercrops, whereas those not involving maize were simultaneous intercrops. In relay intercrops, wheat, faba bean, and pea were the early-sown species, whereas maize was the late-sown species. In simultaneous

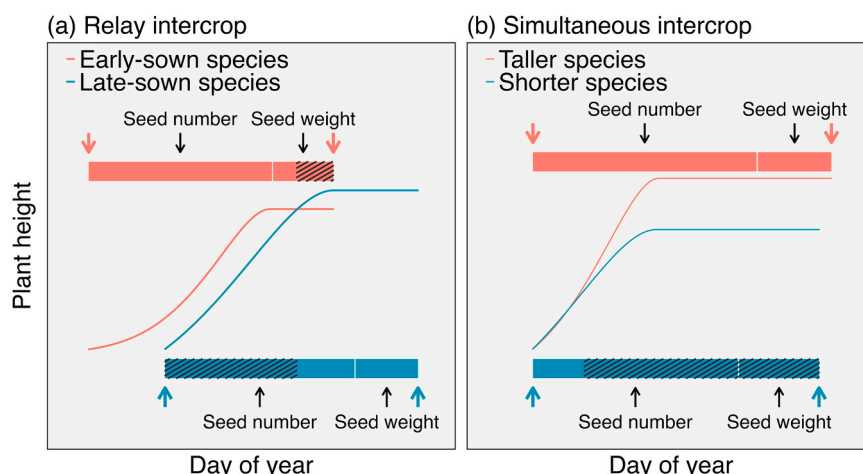


Fig. 1. Illustration of plant height (sigmoid curves) and growth phases (horizontal bars) during which yield components seed number per unit land area and seed weight are determined in relay (a) and simultaneous intercroppings (b). The coloured bars represent the phases in which seed number per unit land area and seed weight are determined. The coloured arrows indicate the sowing and harvesting of the component species. Hatching of the bar indicates that a species is shaded by a taller companion species. Black arrows connect the labels 'Seed number' and 'Seed weight' to the corresponding parts of the coloured bars, which are separated by a fine white stripe.

intercrops, faba bean was taller than both wheat and pea. Wheat and pea were of similar height. Wheat, faba bean, and pea were sown on March 21 in 2018, and April 1 in 2019. The late sowing in 2019 was due to heavy rainfall in mid-March. Maize was sown on May 4 in 2018 and May 7 in 2019 (Fig. 2). All cultivars were cultivated for harvesting seeds for human or animal consumption.

An intercrop strip comprised two narrow species strips, each 1.5 m wide. The maize strip had three plant rows at a 50 cm row distance. The strips of the other three species each had six plant rows at a 25 cm row distance among inner rows and a 20 cm row distance at the strip border to allow space for the tractor wheels during sowing (Fig. 3). The row configuration for a species was identical in its monocrop and intercrops in species strips. The sowing density per unit area of the species strip was also the same in both the intercrops and the monocrop, i.e., the species had a density per unit area of the whole intercrop equal to half of that in

its monocrop so that their relative density was 0.5 (van der Werf et al., 2021). Randomised complete block designs were used, with six blocks in 2018 and four blocks in 2019. The row direction was approximately north-south; see Wang et al. (2023) for further details.

Fertiliser was applied according to species-specific recommendations for conventional agriculture in the Netherlands (Ministerie van Landbouw Natuur en Voedselkwaliteit, 2019). Before the first sowing, potassium (K) and phosphorus (P) fertiliser were spread uniformly over the entire field, at 87 kg K ha⁻¹ in both seasons and 29 and 34 kg P ha⁻¹ in 2018 and 2019, according to pre-sowing soil nutrient analyses. Nitrogen (N) fertiliser application to species grown in intercrops was equal in timing and amount to that in monocrops, with an equal amount per unit species area in the intercrop as per unit field area in the monocrop. Consequently, N fertiliser application in intercrops at a whole field level was the average of that of the monocrops of the component species. The

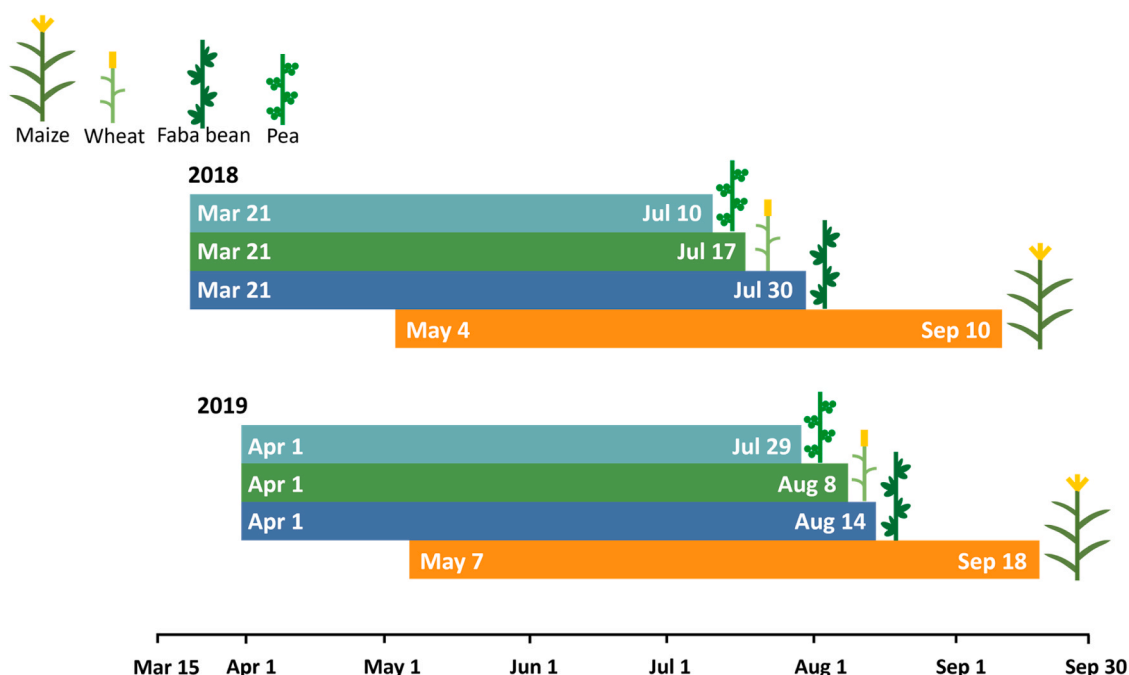


Fig. 2. Dates of sowing and harvesting for maize, wheat, faba bean, and pea in 2018 and 2019. Illustration adapted from Wang et al. (2023).

