Productivity and resource use efficiency in strip intercropping in the Netherlands

Zishen Wang

Propositions

1. Temporal complementarity is the main driver of yield advantage of intercropping under good growing conditions (this thesis).
2. Intercropping is capable of improving resource capture rather than resource conversion (this thesis).
3. Feedback from PhD supervisors is solely for enhancing the quality of the scientific argument.
4. Fertilisers and pesticides, used in moderation, are compatible with sustainable agriculture.
5. There is no way to resolve mutual disdain between academia and industry.
6. Artificial intelligence cannot ask good questions.

Propositions belonging to the thesis, entitled

Productivity and resource use efficiency in strip intercropping in the Netherlands

Zishen Wang
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To my ever-supportive parents

Abstract

Intercropping is the planned cultivation of multiple crop species in one field for at least a portion of their growing periods. Most intercropping in Western Europe is in the form of full mixtures or alternate row intercrops of cereals and legumes in low-input or organic agriculture, usually harvesting species as bulk. Little use is made of strip intercropping with synthetic inputs such as fertilisers and biocides, which are routinely used in conventional agriculture. Strip intercropping with conventional management is the prevalent intercropping system in China. In these systems, the products are usually harvested separately. Yield advantages in strip intercropping mainly arise from border row plants in intercrop strips outperforming inner row plants and monocropped plants. Limited knowledge exists on yield and resource use in strip intercropping under conventional management in Western Europe. This thesis explores relationships between yield and the acquisition of light and nitrogen (N) in strip intercropping of various species combinations under conventional management in the Netherlands.

A two-year field experiment was conducted with conventional management in Wageningen, the Netherlands. Four crop species, maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.), were combined as six bi-specific strip intercrops. Species were grown in 1.5 m-wide strips comprising several plant rows. N fertiliser was applied according to locally recommended doses tailored to species growth demands. In intercrops, the species strips were managed identically to the monocrops, for instance with the same N input per unit area within the species strip in the intercrop compared to the whole field of the corresponding monocrop. Grain yield, biomass, and N uptake were determined on a per-row and per-strip basis. Intercrop light capture at the per-strip level was estimated using an intercrop light capture model, while at the per-row level, it was estimated through a random ray tracing model, using measured plant height and leaf area index as inputs. Light use efficiency (LUE) was then calculated as the ratio of aboveground biomass to captured light.

Intercrops involving maize were relay intercrops due to the later sowing and harvesting of maize compared to the other species. These relay intercrops had in most cases a land equivalent ratio (LER) for grain yield and biomass higher than one, and a net effect (NE; the difference between total intercrop production and expected intercrop production) for grain yield and biomass

greater than zero. The simultaneous intercrops, involving wheat, faba bean, and pea, did not show such advantages.

In both monocrops and intercrops, grain yield showed a stronger correlation with total grain number per unit land area (GN) than with thousand-grain weight (TGW). In relay intercrops, improved early-season light availability favoured early-sown species, increasing their GN, while TGW decreased, likely due to a grain number-grain weight trade-off. Maize had increased GN when combined with short-statured wheat and pea, with more cobs formed, possibly due to improved light availability after maize overtopped these companion species. Maize did not have increased GN with tall-statured faba bean. No grain number-grain weight trade-offs occurred in intercropped maize with wheat or pea, despite increased GN, likely because all grains were sufficiently filled under improved light conditions after harvest of wheat and pea. Simultaneous intercrops involving faba bean resulted in reduced GN and TGW in wheat and pea, putatively due to shading by faba bean.

In relay intercrops, all early-sown species had higher biomass in the border rows compared to the monocrops. This increased biomass resulted from enhanced light capture, but not increased LUE. Faba bean, but not the other early-sown species, had increased biomass in inner rows with maize, due to an increased LUE with unchanged light capture compared to monocropped faba bean. Both border and inner rows of intercropped maize had higher LUE in all relay intercrops, but this resulted in increased biomass only when maize also captured more light, i.e., in the intercrops with wheat and pea but not with faba bean. In simultaneous intercrops, the tall faba bean significantly reduced both light capture and LUE of wheat and pea in all rows. Faba bean captured more light in the border rows, while its LUE remained unchanged. Compared to relay intercrops, light utilisation in simultaneous intercrops was not efficient because faba bean, with increased light capture and unchanged LUE, did not compensate for the reductions in biomass production resulting from reduced light capture and light conversion in both border and inner rows of wheat and pea. In the wheat/pea intercrop, row effects on light capture and conversion were minor due to the similar stature of the two species.

The species-tailored N strategy used in the experiment ensured that cereals did not experience significant N stress on growth, while enabling (and requiring) legumes to exploit N fixation. Relay intercrops captured more N than simultaneous intercrops did. In relay intercrops, early-

sown species had increased N uptake, particularly in border rows. Maize had increased N uptake in intercrops with wheat and pea, but not with faba bean. In simultaneous intercrops, faba bean significantly reduced N uptake of wheat and pea. On average, relay intercrops saved 14% on fertiliser N compared to monocrops for the same yield, whereas simultaneous intercrops did not demonstrate such advantages in saving fertiliser N.

This thesis shows that relay strip intercropping of species with temporal complementarity enhances production and resource capture under conventional management in the Netherlands. The significance of temporal complementarity applies to various species combinations, including cereal/legume and cereal/cereal combinations. The findings are not only helpful for advancing the potential implementation of strip intercropping in conventional agriculture under Western-European conditions, but they also contribute to an improved general insight in how plant-plant interactions affect resource use and agricultural productivity in intercrops.

Keywords: Europe; Strip intercropping; Land equivalent ratio; Net effect; Border row effects; Light capture; Light use efficiency; Nitrogen uptake; Fertiliser nitrogen equivalent ratio

Table of contents

Chapter 1

General introduction

1.1 Intercropping is promising to promote agricultural sustainability

The global need for food is anticipated to markedly rise in the coming decades, placing greater pressure on agricultural production (Alexandratos and Bruinsma, 2012; van Dijk et al., 2021). The environmental impacts of agriculture, however, such as greenhouse gas emission, nutrient spillover, and biodiversity loss, are of concern (Clark and Tilman, 2017; Köthe et al., 2023). Thus, modern agriculture has simultaneous requirements for enhancing productivity, reducing anthropogenic inputs, and protecting biodiversity by developing sustainable agricultural systems (Lankoski and Thiem, 2020; Lind et al., 2019). Intercropping is the cultivation of multiple crop species in one field for a specific duration during their growing cycles (Willey, 1990). Intercropping has several advantages over monocropping, e.g., increased productivity (Li et al., 2020b; Li et al., 2023), enhanced product quality (Fischer et al., 2020; Li et al., 2023), higher resource use efficiency (including land, light, water, and nutrients) (Guiducci et al., 2018; Rodriguez et al., 2020; Tan et al., 2020; Zhu et al., 2015), higher soil organic carbon and nutrient content (Cong et al., 2015; Li et al., 2021), better resilience to abiotic stresses (Nyawade et al., 2019; Renwick et al., 2020), better control of pests and diseases (Boudreau, 2013; Tooker and Frank, 2012; Zhang et al., 2019), and improved suppression of weeds (Gu et al., 2022, 2021; Liebman and Dyck, 1993). Therefore, it has been advocated as a model for a more sustainable agriculture (Brooker et al., 2015; Chai et al., 2021).

1.2 Intercropping performance depends on species complementarity and competition

Many intercropping advantages arise from interspecific complementarity, enabling the component species to acquire resources from different spatial or temporal domains and (or) utilise captured resources through different pathways (Bedoussac and Justes, 2010a; Justes et al., 2021; Li et al., 2020a). In intercropping, various complementarities can be realised by incorporating species with different traits, such as temporal complementarity between early- and late-season species (Yu et al., 2015), spatial complementarity between deep- and shallow-rooted species (Homulle et al., 2021; Li et al., 2006), functional complementarity between C_3 and C_4 species (Yu, 2016), and between nitrogen-fixing and non-nitrogen-fixing species (Rodriguez et al., 2020). Moreover, intercropped species can express plasticity in plant traits in response to the heterogeneous environment, promoting complementarity in addition to the intercropping design (Barillot et al., 2019; Li et al., 2021; Liu et al., 2020; Zhu et al., 2015).

Alongside interspecific complementarity, interspecific competition is also a key process in intercropping. When one species dominates the other in shoot or root size, competition dominance occurs (Seabloom et al., 2003; Weiner, 1990). In the context of competition dominance, yield gains of the dominant species may go along with yield losses of the dominated species. Early sowing can also confer dominance to a species, as observed during the early season in relay intercrops, such as the shading effect of early-sown wheat on late-sown maize (Gou et al., 2017a; Wang et al., 2017; Zhu et al., 2014), and the more developed wheat root system compared to maize root system (Li et al., 2006). In the context of competition, the intercrop would still have yield advantages if the yield gain of the dominant species is more than the loss it causes to the dominated species (Feng et al., 2021; Li et al., 2020a).

1.3 Intercropping syndromes differ depending on production purposes

1.3.1 Cereal/legume full mixtures or row intercrops prevail in low-input/organic agriculture

The current prevailing intercropping in Western Europe usually involves cereal/legume combinations at low levels of anthropogenic inputs such as fertiliser or pesticides, often in low-input or organic agriculture (Bedoussac et al., 2015; Carof et al., 2019; Hauggaard-Nielsen et al., 2008; Jannoura et al., 2014). Species are usually grown as full mixtures or alternating rows, enabling strong rhizosphere interactions, facilitating the utilisation of nitrogen (N) fixation by legume components to maintain an acceptable level of N in the system (Bedoussac et al., 2015; Rodriguez et al., 2020). Such an intercropping pattern can also be found in Africa and Latin America (Chaves et al., 2020; Mudare et al., 2022). In these low-input intercrops, absolute yield increases are not necessarily the aim, but they offer advantages such as increased land use efficiency, improved cereal quality, enhanced nutrient use efficiency, and effective weed suppression and pest control (Bedoussac et al., 2015). Despite these benefits, the low-input intercrops are not well-suited for conventional agriculture, which to date constitutes over 90% of the total agriculture area in the EU (European Commission, Eurostat, 2021). The primary objective of conventional agriculture is to increase both yield and the associated revenue. The low availability of mineral N in low-input intercrops hinders yield increases, especially for cereal components (Li et al., 2020b).

1.3.2 Strip intercrops provide notable yield increases in high-input/conventional agriculture

Contrasting with low-input intercropping, there is an intercropping pattern where component species receive relatively high levels of resource inputs, which is mostly adopted in China (Li et al., 2020b). These high-input intercrops are mostly practised in regions where the primary interest is absolute yield increase (Gou et al., 2017b; Hong et al., 2020; Li et al., 2020a; Wang et al., 2021; Wu et al., 2023). Different than full mixture or row designs, species in these high-input intercrops are often grown in alternating strips comprising several plant rows, enabling distinct management of different species (Li et al., 2020b). Species strips are typically 1–2 m wide, allowing strong interspecific interactions, especially in the border rows of strips (Wang et al., 2021, 2020). Plants in border rows can express plasticity in leaf and root growth in response to the increased resources in the border rows (Li et al., 2021; Zhang et al., 2022; Zhu et al., 2015). This plasticity amplifies the complementarity in resource capture in addition to the border row position itself. Therefore, yield increases in intercrop border rows, compared to intercrop inner rows and monocrops, are the main contributor to the overall increases of the whole intercrop (Gou et al., 2016; Zhu et al., 2015). A high border row proportion is important for increasing resource capture and thus yield in strip intercropping (van Oort et al., 2020; Wang et al., 2021, 2020).

According to the stress gradient hypothesis, high availability of resources will increase the importance of species competition whereas resource stress will tend to increase the importance of complementarity (He et al., 2013). In intercropping, intense interspecific competition can lead to yield increases in dominant species but yield losses in dominated species (Feng et al., 2021). To enhance overall yield increases in the system, it is beneficial for interspecific complementarity to play a significant role rather than competition. Therefore, relay succession, in which component species are sown and harvested asynchronously, is often employed with high inputs, enabling the early- and late-sown species to more completely exploit resources during their respective sole-growing periods (Li et al., 2020b; Yu et al., 2015). The sole-growing periods create competition avoidance. According to a global meta-analysis, high-input intercropping with a relay design, where one of the component species is maize (*Zea mays* L.), has comparable land use efficiency to low-input intercropping, but results in greater yield gains and increased nitrogen (N) and phosphorus (P) fertiliser use efficiency, indicating promising potential to contribute to agricultural sustainability in conventional agriculture (Li et al., 2020b; Tilman, 2020).

1.4 Strip intercropping benefits Western-European conventional agriculture, but more exploration is needed

1.4.1 More species combinations need exploration other than maize/wheat

Maize/wheat relay strip intercropping is widely practised in conventional agriculture by smallholder farmers in the temperate regions of China (Gou et al., 2017b; Hong et al., 2020). The yield advantages result – at least in part – from temporal complementarity, with wheat sown earlier than maize and maize harvested considerably later than wheat. Consequently, wheat experiences reduced interspecific competition for resources in the early season, and maize is negatively affected by tall wheat plants; maize can compensate for its losses during the late season once it overtops wheat and benefits from a sole-growing period after wheat is harvested (Ma et al., 2020; Wang et al., 2017). Moreover, the species can benefit from trait differences. For instance, once maize overtops wheat, wheat as a C_3 species receives reduced light under maize shading, and high light in the top of the canopy may be efficiently used through maize C_4 photosynthesis (Li et al., 2020; Ma et al., 2020). Wheat and maize also show different root distributions in the early and late season, enhancing an efficient capture of water and nutrients (Li et al., 2006; Liu et al., 2020).

In light of these advantages, maize/wheat relay strip intercropping has recently been studied in the Netherlands to assess if its benefits persist under the cooler climate conditions of Western Europe (Gou et al., 2016; Zhu et al., 2015). In these studies, intercrops were fertilised according to local practice for conventional agriculture. Temporal complementarity between wheat and maize resulted in an increased light capture by both species compared to their monocrops, and thus overyielding (Gou et al., 2016; Zhu et al., 2015). Maize/wheat is, however, an N demanding system, and it has not been explored in strip intercropping in the Netherlands whether systems with legumes would have similar advantages as a relay system involving only cereals. Thus, little is known about species complementarity in strip intercropping at conventional input levels under West-European conditions. Since intercropping performance depends on species complementarity and competition under specific environment and management (Fukai and Trenbath, 1993; van der Werf et al., 2021), it is necessary to explore species combinations other than maize/wheat for potential implementation of strip intercropping in Western-European conventional agriculture. Intercrops involving different species types, such as cereal/legume combinations, and those featuring simultaneous cultivation rather than relay cultivation, will be of interest.

1.4.2 A more efficient fertilisation in intercropping is needed in the context of Good Agriculture Practices

Although high-input intercropping brings yield increases, there is potential for improving the present fertilisation strategy, especially for N. The typical N fertilisation strategies in high input intercropping involve: 1) assigning a specific high N dose for annual crops as the total N rate for the entire intercrop (Li et al., 2011; Xing et al., 2023); 2) the N doses for the intercrop are determined by calculating the weighted average of the respective N doses of the individual species when grown as monocrops, considering their land shares in the intercrop (Gao et al., 2022); 3) setting the intercrop N rate as the sum of those in the corresponding monocrops to maintain a consistent N rate per plant for each component species in intercrops and monocrops (Feng et al., 2020; Yang et al., 2017). These N fertilisation strategies can be as high as 300 kg N ha^{-1} (e.g., Li et al., 2009), and usually do not account for differences in N requirements between species , e.g., legumes agronomically do not need much mineral N input but a small dose for their early development (Giller, 2001). N surpluses and consequent N losses from the soil in intercropping can be caused by over-fertilisation, imposing environmental concerns (Wang et al., 2022). Therefore, it is important to apply fertilisers appropriately to balance species needs and environmental costs (Falconnier et al., 2023). According to the standard of Good Agriculture Practices, fertilisation should be applied based on an understanding of species responses to fertiliser and at appropriate doses and timing for agronomic and environmental requirements (FAO, 2003). A species-tailored fertilisation strategy, providing distinct N doses to meet growth demands of component species, can be an effective approach (Falconnier et al., 2023). Such a strategy will provide moderate N rates to species, compared to low or zero N rates in low-input/organic agriculture or the very high N rates in high-input agriculture. Practically, the strip design allows for separate applications.

1.4.3 Light is an important resource to be studied in intercropping under conventional agriculture

In conventional agriculture, light is considered a key resource limiting production, given the expectation that water and nutrients are provided in non-limiting quantities (Gallagher and Biscoe, 1978; Monteith, 1977). When water and nutrients are provided to meet species requirements, intercropping benefits on yield are primarily the result of enhanced light use (Stomph et al., 2020). Previous studies have made efforts through experimental and modelling approaches and indicated that intercropping has the potential to increase light capture. For instance, temporal complementarity in relay intercropping allows the early- and late-sown species to capture more light in their sole-growing periods (Gou et al., 2017a; van Oort et al., 2020; Zhang et al., 2008a; Zhu et al., 2015). Differences in canopy structure among species may facilitate a more efficient light distribution than a homogenous monocrop canopy, thereby contributing to enhanced light capture in intercropping (Zhu et al., 2020). Furthermore, plant plasticity, due to changes in tiller or branch number, leaf angle, leaf shape, and internode length, can significantly contribute to light capture on top of the intercropping design (Barillot et al., 2019; Li et al., 2020; Liu et al., 2017; Wang et al., 2017; Zhu et al., 2015). Light conversion, i.e., light use efficiency (LUE), can also be enhanced in intercropping. For instance, in C_3/C_4 intercropping, the tall-statured C_4 species could potentially have an increased LUE when it overtops the short-statured C_3 species, because the high light condition in the top of the canopy favours C_4 photosynthesis (Ma et al., 2020; Yu, 2016). In cereal/legume intercropping, even when shaded by cereals, legumes can acclimate through morphological adjustments to improve light distribution within the canopy, thereby contributing to improved light conversion (Liu et al., 2017).

How light capture affects intercropping yield can be reflected by yield components

Yield components reflect impediments to yield formation (Grafius, 1978), and have therefore been extensively studied in intercropping research to explain the consequences of interspecific interactions for yield (Ahmed et al., 2020; Ajal et al., 2022; Gou et al., 2016; Hu et al., 2020; Wang et al., 2020). In intercropping, the resource availability per each species is usually different from that in monocropping because of complementarity or competition (Ajal et al., 2022). Yield components are good indicators for assessing the level and timing of complementarity or competition effects on resource acquisition by a species. This is because yield component determination follows a chronological sequence which can then reflect the competitive relationship between species during different growth phases (Evans, 1975). For instance, in a relay strip intercrop, early-sown wheat had more ears and more grains per ear in the intercrop border rows than monocropped wheat due to good light availability in the early season; the thousand-grain weight was, however, reduced because the large number of grains per plant (high sink demand) in combination with maize shading during the wheat grain-filling stage (low source supply) (Gou et al., 2016). Yield components determined at an early stage might affect the yield components determined at a late stage because of within-plant competition for assimilates (Patrick and Colyvas, 2014), as exemplified by the trade-off between grain number and weight (Venable, 1992).

While yield components have received much attention in intercropping studies, they have not often been used to gain deeper insights into the temporal dynamics of complementarity or competition experienced by the component species. Such information is valuable for summarising species strategies in coping with interspecific interactions. It can also assist in identifying the yield components most responsible for yield differences between intercrops and monocrops, aiding in species selection, configuration design, and resource management for intercropping. To achieve this, the relationship of each yield component with yield in intercrops and monocrops will need to be quantified. Intercropping effects on yield components will need to be studied in alignment with the resource capture during the critical growth phases in which they are determined.

Border row contribution to light capture and conversion needs to be quantified

Border row responses are important for production in strip intercropping. For more insights into species interactions, it is essential not only to compare yield but also to compare resource capture and conversion in intercrop border rows and inner rows, and monocrops. It is difficult to measure experimentally light capture per species in mixed canopies, hence researchers have usually made use of modelling to partition light capture between species, e.g., by using the functional-structural plant models (Li et al., 2021; Zhu et al., 2015). Most studies, however, have inferred the contribution of border rows by comparing light capture and conversion of the whole strips with different border row proportions (van Oort et al., 2020; Wang et al., 2021, 2020).

Moreover, light capture and conversion in intercropping can be affected by different heterogeneities. For instance, early-sown species have advantages in light capture over late-sown species because of height dominance (Gou et al., 2017a; Raza et al., 2021; Wang et al., 2017). High light and high temperature conditions favours C_4 species more than C_3 species (Anten and Hirose, 2003; Sage and Kubien, 2007). Studying border row contribution to light capture and conversion in various species combinations provides the opportunity to uncover inter-system distinctions in light use. This will support species and system selection for practice more effectively than only focusing on a specific combination. Supply of water and nutrients, especially N, can also impact light capture and conversion by influencing canopy growth and photosynthesis (Slattery and Ort, 2021). Therefore, it is also important to study light capture and conversion under the local input strategy.

1.4.4 Intercropping effects on N uptake under species-tailored N fertilisation are unknown

Improving N uptake is essential for efficient N use, good yield quantity and quality (Fageria and Baligar, 2005). In the low-input/organic cereal/legume intercrops, cereals can have more N uptake and thus a higher grain protein (Bedoussac et al., 2015; Li et al., 2023). This is because legumes mainly rely on N fixed from the atmosphere when the available mineral N from the soil is low, leaving the N released from mineralisation as a bonus to cereals (Jensen et al., 2020; Rodriguez et al., 2020). In high-input intercrops, increased N uptake often occurs when species are grown in relay succession because temporal complementarity reduces interspecific competition for N (Chen et al., 2019; Li et al., 2011). Moreover, increased capture of other resources such as light can promote N uptake through positive shoot-root feedback (Evers et al., 2019). Species can also express root plasticity, exploiting the soil volume with increased root length densities and more laterally distributed roots, leading to enhanced N uptake (Li et al., 2006; Liu et al., 2020). Intercropping effects on N uptake under a species-tailored N fertilisation strategy remain unknown. Investigating N uptake in various species combinations can contribute to a better understanding of how interspecific interactions affect N uptake of intercropped species and identify the species combinations that can increase N uptake of component species and the entire system.