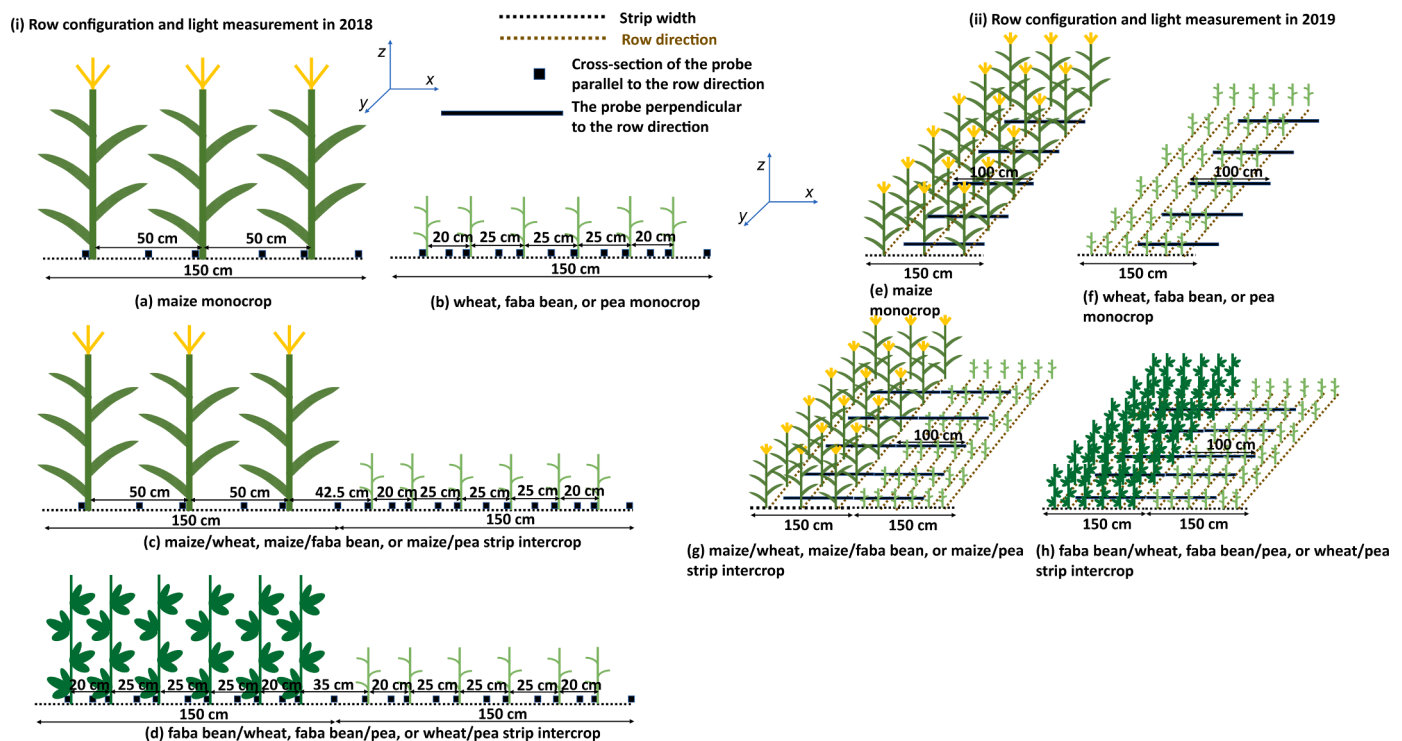


Fig. 3. Row configurations and light measurement locations in 2018 and 2019. (a, e) maize monocrop strip; (b, f) monocrop strip of wheat, faba bean, or pea; (c, g) intercrop strip comprising one maize strip and one species strip of wheat, faba bean, or pea; (d, h) intercrop strip comprising two species strips of a bi-specific combination of wheat, faba bean, and pea. Each species strip in intercrops was 150 cm wide. Incident and transmitted photosynthetically active radiation (PAR) were measured in intercrops and monocrops using an SS1 SunScan Canopy Analysis System (Delta-T Devices Ltd, UK). In 2018 (a–d), the one-metre-long probe was placed parallel to the rows; in 2019 (e–h), the probe was placed perpendicular to the rows (Supplementary Method S1). The black squares in panels a–d (2018) represent the cross-sections of the one-metre-long probe; the black bars in panels e–h (2019) represent a probe in sideview. Illustration adapted from Wang et al. (2023).

N rate was 20 kg N ha⁻¹ for faba bean and pea (applied three and two weeks after sowing in 2018 and 2019 respectively), 125 kg N ha⁻¹ for wheat (80 kg at three and two weeks after sowing in 2018 and 2019 respectively, and 45 kg at stem elongation), and 170 kg N⁻¹ for maize (80 kg at sowing and 90 kg at stem elongation). Weeds and pests were controlled following the local recommendations. The whole field was regularly and uniformly irrigated by an overhead sprinkler beam from June to August in both years to mitigate drought; see Wang et al. (2023) for details.

2.2. Measurements in the field

2.2.1. Phenology monitoring

The BBCH scale for crop development, developed by BASF, Bayer, Ciba-Geigy, and Hoechst, was used to record the start of seed filling in each species (Lancashire et al., 1991). The start of seed filling is at silking (BBCH scale 65) in maize and at full flowering (BBCH scale 65) in wheat (Evans, 1975). Faba bean and pea are indeterminate species, meaning that formation of new phytomers and pods continues while the pods at lower-ranked phytomers have already started filling (Patrick and Stoddard, 2010). The BBCH scale 75, indicating that 50 % of the emerged pods have reached their final sizes and are ready to be filled, was used as the start of seed filling in faba bean and pea. The moments of emergence (BBCH scale 09) and harvest maturity (BBCH scale 89) were recorded for all species.

2.2.2. Plant height

Plant height was measured to assess when a component species was shaded by its companion in an intercrop, indicating whether the light environment was more or less favourable for a species in an intercrop compared to the monocrop. Plant height was measured using a

measuring stick. It was defined as the distance from the soil to the base of the last fully developed leaf, specific to each species. For wheat and maize, height was measured to the base of the last fully developed leaf blade. In wheat, a leaf was considered fully developed if the blade had fully expanded; in maize, once the leaf collar was visible. For faba bean, plant height was measured to the base of the last fully expanded compound leaf. In pea, height was measured to the base of the last fully expanded stipule, as it lacks true leaves. In intercrops, we determined plant height on one to five plants from each row type in each plot. In maize there are two row types: border rows and inner rows. In the other species, there are three row types: border rows (rows 1 and 6), first inner rows (rows 2 and 5), and second inner rows (rows 3 and 4) (Supplementary Method S3). In monocrops, we measured plant height on at least two randomly selected plants from each plot. Measurements were made from the day on which a species had three fully developed leaves to the day when the maximum plant height was reached.

2.2.3. Seed yield, seed number, and seed weight

We harvested 4 m row length (3 m in pea in 2018) of one intercrop strip (3 m wide) in the centre of each intercrop plot and of one 1.5 m-wide strip in the centre of each monocrop plot at maturity. After harvesting, wheat, faba bean, and pea samples were dried against a drying wall (ACT-20, Omnivent Co., Netherlands) with artificial ventilation at 25 °C to an approximate moisture content of 15 %. The samples were then threshed. Maize cobs were removed from the plants immediately after harvesting and dried at 105 °C for 48 h. Cobs were shelled.

A subsample of seeds was randomly taken from each sample and weighed. The seed number of the subsample was counted using an electronic seed counter (CONTADOR, Pfeuffer Co., Germany). Seed number per unit area of the species strip (SN) was calculated. The subsample was then dried at 105 °C for 48 h to quantify the moisture

content and convert the fresh weight to dry weight. Seed yield per unit area of the species strip and thousand-seed weight (TSW) were calculated for each species on an oven dry weight basis.

We focus in this paper on seed number per unit land area (SN) and thousand-seed weight (TSW). However, we also collected data to determine other yield components such as plant number per unit land area, cob number per plant, and seed number per cob for maize; ear number per unit land area and seed number per ear for wheat; shoot number per unit land area, pod number per shoot, and seed number per pod for faba bean and pea (Supplementary Fig. S5).

2.3. Accumulated light capture

Accumulated light capture during a growth phase was calculated as the sum of daily light capture during that phase. Daily light capture was calculated as the product of the daily light capture fraction and the incident PAR. The daily incident PAR was taken as 50 % of the global radiation recorded by the Wageningen University weather station 'De Veenkampen', located 4 km west of the experimental location.

2.3.1. Light capture fraction in monocrops (f_{mono})

Daily values for the proportion of light capture in monocrops, f_{mono} , were calculated using Lambert-Beer's Law for a homogeneous canopy (Monsi et al., 2005):

$$f_{\text{mono}} = 1 - e^{-k \times \text{LAI}} \quad (1)$$

where LAI is the daily leaf area index linearly interpolated by the measured LAI (Supplementary Method S4) using the 'approx' function in R (R Core Team, 2023). k is the light extinction coefficient estimated by fitting Lambert-Beer's Law using the measured light capture fraction and LAI for each monocrop in the experiment. The estimated values of k were 0.638 for maize, 0.636 for wheat, 0.686 for faba bean, and 0.704 for pea (Supplementary Fig. S1).

2.3.2. Light capture fraction in intercrops (f_{inter})

The proportion of light capture by a species in intercrops, f_{inter} , was calculated using a geometry-based model (Gou et al., 2017). This model was initially developed for maize/wheat relay strip intercropping, based on a light capture model for wheat/cotton strip intercropping (Zhang et al., 2008a). It has been shown to perform well (Gou et al., 2017) and has been used in various intercrops with different configurations (van Oort et al., 2020; Wang et al., 2021b; Zhang et al., 2018). We did not make adaptations to this model and refer the readers to Supplementary Method S2 and to Gou et al. (2017) for details. The model inputs are daily LAI, daily plant height, constant species-specific values of light extinction coefficient (k), and the designed strip and path widths of 1.5 m for each species.

Daily LAI (green leaves, on the system level) and plant height of each species were linearly interpolated using the measured data (Supplementary Fig. S2). k is taken to be the same for a species in the intercrops and monocrop (Supplementary Fig. S1).

The light model was validated by comparing the estimated and measured light capture fractions (f_{cap}) on selected days; see Supplementary Method S1 for more details on the light measurements. Root Mean Square Error (RMSE) was calculated to assess the agreement between model estimates and field measurements for a complete strip:

$$\text{RMSE} = \sqrt{\frac{1}{N} \times \sum_i^N (f_{\text{cap}_{Ei}} - f_{\text{cap}_{Mi}})^2} \quad (2)$$

where $f_{\text{cap}_{Ei}}$ and $f_{\text{cap}_{Mi}}$ are the light capture fractions estimated by the model and measured in the field, respectively. N is the number of measurements, which ranged from 9 to 13 depending on treatments.

2.4. Data analyses

2.4.1. Treatment effects on plant height, seed yield, yield components, and accumulated light capture per species

Statistical analyses were performed using R (R Core Team, 2023). To assess the effects of treatments on plant height, seed yield, yield components, and accumulated light capture for each species, linear mixed-effect models were applied for each year. The 'lmer' function from the 'lme4' package was used for fitting these models (Bates et al., 2015). Treatment (one monocrop plus three intercrops for each species) was included as a fixed effect. Block was included as a random effect to account for inter-block variance in each year. The 'anova' function was used to evaluate the treatment effects. Fisher's LSD test was used for multiple comparisons of means. Student's t-test was used to compare the means between an individual intercrop and the monocrop for each species.

2.4.2. Relationships between seed yield and yield components per species

In each year, a linear mixed-effect model was fitted between SN (or TSW) as an explanatory variable and seed yield as a response variable for each species to explore to what extent the differences in seed yield across different species combinations in different blocks were correlated with SN or TSW. Models were fitted to measurement data in individual replicates in each year. Each species had 24 data points in 2018 [(one monocrop + three intercrops) $\times$ six blocks] and 16 data points in 2019 [(one monocrop + three intercrops) $\times$ four blocks]. Block was specified as a random intercept to account for inter-block variability within year, ensuring robust estimation of the relationship between seed yield and yield components (Eq. 3).

$$y_{ij} = \beta_0 + \beta_1 \cdot x_{ij} + b_j + \epsilon_{ij} \quad (3)$$

where i and j are treatment ID and block ID; x_{ij} is the value of explanatory variable of treatment i in block j ; y_{ij} is the value of response variable of treatment i in block j ; b_j is a random intercept accounting for inter-block variability; ϵ_{ij} is a random residual on the plot level. The 'lmer' function from the 'lme4' package was used for fitting the model (Bates et al., 2015). The function 'r2_nakagawa' (Nakagawa and Schielzeth, 2013) in the package 'performance' (Lüdtke et al., 2021) was used to obtain the marginal coefficient of determination (R^2), i.e., the R^2 only accounting for the fixed effect.

2.4.3. Relationships between seed yield, yield components, and the corresponding accumulated light captured per species

To explore to what extent the seed yield, SN, and TSW were correlated with light capture, linear mixed models were fitted to plot-level measurements of seed yield $\sim$ total accumulated PAR over the season, and SN $\sim$ accumulated PAR before seed filling. For TSW, a multiple-linear mixed model with accumulated PAR during seed filling and SN as two explanatory variables was fitted to explore the effect of light capture conditional on the SN that had been determined during earlier growth. All models were fitted to plot-level measurements in each year, with block specified as a random intercept (Eq. 3).

3. Results

3.1. Plant height

From the beginning, faba bean was taller than wheat and pea, with a height difference of about 45 cm at maturity of the species (Fig. 4 a–f). Pea was 10 cm taller than wheat at maturity. In relay intercrops, the three early-sown species were initially taller than maize. However, from about the start of July, maize overtopped the companion species. Maize was taller than the companion species for about 50 % of the total growing period of maize, including the whole seed filling period and a short proportion of the time before silking, except when growing with