1.5 Overall research questions of this thesis

Given the potential of strip intercropping in increasing yield and enhancing resource use efficiency in conventional agriculture, this thesis addresses the research questions: *To what extent can strip intercropping under conventional management in Western-European conditions with species-tailored N fertilisation provide yield advantages? To what extent do species interactions in strip intercropping affect light capture and conversion, and N uptake?* To address the questions, a two-year experiment was conducted that provided data for all of the chapters (Fig. 1.1).

1.6 Outline of this thesis

Chapter 2 addresses the research question: *Can strip intercropping, involving commonly cultivated crop species, provide yield advantages under conventional management in Western-European conditions with species-tailored N fertilisation?* I conducted a two-year field experiment in which four crop species, maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.), were combined as six bi-specific strip intercrops. The three intercrops involving maize i.e., maize/wheat, maize/faba bean, and maize/pea, were relay intercrops because of later sowing and harvesting of maize compared to the companion species. The other three intercrops, i.e., faba bean/wheat, faba bean/pea, and wheat/pea are nearly simultaneous because wheat, faba bean, and pea had the same sowing date and similar harvesting dates. Species within this experiment were managed according to the locally conventional production practices. Species received the same N fertiliser within the species strip in intercrops as they did in monocrops. Species performance was assessed based on yield differences per species between intercrops and monocrops. Competitiveness of species in intercrops was assessed by competitive ratio (CR; Willey and Rao, 1980). Land equivalent ratio (LER; Willey and Rao, 1980) and net effect (NE; Loreau and Hector, 2001) for grain yield and vegetative biomass were used to assess intercrop land productivity and absolute yield change, respectively. For definitions of these metrics see Box 1.1.

Chapter 3 addresses the research questions: *What are the key yield components determining grain yield differences of species in strip intercropping? To what extent are the yield component and grain yield responses associated with light capture?* I explored relationships between grain yield per unit land area and the total grain number per unit land area (GN) and thousand-grain weight (TGW) of the four species in all treatments from the field experiment in Chapter 2. Based on plant height and leaf area index (LAI) collected from the field experiment, light captured before and during grain filling, and throughout the season of species in all intercrops was estimated using an intercrop light model (Gou et al., 2017a). Relationships between GN and cumulatively captured light before grain filling, and between TGW and cumulatively captured light during grain filling were explored. The relationship between LER and light capture throughout the season was also explored.

Chapter 4 addresses the research question: *How do the intercropping effects on light capture and conversion contribute to the border row effects and overall intercropping effects on above-*

ground biomass in strip intercropping? Based on the data collected in the second year of the field experiment in Chapter 2, I estimated cumulative light captured of different row types, border and inner rows, of all species in all treatments using a random ray tracing model (Gijzen and Goudriaan, 1989; Schnieders, 1999; Tsubo and Walker, 2002; Wang et al., 2017). Light conversion was quantified using the light use efficiency (LUE). LUEs of border and inner rows were determined as the slopes of the regressions between biomass and cumulative light captured.

Chapter 5 addresses the research questions: *What are the effects of strip intercropping on N uptake of species and system under conventional management in Western-European conditions with species-tailored N fertilisation? What are the effects on fertiliser N use efficiency?* I analysed above-ground N uptake and N concentration of all species in all treatments throughout the season in the field experiment in Chapter 2. Species performances were assessed based on N uptake differences for species between intercrops and monocrops. Land equivalent ratio for N uptake (LER_N; Bedoussac and Justes, 2010b; Li et al., 2011) was used to assess intercrop land use efficiency for capturing N relative to the combined monocrops. Fertiliser N equivalent ratio (FNER; Xu et al., 2020) was used to assess intercrop fertiliser N use efficiency in producing grain yield relative to the combined monocrops.

Chapter 6 synthesises the findings of the preceding chapters. I reflect on how species interactions influence light and N use, consequently affecting yield in strip intercropping under the experimental management. Following this reflection, I discuss the significance and limitations of the work presented in this thesis. Through the integration of these findings, I will suggest implications of my thesis results regarding the adoption of strip intercropping for conventional agriculture in Western Europe.

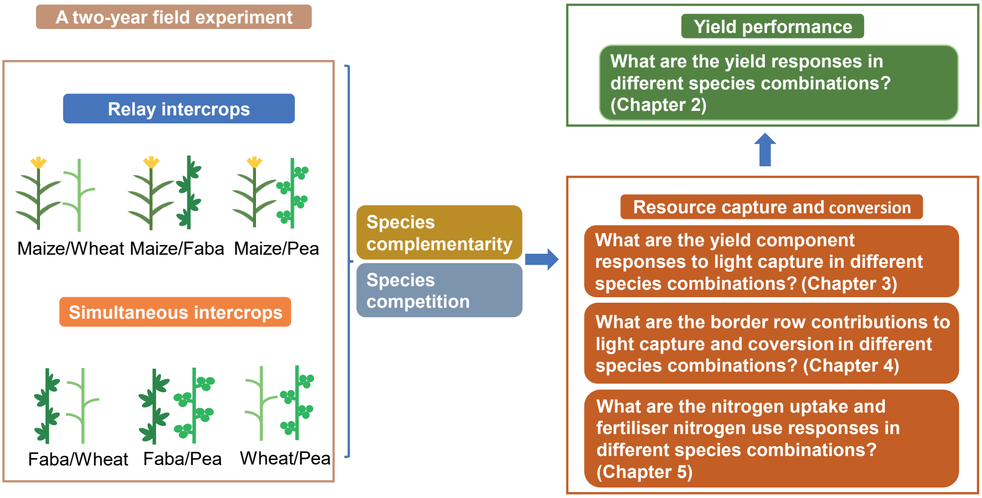

Fig. 1.1 Schematic representation of this thesis. A two-year field experiment was conducted in Wageningen, the Netherlands, as a case study for strip intercropping under conventional management in Western Europe. Six bi-specific intercrops were tested. Yield performance of each species and each intercrop was studied in Chapter 2. Intercropping effects on light capture and conversion, N uptake, and fertiliser N use were described and analysed in Chapters 3, 4, and 5.

Box 1.1 Relevant metrics and definitions in this thesis

In this thesis, I used various metrics to assess intercropping effects on production, resource capture, and resource conversion at the species row level, the species strip level, and the intercrop level. Their definitions are presented as follows:

Temporal niche differentiation (TND)

Temporal niche differentiation (TND; Yu et al., 2015) is used to quantify temporal complementarity in intercrops:

$$\mathrm{TND} = 1 - \frac{T_{\mathrm{overlap}}}{T_{\mathrm{system}}} \qquad \text{(Eq. 1.1)}$$

where T_{overlap} is the duration when the component species grow together in the intercrop; T_{system} is the total season length of the intercrop, from sowing the first species to harvesing the last species.

Box 1.1 (continued)

Land equivalent ratio (LER)

Land equivalent ratio (LER; Willey and Rao, 1980) is used to assess the land use efficiency of intercrops relative to monocrops:

$$\mathrm{LER} = \mathrm{pLER}_1 + \mathrm{pLER}_2 = \frac{Y_{\mathrm{I},1}}{Y_{\mathrm{M},1}} + \frac{Y_{\mathrm{I},2}}{Y_{\mathrm{M},2}} \qquad \text{(Eq. 1.2)}$$

where pLER_i is the partial land equivalent ratio of species i; $Y_{\mathrm{I},i}$ is the yield of species i in the intercrop on per unit land area of the intercrop; $Y_{\mathrm{M},i}$ is the yield of species i in the monocrop on per unit land area of the monocrop.

Grain yield can be replaced by biomass, light capture, and N uptake to assess the land use efficiency of intercrops in producing biomass, capturing light, and capturing N, compared to monocrops.

Net effect (NE)

Net effect (NE; Loreau and Hector, 2001) is used to assess the absolute yield change in the intercrop compared to the expected yield:

$$\mathrm{NE} = \left(Y_{\mathrm{I},1} - EY_1\right) + \left(Y_{\mathrm{I},2} - EY_2\right) = \left(Y_{\mathrm{I},1} - Y_{\mathrm{M},1} \times p_1\right) + \left(Y_{\mathrm{I},2} - Y_{\mathrm{M},2} \times p_2\right) \qquad \text{(Eq. 1.3)}$$

where $Y_{\mathrm{I},i}$ is the yield of species i in the intercrop on per unit land area of the intercrop; $Y_{\mathrm{M},i}$ is the yield of species i in the monocrop on per unit land area of the monocrop; EY_i is the expected yield of species i; p_i is the land share of species i in the intercrop.

Competitive ratio (CR)

Competitive ratio (CR; Willey and Rao, 1980) is used to assess the competitiveness of one species relative to its companion species in the intercrop. It is calculated using the partial land equivalent ratios pLER and land shares of the component species:

Box 1.1 (continued)

$$\mathrm{CR}_1 = \frac{\mathrm{pLER}_1}{\mathrm{pLER}_2} \times \frac{p_2}{p_1}; \mathrm{CR}_2 = \frac{\mathrm{pLER}_2}{\mathrm{pLER}_1} \times \frac{p_1}{p_2} \qquad \text{(Eq. 1.4)}$$

where the land shares p_1 and p_2 represent the theoretical proportions of the intercropped land area assigned to each species. The land shares sum to one: $p_1 + p_2 = 1$.

Land equivalent ratio for light capture (LCER)

Land equivalent ratio for light capture (LCER) is used to assess the land use efficiency of intercrops for light capture relative to monocrop:

$$\mathrm{LCER} = \mathrm{pLCER}_1 + \mathrm{pLCER}_2 = \frac{CPAR_{\mathrm{I}1}}{CPAR_{\mathrm{M}1}} + \frac{CPAR_{\mathrm{I}2}}{CPAR_{\mathrm{M}2}} \qquad \text{(Eq. 1.5)}$$

where the pLCER_i is the partial equivalent ratio for light capture of species i; $CPAR_{\mathrm{I}i}$ is the cumulative light captured throughout the season of species i in the intercrop on per unit area of the intercrop; $CPAR_{\mathrm{M}i}$ is the cumulative light captured throughout the season of species i in its monocrop.

Light use efficiency (LUE)

In this thesis, light use efficiency (LUE; g MJ^{-1}) represents the efficiency of plants in converting photosynthetically active radiation (PAR; MJ m^{-2}) captured to above-ground biomass. It is estimated as the slope of the linear regression between above-ground biomass and cumulative PAR captured.

Land equivalent ratio for nitrogen uptake (LER_N)

Land equivalent ratio for nitrogen uptake (LER_N) (Bedoussac and Justes, 2010b; Li et al., 2011) is used to assess the land use efficiency for N uptake of intercrops relative to monocrops:

$$\mathrm{LER}_\mathrm{N} = \mathrm{pLER}_{\mathrm{N},1} + \mathrm{pLER}_{\mathrm{N},2} = \frac{N_{\mathrm{I},1}}{N_{\mathrm{M},1}} + \frac{N_{\mathrm{I},2}}{N_{\mathrm{M},2}} \qquad \text{(Eq. 1.6)}$$

Box 1.1 (continued)

where $N_{\mathrm{I},i}$ is the N uptake of species i in an intercrop at final harvest, expressed at per unit of total area of the intercrop; $N_{\mathrm{M},i}$ is the N uptake of species i in its monocrop at final harvest, expressed at per unit area of the monocrop; $\mathrm{pLER}_{\mathrm{N},i}$ is the partial land equivalent ratio for N uptake of species i.

Fertiliser nitrogen equivalent ratio (FNER)

Fertiliser nitrogen equivalent ratio (FNER; Xu et al., 2020) is used to assess the fertiliser N use efficiency of intercrops relative to monocrops:

$$\mathrm{FNER} = \left(\frac{Y_{\mathrm{I},1}}{Y_{\mathrm{M},1}} \times \frac{F_{\mathrm{M},1}}{F_{\mathrm{IC}}}\right) + \left(\frac{Y_{\mathrm{I},2}}{Y_{\mathrm{M},2}} \times \frac{F_{\mathrm{M},2}}{F_{\mathrm{IC}}}\right) \quad \text{(Eq. 1.7)}$$

where $Y_{\mathrm{I},i}$ is the grain yield (per unit of total area of an intercrop) of species i in the intercrop; $Y_{\mathrm{M},i}$ is the grain yield (per unit area of a monocrop) of species i in the monocrop; $F_{\mathrm{M},i}$ is the rate of fertiliser N applied per unit area of the monocrop of species i; F_{IC} is the rate of fertiliser N applied per unit area of the whole intercrop.

Row level

In this thesis, "row level" indicates that the analysis is conducted on a per-unit length basis of a row for a species.

Species strip level

A species strip consists of several plant rows of the same species. In this thesis, it is referred to as "species strip", "species level", indicating that the analysis is conducted for a species on a per-unit land area basis of its species strip.

Intercrop strip level

An intercrop strip consists of two species strips, one for each species. In this thesis, it is referred to as "intercrop strip", "intercrop level", "system", and "system level", indicating that the analysis is conducted for a species or an intercrop on a per-unit land area basis of the whole intercrop.

Chapter 2

Temporal complementarity drives species combinability in strip intercropping in the Netherlands

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Abstract

Combinability of species in intercrops depends on the production conditions and there is limited information on the potential of intercropping under conventional (i.e., non-organic) management in Western Europe. Here we determined productivity of four crop species (maize, *Zea mays* L.; wheat, *Triticum aestivum* L.; faba bean, *Vicia faba* L.; pea, *Pisum sativum* L.) in six different bi-specific mixture compositions. Species were spring-sown and fertilised in their strips according to common practice for monocrops. Strips were 1.5 m wide enabling strong interspecific interactions. Intercrops with maize, a species sown and harvested later than the other three species, had land equivalent ratio (LER) values that were in four out of six cases significantly greater than one, from 1.14 ± 0.04 to 1.22 ± 0.05 in 2018, and from 0.98 ± 0.06 to 1.15 ± 0.01 in 2019. Simultaneous intercrops comprising two of the other three species had LER values that tended to be lower than one, even though many LERs were not significantly different from one: from 0.94 ± 0.02 to 0.95 ± 0.04 in 2018, and from 0.80 ± 0.08 to 0.93 ± 0.04 in 2019. The yield gain (net intercropping effect; NE) in relay intercrops with maize ranged from 1.33 ± 0.59 to 2.01 ± 0.54 Mg ha^{-1} in 2018, and from 0.29 ± 0.41 to 1.04 ± 0.14 Mg ha^{-1} in 2019. The NE of simultaneous intercrops ranged from −0.43 ± 0.13 to −0.27 ± 0.22 Mg ha^{-1} in 2018, and from −1.17 ± 0.49 to −0.36 ± 0.22 Mg ha^{-1} in 2019. Results indicate that temporal complementarity between species drove the LER (or NE) in these experiments. On the other hand, values of the LER (or NE) were similar in species combinations with or without legumes, suggesting no major role for complementarity for nitrogen capture under the conditions of the study. Faba bean was the most competitive species and reached high partial LER and NE values in intercrops at the expense of the companion species. Competition from faba bean reduced the grain yield of wheat and pea more than it increased faba bean grain yield, resulting in negative net effects. Results suggest that relay strip intercropping can improve land use efficiency and total grain yield in conventional farming in Western Europe if species have temporal complementarity.

Keywords: Europe; Species combinability; Strip intercropping; LER; Net effect

2.1 Introduction

Intercropping is the planned cultivation of multiple crop species in one field for at least part of their growing periods (Willey, 1990). It provides a suitable cropping model for sustainable intensification (Brooker et al., 2015) because of improved use efficiency of land (Li et al., 2020b; Yu et al., 2015), light (Gou et al., 2017a; Liu et al., 2017; Raza et al., 2019; Tsubo et al., 2001), water (Morris and Garrity, 1993; Tan et al., 2020; Yin et al., 2020), and nutrients (Darch et al., 2018; Guiducci et al., 2018; Tang et al., 2021; Xu et al., 2020). Furthermore, intercropping can lead to higher organic soil carbon and nitrogen content (Cong et al., 2015; Li et al., 2021; Wang et al., 2014), better pest and disease control (Boudreau, 2013; Risch, 1983; Tooker and Frank, 2012; Trenbath, 1993; Zhang et al., 2019), and better weed suppression (Corre-Hellou et al., 2011; Gu et al., 2021; Gu et al., 2022; Liebman and Dyck, 1993).

Many advantages of intercropping are associated with plant-plant complementarity. That is, intercropped species can use resources more completely because they exploit above-ground resources (light) and below-ground resources (water, nutrients) differently, e.g., due to differences in the temporal pattern of growth, light interception and soil resource uptake (Yu et al., 2015), above- or below-ground morphology (Li et al., 2021; Sun et al., 2019), and (or) functional traits for resource capture (Gou et al., 2018; Rodriguez et al., 2020).

Intercropping is usually considered advantageous at low levels of resource availability (Brooker et al., 2015; Franco et al., 2015; Jensen et al., 2020) because complementarity is dominant with constrained resources, but competition prevails with ample resources (He et al., 2013; Justes et al., 2021). Nevertheless, meta-analyses indicate that yield advantages in intercropping increase with nitrogen (N) input in high-input agriculture (Li et al., 2020b; Yu et al., 2015). In high-input systems in China, bi-specific intercrops (one component species of which is often maize, *Zea mays* L.) are planted in alternating narrow strips of a few crop rows whereby the combined species are sown and harvested in a relay succession. The yield increase is related to the difference in growing periods, which decreases interspecific competition for light and other resources, while the extended total growth duration increases the aggregate resource capture of the system as a whole (Gou et al., 2017a; Li et al., 2020b; Yu et al., 2015; Zhang et al., 2008a). Policymakers are interested in increasing sustainability of farming, but they want to maintain as much as possible high levels of productivity, to ensure food security and healthy diets (Lankoski and Thiem, 2020). Hence, this high-input syndrome of intercropping fits the pursuit of sustainable intensification because it may save 16–29% land and 19–36% nitrogen and phosphorus fertiliser per unit yield produced compared to monocrops, while maintaining high yield levels (Li et al., 2020b).

In strip intercrops, interspecific interactions mainly occur in the border rows of adjacent species strips, hence narrow strips and a high proportion of such border rows are essential for achieving a large yield gain in strip intercropping (van Oort et al., 2020; Wang et al., 2020). Yield gain is usually due to complementarity for resource capture, which occurs because crop species usually differ in one or more of the following traits: phenology (Gou et al., 2018), height (Wang et al., 2017), canopy structure (Li et al., 2021; Zhu et al., 2015), root distribution (Liu et al., 2020), ability to symbiotically fix N from the soil (Bedoussac et al., 2015; Jensen et al., 2020; Rodriguez et al., 2020), water consumption (Ren et al., 2019; Zhang et al., 2022), ability to solubilise immobile soil phosphorus (Li et al., 2007; Li et al., 2019; Tang et al., 2021) and photosynthetic capacity (Gou et al., 2018). Yield increases in border rows compared to yields in inner rows or in monocrops are the result of resource complementarity that results in comparatively weak competition from allospecific neighbours, when averaged out over time, even if it can be strong at specific times of co-growth (Gou et al., 2016; Zhang et al., 2007; Zhu et al., 2015). Border row plants can express plasticity in leaf and root growth in response to the extra resources available at the border, which can amplify the complementarity in resource use on top of the extra resource capture due to the border row position itself (Evers et al., 2019; Liu et al., 2020; Zhang et al., 2022; Zhu et al., 2015). Furthermore, complementarity for a limiting resource can promote resource capture and plant growth, such that uptake of other, less limiting, resources is also enhanced (Evers et al., 2019).

Competition is a key process in intercrops, and a yield gain of one species may be associated with a yield loss of the companion species. Nevertheless, if one of the species has reduced yield, the intercropping system as a whole may have a yield advantage, provided the relative (or absolute) yield gain of the dominant species is greater than the loss of the dominated species (Feng et al., 2021; Li et al., 2020a). If the sum of relative yield changes is larger than zero, the system has a land equivalent ratio (LER) > 1, and if the sum of absolute yield changes is larger than zero, the system has a net effect (NE) > 0 (van der Werf et al., 2021). If, however, the loss of the dominated species is greater than the gain of the dominant species, the system will have a yield disadvantage. Reduced resource capture and decreased yield in border rows may occur because of competition (Wang et al., 2020) and (or) expression of plastic responses that do not result in improved resource capture and yield (Li et al., 2021). Since intercrop productivity is contingent upon the performance of component species under particular growing conditions, it is important to investigate the performance per each species in a specific cropping systems context, to ascertain their combinability for intercropping, given a production situation (Fukai and Trenbath, 1993; van der Werf et al., 2021).

Narrow strip intercropping with high resource input is rare in Western Europe, mainly due to as yet unresolved technology challenges related to sowing, harvesting, and crop management. Instead, intercropping in Europe is mostly confined to mixtures of simultaneously sown and harvested C_3 cereals and legumes, usually with low or moderate inputs in organic systems (Bedoussac et al., 2015). Such mixtures exploit the biological N fixation potential of legumes to keep sufficient N in the system to support quality cereal production with low organic manure inputs (Bedoussac et al., 2015). Yet, the organic farming area is currently only 8% of the total farming area in the EU despite the recent increase (European Commission, Eurostat, 2020). This raises the question whether intercropping could be tailored to conventional production practices. In this context, strip intercropping is of interest, as strip intercropping systems have higher yield gains than fully mixed intercropping systems under conditions of moderate or high resource input (Li et al., 2020b).