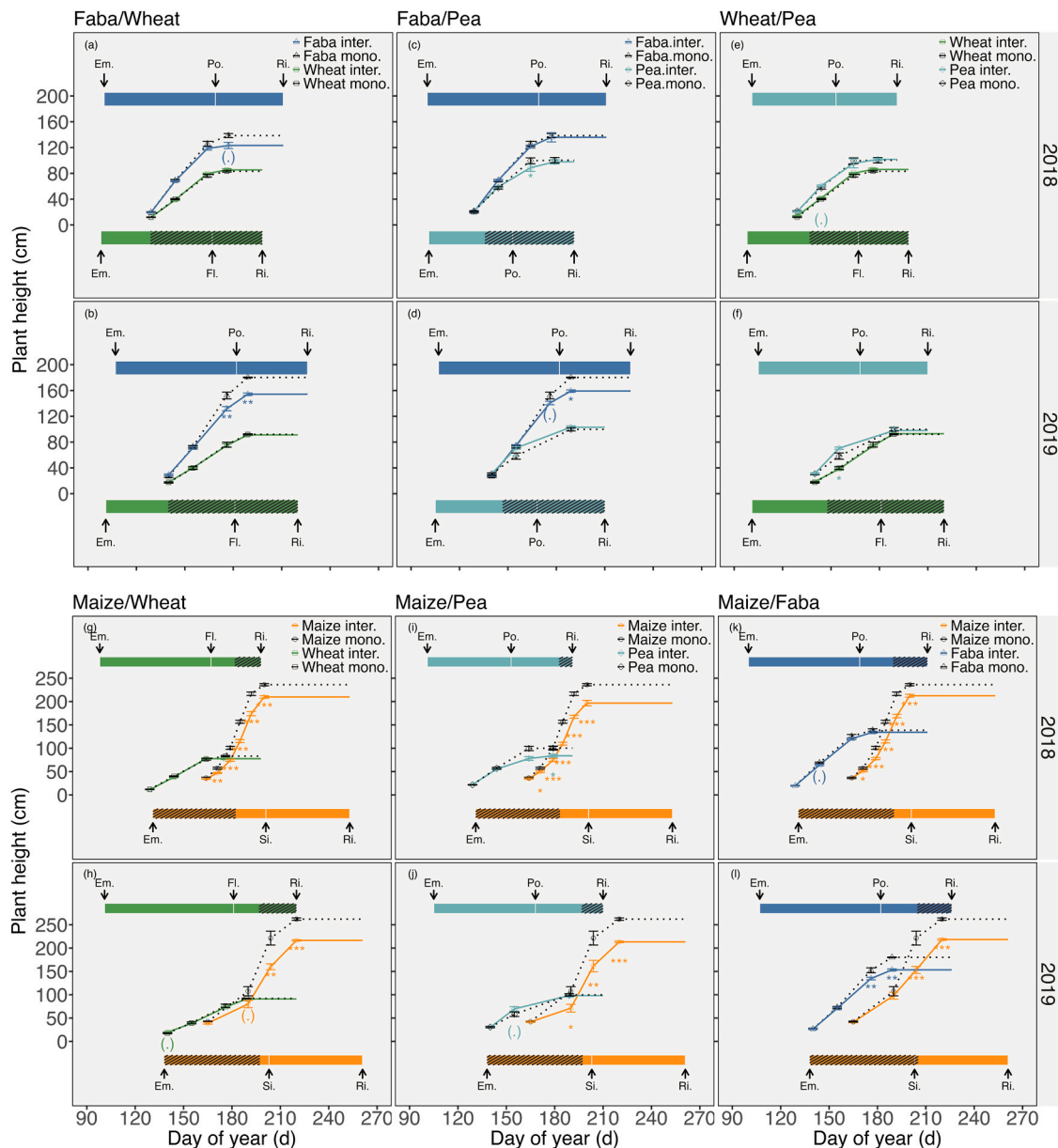


Fig. 4. Plant heights of maize (orange circles), wheat (green squares), faba bean (blue triangles), and pea (cyan diamonds) in simultaneous (a–f) and relay intercrops (g–l). Error bars represent the standard error of the mean. Coloured blocks represent the phases before and during seed filling. Each phase is defined by phenological events observed according to the BBCH scale (Lancashire et al., 1991): Em.: Emergence (09) (all species); FL.: Full flowering (65) (wheat); Si.: Silking (65) (maize); Po.: start of Pod filling (75) (faba bean and pea); Ri.: Ripe (89) (all species). The hatching on the blocks indicates that the focal species was shorter than the companion species. Asterisks denote a significant difference in height of a focal crop species when grown in an intercrop or monocrop at a specific date (Student t-test): $P \leq 0.001$: ***, $P \leq 0.01$: **, $P \leq 0.05$: *, $P \leq 0.1$: (.).

faba bean in 2019. At maturity, the height difference between maize and wheat or pea was more than 1 m, but the height difference was only 70 cm in the intercrop with faba bean (Fig. 4 g–l).

Intercropped maize achieved a lower maximum plant height than monocropped maize in both years, with a difference of approximately 30 cm in 2018 and 45 cm in 2019 (Fig. 4 g–l; $P < 0.001$). The early-sown species reached similar maximum heights in relay intercrops as in monocrops. In simultaneous intercrops, faba bean had a lower maximum height in intercrops with wheat or pea than in monocrops in 2019, with a decrease of about 20 cm (Fig. 4 a–d; with wheat: $P = 0.004$; with pea: $P = 0.013$), but a difference was not found in 2018. In the wheat/pea intercrop, the maximum heights of both species were similar in intercrops and monocrops (Fig. 4 e and f).

3.2. Relationships between seed yield and yield components and intercropping effects

There were strong relationships between SN and seed yield in all species, both in monocrops and intercrops in both years (Fig. 5). For the same SN, maize seed yield was approximately 300 g m^{-2} higher in 2018 than in 2019. The positive effects of SN on seed yield were similar between years for the other three species. Relationships between TSW and seed yield varied between species, with a distinct year-effect on the slope in maize (Fig. 5 b), a positive relationship in wheat and pea (Fig. 5 d and h) and a negative relationship in faba bean (Fig. 5 f).

In relay intercrops, maize intercropped with wheat ($P = 0.009$ in 2018; $P = 0.002$ in 2019) and pea ($P = 0.007$ in 2018; $P = 0.003$ in 2019) had higher seed yields than monocropped maize in both years,

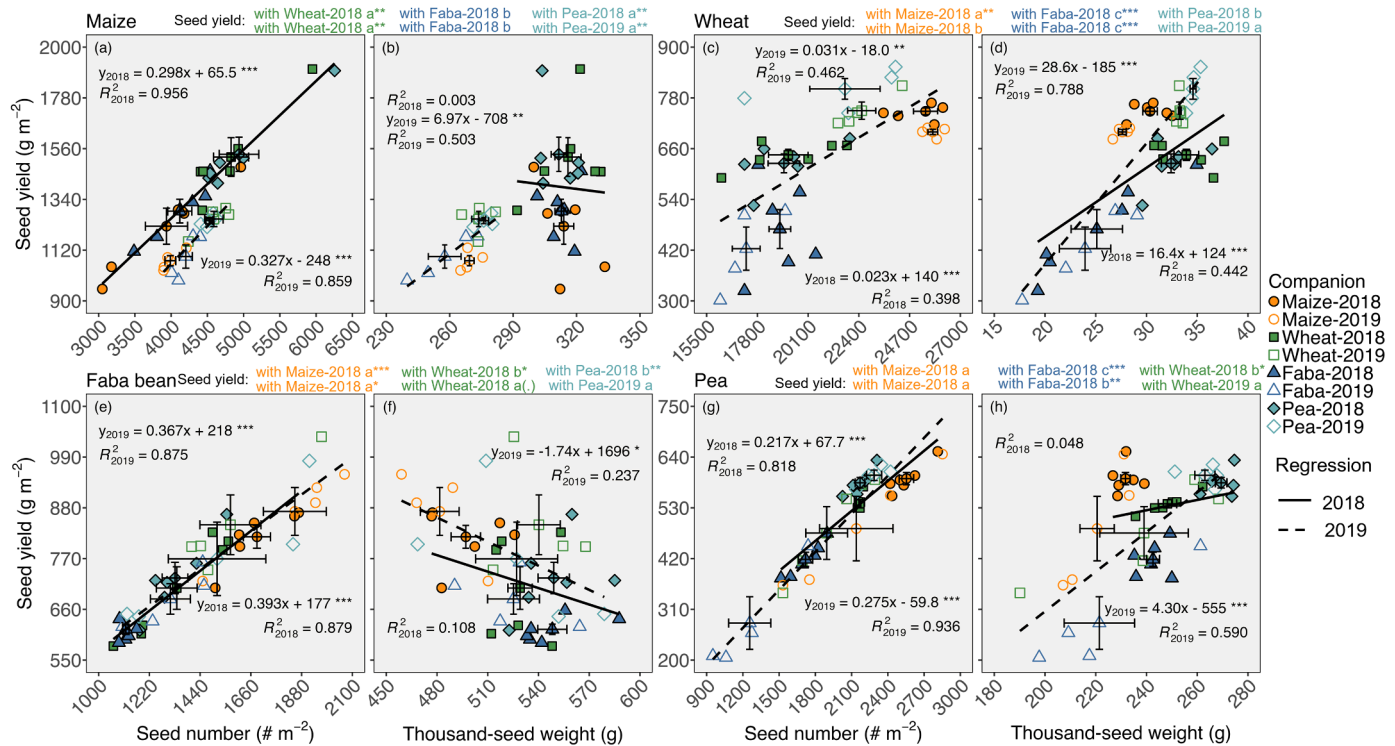


Fig. 5. Relationships between seed yield and seed number per unit land area (SN) and thousand-seed weight (TSW) of maize (a, b), wheat (c, d), faba bean (e, f), and pea (g, h). Different symbols indicate that the focal species was combined with different companion species: maize (orange circles), wheat (green squares), faba bean (blue triangles), and pea (cyan diamonds). Data collated in 2018 and 2019 are indicated by filled and open symbols, respectively. Error bars represent standard errors of the means. Symbols without error bars attached are the data collected from a specific block in a particular year. Equations are presented only when the slopes are significantly different from zero according to Student's t-test: $P \leq 0.001$: ***, $P \leq 0.01$: **, $P \leq 0.05$: *, $P \leq 0.1$: (. R^2 is the marginal R^2 , i.e., the R^2 for fixed effects only. For a focal species, seed yield is compared between its monocrop and intercrops. Asterisks denote significant differences between the intercrops and the monocrop for a focal species within an individual year (Student's t-test: $P \leq 0.001$: ***, $P \leq 0.01$: **, $P \leq 0.05$: *, $P \leq 0.1$: (. Shared letters denote non-significant differences among intercrops within an individual year (Fisher's LSD test; $P \leq 0.05$). More details about multiple comparisons of the means are presented in [Supplementary Fig. S4](#).

whereas maize intercropped with faba bean showed no yield increase. Intercropping did not affect maize TSW. Yield increases for maize with wheat ($P = 0.022$ in 2018; $P = 0.001$ in 2019) and pea ($P = 0.012$ in 2018; $P = 0.002$ in 2019) were due to increased SN. The increased SN in intercropped maize was due to increased cob number per plant ([Supplementary Fig. S5](#)). Faba bean intercropped with maize had increased yield in both years ($P < 0.001$ in 2018; $P = 0.039$ in 2019), whereas wheat intercropped with maize showed an increase only in 2018 ($P = 0.009$) and pea intercropped with maize had a similar yield as monocropped pea in both years. TSW of wheat ($P = 0.054$ in 2018; $P = 0.012$ in 2019), faba bean ($P < 0.001$ in 2018; $P = 0.098$ in 2019), and pea ($P < 0.001$ in 2018; $P = 0.032$ in 2019) was reduced in relay intercrops. In simultaneous intercrops, intercropped faba bean showed yield increases, but significant only in 2018 ($P = 0.030$ with wheat; $P = 0.009$ with pea). Intercropping with faba bean reduced the seed yield of wheat and pea by reducing both SN and TSW. In the wheat/pea intercrop, most wheat yield components were unaffected. Pea TSW was decreased in 2018 ($P < 0.001$).

3.3. Light capture

The estimation of seasonal light capture fraction per system f_{cap} , averaged across the whole strip, showed good agreement with field measurement in both monocrops and intercrops ([Supplementary Fig. S6](#)). In 2018, the RMSE of light capture fraction over the season ranged from 0.035 (wheat monocrop) to 0.136 (faba bean monocrop); in 2019, it ranged from 0.041 (maize/wheat intercrop) to 0.099 (maize monocrop).

Maize intercropped with wheat ($P = 0.046$ in 2018; $P = 0.024$ in

2019) or pea ($P = 0.016$ in 2018; $P = 0.012$ in 2019) captured more light over the whole season than monocropped maize, whereas maize intercropped with faba bean showed similar total light capture as monocropped maize ([Fig. 6](#)). Before seed filling, intercropped maize captured less light than monocropped maize, but during seed filling, maize captured significantly more light if it was intercropped with wheat ($P < 0.001$ in both years), faba bean ($P = 0.007$ in 2018; $P = 0.008$ in 2019), and pea ($P < 0.001$ in both years) than if it was grown as the monocrop. Early-sown species intercropped with maize captured significantly more light before seed filling than their monocrops, except intercropped wheat in 2019. During seed filling, early-sown species in most cases showed similar light capture to the corresponding monocrops. In intercrops with faba bean, intercropped wheat and pea captured less light over the season (wheat: $P < 0.001$ in 2018 and $P = 0.067$ in 2019; pea: $P < 0.001$ in both years) due to decreases both before (wheat: $P < 0.001$ in 2018 and $P = 0.024$ in 2019; pea: $P < 0.001$ in 2018; $P = 0.041$ in 2019) and during seed filling (wheat: $P < 0.001$ in 2018 and $P = 0.225$ in 2019; pea: $P < 0.001$ in both years), whereas intercropped faba bean captured more light than monocropped faba bean during seed filling (with wheat: $P < 0.001$ in 2018 and $P = 0.002$ in 2019; with pea: $P < 0.001$ in both years). In the wheat/pea intercrop, intercropped wheat captured less light before seed filling ($P = 0.079$ in 2018; $P = 0.075$ in 2019) but more light during seed filling ($P < 0.001$ in 2018; $P = 0.025$ in 2019). We found no significant effects from intercropping with wheat in pea.