Recently, maize/wheat relay narrow strip intercropping has been studied in the Netherlands at locally conventional input levels. Yield increases over monocropping were observed due to temporally complementary resource capture (Gou et al., 2016; Zhu et al., 2015). Information on narrow strip intercropping under Western-European conditions is still lacking for other potential species combinations under conventional management, including various popular cereal/legume combinations, particularly with simultaneous cultivation rather than relay intercropping.

Therefore, this study addresses the question to which extent four commonly grown crop species, two cereals and two legumes, are combinable in narrow strip intercrops with recommended levels of fertilisation in conventional agriculture under Western-European conditions. We aim to quantify the possible production advantages of this type of intercropping under Dutch growing conditions. We report on a two-year experiment comparing all six bi-specific combinations of four species: maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.). We explored the land use efficiency using the land equivalent ratio and determined the absolute yield gain of these intercrops (net effect) compared to expectation based on monocrop yields under good agricultural practice for conventional farming. Species were sown at their typical sowing time and were fertilised in their strips in accordance with recommendations for the species under conventional farming, i.e., with the use of industrial N fertiliser. The importance of temporal complementarity is exemplified by comparing relay intercrops with maize and simultaneous intercrops without maize; the importance of N capture complementarity between a cereal and a legume is exemplified by comparing cereal/legume intercrops with cereal/cereal or legume/legume intercrops.

2.2 Materials and methods

2.2.1 Experimental design

Field experiments were conducted in 2018 and 2019 at Droevendaal Experimental Farm in Wageningen, the Netherlands (51° 59' 20" N, 5 ° 39' 16" E). The local climate is temperate oceanic. The growing seasons from March 21 to September 10 in 2018 and from April 1 to September 18 in 2019 (both counted from the first sowing date to the last harvesting date) had average air temperature of 16 and 15 °C, cumulative photosynthetically active radiation of 1537 and 1514 MJ m^{-2}, and cumulative precipitation of 300 and 252 mm (Fig. S2.1). Both years had hotter and drier summer (18.9 and 18.4 °C from June to August in 2018 and 2019) than the long-term average (17 °C) (Koninklijk Nederlands Meteorologisch Instituut, 2019). The farm has a sandy soil with a pH of 5.7 and 3.4% organic matter with a C/N ratio of 11 in the top 30 cm. Different fields were used in the two years. The pre-crop of the 2018 experiment was winter wheat (*Triticum aestivum* L.), which was sown in the autumn of 2016 and harvested in the summer of 2017. Following winter wheat harvest, a mixture of bristle oat (*Avena strigosa* Schreb.) and fodder radish (*Raphanus sativus* L.) was grown as a green manure and nitrogen catch crop. Before the 2019 experiment, sugar beet (*Beta vulgaris* L.) was grown, and the field was fallow during late autumn and winter (Table S2.1).

Four crop species, maize (*Zea mays* L., var. 'LG30.223'), wheat (*Triticum aestivum* L., var. 'Nobless'), faba bean (*Vicia faba* L., var. 'Fanfare'), and pea (*Pisum sativum* L., var. 'Astronaute'), were combined as pairs to form six strip intercrops, i.e., maize/wheat, maize/faba bean, maize/pea, faba bean/wheat, faba bean/pea and wheat/pea (Fig. 2.1). In addition, each species was grown as a monocrop. All cultivars were suited for spring sowing, and they were sown in late March, April, or May.

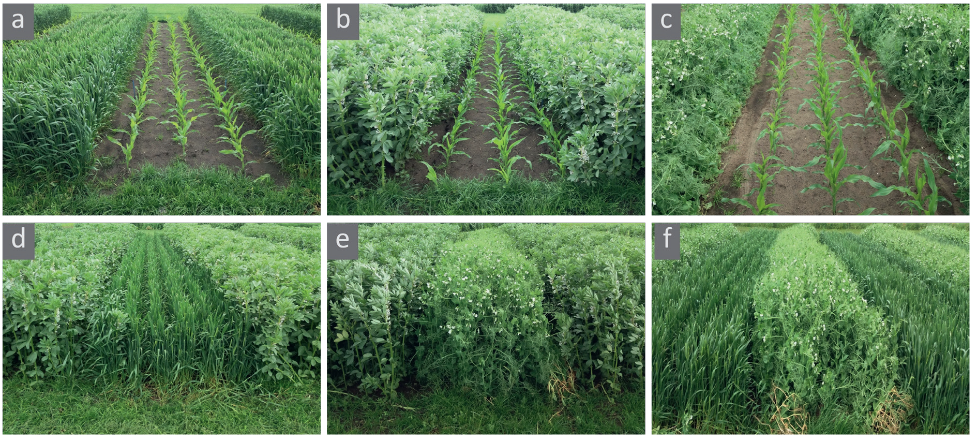
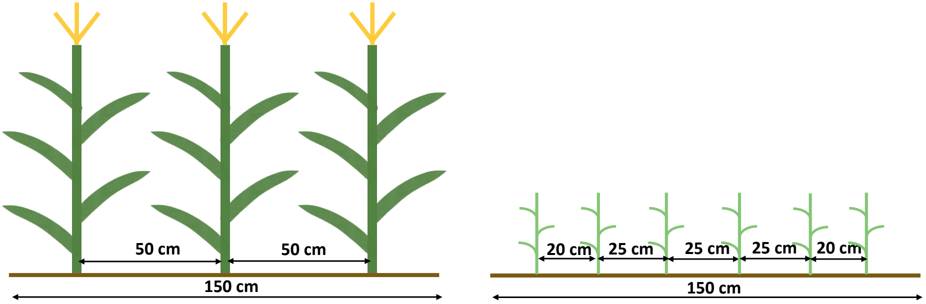


Fig. 2.1 Six intercrops on June 15, 2019: a. maize/wheat; b. maize/faba bean; c. maize/pea; d. faba bean/wheat; e. faba bean/pea; f. wheat/pea.

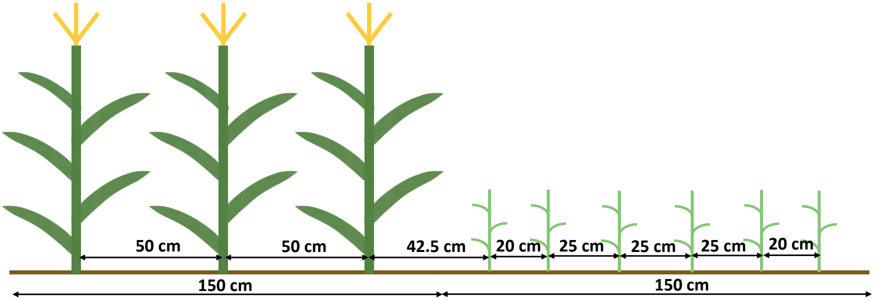
Maize was grown at a 50 cm row distance, while the other species were grown at a 25 cm row distance except for a 20 cm row distance at the border of strips in both monocrops and intercrops to avoid the tractor wheel tracks. Species strips were 1.5 m wide, comprising three rows of maize or six rows of the other species (Fig. 2.2). The intercrops therefore had a replacement design with a relative density of 0.5 of both species with expected species yields in the intercrops being half the monocrop yields.

In both years, the sowing density was 10 seeds m^{-2} for maize, 83 seeds m^{-2} for pea, and 44 seeds m^{-2} for faba bean. Sowing density of wheat was 383 seeds m^{-2} in 2018 and 369 seeds m^{-2} in 2019. The same sowing density was used in monocrops and – per unit area of the species strips – in intercrops. Wheat, faba bean, and pea were sown on March 21, 2018, and April 1, 2019. The late sowing in 2019 was due to heavy precipitation (85 mm) from March 12 to 18 (Fig. S2.1). Maize was sown on May 4 in 2018, and May 7 in 2019. Species were harvested at maturity. The three intercrops with maize were relay intercrops, with maize being sown and harvested later than the companion species, while the other three intercrops were nearly simultaneous, due to a single sowing date and similar harvesting dates (Fig. 2.3). In 2018, the plot size was 9 m width × 11 m length comprising six species strips in intercrops (three for each species). In 2019, the plot size was 12 m width × 11 m length for monocrops and 15 m width

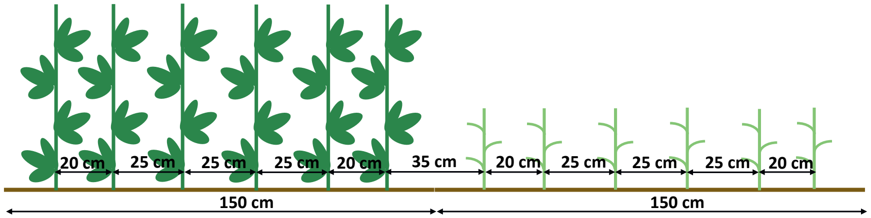
× 11 m length for intercrops, comprising 10 species strips (five for each species) to allow five periodic harvests. Experiments were arranged as randomised complete block designs with six (2018) or four (2019) replicates. The row orientation was approximately north-south.



(a) maize monocrop (b) wheat, faba bean, or pea monocrop



(c) maize/wheat, maize/faba bean, or maize/pea strip intercrop



(d) faba bean/wheat, faba bean/pea, or wheat/pea strip intercrop

Fig. 2.2 Row configuration in the monocrops and intercrops. Sowing was done with a narrow sowing machine (Belt Cone Seeder, Haldrup Co., Germany) and a small tractor with 133 cm space between the wheel tracks (Fendt 207, Fendt Co., Germany). (a) monocrop of maize with a 50 cm row distance; (b) monocrop of wheat, faba bean, or pea with six rows per strip, with 25 cm between rows 2 to 5 and 20 cm between rows 1 and 2, and between rows 5 and 6, to avoid the tractor wheel tracks; (c) strip intercrops with three rows of maize alternating with six rows of wheat, faba bean, or pea; (d) strip intercrops consisting of a bi-specific combination of wheat, faba bean, and pea. Sowing was done such that each species strip had a 150 cm growing space. In intercrop maize, rows 1 and 3 were border rows and row 2 was an inner row of the strip, while in the intercrops of other species, rows 1 and 6 were border rows of the strip, rows 2 and 5 were inner row I, and rows 3 and 4 were inner row II. In intercrops, the maize strip had a border row proportion of 2/3, and the strips of wheat, faba bean, and pea had a border row proportion of 1/3.

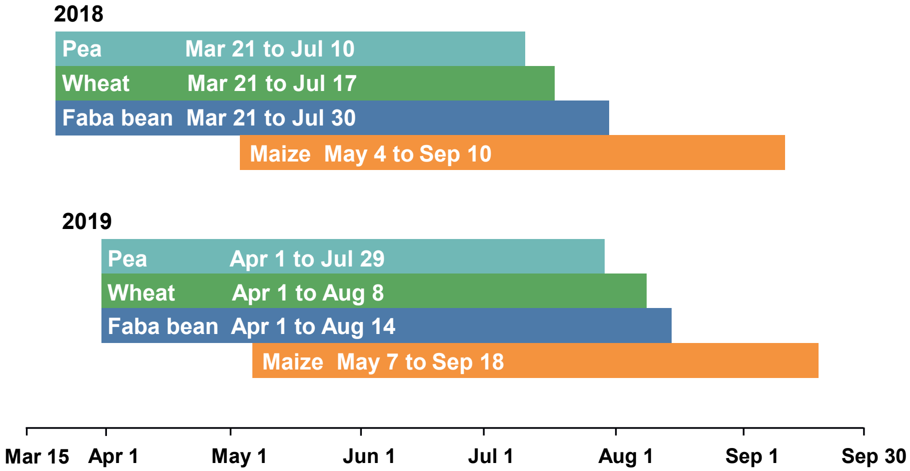


Fig. 2.3 Growing periods (from sowing to harvesting) of maize, wheat, faba bean, and pea in 2018 and 2019. In 2019, the later sowing of early species extended the period of co-growth, aggravated competition, and reduced temporal complementarity.

In relay intercrops, the growing periods of the two species overlapped only partially. Relay intercrops thus show 'temporal niche differentiation' (TND) that can be quantified as (Yu et al., 2015):

$$\text{TND} = 1 - \frac{T_{\text{overlap}}}{T_{\text{system}}} \qquad \text{(Eq. 2.1)}$$

where T_{overlap} is the co-growth duration of two species, and T_{system} is the total growth duration of the intercropping system.

Due to a longer period of co-growth in 2019, the relay intercrops had larger TND in 2018 than in 2019 (0.57 vs. 0.45 for maize/wheat, 0.50 vs. 0.42 for maize/faba bean, and 0.61 vs. 0.51 for maize/pea). The simultaneous intercrops had much lower TND values than the relay intercrops and they were similar for the same system in the two years (0.10 vs. 0.04 for faba bean/wheat, 0.15 vs. 0.12 for faba bean/pea, and 0.06 vs. 0.08 for wheat/pea).

Potassium (K) and phosphorus (P) fertiliser was applied homogeneously over the whole field before the first sowing (i.e., sowing of wheat, faba bean, and pea). The dose of K was 87 kg K ha^{-1} in both years, while P was applied at a rate of 29 kg P ha^{-1} in 2018 and 34 kg P ha^{-1} P_2O_5 in

2019 (Table S2.2). The amount of N fertiliser for each species was based on recommendations for arable crop fertilisation in the Netherlands for non-organic agriculture (Ministerie van Landbouw, Natuur en Voedselkwaliteit, 2019). Legumes received only a 'starter' input of 20 kg N ha^{-1}, three weeks after sowing in 2018 and two weeks after sowing in 2019. After considering the residual mineral N (approx. 10 to 20 kg N ha^{-1}) and N release expected from soil organic matter during the growing season in the top 30 cm soil (approx. 90 kg N ha^{-1}), wheat was given 125 kg N ha^{-1}, and maize 170 kg N ha^{-1}, in both years (Table S2.2). Fertiliser input in wheat and maize was given in two splits. All N fertiliser in monocrops and intercrops was applied next to the rows by a machine (ENTI Co., the Netherlands), except the N fertiliser of the second split in maize, which was applied by hand. Species strips in intercrops received the same fertilisation as monocrops. Supplementary water was applied by sprinkler from June to August whenever water storage in the top 25 cm soil layer was close to 25 mm (Fig. S2.1).

2.2.2 Measurements: final harvest

All species were harvested at maturity. Two neighbouring species strips in the middle of each intercropping plot and one species strip in the middle of each monocropping plot were selected for harvest. 4 m of each row in the middle of a single species strip was harvested and processed separately. For pea in 2018, 3 m was harvested. After harvesting, the samples of wheat, faba bean, and pea were immediately dried against a drying wall (ACT-20, Omnivent Co., the Netherlands) with artificial ventilation at 25 °C until an approximate moisture content of 15% was reached. Then, wheat, faba bean, and pea plants were disassembled into stems with leaves, grains, and chaffs for wheat or pod shells for faba bean and pea, and these partitions were weighed. Maize samples were disassembled immediately after harvesting, separating stems with leaves, grains, and cob shafts and husks. Fresh weights were determined.

A subsample was randomly taken from each partition of each sample of each species to determine the moisture percentage after drying at 105 °C for 48 h, allowing to convert fresh weights to dry weights. Vegetative biomass was defined as the sum of all partitions at final harvest other than grains. Harvest index was calculated by dividing grain yield by total biomass.

2.2.3 Data analysis

Land equivalent ratio (LER; Willey and Rao, 1980) was used to assess the land productivity of intercrops relative to monocrops:

$$\mathrm{LER} = \mathrm{pLER}_1 + \mathrm{pLER}_2 = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \qquad \text{(Eq. 2.2)}$$

where the pLER_i is the partial land equivalent ratio of species i, Y_i is the grain yield or vegetative biomass (per unit area of the whole intercrop) of species i in the intercrop, and M_i is the grain yield or vegetative biomass (per unit area of the monocrop) of species i in the monocrop. An LER greater than one indicates that the monocrops need more land than the intercrop to produce the same grain yield or vegetative biomass for each species, i.e., the intercrop uses land more efficiently than the monocrops. The LER is also the relative yield total, and the pLER is the relative yield of a species in an intercrop compared to its monocrop.

The relative yield gain (or loss) of a species is the difference between its relative yield and its relative density:

$$\Delta RY_i = RY_i - RD_i \qquad \text{(Eq. 2.3)}$$

where ΔRY_i is the relative yield gain (or loss) of a species in an intercrop compared to its monocrop, RY_i is the relative yield of a species in an intercrop to its monocrop, and RD_i is the relative density of a species in an intercrop to its monocrop, which is 0.5 in the experiments described here.

The following equality holds (Loreau and Hector, 2001):

$$\mathrm{LER} = \mathrm{pLER}_1 + \mathrm{pLER}_2 = (\Delta RY_1 + RD_1) + (\Delta RY_2 + RD_2) = \Delta RY_1 + \Delta RY_2 + 1 \qquad \text{(Eq. 2.4)}$$

Competitive ratio (CR; Willey and Rao, 1980) was used to assess the competitiveness of one species compared to its companion species in an intercrop:

$$\mathrm{CR}_1 = \frac{\mathrm{pLER}_1}{\mathrm{pLER}_2} \times \frac{p_2}{p_1}; \mathrm{CR}_2 = \frac{\mathrm{pLER}_2}{\mathrm{pLER}_1} \times \frac{p_1}{p_2} \qquad \text{(Eq. 2.5)}$$

where CR_1 and CR_2 are the competitive ratios of species 1 and species 2, and p_i is the area proportion of species i in the intercrop, which is 0.5 for all species in the experiments described here, so the formulas simplify to:

$$\mathrm{CR}_1 = \frac{\mathrm{pLER}_1}{\mathrm{pLER}_2}; \mathrm{CR}_2 = \frac{\mathrm{pLER}_2}{\mathrm{pLER}_1} = \frac{1}{\mathrm{CR}_1} \qquad \text{(Eq. 2.6)}$$

If $\mathrm{CR}_i > 1$, species i is more competitive than its companion species. Since CR_1 and CR_2 are each other's reciprocal, CR of only one of the species was calculated for a particular intercrop.

The net effect (NE; Loreau and Hector, 2001) was used to assess the absolute yield difference between the observed yield of a species in the intercrop and the expected yield, based on monocrop yields and land share:

$$\mathrm{NE} = \mathrm{NE}_1 + \mathrm{NE}_2 = (Y_1 - EY_1) + (Y_2 - EY_2) \qquad \text{(Eq. 2.7)}$$

where Y_i is the grain yield or vegetative biomass (per unit area of the whole intercrop) of species i and EY_i is the *expected* grain yield or vegetative biomass. This expected yield in the intercrop is calculated as:

$$EY_i = M_i \times p_i \qquad \text{(Eq. 2.8)}$$

where M_i is the grain yield or vegetative biomass of the monocrop i and p_i is the area proportion of species i in the intercrop (0.5 for all species).

Overyielding of an intercrop is defined as NE > 0, while overyielding of a species in an intercrop is defined as NE_1 (for species 1) or NE_2 (for species 2) greater than zero. Overyielding of a species requires pLER > 0.5 (i.e., both the absolute and relative yields are greater than expected) but overyielding of the system does not require an LER greater than one, because overyielding in absolute terms is also determined by the selection effect which depends on the correlation (positive or negative) between relative yield gain, ΔRY, and monocrop yield (Loreau and Hector, 2001).

Statistical analyses were conducted in R (R Core Team, 2022). Linear mixed effects models were fitted to analyse the effects of species combination and experimental year on the grain yield, vegetative biomass, harvest index, the pLER, and the NE of each species, and the LER and the NE of the intercrops. The function 'lmer' from the package 'lme4' was used to fit the linear mixed models (Bates et al., 2015). Species combination, experimental year, and their interaction were specified as fixed effects (all categorical), while block (categorical) was specified as a random effect within year to describe the inter-block variance within each year (Eq. 2.9).

$$Y_{ijk} = Y + \beta_i + \tau_j + \beta\tau_{ij} + b_{ik} + \epsilon_{ijk} \qquad \text{(Eq. 2.9)}$$

where i, j, and k represent year ID, species combination ID, and block ID; Y is the overall population mean of the relevant response variable; β_i is the year effect; τ_j is the species combination effect; $\beta\tau_{ij}$ is the interaction between year and species combination; b_{ik} is a random block effect nested in year; ϵ_{ijk} is a plot-level random error term; Y_{ijk} is the sample mean of the response variable of species combination j in block k in year i. For notation, see Makowski et al. (2019).

The relationships between TND as a continuous predictor and LER and NE as indices for intercrop performance were investigated. Thereby, four categorical covariables were defined to evaluate whether the effect of TND differed between intercrops with or without a legume species (0/1), between intercrops that could be characterised as cereal/legume combinations or not (0/1), between intercrops with or without maize (0/1), or even between all different species combinations, i.e., whether each species combination had specific relationships between TND and LER, and between TND and NE (a categorical covariable with six levels). For each covariable, models were fitted with and without the interaction between TND and the covariable. All models and the simplest candidate model (only TND as the predictor) were compared (Table 2.1). Akaike's information criterion (AIC; Akaike, 1998) in the function 'anova' was used to select the optimal model. For the models with very close AIC values, the simpler model was selected to avoid overfitting.

A categorical variable 'Combination_Row' was defined to identify a specific row of a species in a specific species combination, to study intercropping border row effects on grain yield, vegetative biomass, and harvest index of each species. Linear mixed models were then fitted to analyse border row effects, with experimental year and 'Combination_Row' and their interaction as fixed effects, and block as a random effect nested in year (Eq. 2.9). Multiple comparisons of means within an individual year and across two years for treatment effect were conducted using Tukey's Post-Hoc Test ($P = 0.05$) in the package 'emmeans' (Lenth, 2021). The package 'ggplot2' was used for data visualisation (Wickham, 2016).

Table 2.1 Specification of the models to determine the relationship between LER (or NE) and TND. In the equations, i, j, and k represent year ID, species combination ID, and block ID. In all models, b_{ik} is a random block effect nested in year, and ϵ_{ijk} is a plot-level random error term. Meaning of the categorical covariables: Legume.Incl.: an intercrop comprised or comprised not a legume component; Cereal.Legume: an intercrop was a cereal/legume combination or not (contrasting maize/faba bean, maize/pea, faba bean/wheat, and wheat/pea with maize/wheat and faba bean/pea); Maize.Incl.: an intercrop comprised or comprised not maize; Comb.: the categorical covariable representing all six species combinations as levels.

Models	Equations	Degrees of freedom
1	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + b_{ik} + \epsilon_{ijk}$	4
2	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Legume.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	5
3	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Cereal.Legume}_{ijk} + b_{ik} + \epsilon_{ijk}$	5
4	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Maize.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	5
5	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Legume.Incl.}_{ijk} + \beta_3 * \mathrm{TND}_{ijk} * \mathrm{Legume.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	6
6	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Cereal.Legume}_{ijk} + \beta_3 * \mathrm{TND}_{ijk} * \mathrm{Cereal.Legume}_{ijk} + b_{ik} + \epsilon_{ijk}$	6
7	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Maize.Incl.}_{ijk} + \beta_3 * \mathrm{TND}_{ijk} * \mathrm{Maize.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	6
8	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Comb.}_{ijk} + b_{ik} + \epsilon_{ijk}$	9
9	$\mathrm{LER(or\ NE)}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Comb.}_{ijk} + \beta_3 * \mathrm{TND}_{ijk} * \mathrm{Comb.}_{ijk} + b_{ik} + \epsilon_{ijk}$	14

2.3 Results

2.3.1 Grain yield, vegetative biomass, and harvest index per species strip

Maize

At harvest, maize had 25% higher ($P = 0.014$) and 26% higher ($P = 0.010$) grain yield in intercrops with wheat and pea than expected, while it had a similar grain yield as expected in the intercrop with faba bean in 2018, and it had a similar grain yield as expected in all intercrops in 2019 (Fig. 2.4 i; Table S2.3 i). In both years, maize vegetative biomass (i.e., stover) per unit area of maize, was higher than expected in intercrops with wheat and pea ($P < 0.001$), but there was no significant increase in vegetative biomass in the intercrop with faba bean. The harvest index of maize was similar among treatments in both years.

Wheat

Wheat had on average higher grain yield than expected in the maize/wheat intercrop, lower grain yield than expected in the faba bean/wheat intercrop, and similar grain yield, compared to expected, in the wheat/pea intercrop (Fig. 2.4 ii; Table S2.3 ii). Wheat overyielding with maize was significant in 2018 but not in 2019. Wheat underyielding with faba bean was found in both years, averaging 36% lower than the monocrop wheat ($P < 0.001$). Lower vegetative biomass of wheat with faba bean was only significant in 2019. Averaged over two years, wheat harvest index was 20% lower in the faba bean/wheat intercrop than in the monocrop wheat ($P < 0.001$).

Faba bean

Averaged over two years, faba bean in the maize/faba bean intercrop produced 30% higher grain yield than expected ($P < 0.001$; Fig. 2.4 iii; Table S2.3 iii). The grain yield increase of faba bean in the faba bean/wheat intercrop was 14% in 2018 ($P = 0.363$) and 24% in 2019 ($P = 0.095$), but not statistically significant in either year. The grain yield increase in the faba bean/pea intercrop was also substantial but not significant in 2018 (18%; $P = 0.191$) and 2019 (13%; $P = 0.559$). Faba bean harvest index was similar across treatments within the same year, except for faba bean with wheat in 2019, which had a significantly higher harvest index than the monocrop faba bean ($P = 0.040$).

Pea

Pea had on average over the two years 41% lower grain yield in the faba bean/pea intercrop than in the monocrop pea ($P < 0.001$; Fig. 2.4 iv; Table S2.3 iv). Pea grain yield in the maize/pea intercrop in both years and in the wheat/pea intercrop in 2018 was similar to expected, but significantly lower than expected with wheat in 2019. Pea vegetative biomass was reduced in the faba bean/pea intercrop in 2019 but not in 2018. Compared to the monocrop, pea had a similar harvest index when intercropped with wheat in both years and with maize in 2018, but a significantly lower harvest index with faba bean in both years and with maize in 2019.

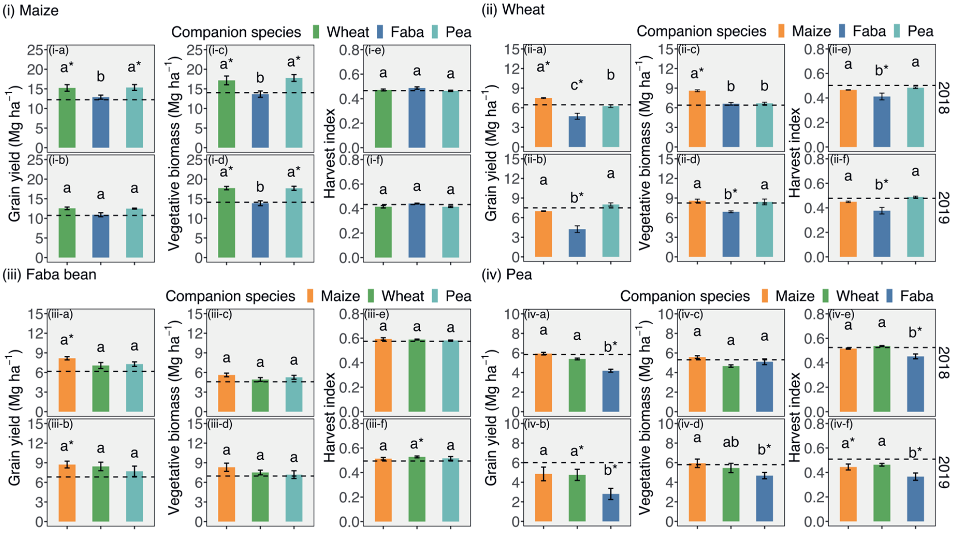


Fig. 2.4 Grain yield, vegetative biomass, and harvest index of maize (i), wheat (ii), faba bean (iii), and pea (iv) when growing with different companion species in 2018 (a, c, e) and 2019 (b, d, f). Grain yield and vegetative biomass are expressed per unit species area of the species to allow comparison of intercrops and monocrops. Colours represent the companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Panels i–iv indicate different focal species. The dashed lines represent the focal species in its monocrop (the expected values of the species in the intercrops if there were no intercropping effects). Error bars represent standard errors of the means. Multiple comparisons of means were conducted within an individual year using Tukey's Post-Hoc Test using the 'emmeans' function (i.e., *emmeans*(*Response variable, pairwise* ~ *Combination* | *Year*)). Shared letters denote non-significant differences among intercrops within an individual year. Asterisks denote significant differences between the intercrops and monocrop within an individual year according to Tukey's Post-Hoc Test ($P \leq 0.05$). Further details showing the multiple comparisons across two years are presented in Table S2.3.

2.3.2 LER, NE, and CR for grain yield and vegetative biomass

In 2018, the grain yield LER ranged from 0.95 ± 0.04 (faba bean/pea) to 1.22 ± 0.05 (maize/wheat), while in 2019, it ranged from 0.80 ± 0.08 (faba bean/pea) to 1.15 ± 0.01 (maize/faba bean) (Fig. 2.5; Table S2.4 i). In 2018, the relay systems with maize all obtained grain yield LER values significantly higher than one, but in 2019, only the maize/faba bean intercrop did. Simultaneous intercrops without maize, in contrast, obtained grain yield LER values close to one and usually below one, though in all cases except one not significantly below one. The faba bean/pea intercrop in 2019 had a grain yield LER that was significantly lower than one.

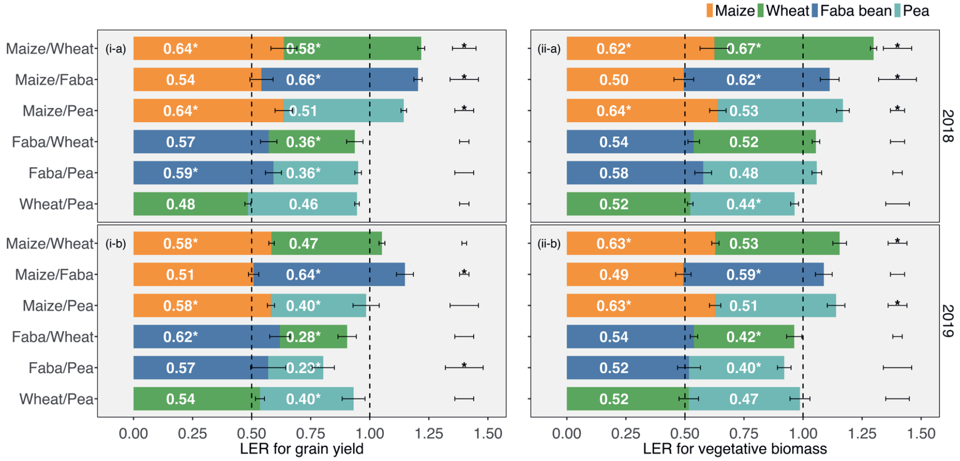


Fig. 2.5 Land equivalent ratio of intercrops and partial land equivalent ratio of component species for grain yield (i) and vegetative biomass (ii) in six species combinations in 2018 (a) and 2019 (b). Colours represent four different component species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Error bars attached to the bars indicate the standard errors of pLER. Error bars at the right of the panels indicate the standard errors of LER. The asterisks denote significant differences from 0.5 for pLER values and from one for LER values by examining if 0.5 (or one) was located outside the 95% confidence interval of pLER (or LER). Further details are presented in Table S2.4.

In the relay intercrops, combining maize with the legume species faba bean or pea did not result in a higher LER than combining maize with the non-legume wheat. Likewise, the LER was similar in the simultaneous intercrops when faba bean and pea were combined with each other (legume/legume) or with wheat (cereal/legume).

In the maize/wheat intercrop in 2018, both maize and wheat had a pLER for grain yield and vegetative biomass significantly exceeding the relative density of 0.5. In four other cases of relay intercropping (maize/faba bean in both years, maize/pea in 2018, and maize/wheat in 2019), one species had a pLER significantly higher than 0.5, and the other had a pLER close to 0.5. In one case, the maize/pea intercrop in 2019, maize had a pLER significantly higher than 0.5, and pea had a pLER significantly lower than 0.5. In the intercrops with faba bean, faba bean had a grain yield pLER higher than its companions, with the grain yield pLER of maize close to 0.5, and those of wheat and pea were substantially lower than 0.5.

The intercrop and species NE values showed identical trends to the LER values and pLER values. Relay intercrops had positive NE on grain yield, but the other intercrops had near zero NE on grain yield (Fig. 2.6; Table S2.5).

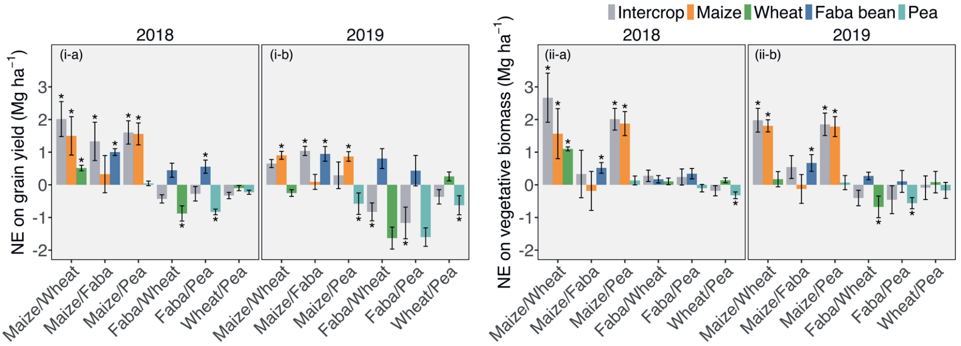


Fig. 2.6 Net effects on grain yield (i) and vegetative biomass (ii) in 2018 (a) and 2019 (b) of intercrops (grey) and the component species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Error bars represent standard errors of the means. The asterisks denote significant differences from zero by examining if zero was located outside the 95% confidence interval of NE. Further details are presented in Table S2.5.

In relay intercrops with maize, faba bean had a CR for grain yield higher than one, but only significant in 2018, wheat had a CR for grain yield lower than one, but only significant in 2019, pea had a CR for grain yield significantly lower than one in both years (Table 2.2). In intercrops with faba bean, faba bean was significantly more competitive than wheat and pea in both years. In wheat/pea, wheat and pea were equally competitive in both years.

Table 2.2 Competitive ratios (CR) for grain yield and vegetative biomass in 2018 and 2019. Intercrops are indicated by the focal species (columns) and the companion species (rows). Since CRs of the two species are each other's reciprocal, only the CRs of the focal species are shown. Asterisks denote significant differences from one for CRs: ***$P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$, (.) $P \leq 0.1$ (Student's t-test).

		Competitive ratio for grain yield			Competitive ratio for vegetative biomass		
Year	Companion species	Focal species			Focal species		
		Wheat	Faba bean	Pea	Wheat	Faba bean	Pea
2018	Maize	0.96 ± 0.10	1.27 ± 0.12 (.)	0.81 ± 0.04 **	1.13 ± 0.11	1.27 ± 0.07 *	0.84 ± 0.07 (.)
	Wheat	-	1.70 ± 0.27 (.)	0.96 ± 0.04	-	1.04 ± 0.05	0.85 ± 0.03 **
	Faba bean		-	0.61 ± 0.04 ***		-	0.84 ± 0.04 *
2019	Maize	0.80 ± 0.03 **	1.27 ± 0.12	0.69 ± 0.09 *	0.84 ± 0.04 *	1.23 ± 0.13	0.82 ± 0.07 (.)
	Wheat	-	2.36 ± 0.52 (.)	0.75 ± 0.11	-	1.30 ± 0.14	0.93 ± 0.11
	Faba bean		-	0.43 ± 0.10 *		-	0.79 ± 0.07 (.)

2.3.3 Relationships between TND and LER (and NE) for grain yield

Model selection indicated that Model 8 was the most supported model to describe the data, both for LER and NE (Table S2.6). This model implies that LER and NE increased with TND with a common slope across all species combinations (no interaction), while the six different species combinations had different intercepts. LER increased by 1.08 units per unit TND and NE increased by 9.33 Mg ha^{-1} per unit TND (Fig. 2.7). Model selection did not support models that contrasted intercrops with maize vs. those without, or with a legume vs. without, or were cereal/legume combinations vs. were not. This result of model selection confirmed the importance of TND and its uniform effect across combinations, but also highlighted that each species interaction brought something particular to the LER and NE, and this 'plant team' effect could not be simplified to the presence of a particular species or species groups, such as a cereal or a legume or a cereal/legume combination.

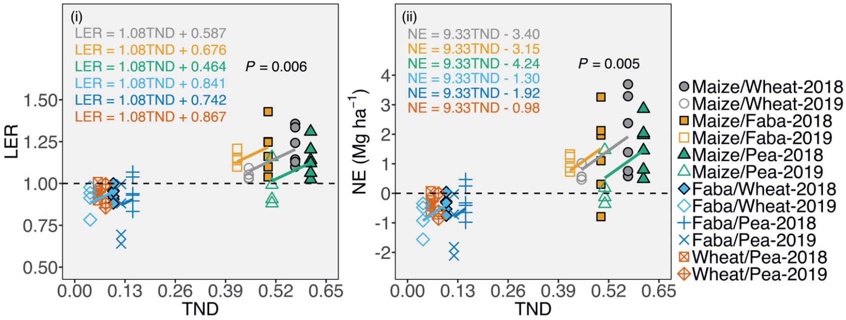


Fig. 2.7 Relationships between TND and LER (i) and NE (ii) for grain yield. The equations and symbols are in the same colour for a particular species combination. The *P*-values are related to the slopes, indicating whether they are significantly different from zero (F-test).

2.3.4 Border row effects

In each monocrop, rows were similar to each other, except for the rows 1 and 6 of the harvested strip in the monocrop wheat in 2019, which had 33% higher ($P < 0.001$) vegetative biomass than the rows 2 and 5, and 24% higher ($P = 0.005$) vegetative biomass than the rows 3 and 4 (Fig. S2.2). However, there was no row effect on grain yield per row in any of the monocrops in any year, including the wheat in 2019. We used the average grain yield, vegetative biomass, and harvest index of monocrop rows as the expected value for intercrop rows.

Relay intercrops

Border rows of maize strips had a 22% higher grain yield than expected in the maize/wheat intercrop ($P = 0.026$) and a 31% higher grain yield than expected in the maize/pea intercrop ($P < 0.001$) in 2018 (Fig. 2.8 i; Table S2.7 i). In 2019, however, no such yield increases occurred. In the maize/faba bean intercrop, border row maize had a yield similar to the monocrop maize in both years. Positive border row effects were observed for faba bean grain yield in the maize/faba bean intercrop in both years (Fig. 2.8 iii; Table S2.7 iii). Border row faba bean in the maize/faba bean intercrop on average over two years had a 43% higher grain yield than expected ($P < 0.001$). In 2018, border row wheat had a 42% higher grain yield in the maize/wheat intercrop than expected ($P < 0.001$; Fig. 2.8 ii; Table S2.7 ii). In 2019, however, no such yield increase was found. Border row wheat in the maize/wheat intercrop on average over two years had a 13% lower harvest index than the monocrop wheat ($P < 0.001$). No border row effects on grain yield were observed in pea, even though border row pea produced a 47% higher vegetative biomass in the maize/pea intercrop than expected in 2019 ($P < 0.001$; Fig. 2.8 iv; Table S2.7 iv).

Simultaneous intercrops

In the faba bean/wheat intercrop in 2019, border row faba bean had a 66% higher grain yield than expected ($P < 0.001$), while no such a yield increase was found in 2018 (Fig. 2.8 iii; Table S2.7 iii). In the faba bean/pea intercrop, border row faba bean had a grain yield increase in both years, with on average over two years a 32% higher grain yield than expected ($P < 0.001$). The grain yields of intercropped wheat and pea were decreased in all rows in the intercrops with faba bean in both years, and the border rows had the largest decreases (Fig. 2.8 ii and iv; Table S2.7 ii and iv). Averaged over two years, the grain yield in the border rows of intercropped wheat and pea was reduced by 47% and 52%, respectively ($P < 0.001$). The harvest indices of wheat and pea were also substantially decreased in all intercrop rows. In the wheat/pea intercrop in 2019, border row wheat had a 22% higher grain yield and a 22% higher vegetative biomass than expected ($P < 0.001$), but no such increases were found in 2018 (Fig. 2.8 ii; Table S2.7 ii). The harvest index of wheat was 10% lower in border row wheat in the wheat/pea intercrop than expected in 2018 ($P = 0.015$), but no such a decrease was found in 2019. The harvest index of pea was 20% lower in border row pea in the wheat/pea intercrop than in the monocrop pea in 2019 ($P = 0.014$), but no such a decrease was found in 2018 (Fig. 2.8 iv; Table S2.7 iv).