3.4. Relationships between light capture and seed yield (and yield components)

There were large differences between species in the relationship

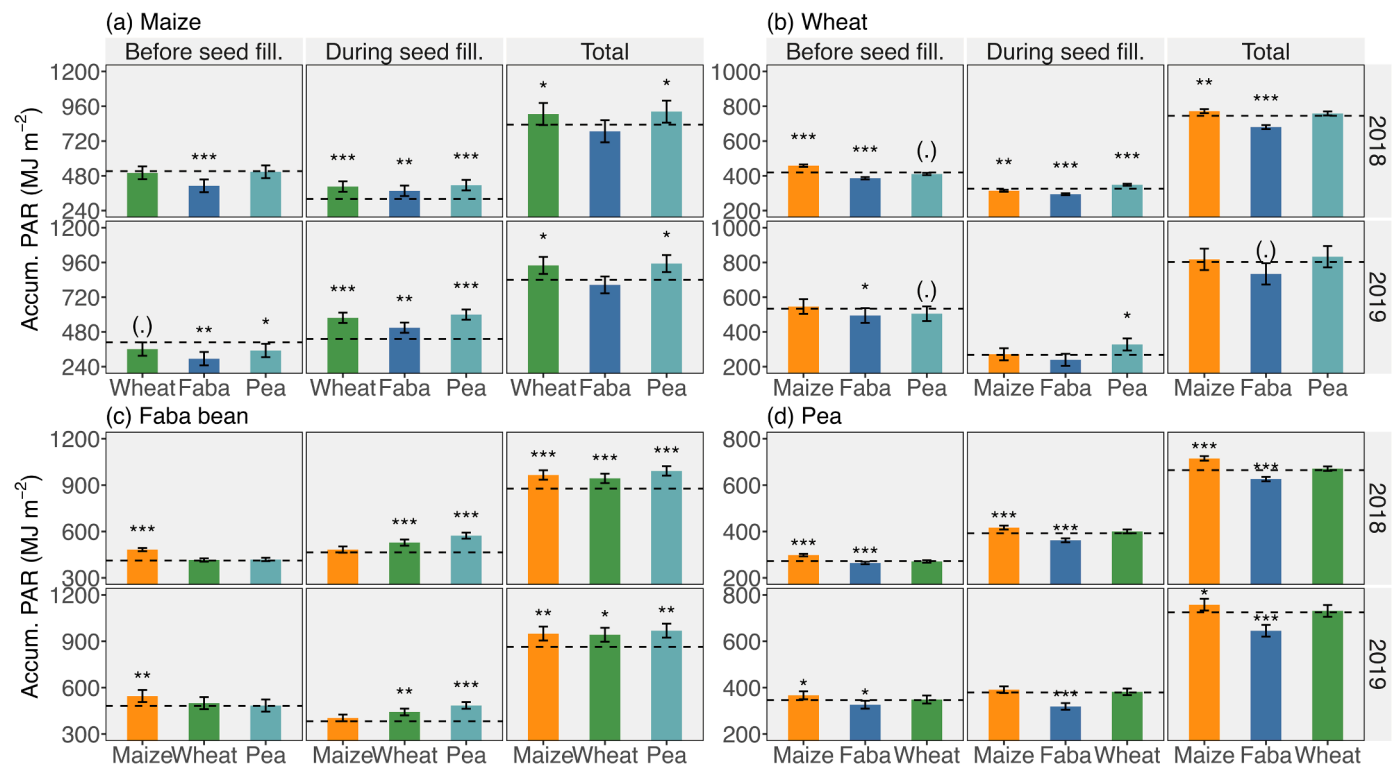


Fig. 6. Accumulated capture of photosynthetically active radiation (PAR) by maize (a), wheat (b), faba bean (c), and pea (d). For a focal species in each panel, different colours indicate that it was combined with different companion species: maize (orange), wheat (green), faba bean (blue), or pea (cyan). Accumulated PAR capture is expressed per unit area of the species strip in intercrops to make it directly comparable to PAR capture in monocrops. The dashed lines represent the accumulated PAR capture of the focal species in its monocrop. Error bars represent the 95 % confidence intervals of the means. Asterisks denote significant differences between the intercrops and the monocrop for a focal species (Student's t-test): $P \leq 0.001$: ***, $P \leq 0.01$: **, $P \leq 0.05$: *, $P \leq 0.1$: (.).

between seed yield or yield components and light capture, with overall much weaker relationships in maize (Fig. 7 a–c) than in the other three species (Fig. 7 d–l). In maize, there was no significant relationship between seed yield and light interception in 2018, whereas there was a significant positive relationship in 2019. In wheat, faba bean and pea, there were significant positive relationships between light capture and yield as well as SN. There was also a significant positive relationship between light capture and TSW in wheat and faba bean. There was, however, no significant relationship between light capture and TSW in pea.

In faba bean, apart from the positive effect of light capture during seed filling on TSW, SN that had been determined earlier had a negative effect on TSW. However, SN did not have a significant effect on TSW in the other three species (Supplementary Fig. S3).

4. Discussion

We expected that acquisition of light would be the main limitation for crop growth under the condition of this study due to the water and nutrient management that targeted non-limiting availability of these production factors. Therefore, we hypothesised that yield component determination of the component species would respond to the intercropping effects on light capture. The early-sown species would have an increased seed number per unit land area (SN) compared to their monocrops due to capturing more light before seed filling. In contrast, maize would have an increased thousand-seed weight (TSW) compared to its monocrop as it captured more light during seed filling in the intercrops.

4.1. Relay intercrops enable seed number increases in both early- and late-sown species

In contradiction to the hypothesis, the early-sown species and late-sown maize both showed increases in SN in intercropping, whereas none of the species showed increases in TSW (Fig. 5; Supplementary Fig. S4). In both cereals and legumes, SN was correlated with light availability before seed filling. Considering the relatively low R^2 for the random block effect (Supplementary Table S1), and the significant treatment effects on SN and light capture (Supplementary Fig. S4; Fig. 6), the significant SN ~ light capture relationships of the three early-sown species mostly resulted from the treatment differences in SN and light capture. Our results support the view that relay intercropping is beneficial for seed setting of early-sown species, as they receive extra light due to the absence or low competitiveness of the late-sown species (Gou et al., 2016; Li et al., 2020b; Qian et al., 2018; Zhu et al., 2016).

Reduced light capture before seed filling in intercropped maize (Fig. 6) is due to light competition from the early-sown species, as observed in several previous studies (Huang et al., 2017; Zhang et al., 2008b; Zhu et al., 2014). However, intercropped maize with wheat and pea showed increased SN despite this decrease in light capture before seed filling (Fig. 5; Supplementary Fig. S4). Our maize cultivar had cobs initiated at leaf 9 or 10. Maize outgrew wheat and pea around the ten-leaf stage (Fig. 4), with better light conditions supporting cob initiation and development. This may explain the higher cob number (approximately 1.1–1.2 cobs per plant; Supplementary Fig. S5) and the consequent increased SN in intercropped maize, because improved light conditions may aid cob development through light capture and CO₂ assimilation by cob leaves (Cagnola et al., 2021) and assimilate translocation from the upper leaves (Subedi and Ma, 2005). In monocropped maize, mutual shading may lead to abortion or absence of a second cob (Prine, 1971). In essence, although intercropped maize experienced