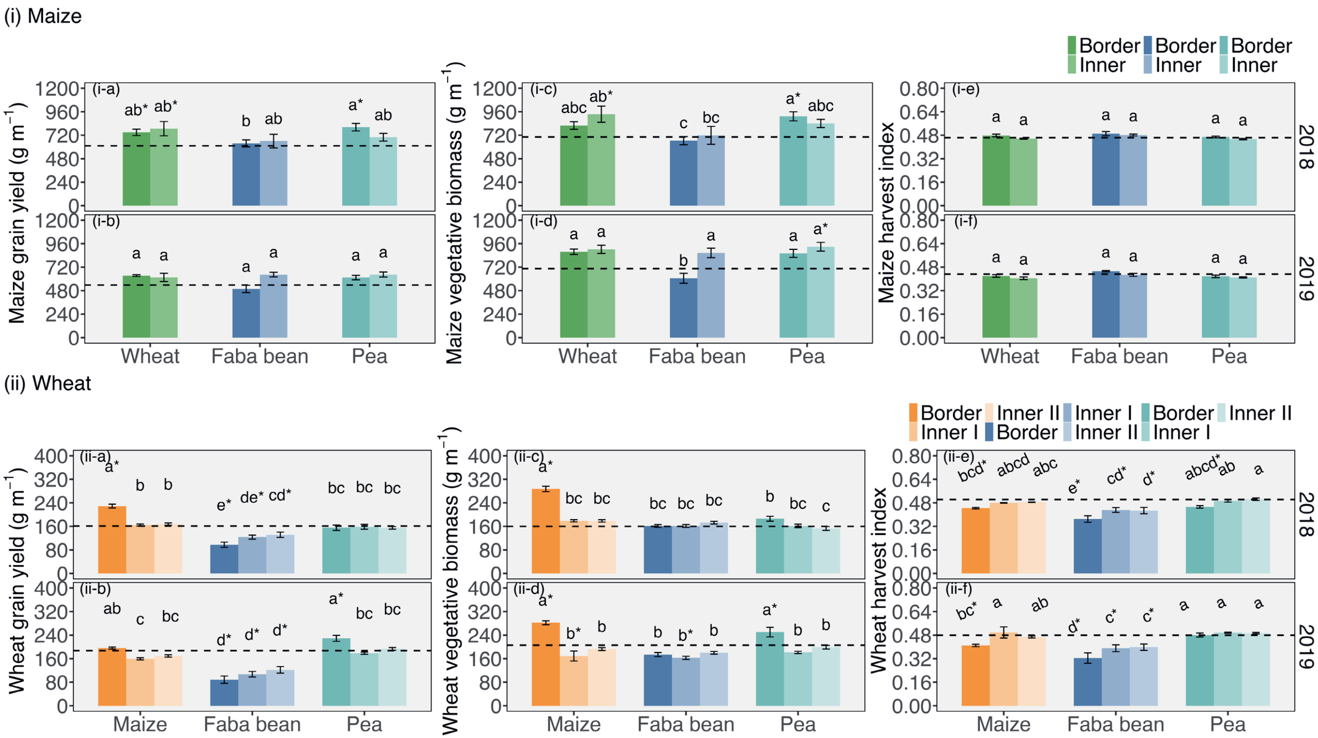
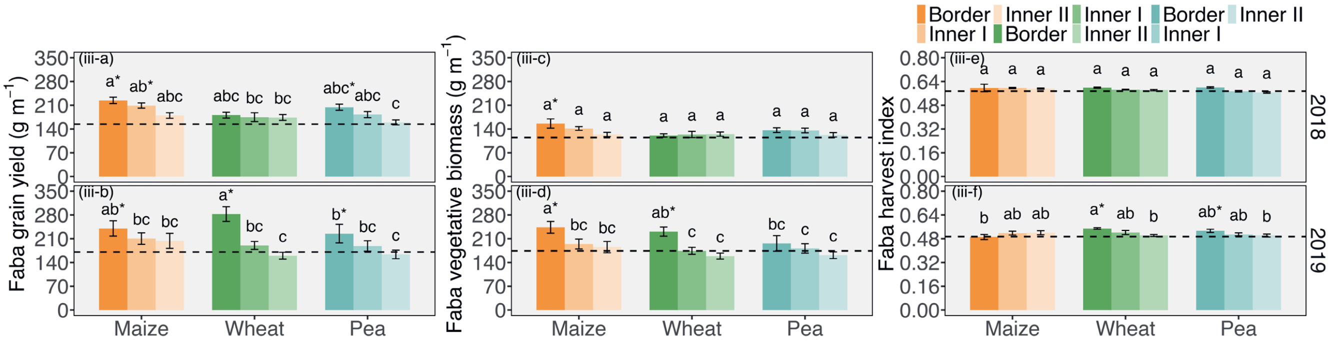


Fig. 2.8 Grain yield, vegetative biomass, and harvest index of different rows in intercrops for maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a, c, e) and 2019 (b, d, f). Companion species are indicated along the X-axis. Dashed lines represent grain yield, vegetative biomass, and harvest index of the monocrop of the focal species indicated along the Y-axis (these monocrop values represent the expected values of intercrop rows). Each colour intensity represents a different row. Error bars represent standard errors of the means. Multiple comparisons of means were conducted within an individual year using Tukey's Post-Hoc Test in the 'emmeans' function (i.e., *emmeans*(*Response variable, pairwise* ~ *Combination_Row* | *Year*)). Shared letters denote non-significant differences among 'Combination_Row's within an individual year. Asterisks denote significant differences between 'Combination_Row's and the monocrop within an individual year according to Tukey's Post-Hoc Test ($P \leq 0.05$). Further details showing the multiple comparisons across two years are presented in Table S2.7.

(iii) Faba bean



(iv) Pea

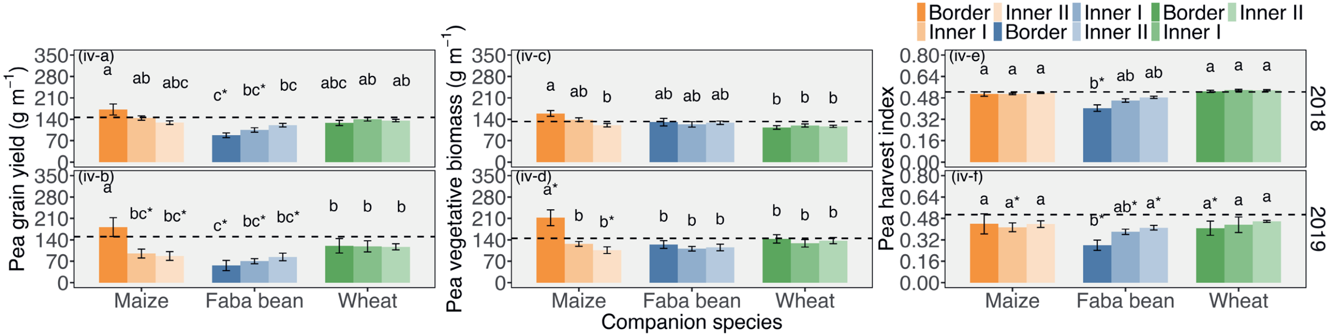


Fig. 2.8 (continued) Grain yield, vegetative biomass, and harvest index of different rows in intercrops for maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a, c, e) and 2019 (b, d, f). Companion species are indicated along the X-axis. Dashed lines represent grain yield, vegetative biomass, and harvest index of the monocrop of the focal species indicated along the Y-axis (these monocrop values represent the expected values of intercrop rows). Each colour intensity represents a different row. Error bars represent standard errors of the means. Multiple comparisons of means were conducted within an individual year using Tukey's Post-Hoc Test in the 'emmeans' function (i.e., *emmeans*(*Response variable, pairwise ~ Combination_Row | Year*)). Shared letters denote non-significant differences among 'Combination_Row's within an individual year. Asterisks denote significant differences between 'Combination_Row's and the monocrop within an individual year according to Tukey's Post-Hoc Test ($P \leq 0.05$). Further details showing the multiple comparisons across two years are presented in Table S2.7.

2.4 Discussion

Here we explored production effects of narrow strip intercropping for various species combinations including C_3- and C_4-cereals and legumes in conventional farming under Western-European growing conditions in the Netherlands. Despite substantial inter-year variability, relay intercrops consistently showed positive responses: they achieved LERs greater than one and NEs greater than zero. Such advantages in land use and yield production were not found in simultaneous intercrops. Across all intercrops, TND was an important driving factor for LER and NE, but there were also differences in LER and NE related to the particular species combinations. Under the strip- and species-specific N application strategy of this study, the combinations of a cereal and a legume did not achieve consistently higher LER or NE values than intercrops that did not combine a cereal and a legume, e.g., maize/wheat and faba bean/pea.

The LER and NE values showed that relay strip intercrops grown with sufficient water and species-specific N inputs used land more efficiently than their corresponding monocrops (Figs 2.5 and 2.6). The positive effects of TND on LER and NE were significant in all intercrops (Fig. 2.7). Our results and those of previous studies on maize/wheat relay systems (Gou et al., 2016; Zhu et al., 2015) indicate that the globally positive effect of temporal complementarity on land use efficiency (Yu et al., 2015) and absolute yield increases (Li et al., 2020b) in C_3/C_4 mixtures with sufficient resources is therefore more generally valid for conventional farming in the Netherlands. In other words: temporal complementarity is equally relevant for efficient land use in cereal/legume mixtures (maize/faba bean and maize/pea) as in a cereal/cereal mixture (maize/wheat), while combinations without temporal complementarity under the conditions of the study did not result in agronomically relevant overyielding. Border rows of strips were affected the most by intercropping (Fig. 2.8). We found in general no differences in grain yield, vegetative biomass, and harvest index between rows within the monocrops, with one exception: the vegetative biomass of wheat was higher in the outer rows of the strip in 2019. This was the only difference found between rows in the monocrops, and may have been due to chance, or to an effect of the wheel tracks, which caused some soil compaction which could be advantageous under drought conditions.

A larger TND grants each species a longer period to grow alone and allows the exploitation of all the available light and soil resources by a single species for a longer time, provided season length is sufficient. A larger TND also enlarges the proportion of the growing season that there is a crop in the field because it is achieved by sowing the early-sown species earlier or harvesting the late-harvested species later. The LER-increasing effect of a large TND is strongest at high N input (Yu et al., 2015). Light is a key limiting resource in conventional farming because water and nutrients are supplied in quantities that aim to alleviate constraints, hence temporal complementarity, which increases light capture per species and of the system as a whole, is expected to be of major importance in conventional farming (Gallagher and Biscoe, 1978; Monteith, 1977). Such temporal complementarity leads to a pLER greater than expected based on the relative density and a positive NE for both species. All in all, the entire intercrop is a ‘win-win’ system having aggregate advantages.

In addition to increased light capture, increased light conversion efficiency (also known as the light use efficiency, LUE) is expected, because maize as a C_4 plant has greater photosynthetic capacity during high summer temperatures while C_3 plants can have enhanced LUE in the shading of maize (Gou et al., 2017a; Liu et al., 2017). However, an enhanced maize canopy LUE is not guaranteed even though higher leaf photosynthesis has been found in intercropped maize (Gou et al., 2017a; Gou et al., 2018) because maize needs a long enough recovery growth period after harvest of a companion species (i.e., a large TND) to make full use of its photosynthetic capacity at the canopy level (Yu, 2016). Next to recovery from shading, also recovery from competition for nutrients like N might have played a role (Gou et al., 2018).

With lower TND in 2019 than in 2018, the relay intercrops obtained lower LER and NE values in 2019 than in 2018. The lower TND means that maize and the early-sown species had a longer co-growth period and thus experienced greater interspecific competition in 2019 than in 2018. As a result, the early species may not have captured adequate light during grain filling due to shading by maize, and maize may not have had enough recovery time to compensate for the effects of early competition with the early-sown companion species (Zhu et al., 2014). Thus, these results indicate that relay intercropping with maize under conditions of sufficient water and nutrients requires a sufficient TND to avoid shading on the early-sown species during its grain filling and enough recovery time after harvest of the early-sown species to let maize benefit from a ‘growing alone’ phase.

A sufficient TND and enough recovery time could be obtained by sowing the early species earlier or by sowing the late species later. However, at a specific location, the total number of growing degree days may constrain the TND that may be achieved. If the early species are spring cultivars as in the current study, premature sowing could cause low emergence or damaged seedlings because of frost. Maize could not mature if it is sown too late. Intercropping with winter-sown species could be explored as an option to increase the TND under Dutch climate conditions. Winter wheat that is harvested in mid-June, for instance, can offer maize a recovery period of approximately 10 weeks in relay intercropping in China, during which maize photosynthesis and root growth are stimulated (Ma et al., 2020). Using a winter wheat cultivar could possibly increase the LER in maize/wheat combinations. In contrast, maize in the present study only had a recovery period of six weeks after wheat had been harvested in 2019. The appropriate winter-sown species and the recovery time it can grant maize need to be explored under local climate conditions. Late maturing cultivars of the late species could also be considered to increase the TND (Mohammed et al., 2022).

Cultivating relay intercrops with a larger TND might limit options for growing subsequent or preceding crops in regions with a warmer winter, where the degree days allow a second crop to grow after harvest of the first crop, i.e., double cropping (Liang et al., 2022). For those regions, it is necessary to compare whole cropping systems and go beyond only comparing intercrops to their monocrops (Feng et al., 2017). Moreover, the lower intercepts of the relationships between LER (or NE) and TND in the relay intercrops as compared to the simultaneous intercrops (Fig. 2.7), suggest that the relay intercrops may be in some ways less complementary than the simultaneous intercrops. For instance, lodging of the late species due to the shading by the early species is a concern in relay intercrops (Cheng et al., 2020; Hussain et al., 2021). Designing a satisfactory TND requires comprehensive consideration of the species selection and the local production systems and climate, also considering possibilities under climate change.

Resource supply is a concern during recovery growth. N fertilisation to maize at harvesting of the early species in relay intercropping can improve maize recovery (Hu et al., 2016). In the present study, such a fertilisation strategy was not employed because European good agricultural practice aims to achieve low levels of mineral N left in the soil after harvest. Maize performance could probably be enhanced in our system, but this might also increase N surplus and N losses (Wang et al., 2022).

Under the strip- and species-specific fertilisation strategy applied in this study, the cereals received moderate N fertilisation, and the legumes received low starter N fertilisation. This strategy differs from the high-input strategy giving full fertilisation to both cereals and legumes which is often applied in China (Li et al., 2006; Ren et al., 2017; Zhang et al., 2020). It also differs markedly from the low-input strategy in organic agriculture in Europe, where N limitation is a key constraint to yield (Hauggaard-Nielsen et al., 2008; Hauggaard-Nielsen et al., 2009). We adopted this species-specific fertilisation strategy to avoid over-fertilisation of the legumes, and achieve policy targets of lowering N application in agriculture, and at the same time avoiding under-fertilisation of the cereals to maintain high yields. Such an approach is in accordance with principles of good agricultural practice in conventional farming. It is a suitable strategy to determine whether intercropping could be an option for conventional growers in Western Europe, as moderation of N input and safeguarding of yield levels are both important.

We expected that legumes would not contribute much to overyielding with the chosen levels of N input in the cereals, because we removed the N stress. We also grew the faba bean/pea intercrop as a negative control for the cereal/legume intercrops and confirmed that simultaneously grown legumes did not result in intercropping benefits, but neither did simultaneously grown cereal/legume intercrops, indicating that complementarity for N acquisition was not influential in the studied simultaneous systems. The observed yield advantages for maize were comparable when grown with wheat or the legumes and therefore most likely due to its later sowing and harvesting rather than to any legume-specific interactions.

The mineral N application in the present study ensured sufficient N input to meet the demand of cereals, and thus the cereals did not benefit much from the legumes compared to those under low to zero N input in organic farming where the competition for mineral N can be alleviated by legume N fixation (Bedoussac et al., 2015). Nevertheless, root foraging of species in their neighbouring strips can occur (Zhang et al., 2022) and could affect species access to the designed N fertiliser amount (Liu et al., 2020), but we did not identify species interactions that suggested this played a large role. Even if maize and wheat extended their roots into the neighbouring strip as earlier reported for fully fertilised intercropping (Gao et al., 2010; Li et al., 2006; Liu et al., 2020), the amount of mineral N applied in the legume strip would largely be taken up during early legume growth, leaving little N for the neighbouring cereals. On the other hand, it is entirely possible that legumes acquired N from the neighbouring cereal strips.

This may have played a role particularly in cereal/faba bean intercrops because the biomass growth of faba bean was large, thus augmenting its N demand.

Legumes still played a positive role in the relay intercrops because the land use efficiency and the absolute yield were increased with a much lower N fertilisation rate than used in the maize/wheat intercrop. Pea in 2019 was an exception as it did not result in land use and yield advantages in the maize/pea intercrop. Pea lodged in June 2019 because of heavy rain. The young maize plants could not support the lodging pea and this problem was therefore more serious in the intercrop than in the monocrop in which the pea plants were intertwined and thus supported each other more efficiently than they did in the narrow strips. In the intercrop with maize, pea plants leaned over to one side of the strip, whereas maize plants remained erect. The lodging resulted in large grain yield decreases in inner rows I and II of pea (Fig. 2.8 iv-b), which were squeezed by the lodging border rows. This suggests that legumes having firm stems, such as faba bean, are more suited for strip intercropping with maize than bushy plant types that may be more prone to lodging. Pea is a reliable companion species when grown in a full mixture in which its canopy can be supported by a companion cereal species (Barillot et al., 2012).

In contrast with the ‘win-win’ situation in the relay intercrops, the gain in pLER or NE of one species went along with a reduction in pLER or NE in the companion species in the simultaneous intercrops (Figs 2.5 and 2.6). Competition for light is a plausible reason for the ‘win-lose’ situation in the simultaneous intercrops, especially when faba bean was grown with wheat or pea. The faba bean cultivar ‘Fanfare’ is a fast-growing and tall-statured cultivar. It has been demonstrated to have a large total root length (Homulle, 2020) and rapid ground cover (Andersen et al., 2020). It has also been documented with the highest and most stable yield among various cultivars studied in Belgium, Denmark, and Finland (Segers et al., 2022; Skovbjerg et al., 2020). Given the high competitiveness of the studied faba bean cultivar, a less competitive cultivar with a less vigorous canopy and a dwarf stature could be an alternative (Hughes et al., 2020).

In the present study, faba bean received a starter N fertiliser of 20 kg N ha^{-1}. The applied N and the N released from soil significantly stimulated the growth of faba bean, leading to a tall canopy. At full canopy cover, the light is fully captured in both monocrops and intercrops, and competition for light then becomes a zero-sum game in intercrops where the gain of one species and the loss of the other cancel out for zero net benefit. The faba bean plants were tall, growing fast and thus gradually shaded the shorter wheat and pea plants. This likely resulted in lower light capture by wheat and pea. The low grain yield and harvest index of wheat and pea indicate constraints during grain filling, which may be due to shading by faba bean (Fig. 2.4 ii and iv). The border rows suffered the most due to the close proximity (Fig. 2.8 ii and iv).

Relative yield gains in faba bean did not fully compensate for the relatively large yield reductions in intercropped wheat and pea, resulting in LER values < 1. The asymmetry in yield responses of faba bean and wheat or pea was greatest in the border rows (Fig. 2.8 ii, iii, and iv). In contrast, faba bean with maize produced substantially higher grain yield at only a slight penalty for maize (Fig. 2.4 i and iii; Fig. 2.8 i and iii), leading to overall gains of the system (Figs 2.5 and 2.6). The largest intercepts of the LER ~ TND and the NE ~ TND relationships of the maize/faba bean intercrop among the three relay intercrops indicate that resources were maximally captured with the presence of a strong competitor (Fig. 2.7). From our data we cannot identify whether this is competition for light, nutrients, or water. In principle, faba bean had better access to P and K in the intercrop with maize, because the fertiliser was broadcast over the whole field before the first species was sown, whereas maize was only sown later, allowing faba bean to forage pre-emptively in the maize strip. Furthermore, faba bean could benefit from its large stature which increases light capture, supporting better root growth which would increase acquisition of nutrients and water in a positive feedback loop (Evers et al., 2019).

In relay intercrops, low-statured species such as wheat and pea are usually grown as early companions of maize because strong early light competition can substantially decelerate maize growth (Zhu et al., 2014), while a low-statured species is not too aggressive. Growth delay due to strong early competition was also observed in other species combinations, e.g., wheat/cotton, particularly if the species were grown in narrow strips, which aggravates interspecific interactions, like shading (Zhang et al., 2008b). Overyielding in the maize/faba bean intercrop exemplifies that maize can be combined with a strongly competitive tall species, provided the yield gain of this species exceeds the yield loss in maize.

Due to the later sowing of the early species in 2019 as compared to 2018, the co-growth period was longer in the second year, strengthening interspecific competition in the relay intercrops with maize. We found that the smaller TND in 2019 mainly reduced the yield increases in the border rows, as well as the pLER and the NE of the less competitive species (maize in maize/faba bean, wheat in maize/wheat, and pea in maize/pea), but did not affect much the performance of the more competitive species. There is, therefore, a need for a sufficient TND to allow the less competitive species to take substantial border row advantages.

The present study shows yield advantages of relay strip intercrops with maize and various companion species at conventional nutrient input levels. The relay and narrow strip design enables species-specific management, such as distinct times and amounts of fertilisation per strip according to the species demands (Hu et al., 2017), and separate harvest of each species grain. Maize is often used in relay intercrops in China (Li et al., 2020b) but there are also other C_4 species that could be combined with C_3 plants for temporal complementarity, such as sorghum (*Sorghum bicolor* L.) and foxtail millet (*Setaria italica* L.). More species combinations can be explored, and sowing and harvesting times may be optimised to exploit temporal complementarity for growing conditions in Western Europe. Particularly, it is interesting to explore species combinations that do not require separate management and harvesting of species, but which can be harvested as bulk without post-harvest separation (Bedoussac et al., 2015).

Narrow strips are challenging to manage in Western Europe because agricultural mechanisation has evolved to fit large and homogeneous cultivated areas (van Oort et al., 2020). Therefore, currently, the focus on crop diversification under Dutch growing conditions is on strip cropping with strip widths from 3 m up to 20 m (Juventia et al., 2021). Such diversification with wider strips provides advantages through interference with the spread of plant diseases (Ditzler et al., 2021) and easier dispersal of pest natural enemies from one crop to another (Ma et al., 2006; Parajulee et al., 2010; Xia, 1997), but due to the low proportion of border rows, such systems have little benefit from border row effects on resource capture and yield. Such systems have therefore limited scope for complementary resource capture and yield increase (van Oort et al., 2020), but they have the advantage that they can be managed with conventional equipment and tailored management per species. Moreover, mixtures can be used in each strip, enhancing crop species or cultivar diversity with associated diversity benefits. Since intercropping benefits related to complementary resource capture tend to attenuate with decreasing border row proportion (van Oort et al., 2020; Wang et al., 2020), appropriate mechanisation options need to be explored to benefit from the application of intercropping with narrower strips.

2.5 Conclusion

We found that relay intercrops with temporal complementarity use land efficiently at conventional nutrient input levels in the Netherlands. We infer from our results that relay intercropping is a promising intercropping mode in situations in which production is not limited by shortage of nutrients or water but mainly by light capture over time. Both cereal/cereal and cereal/legume mixtures can be grown as relay systems, and maize and other C_4 species are important candidate species for late sowing and harvesting in relay intercrops due to their natural growth cycle that peaks later in the year than the growth cycle of C_3 species. Species combinations should exhibit complementary seasonal trends in resource demand to best capture intercrop advantages in narrow strip intercropping. Legumes can be readily integrated in relay systems, and may help reduce the need for use of anthropogenic nitrogen while contributing to the production of healthy plant-based diets, thereby strongly supporting the sustainable development goal of mitigating climate change.

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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/dans-266-ws85.

Chapter 3

On the relationship between light capture and yield components in strip intercropping

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Abstract

The partitioning of light between species in intercrops changes over time in relation to the earliness of canopy development of each species and the final plant height. The consequences of these shifts in light capture in crop species mixtures may be reflected in the yield components of the species. We test the hypothesis that shifting light capture in intercrops can explain intercropping effects on grain number, grain weight and yield in different species mixture compositions. We determined grain number per unit area, thousand-grain weight, and grain yield of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.), grown as monocrops or as bi-specific strip intercrops 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 before and during grain filling was estimated using a model based on strip width, crop height and leaf area index. We then assessed the relationships between cumulative light captured per species, yield and its components, and land equivalent ratio. Differences in species yield in intercrops and monocrops were strongly related to differences in grain number. In relay intercrops, both species had increased yield due to an increased number of grains. Species grown in simultaneous intercrops did not have higher yield or grain number than the monocrop, except for faba bean with wheat or pea. Increased grain number of early-sown species in relay intercrops was related to greater light capture before grain filling compared to monocrops. Increased grain number in maize may be due to better light availability after maize overtopped the companion species. The early-sown species showed trade-offs between grain number and weight, whereas the improved light availability resulting from the early harvesting of companions allowed intercropped maize to fill all grains to the same extent as monocropped maize did. Yield was more strongly related to grain number than grain weight in all species in both monocrops and intercrops. In relay intercrops, grain yield increases were realised by species effectively filling grains to take advantage of the larger grain number. The findings show the importance of achieving large grain number and effective grain filling for increasing grain yield in conventionally managed strip intercrops under Dutch growing conditions.

Keywords: Europe; Light capture; LER; Relay intercropping; Strip intercropping; Yield components

3.1 Introduction

Intercropping is the 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 at various levels of resource input (Bedoussac et al., 2015; Feng et al., 2021; Gou et al., 2016; Li et al., 2020b, 2020a; Li et al., 2023; Xu et al., 2020; Yu et al., 2015). Thus, intercropping is viewed as an interesting option for ecological intensification in both organic and conventional farming that can achieve high yields with reduced anthropogenic inputs (Bedoussac et al., 2015; Gong et al., 2022; Li et al., 2020b; Li et al., 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 yield increase or decrease as compared to monocropping (Feng et al., 2021; Gou et al., 2016; Wang et al., 2023). Yield components provide insights 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., 2020; 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 between the intercrop and monocrop (Bloom et al., 1985; Sadras and Slafer, 2012). 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., 2021; Zhu et al., 2016).

Yield components such as grain number and grain weight are usually determined in a chronological order, and each yield component has a critical phase during which it is significantly affected by resource capture (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. A temporal differentiation in the capture of resources occurs naturally in relay intercrops in which the component species overlap only for a portion of their growth durations (Li et al., 2020b; 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 attributes that affect resource capture and thus yield components, such as growth cycle (e.g., sown and harvested early vs. sown and harvested late), developmental pattern (e.g., determinate vs. indeterminate), shoot and root architecture (e.g., tall vs. short; deep rooting vs. shallow rooting), and physiology (e.g., C_3 vs. C_4; nitrogen-fixing vs. non-nitrogen-fixing). Therefore, studying yield component determination in response to resource capture in various species combinations allows determining whether those combinations are suitable in a given production situation. Yield components indicate how different types of species interaction during different growth phases (e.g., shading, complementarity for nitrogen acquisition) affect the determination of final yield. This can help to identify 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., 2017a; Li et al., 2021; Mao et al., 2014; van Oort et al., 2020; Wang et al., 2021; Zhang et al., 2008a; Zhu et al., 2015). The relationship between grain yield and light capture in intercrops has been investigated by various authors (Gou et al., 2017a, 2016; van Oort et al., 2020; Wang et al., 2021; Zhu et al., 2016), but the effects of dynamics in light capture over the growth phases on yield components have not previously been quantified. Therefore, this study addresses the question to which extent the differences in two most important yield components (grain number per unit land area and grain weight), and grain yield between intercrops and monocrops are related to differences in light capture over time.

We conducted a two-year field experiment in which grain number per unit land area, grain weight, and yield of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.) were investigated in all six bi-specific combinations in strip intercrops comprising 1.5 m-wide strips of component species. The combinations with maize were relay intercrops because of the later sowing and harvesting of maize as compared to the other species. In contrast, species combinations without maize were nearly simultaneous because wheat, faba bean, and pea were sown at the same time, and they differed little in harvesting date. We conducted this experiment by supplying water and nutrients in intercrops tailored to species demand as proposed within the EU framework of Good Agricultural Practices (FAO, 2003), and in search of sustainable intensification options for conventional farming in Western Europe (Wang et al., 2023). The species demand was assumed to be equal to that of the monocrops, i.e. the fertiliser supply to a species per unit area of the whole monocrop and per unit area of the species strip in intercrops was the same, allowing a fair comparison of species performance in monocrops and intercrops.

Two hypotheses were tested:

1) Due to the temporal complementarity in relay intercrops and related dynamics in plant stature, the early-sown and shorter species captures more light during its early growth, while the late-sown and taller maize captures more light during later growth. Consequently, it is expected that the early-sown species show an intercropping advantage in grain number but a disadvantage in grain weight due to shading by maize during grain filling, whereas the late-sown but taller species (i.e., maize) shows an intercropping disadvantage in grain number due to shading during grain formation but a compensatory advantage in grain 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. Here, we expect that taller species benefit from intercropping due to greater light capture, both with respect to grain number and grain weight, whereas shorter species have both components reduced due to shading by the companion species (Fig. 3.1). We also expect that the greater grain number of early-sown species in relay intercrops results in intensified competition for assimilates, aggravating the grain-weight-reducing effect of light competition from maize during the grain filling of the early-sown species.

2) Land equivalent ratios (LER) of intercrops are positively related to increases in light capture in comparison to the corresponding monocrops. As a consequence, greater land equivalent ratios are expected in relay intercrops than in simultaneous intercrops.

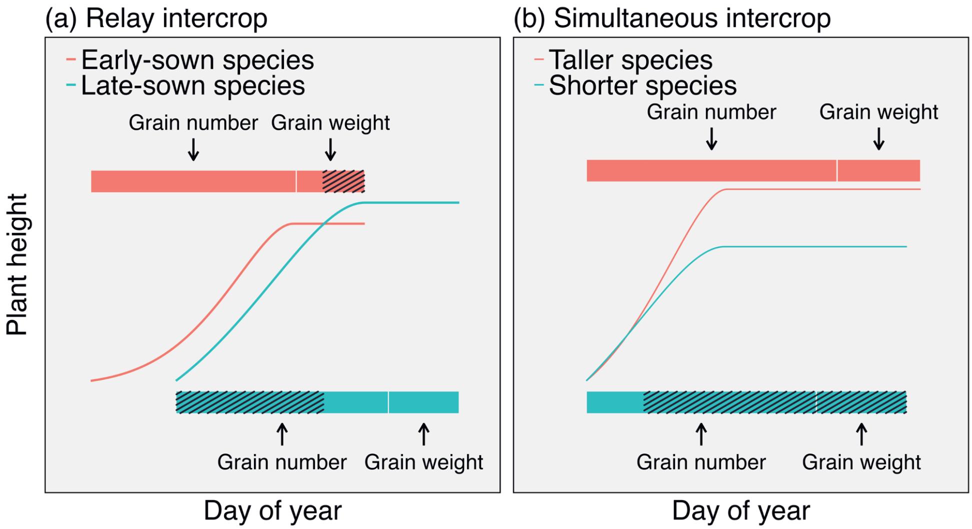

Fig. 3.1 Illustration of plant height (sigmoid curves) and growth phases (horizontal bars) during which yield components grain number and grain weight are determined in relay (a) and simultaneous intercrops (b). The coloured bars represent the phases in which grain number per unit land and grain weight are determined. Hatching of the bar indicates a species is shaded by the companion species.

3.2 Materials and methods

3.2.1 Experimental design

A two-year field experiment was conducted at Droevendaal Experimental Farm of Wageningen University & Research, Wageningen, the Netherlands (51° 59' 20" N, 5° 39' 16" E) in 2018 and 2019. The growing seasons, counted from sowing the first-sown species to harvesting the last-sown species, 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, cumulative photosynthetically active radiation (PAR) of 1537 and 1514 MJ m^{-2}, and cumulative precipitation of 300 and 252 mm. Both seasons were hotter and drier than the long-term record (Koninklijk Nederlands Meteorologisch Instituut, 2019). The farm has a sandy soil with a pH of 5.7, an organic matter 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 Chapter 2 for more details.

Six strip intercrops were cultivated by pairing 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. Wheat, faba bean, and pea were spring cultivars, and they 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 a spring cultivar and was sown on May 4 in 2018 and May 7 in 2019.

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. 3.2). The sowing densities were 10 seeds m^{-2} for maize, 83 seeds m^{-2} for pea, and 44 seeds m^{-2} for faba bean in both years. Sowing density of wheat was 383 seeds m^{-2} in 2018 and 369 seeds m^{-2} in 2019. For a species, the sowing density was the same per unit area of the species strip in the intercrops and in 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 Chapter 2 for more details.

Fertiliser was applied according to species-specific recommendation 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 N fertilisation 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 to reduce drought stress; see Chapter 2 for details.

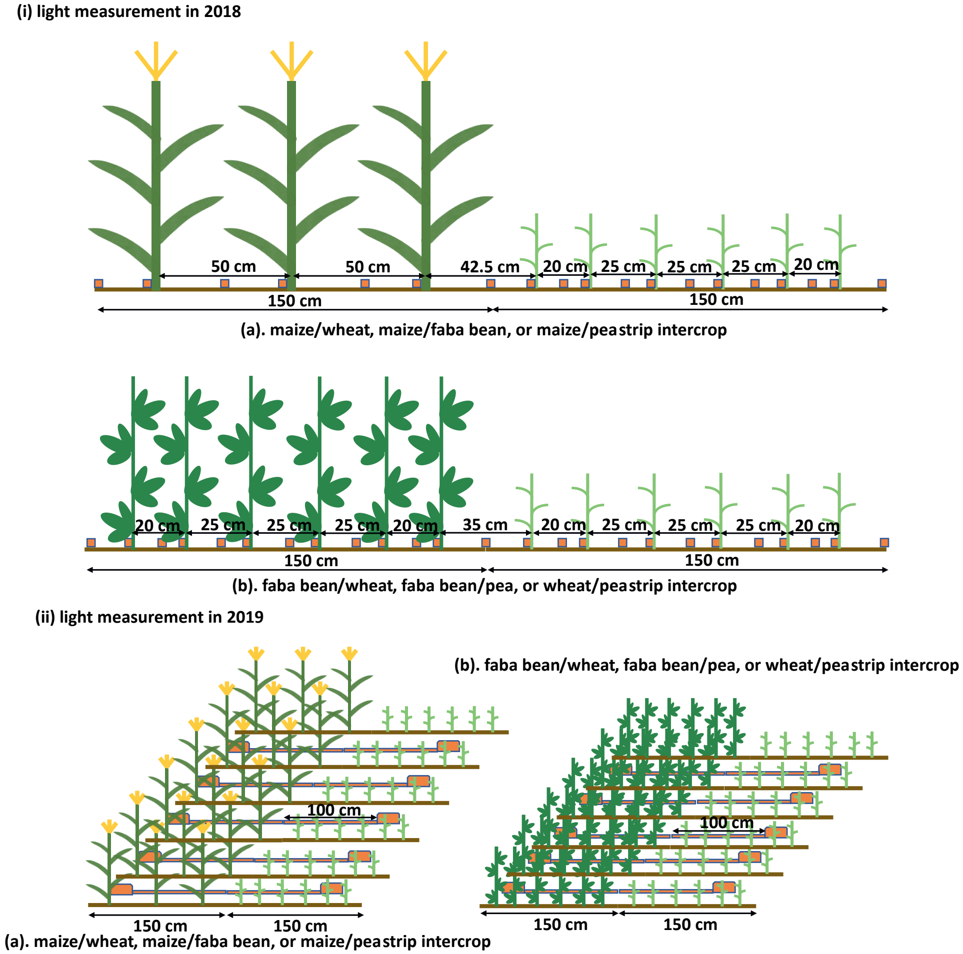

Fig. 3.2 Row configurations and light measurement locations in 2018 and 2019. (a) the intercrop strip comprising one maize strip and one species strip of wheat, faba bean, or pea; (b) the intercrop strip comprising two species strips of a bi-specific combination of wheat, faba bean, and pea. Each species strip was designed to be 150 cm wide. The orange squares, bars, and trapezoids represent position of the SunScan probe (Delta-T Devices Ltd, UK), which was used to measure transmitted PAR under the canopy on selected days to calculate the proportion of light captured (Method S3.1). These measurements were used to verify the light capture model.

3.2.2 Field measurements

Phenology monitoring

The universal scale for crops, developed by BASF, Bayer, Ciba-Geigy and Hoechst (BBCH scale), was used to observe the critical phenological event marking the start of grain filling for each species (Lancashire et al., 1991). The start of grain filling is at silking (65) in maize and at full flowering (65) in wheat (Evans, 1975). Faba bean and pea are indeterminate, meaning that formation of new phytomers and pods continues while the pods at lower-ranked phytomers have started filling (Patrick and Stoddard, 2010). The BBCH scale '75', i.e., 50% of the emerged pods have reached the final size and are ready to be filled, was used as the critical event for faba bean and pea. The moments of emergence (09) and harvest maturity (89; the harvesting days) were observed for all species.

Plant height

Plant height was measured to assess when a component species was shaded by its companion in intercrops, indicating whether the light environment was more or less favourable for a species in intercrops compared to the monocrop. Plant height was measured using a measuring stick. It was defined as the distance from the bottom of the main stem to the base of the last fully developed leaf. In wheat, faba bean, and pea, a leaf was considered fully developed if the blade had fully expanded; in maize, once the leaf collar was visible. Plants from different rows of one species strip in the middle of the plot were randomly selected for measurement. Measurements were made from the day on which a species had three fully developed leaves to the day when the maximum plant height was attained (Method S3.3).

Yield, grain number and grain weight

We harvested 4 m row length of one intercrop strip (3 m wide) in the centre of each intercrop plot and one 1.5 m-wide strip in the centre of each monocrop plot at maturity. As an exception, for pea, we harvested 3 m row length in 2018. 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 grains was randomly taken from each sample and weighed. The grain number of the subsample was counted using an electronic seed counter (CONTADOR, Pfeuffer Co., Germany). Grain number per unit area of the species strip (GN) 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. Grain yield per unit area of the species strip and thousand-grain weight (TGW) were calculated for each species on an oven dry weight basis.

3.2.3 Cumulative light capture

Cumulative 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', 4 km west of the experimental location.

Light capture fraction in monocrops (f_{mono})

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

$$f_{\text{mono}} = 1 - e^{-k \times \text{LAI}} \qquad \text{(Eq. 3.1)}$$

where LAI is the daily leaf area index linearly interpolated by the measured LAI (Method S3.4) using the 'approx' function in R (R Core Team, 2022). 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 (Fig. S3.1).

Light capture fraction in intercrops (f_{inter})

The proportion of light capture in intercrops, f_{inter}, was calculated using a geometry-based model (Gou et al., 2017a). 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., 2017a) and has been used in various intercrops with different configurations (van Oort et al., 2020; Wang et al., 2021; Zhang et al., 2018). We did not make adaptations to this model and refer the reader to Method S3.2 and to Gou et al. (2017a) for details. The model inputs are daily LAI, plant height, 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 (Fig. S3.2). *k* is taken to be the same for a species in intercrops and monocrops (Fig S3.1).

The light model was validated by comparing the estimated and measured light capture fractions (f_{cap}) on selected days; see Method S3.1 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:

$$\mathrm{RMSE} = \sqrt{\frac{1}{N} \times \sum_{i}^{N} \left(f_{\mathrm{cap}_{\mathrm{E}\,i}} - f_{\mathrm{cap}_{\mathrm{M}\,i}}\right)^{2}} \qquad \text{(Eq. 3.2)}$$

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

3.2.4 Data analyses

Relationships between grain yield and yield components per species

In each year, a linear mixed effects model was fitted between GN (or TGW) as an explanatory variable and grain yield as a response variable for each species to explore to what extent the differences in grain yield across different species combinations in different blocks were correlated with GN or TGW. Block was specified as a random effect. The function 'r2_nakagawa' (Nakagawa and Schielzeth, 2013) in the package 'performance' (Lüdecke 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.

Relationships between grain yield, yield components, and the corresponding cumulative PAR captured per species

To explore to what extent the differences in grain yield, GN, and TGW were correlated with light capture, linear mixed models were fitted for grain yield ~ total cumulative PAR over the season, and GN ~ cumulative PAR before grain filling. For TGW, a multiple-linear mixed model with cumulative PAR during grain filling and GN as two explanatory variables were fitted to explore the effect of light capture conditional on the GN that had been determined during earlier growth. All models were fitted for the two years separately while block was specified as a random effect.

Land equivalent ratios for grain yield (LER) and light capture (LCER)

Land equivalent ratio (LER; Willey and Rao, 1980) was used to quantify the land use efficiency of intercrops compared with monocrops:

$$\mathrm{LER} = \mathrm{pLER}_1 + \mathrm{pLER}_2 = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \qquad \text{(Eq. 3.3)}$$

where the pLER_i is the partial land equivalent ratio of species i, Y_i is the grain yield of species i in the intercrop (per unit area of the intercrop), and M_i is the grain yield of species i in the monocrop. The species combination effects on pLER and LER have been presented in Chapter 2.

By extension of the land equivalent ratio for grain yield, the land equivalent ratio for light capture (LCER) was defined to quantify the relative land area used in monocrops to capture the same amount of light as captured on a unit area of the intercrop:

$$\mathrm{LCER} = \mathrm{pLCER}_1 + \mathrm{pLCER}_2 = \frac{CPAR_{\mathrm{I}1}}{CPAR_{\mathrm{M}1}} + \frac{C\,PAR_{\mathrm{I}2}}{CPAR_{\mathrm{M}2}} \qquad \text{(Eq. 3.4)}$$

where the pLCER_i is the partial equivalent ratio for light capture of species i, $CPAR_{\mathrm{I}i}$ is the cumulative light captured throughout the season of species i in the intercrop (per unit area of the intercrop), and $CPAR_{\mathrm{M}i}$ is the cumulative light captured throughout the season of species i in its monocrop. An LCER higher than one indicates that the monocrops require more land than the intercrop to capture the same amount of light with the component species, i.e., the intercrop is more efficient in capturing light than the monocrops, a value below one indicates the reverse.

Relationships between land equivalent ratios for grain yield (LER) and light capture during the whole season (LCER)

To explore the effects of light capture on LER for grain yield, linear mixed models were fitted between LCER as a numeric explanatory variable and LER as a response variable. Four categorical covariables were introduced to examine if the effect of LCER differed between intercrops with or without maize (two levels), between intercrops with or without a legume (two levels), between intercrops that were or were not cereal/legume combinations (two levels), or between all different species combinations (six levels). Models with and without the interaction between the covariable and LCER were fitted for each covariable. The simplest model with only LCER as a predictor was also fitted (Table 3.1). The most supported model was selected using Akaike's information criterion in the function 'anova' (Akaike, 1998). Between models with AIC values differing less than two, the simpler model was selected to avoid overfitting (Burnham and Anderson, 2004).

Table 3.1 Model specifications for exploring the relationships between LER for grain yield and LCER. i, j, and k represent year ID, species combination ID, and block ID. b_{ik} is a random block effect nested in the year. ϵ_{ijk} is a random error on the plot level. Definitions of the categorical covariables: Legume. Incl.: a legume species is included in the intercrop or not (0/1); Cereal.Legume: the intercrop is a cereal/legume combination or not (0/1); Maize.Incl.: maize is included in the intercrop or not (0/1); Comb.: the covariable having all six combinations as levels. Df is the degrees of freedom of the models, representing the number of parameters to be estimated.

Models	Equations	Df
1	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + b_{ik} + \epsilon_{ijk}$	4
2	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Legume.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	5
3	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Cereal.Legume}_{ijk} + b_{ik} + \epsilon_{ijk}$	5
4	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Maize.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	5
5	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Legume.Incl.}_{ijk} + \beta_3 * \mathrm{LCER}_{ijk} * \mathrm{Legume.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	6
6	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Cereal.Legume}_{ijk} + \beta_3 * \mathrm{LCER}_{ijk} * \mathrm{Cereal.Legume}_{ijk} + b_{ik} + \epsilon_{ijk}$	6
7	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Maize.Incl}_{.ijk} + \beta_3 * \mathrm{LCER}_{ijk} * \mathrm{Maize.Incl.}_{ijk} + b_{ik} + \epsilon_{ijk}$	6
8	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Comb.}_{ijk} + b_{ik} + \epsilon_{ijk}$	9
9	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{LCER}_{ijk} + \beta_2 * \mathrm{Comb.}_{ijk} + \beta_3 * \mathrm{LCER}_{ijk} * \mathrm{Comb.}_{ijk} + b_{ik} + \epsilon_{ijk}$	14

3.3 Results

3.3.1 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. 3.3 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 grain filling period and a short proportion of the time before silking, except when growing with 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. 3.3 g–l).