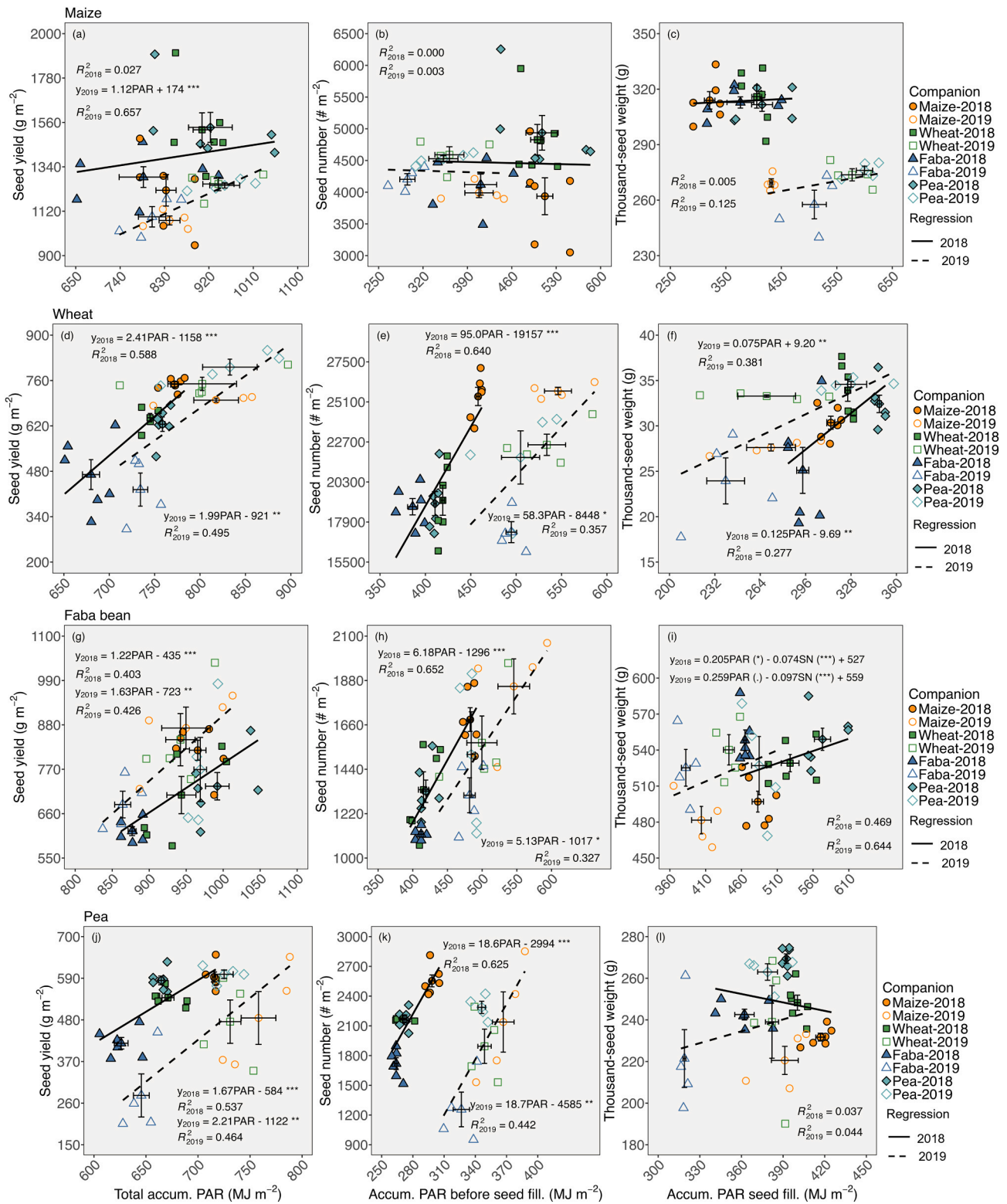


Fig. 7. Relationships of Seed yield ~ Total photosynthetically active radiation (PAR) captured (a, d, g, j), Seed number (SN) ~ PAR captured before seed filling (b, e, h, k), and Thousand-seed weight (TSW) ~ PAR captured during seed filling (c, f, i, l) of maize, wheat, faba bean, and pea. For a focal species, different symbols indicate that it was combined with different companion species: maize (orange circles), wheat (green squares), faba bean (blue triangles), and pea (cyan diamonds). Filled symbols are for 2018 and open symbols for 2019. Error bars represent standard error of the mean. Symbols without error bars attached are the data collected from a specific block in a particular year. Equations are presented only when the slopes are significantly different from zero according to Student's t-test: $P \leq 0.001$: ***, $P \leq 0.01$: **, $P \leq 0.05$: *, $P \leq 0.1$: (.). SN affected TSW in faba bean but not in the other species. The lines shown in panel i (faba bean) show the response of TSW to accumulated PAR during seed filling for the average SN observed in a year. The negative effects of SN on TSW are shown in Supplementary Fig. S3. R^2 is the marginal R^2 , i.e., the R^2 for fixed effects only.

early light competition, it still had increased SN by having better light conditions at the leaves that subtended a cob during cob initiation and development.

Maize intercropped with faba bean also had an increased cob number per plant, but the total SN was not increased because of the decreased seed number per cob (Supplementary Fig. S5). The lower LAI of maize intercropped with faba bean (Supplementary Fig. S2), compared to monocropped maize and maize intercropped with wheat and pea, could be an explanation for this because it can lead to a reduced photosynthate production that constrains seed setting. Furthermore, as faba bean was taller than wheat and pea, the light environment of cob leaves in maize/faba bean was less favourable than in maize/wheat and maize/pea.

Considering the modest values of marginal R^2 of the relationships (maximum around 0.65; Fig. 7), light should not be considered as the sole factor influencing SN in the present study. This is also reflected in our supplementary analysis of the relationship between light capture and land productivity at the system level. The land equivalent ratio for light capture had a uniformly positive effect on the land equivalent ratio for seed yield. However, there were still variances not explained by light, and each species combination had a unique added effect (Supplementary Fig. S9). These variances may be attributed to other resources such as nutrients and water. In this experiment, the fertiliser rates employed were significantly lower than those in high fertilisation regimes, which minimise nutrient stress but incur environmental costs (Li et al., 2020a; Wang et al., 2022). Additionally, the N rates were specific for monocrop growth, neglecting potential allo-specific interactions in intercropping. The early-sown species likely acquired N fertiliser from maize strips through lateral root extension, which may have negatively affected N capture by maize (Li et al., 2006).

Water may also have played a significant role in shaping the results of this study. Both seasons experienced hotter and drier conditions than usual for the location, resulting in substantial evapotranspiration (Supplementary Fig. S7). Although irrigation was given frequently during dry periods, drought and interspecific water competition may still have occurred, especially in May and June of both years. In the simultaneous intercrops, faba bean may have foraged mineral N from wheat as the nodulation can be inhibited by water stress (Egamberdieva et al., 2020). The same might apply to pea, but we expect less foraging of N in the neighbouring strip by pea than by faba bean, because faba bean had more vigorous above-ground biomass growth than pea, which likely corresponded with root growth below-ground, but was not measured in this study. Drought may also have contributed to the reduction in maize seed weight across all treatments in 2019 compared to 2018. In 2019, we reduced the irrigation frequency from mid-July to mid-August to facilitate harvesting of wheat, faba bean, and pea. This resulted in a 31 % reduction in water supply during the maize seed-filling stage compared to 2018 (Supplementary Fig. S7), which could result in reduced seed weight (Grant et al., 1989), considering the precipitation levels compared to 2018.