3.3.2 Relationships between grain yield and yield components

There were strong relationships between GN and grain yield in all species, both in monocrops and intercrops in both years (Fig. 3.4). For the same GN, maize grain yield was approximately 300 g m^{-2} higher in 2018 than in 2019. The positive effects of GN on grain yield were similar between years for the other three species. Relationships between TGW and grain yield varied between species, with a distinct year-effect on the slope in maize (Fig. 3.4 b), a positive relationship in wheat and pea (Fig. 3.4 d and h) and a negative relationship in faba bean (Fig. 3.4 f).

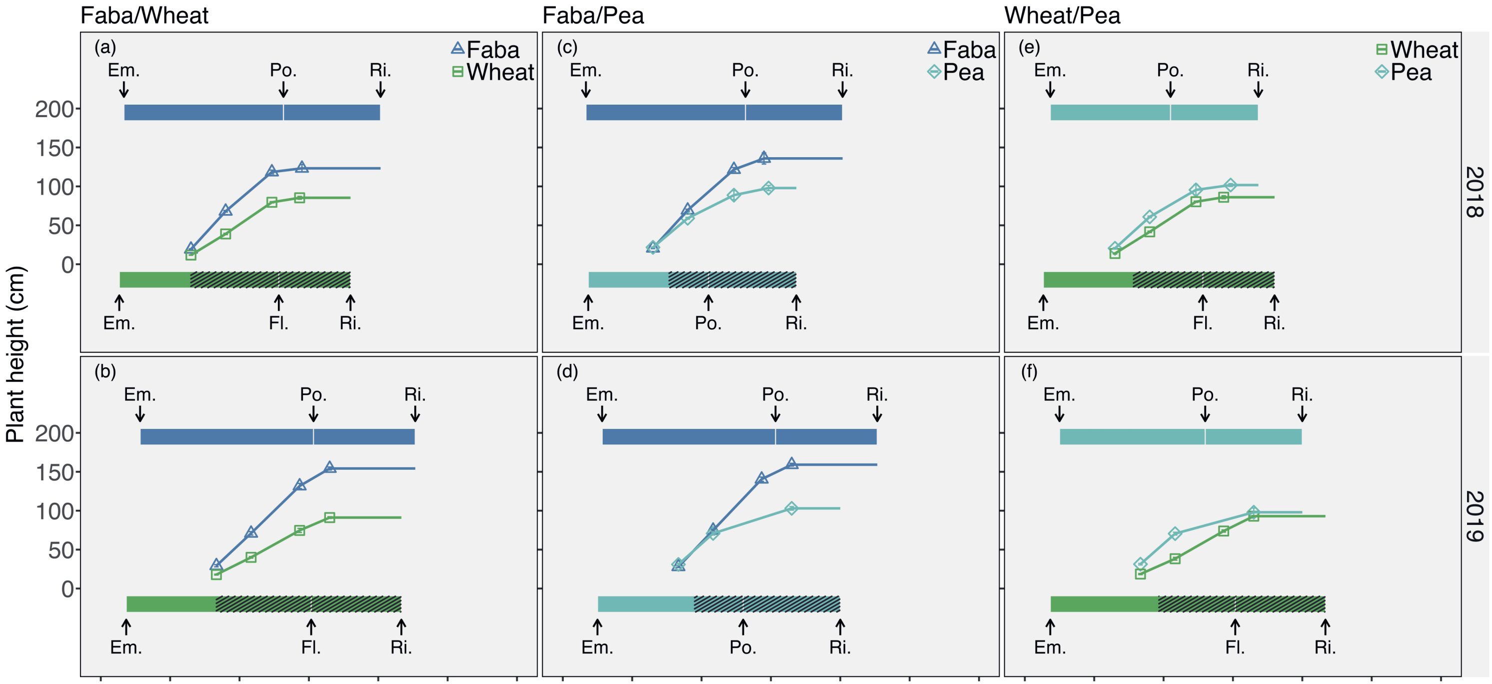

Fig. 3.3 Plant heights of maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond) in simultaneous (a–f) and relay intercrops (g–l). Error bars represent the standard error of the means. Coloured blocks represent the phases before and during grain filling. Each phase is defined by phenological events observed according to 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.

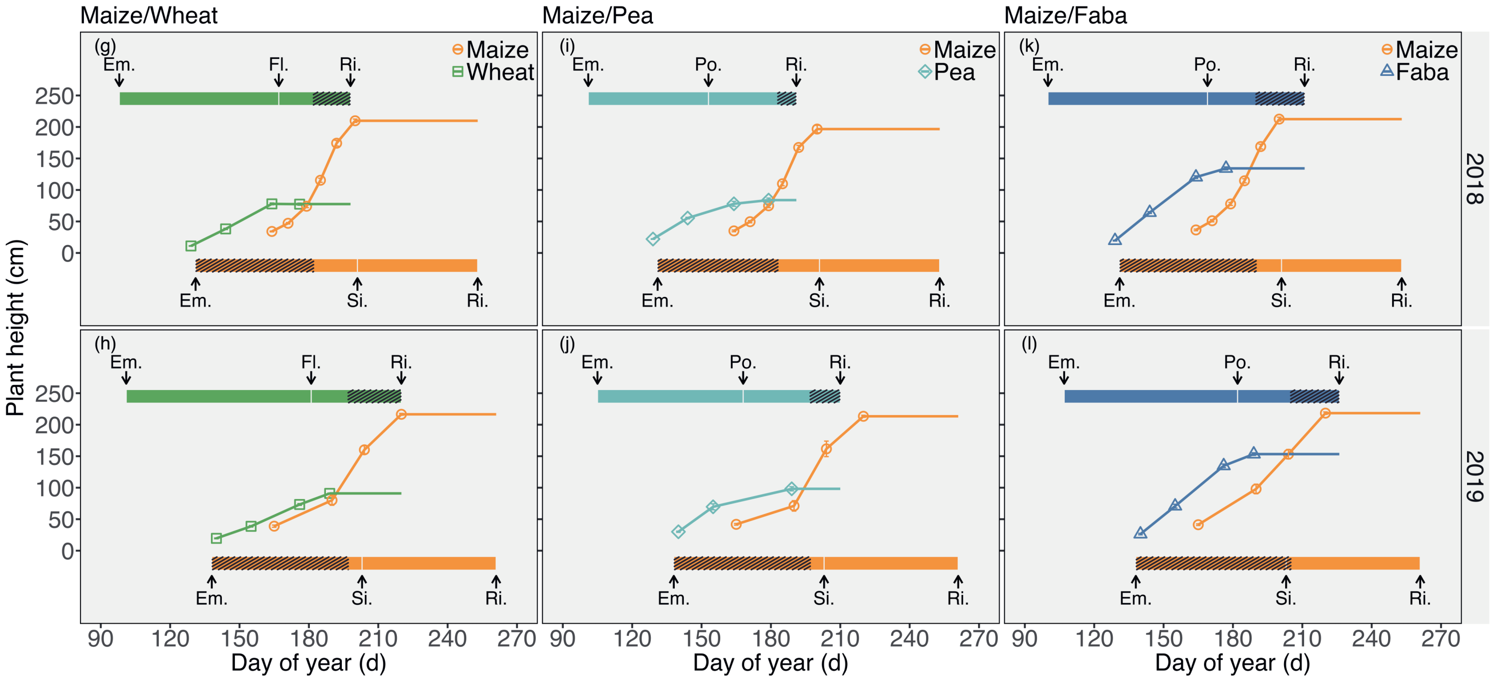

Fig. 3.3 (continued) Plant heights of maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond) in simultaneous (a–f) and relay intercrops (g–l). Error bars represent the standard error of the means. Coloured blocks represent the phases before and during grain filling. Each phase is defined by phenological events observed according to 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.

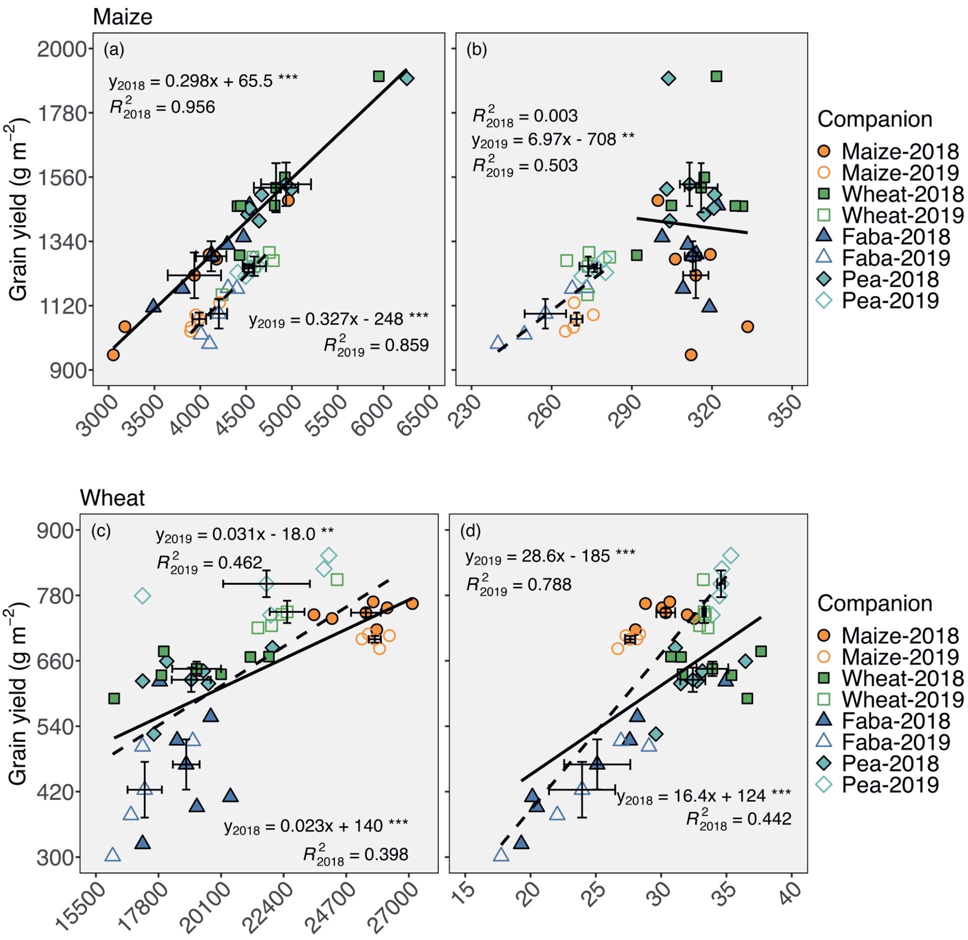

Fig. 3.4 Relationships between grain yield and grain number (GN) and thousand-grain weight (TGW) of maize (a, b), wheat (c, d), faba bean (e, f), and pea (g, h). Different symbols indicate that the focal species was combined with different companion species: maize (orange circle), wheat (grain square), faba bean (blue triangle), and pea (cyan diamond). Data collated in 2018 and 2019 are indicated as 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. More details about multiple comparisons of the means are presented in Fig. S3.4.

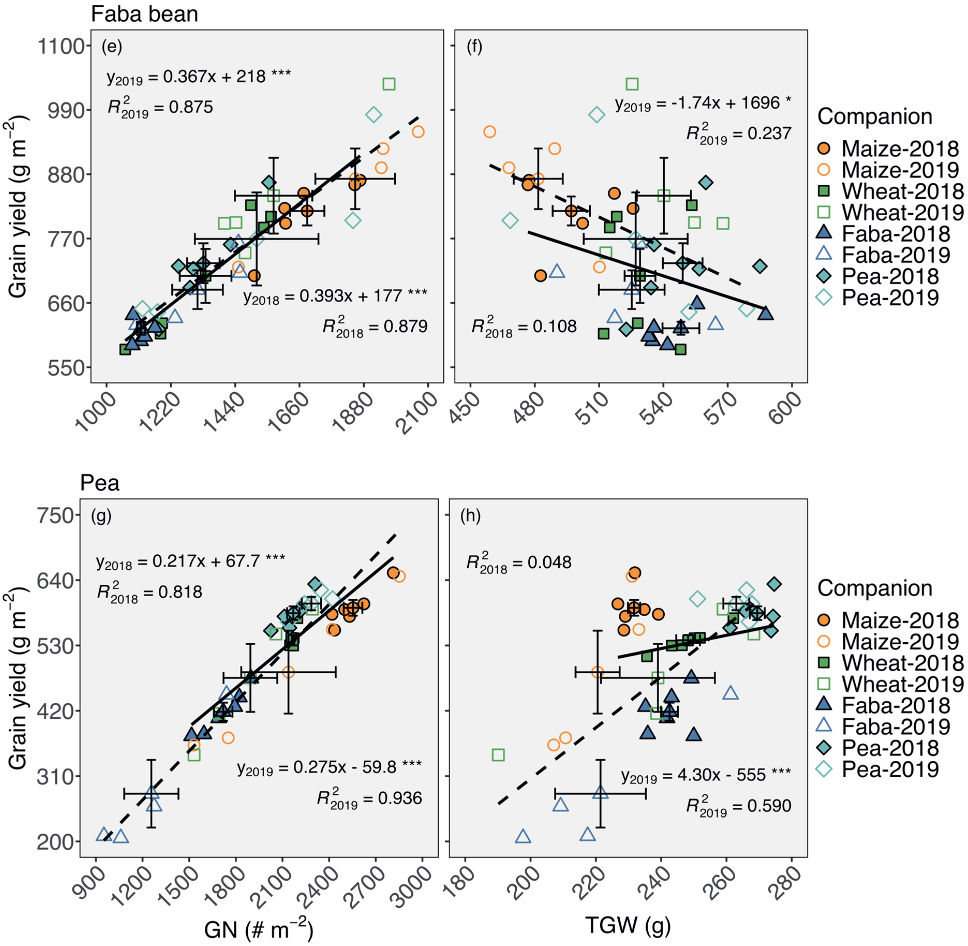

Fig. 3.4 (continued) Relationships between grain yield and grain number (GN) and thousand-grain weight (TGW) of maize (a, b), wheat (c, d), faba bean (e, f), and pea (g, h). Different symbols indicate that the focal species was combined with different companion species: maize (orange circle), wheat (grain square), faba bean (blue triangle), and pea (cyan diamond). Data collated in 2018 and 2019 are indicated as 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. More details about multiple comparisons of the means are presented in Fig. S3.4.

3.3.3 Relationships between light capture and grain yield (and yield components)

The estimation of f_{cap} across the whole strip showed good agreements with field measurement in both monocrops and intercrops (Fig. S3.6). In 2018, the RMSE 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). Table S3.1 provides information on light capture by each species in the monocrop and intercrops.

There were large differences between species in the relationship between grain yield or yield components and light capture, with overall much weaker relationships in maize (Fig. 3.5 a-c) than in the other three species (Fig. 3.5 d-l). In maize, there was no significant relationship between grain 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 GN. There was also a significant positive relationship between light capture and TGW in wheat and faba bean. There was, however, no significant relationship between light capture and TGW in pea.

In faba bean, apart from the positive effect of light capture during grain filling on TGW, GN that had been determined earlier had a negative effect on TGW. However, GN did not have a significant effect on TGW in the other three species.

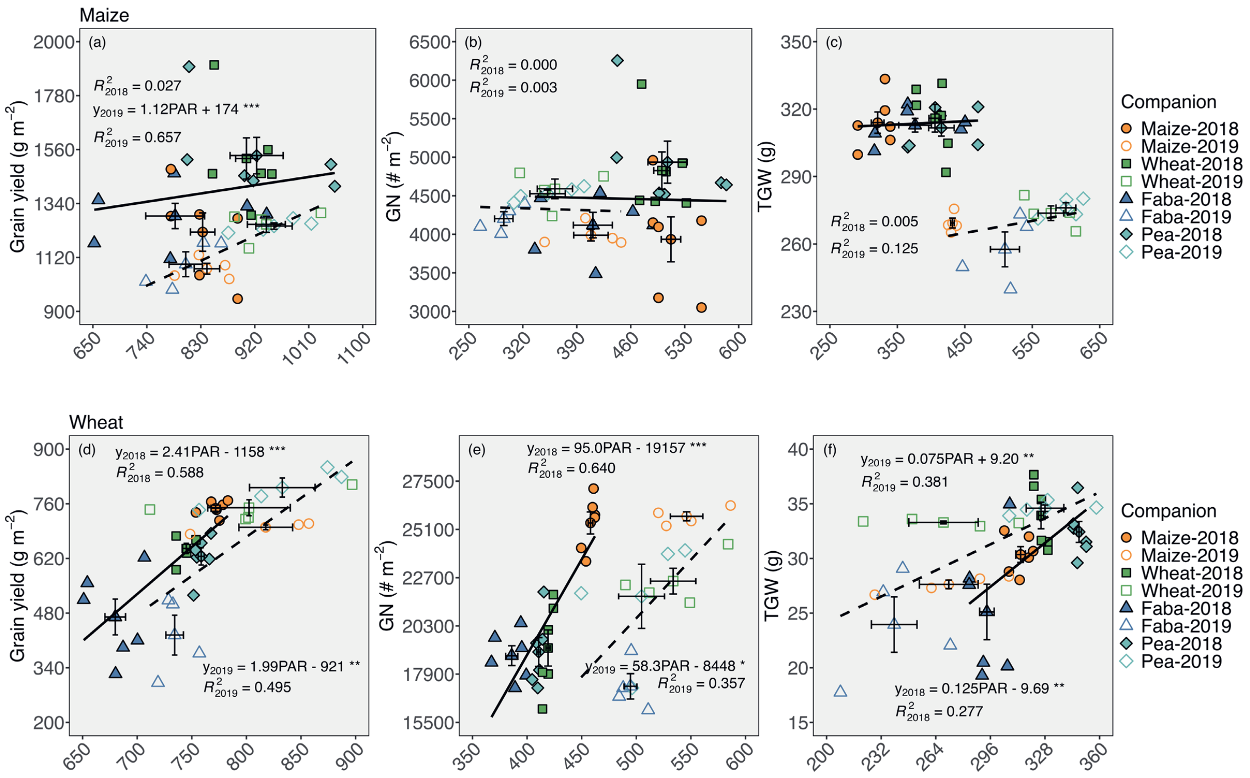

Fig. 3.5 Relationships of grain yield ~ total cumulative PAR captured, GN ~ cumulative PAR captured before grain filling, and TGW ~ GN + cumulative PAR captured during grain filling of maize (a, b, c), wheat (d, e, f), faba bean (g, h, i), and pea (j, k, l). For a focal species, different symbols indicate that it was combined with different companion species: maize (orange circle), wheat (grain square), faba bean (blue triangle), and pea (cyan diamond). Filled symbols are for 2018 and open symbols for 2019. Error bars represent standard errors of 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.

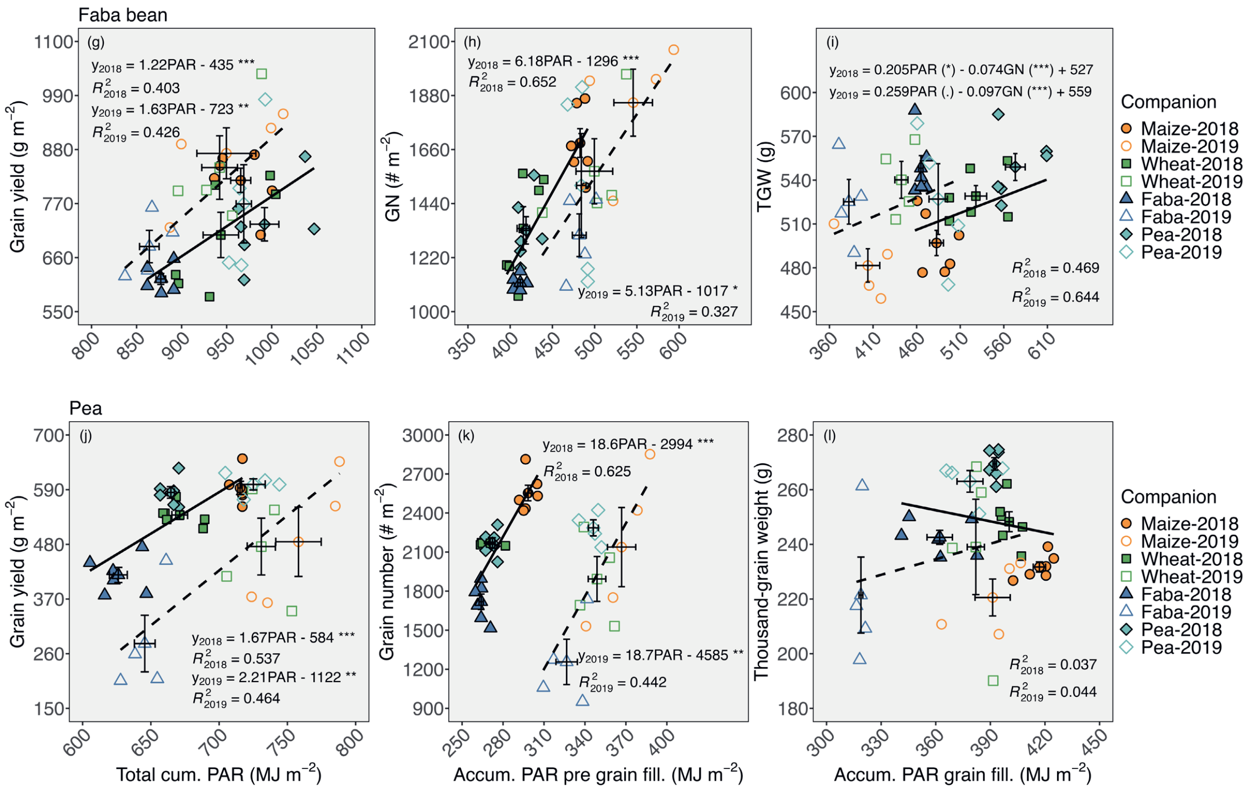

Fig. 3.5 (continued) Relationships of grain yield ~ total cumulative PAR captured, GN ~ cumulative PAR captured before grain filling, and TGW ~ GN + cumulative PAR captured during grain filling of maize (a, b, c), wheat (d, e, f), faba bean (g, h, i), and pea (j, k, l). For a focal species, different symbols indicate that it was combined with different companion species: maize (orange circle), wheat (grain square), faba bean (blue triangle), and pea (cyan diamond). Filled symbols are for 2018 and open symbols for 2019. Error bars represent standard errors of 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.