4.2. Seed weight is not only determined by light capture during seed filling but also by within-plant competition for assimilates

Intercropping effects on TSW were not well explained by light capture during seed filling, except in the case of faba bean (Fig. 7 i). This was either because no significant TSW ~ light capture relationships were detected (maize and pea; Fig. 7 c and l), or due to a large proportion of variance that was not explained by the relationship (wheat; Fig. 7 f). However, this does not imply that light capture during seed filling is not influential for seed weight determination. Seed weight is determined both by assimilation during seed filling and the translocation of assimilates stored in the stem during vegetative growth and the translocation of nitrogen from the leaves (Gao et al., 2022, 2020). The three early-sown species experienced only brief shading by maize before their harvest, and their light capture during seed filling was similar to their monocrops (Fig. 4; Fig. 6). It is more plausible that the

reduced TSW in wheat and faba bean is due to the increased number of reproductive shoots and thereby high SN in intercrops, which increased competition for assimilates between the seeds (Supplementary Fig. S5). In essence, intercropping increased the number of seeds but decreased light capture per seed.

Faba bean exhibited a significant trade-off between TSW and SN, indicating negative feedback between seed number and the available assimilates or translocated nutrients per seed (Supplementary Fig. S3). Seed filling of wheat and faba bean may have been limited by water and nutrients. This is because the senescence of the roots of the early-sown species after anthesis (Robinson et al., 1991; Xue et al., 2003) can significantly hinder their ability to compete for soil resources with the vigorous root system of maize. In the case of pea, negative feedback between seed number and available resources per seed was likely not the only reason for decreases in TSW, as SN was only increased in 2018. The decreased TSW when grown with maize could have been due to lodging in the pea canopy which was not accounted for in the estimated light capture.

The fact that maize TSW was not increased while more light was captured might similarly be attributed to increased competition among seeds for assimilates. The higher SN required more light to achieve comparable TSW compared to monocropped maize. The improved light condition during seed filling enabled all seeds to be filled to the same extent as in monocropped maize; thus, a yield increase was found in maize (Supplementary Fig. S4). Overyielding of late-sown species follows the recovery growth principle (Zhang and Li, 2003). We found that achieving recovery in seed yield relies on sufficient per-seed filling on top of setting more seeds during the early phase.

4.3. Intercropping yield effects are more strongly related to seed number than to seed weight

Differences in species seed yield between intercrops and monocrops were mainly due to differences in SN, as indicated by the higher marginal R^2 of relationships between yield and SN compared to the relationships of yield with TSW (Fig. 5). The only exceptions are wheat and pea intercropped with faba bean for which reductions in both SN and TSW contributed to negative intercropping effects on seed yield. Our findings agree with other intercropping studies in which seed number was the main yield component associated with intercropping effects (Gou et al., 2016; Hu et al., 2020; Monti et al., 2016; Zhang et al., 2022; Zhu et al., 2016). Generally, this could be explained by the principle that seed number is more plastic than seed weight in response to heterogeneous resource conditions because a stable seed weight has evolutionary advantages (Sadras and Denison, 2009). Specifically, in this study, the pre-seed filling phases were the stages when the species interacted the most in both relay intercrops and simultaneous intercrops. In the relay intercrops, early-sown species had increased light capture during early growth, whereas maize benefited during cob initiation. In simultaneous intercrops, species growth periods overlapped completely during pre-seed filling, and partially during seed filling due to different harvest dates (Fig. 4). Thus, our findings highlight that the pre-seed filling phases are critical in determining intercropping productivity, as this is when species interact most intensively, and seed number is established. Maximising capture of light and other resources during this phase is key to achieving the yield advantages of intercropping.

4.4. Practical implications

Results of this study show the importance of light capture for species productivity in strip intercrops under conventional management. It is essential for increasing yields in intercropping to provide the component species with favourable light conditions during their period of seed number determination and ensure efficient seed filling.

In relay intercrops, achieving a higher seed number for both

component species is possible if competition for light is reduced by temporal complementarity. In practice, there are various species differing in natural growth cycles. Early-sown species may have a higher chance to produce more seeds due to early access to light. However, in late-sown species, the shading by the early-sown companions is important. Early shading can slow down the development of a later-sown species (Zhang et al., 2008b; Zhu et al., 2014). An early companion with a tall and vigorous canopy will hinder seed setting of the late-sown species, as exemplified by the lack of seed number advantages of intercropped maize with faba bean (Fig. 5; Supplementary Fig. S4). Therefore, whether the late-sown species produces more seeds depends on the timing when it becomes taller than the companion species, which should align with its seed setting stage. Early overtopping is important to improve light conditions, ensuring sufficient seed filling and thereby capitalising on the higher seed number, to contribute fully to the overall increase in seed yield. However, if a late-sown tall species overtops the early-sown shorter species too early, it may hinder the early species in establishing seed number advantages and filling seeds sufficiently. Thus, the overtopping process in relay intercropping needs to be fine tuned to allow optimal seed filling of the early-sown species and seed setting of the later-sown species. This fine tuning may be achieved by matching variety traits and sowing dates, as well as intercrop configuration, with the local production situation.

Moreover, for tillering/branching species, tiller/branch number is important for final seed number (Altendorf et al., 2021), as observed in the three early species in relay intercrops (Supplementary Fig. S5). Since tillers/branches are initiated during the early growth phase and can be negatively affected by shading – either due to reduced red: far-red ratios ceasing bud outgrowth (Evers et al., 2006) or reduced light intensity triggering the abortion of tillers/branches (Dong et al., 2019) – species in which yield is sensitive to tiller/branch number may not be suitable as late-sown species in relay intercrops.

In conclusion, it is important to comprehensively consider growth patterns of species and combine them to achieve an ideal temporal complementarity, allowing both species to set as many seeds as possible and fill the seeds sufficiently. Furthermore, a sufficient supply of water and nutrients is important, as the acquisition of below- and above-ground resources can mutually promote each other through a positive root and shoot feedback (Evers et al., 2019). This allows intercropped species to efficiently capture all available resources, surpassing the complementarity effects on single limiting resources.

5. Conclusion

Our study revealed that seed number serves as the primary determinant of yield in both monocropped and intercropped species in conventional farming in the Netherlands. Relay intercropping with maize was more productive than simultaneous intercropping because it enabled both the early-sown species and late-sown maize to have increased seed number, primarily due to reduced interspecific competition during stages of seed number determination. The early-sown species showed trade-offs between seed number and weight. Early harvest of the companion species improved light conditions, allowing intercropped maize, with its increased seed number, to fill all seeds as effectively as monocropped maize. Light capture advantages are relevant in increasing seed numbers in relay intercropping, and the supply of nutrients and water should sufficiently support the growth processes enabled by light capture. For intercropping design, if soil resources are non-limiting, component species should exhibit significant temporal complementarity during early growth, ensuring increased resource capture for seed number determination. Sufficient access to light and soil resources is important for species to effectively fill seeds to take advantage of the larger seed number.

CRedit authorship contribution statement

Zishen Wang: Writing – original draft, Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bei Dong:** Methodology, Investigation, Data curation, Conceptualization. **Tjeerd-Jan Stomph:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jochem B. Evers:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Peter E.L. van der Putten:** Resources, Methodology, Investigation. **Wopke van der Werf:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization.

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

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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.2024.109647](https://doi.org/10.1016/j.fcr.2024.109647).

Data Availability

The data supporting the findings of this study are openly available at Data Archiving and Networked Services (DANS) at <https://doi.org/10.17026/PT/XK27U5>

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