3.3.4 Land equivalent ratio for light capture (LCER) and relationships between land equivalent ratios for grain yield (LER) and for light capture (LCER)

The relay intercrops all obtained LCER values higher than one in both years (Fig. 3.6). The simultaneous intercrops obtained LCER values similar to one, except for faba bean/pea in 2018, which had an LCER higher than one. Thus, relay intercropping had a more efficient light capture than monocropping, and simultaneous intercropping did not improve light capture.

Model 8, characterised by a common slope across species combinations, but different intercepts, was selected as the best model for the relationships of LER ~ LCER (Table S3.3; Fig. 3.7). With the same LCER, the relay intercrops had higher LER than the simultaneous intercrops, with the maize/faba bean intercrop having the highest LER, while the faba bean/pea intercrop having the lowest LER.

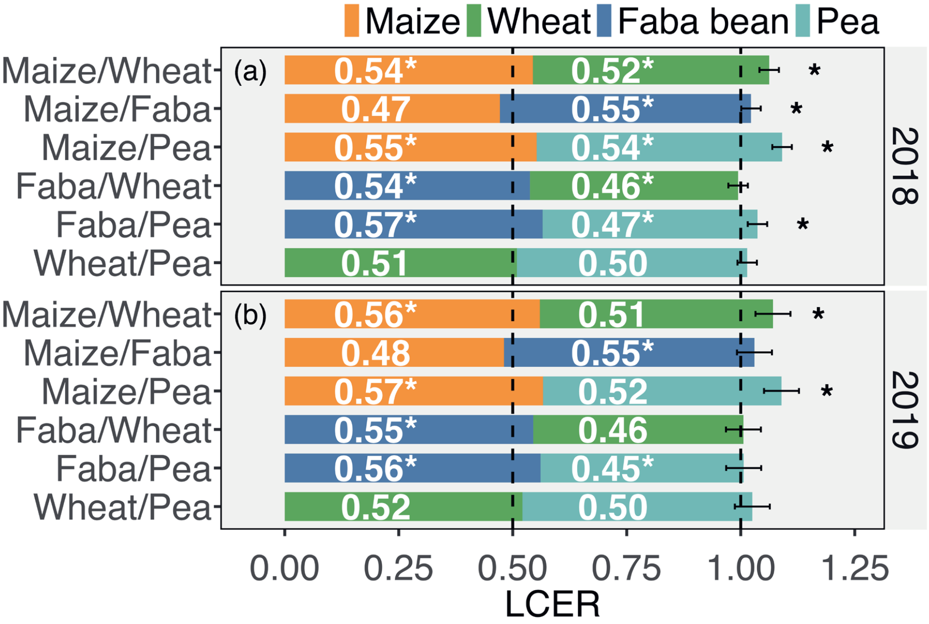

Fig. 3.6 Land equivalent ratios for light capture during the whole season (LCER) of the intercrops in 2018 (a) and 2019 (b). LCER was calculated based on the cumulative PAR captured during whole season (Table S3.1). Colours represent the component species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Error bars represent the 95% confidence interval of LCER. An asterisk indicates that the pLCER of a component species (or the LCER of an intercrop) was significantly different from 0.5 (or one), i.e. 0.5 (or one) was not within the 95% confidence interval of the pLCER (or LCER).

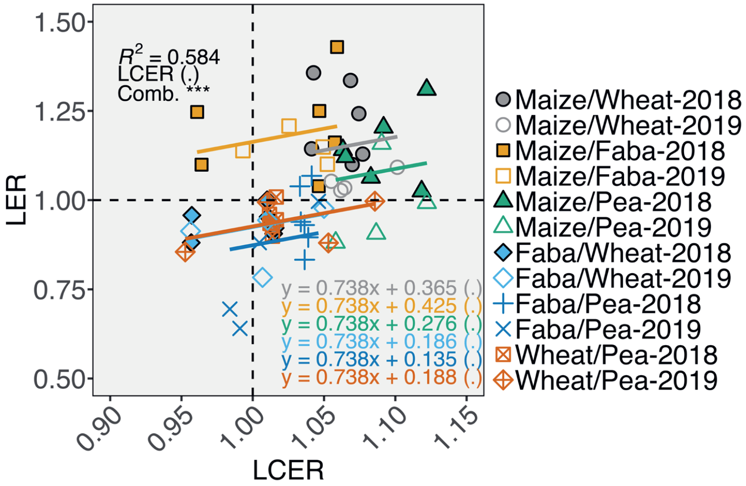

Fig. 3.7 Relationships between land equivalent ratios for grain yield (LER) and light capture during the whole season (LCER). The asterisks attached to the names of the explanatory variable and the covariable indicate such variables significantly contributed to explaining the variance of LER (F-test). Symbols, fitted lines, and equations are all given in the same colour for a certain intercrop. The asterisks attached to the equations indicate that the slopes are significantly different from zero according to the 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.

3.4 Discussion

We hypothesised that acquisition of light would be the main limitation for crop growth under the conditions of the study due to the water and nutrient management that targeted non-limiting availability of these production factors. Therefore, we expected yield component determination of the component species to respond to the intercropping effects on light capture, e.g., the early-sown species would have an increased grain number per unit land area (GN) compared to their monocrops due to more light captured before grain filling compared to monocrops, whereas maize would have an increase in thousand-grain weight (TGW) compared to its monocrop due to more light captured during grain filling in the intercrops than in the monocrop.

3.4.1 Relay intercrops enable grain 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 GN in intercropping, whereas none of the species showed increases in TGW (Fig. 3.4; Fig. S3.4). In both cereals and legumes, GN was correlated with light availability before grain filling. Considering the relatively low R^2 for the random block effect (Table S3.2), and the significant treatment effects on GN and light capture (Fig. S3.4; Table S3.1), the significant

GN ~ light capture relationships of the three early-sown species mostly resulted from the treatment differences in GN and light capture. Our results support the view that relay intercropping is beneficial for grain 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., 2020; Qian et al., 2018; Zhu et al., 2016).

Reduced light capture before grain filling in intercropped maize (Table S3.1) 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 GN despite this decrease in light capture before grain filling (Fig. 3.4; Fig. S3.4). Our maize cultivar had cobs initiated at leaf 9 or 10. Maize outgrew wheat and pea around the ten-leaf stage (Fig. 3.3), with better light conditions supporting cob initiation and development. This may explain the higher cob number (approximately 1.1 to 1.2 cobs per plant; Fig. S3.5) and the consequent increased GN in intercropped maize, because improved light conditions may aid cob development through light capture and CO_2 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 early light competition, it still had increased GN by having better light conditions at the leaves that subtend a cob during cob initiation and development.

Maize intercropped with faba bean also had an increased cob number per plant, but the total GN was not increased because of the decreased grain number per cob (Fig. S3.5). The lower LAI of intercropped maize with faba bean (Fig. S3.2), compared to monocropped maize and maize intercropped with wheat and pea, could be an explanation for this because it can lead to reduced photosynthate production, which did not suffice for adequate grain setting (Schussler and Westgate, 1991). 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. 3.5), light should not be considered as the sole factor influencing GN in the relay or simultaneous intercrops in the present study. 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., 2020b; 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 (Liu et al., 2020).

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 (Fig. S3.7). Although irrigation was given frequently during dry periods, drought stress and interspecific water competition may still have persisted, especially in May and June of both years. In the simultaneous intercrops, faba bean may forage 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.

3.4.2 Grain weight is not only determined by light capture during grain filling but also by within-plant competition for assimilates

Intercropping effects on TGW were not well explained by light capture during grain filling, except in the case of faba bean (Fig. 3.5 i). This was either because no significant TGW ~ light capture relationships were detected (maize and pea; Fig. 3.5 c and l), or due to a large proportion of variance that was not explained by the relationship (wheat; Fig. 3.5 f). However, this does not imply that light capture during grain filling is not influential for grain weight determination. Grain weight is determined both by assimilation during grain 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 grain filling was similar to their monocrops (Fig. 3.3; Table S3.1). It is more plausible that the reduced TGW in wheat and faba bean is due to the increased number of reproductive shoots and thereby high GN in intercrops, which increased competition for assimilates between the grains (Fig. S3.5). In essence, intercropping increased the number of grains but decreased light capture per grain.

Faba bean exhibited a significant trade-off between TGW and GN, indicating negative feedback between grain number and the available assimilates or translocated nutrients per grain (Fig. S3.3). Grain 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, a negative feedback between grain number and available resources per grain was likely not the only reason for decreases in TGW, as GN was only increased in 2018. The decreased TGW when grown with maize could have been due to lodging in the pea canopy which was not accounted for in the calculated light capture.

The fact that maize TGW was not increased while more light was captured might similarly be attributed to increased competition among grains for assimilates. The higher GN, due to a larger cob number per plant, required more light to achieve the same TGW. The improved light condition during grain filling enabled all grains to be filled to the same extent as in monocropped maize; thus, a yield increase was found in maize (Fig. S3.4). Overyielding of late-sown species follows the recovery growth principle (Zhang and Li, 2003). We found that achieving recovery in grain yield relies on sufficient per-grain filling on top of setting more grains during the early phase.

3.4.3 Intercropping yield effects are more strongly related to grain number than to grain weight

Differences in species grain yield between intercrops and monocrops were mainly due to differences in GN, as indicated by the higher marginal R^2 of relationships between yield and GN compared to the relationships of yield with TGW (Fig. 3.4). The only exceptions are wheat and pea intercropped with faba bean for which reductions in both GN and TGW contributed to negative intercropping effects on grain yield. Our findings are in agreement with other intercropping studies in which grain number was the main yield component associated with intercropping advantage (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 grain number is more plastic than grain weight in response to heterogeneous resource conditions because a stable grain weight has evolutionary advantages (Sadras and Denison, 2009). Specifically, in this study, the pre-grain 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 increased light capture in early growth, and also maize benefited during cob initiation. In simultaneous intercrops, species growth periods overlapped completely during pre-grain filling, and partially during grain filling due to different harvest dates (Fig. 3.3).

3.4.4 Practical implications

Results of this study show the importance of light capture for species and intercrop productivity under conventional management, but the role of other below-ground resources cannot be ignored (Fig. 3.7). It is essential for increasing yields in intercropping to provide the component species with favourable light conditions during their period of GN determination and ensure efficient grain filling.

In relay intercrops, achieving a higher grain 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 grains due to early access to light. However, in late-sown species, the shading by the early-sown companions is important. Early shading can retard development of the late-sown species (Zhu et al., 2014). An early companion with a tall and vigorous canopy will hinder grain setting of the late-sown species, as exemplified by the lack of GN advantages of intercropped maize with faba bean (Fig. 3.4; Fig. S3.4). Therefore, whether the late-sown species produce more grains depends on the timing when it becomes taller than the companion species, which should align with its grain setting stage. Early overtopping is important to improve light conditions, ensuring sufficient grain filling and thereby capitalising on the higher grain number, to contribute fully to the overall increase in grain yield. However, if the late species overtops too early, it may hinder the early species in establishing grain number advantages and filling grains sufficiently. Thus, the overtopping process in relay intercropping needs to be fine tuned to allow optimal grain filling of the early-sown species and grain 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 grain number (Altendorf et al., 2021), as observed in the three early species in relay intercrops (Fig. S3.5). 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 grains as possible and fill the grains sufficiently. Supply of water and nutrients is also 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.

3.5 Conclusion

Our study revealed that grain 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 maize to have increased grain number, primarily due to reduced interspecific competition during stages of grain number determination. The early-sown species showed grain number-grain weight trade-offs, whereas the improved light availability resulting from the early harvesting of companions enabled intercropped maize to fill all grains to the same extent as monocropped maize did. Light capture advantages are relevant in increasing grain 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 grain number determination. Sufficient access to light and soil resources is important for species to effectively fill grains to take advantage of the larger grain number.

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Chapter 4

The contribution of border row effects to light capture and light use efficiency in strip intercropping

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Abstract

Strip intercropping results in interspecific interactions between species that affect species yields and land equivalent ratio. Interspecific interactions occur mainly in the border rows of the strips, but there is little information on the comparative effect sizes of species mixture on light capture and light use efficiency (LUE) in the border and inner rows of the species strips. Here, we quantify the light capture and LUE in four crop species in six different intercropping systems, comprising both simultaneous and relay intercrops, and quantify differences in light capture and LUE between border and inner rows of the strips. We grew maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.) in strip intercrops of two species in the Netherlands under otherwise conventional crop management. The intercrops involving the late-sown and harvested maize were relay systems, and the combinations not involving maize were simultaneous systems. We measured leaf area and height over time for all species per row type (border and inner). Light capture of border and inner rows of the 1.5 m-wide species strip were estimated by a random ray tracing model. LUE was then estimated from measured cumulative above-ground biomass and simulated light capture. The model estimated light capture for different row types of all species in different combinations with good agreement with the field measurements. In relay intercrops, the early-sown species all obtained higher biomass in the border rows of the intercrops than in the monocrops. The increased biomass of the early-sown species corresponded to enhanced light capture, but not to increased LUE. Border and inner rows of intercropped maize had higher LUE in all relay intercrops. Border row maize biomass increased when grown with short-statured companions (wheat and pea) with an associated increase in light capture by maize, but maize biomass was not increased when it was combined with tall-statured faba bean. In the simultaneous intercrops, the tall faba bean substantially reduced both light capture and LUE of wheat and pea in all rows. Faba bean captured more light mainly in the border rows, whereas its LUE remained unchanged. Light capture and LUE in the intercrops were mostly consistent with the border row effects on biomass for each species. Relay intercrops enhanced biomass of both component species, particularly in border rows. In relay intercrops, the early-sown C_3 species benefited from increased light capture rather than increased LUE. The late-sown C_4 maize benefited from increased LUE, but biomass was increased only in intercrops with a short-statured companion, i.e., wheat or pea. In C_3/C_3 simultaneous intercrops lacking temporal complementarity, light use was less efficient. The taller species, i.e., faba bean, showed increased light capture in border rows but unchanged LUE. However, it did not compensate for the reductions in both light capture and conversion of the shorter-statured companions, i.e., wheat or pea, in all rows in terms of biomass production. In intercropping, where light is the main limitation, C_3/C_4 combinations, with temporal complementarity between species, have a better chance to increase light capture and conversion than C_3/C_3 combinations facing strong interspecific competition.

Keywords: Strip intercropping; Relay intercropping; Border row; Light capture; Light use efficiency; Light model

4.1 Introduction

Intercropping is the cultivation of multiple crop species on the same field for a portion or the whole of their growing periods. Intercropping has the potential to improve resource use efficiency and increase the production per unit land, due to species complementarities (Brooker et al., 2015; Li et al., 2020b, 2023; van der Werf et al., 2021). Intercropping increases capture and (or) conversion efficiencies of resources such as light, nutrients, and water. Which resources are used more efficiently depends on the production situation and the management (Bedoussac et al., 2015; Castillo et al., 2022; Mudare et al., 2022; Wang et al., 2021; Xu et al., 2020; Yin et al., 2020; Zhang et al., 2022; Zhu et al., 2015). If water and nutrients are supplied at levels that do not constrain production, yield-increasing effects of intercropping are mostly due to improved light capture and conversion (light use efficiency, LUE) (Gou et al., 2016, 2017a; Li et al., 2021). For instance, relay strip intercrops in temperate climates provide temporal complementarity that allows early-sown species to capture an increased quantity of early-season light before canopy development of the late-sown species, whereas the late-sown species benefit from increased late-season light capture after harvest of the early species (Gou et al., 2017a; Zhang et al., 2008a; Zhou et al., 2021; Zhu et al., 2015). In the absence of temporal complementarity, increased light capture is also possible because the heterogeneous canopy allows a more efficient light distribution between canopies of different species (Dzvene et al., 2023; Zhu et al., 2020). Intercropped plants can express plasticity such as increased tillering and leaf growth (Li et al., 2021; Umesh et al., 2023; Zhu et al., 2015) in response to enhanced light conditions or other changes in resource availability, which reinforces the advantages in light capture.

Intercropping can increase light capture and conversion at the same time (Liu et al., 2018; Zhang et al., 2018). This is because good light conditions can support increased photosynthesis by promoting biomass allocation to leaves and uptake of water and nitrogen (N) in leaves (Lambers et al., 2008; Poorter et al., 2009), through a positive above- and below-ground resource capture feedback (Evers et al., 2019). Moreover, increased LUE can be observed in intercropped plants under low-light conditions. This phenomenon has been described in C_3/C_4 intercropping, where a short-statured C_3 species is inferred to benefit from a higher proportion of diffuse light under shading of a tall-statured C_4 species (Liu et al., 2017). The C_4 species, on the other hand, benefit from its high photosynthetic capacity at a high light intensity (Gong et al., 2020; Wang et al., 2021; Yu, 2016).

We define strip intercropping as a system in which two or more species are grown in alternating strips whereby the strips are at least 1 m wide, to allow species-specific management, but not wider than 3 m, to ensure sufficient interspecific interaction. On the other hand, strip systems of arable crops with strips wider than 3 m have very limited interspecific interactions, which may limit the potential for complementarity (van Oort et al., 2020). Intercropping advantages resulting from complementarity are most likely to occur with narrow strips, and particularly in the border rows (Gou et al., 2017a; Zhang et al., 2008a; Zhu et al., 2015). Interspecific competition and complementarity for light capture will occur mainly in those border rows, though shading effects may extend beyond the border row in a shorter, shaded species, grown alongside a taller one.

Little work has been done to quantify light capture in strip intercrops (van Oort et al., 2020; Wang et al., 2021). Not only is light capture affected by the strip canopy structure, but also the availability of other resources, especially N, will be affected. This may, in turn, impact light capture and conversion by altering canopy development, structure, and photosynthesis (Ouyang et al., 2021; Slattery and Ort, 2021). Furthermore, light capture and LUE can be influenced by the choice of companion species, resulting in various types of heterogeneity, such as C_3/C_4, N-fixing/non-N-fixing, early/late sowing, tall/short stature, and dense/sparse canopy differences (Justes et al., 2021; Reynolds et al., 1994; Silva et al., 2023; Wang et al., 2021).

Here, we build on data collected in the intercropping experiment in 2019 described in Chapter 2, with four crop species in six different species combinations, to quantify the relationship between light capture and biomass production in border and inner rows of each species in each mixture. We use modelling to assess light capture in border and inner rows and combine this with the biomass data to calculate LUE. With the results of this study, we aim to determine the contribution of heterogeneity in light capture and heterogeneity in light conversion to the border row effects and overall intercropping effects on biomass production in the different intercrops studied.

4.2 Materials and methods

4.2.1 Experimental design

The field experiment was conducted in 2019 at Droevendaal Experimental Farm of Wageningen University & Research, the Netherlands (51°59'20" N, 5°39'16" E). The experimental season ran from April 1 to September 18, covering the period from sowing the first species to harvesting the last. The local climate, classified as temperate oceanic, is characterised by an average air temperature of 15°C, cumulative photosynthetically active radiation (PAR) of 1514 MJ m^{-2}, and cumulative precipitation of 252 mm during the experimental season. The summer of 2019 had drier and hotter conditions than the historic record (Koninklijk Nederlands Meteorologisch Instituut, 2019). The farm has sandy soil with a 3.4% organic matter and a 5.7 PH.

Four crop species, maize (*Zea mays* L., var. 'LG30.223'), wheat (*Triticum aestivum* L., var. 'Nobless'), faba bean (*Vicia faba* L., var. 'Fanfare'), and pea (*Pisum sativum* L., var. 'Astronaute'), were combined as six bi-specific strip intercrops, each featuring a 1.5 m-wide species strip: maize/wheat, maize/faba bean, maize/pea, faba bean/wheat, faba bean/pea, and wheat/pea. This experiment was designed according to Good Agricultural Practices (FAO, 2003) for the EU. Each species received N fertilisation in accordance with recommendations for monocrops. Inclusion of the legumes was aimed at utilising N-fixation to further reduce the N input (Chapter 2). Intercrops were laid out as 50:50 replacement designs with 1.5 m-wide strips of each species, which were fertilised as monocrops. Hence, the N fertiliser input per unit area of the whole intercrop was the average of the monocrop N fertiliser inputs, but applied heterogeneously within the intercrop according to species demand, higher for maize and wheat than for faba bean and pea.

In the maize strips, three plant rows were sown at a 0.5 m row distance, whereas the other three species had six plant rows at a 0.25 m row distance from rows 2 to 5 and a 0.2 m row distance between the border rows of the strip and the first inner rows to create a wide enough driving lane for passage of a tractor. In a maize species strip, rows 1 and 3 were border rows, and row 2 was an inner row. In a species strip of wheat, faba bean, or pea, rows 1 and 6 were border rows, rows 2 and 5 were called inner rows I, and rows 3 and 4 were called inner rows II; see Chapter 2 for more details.

Sowing densities adhered to the local conventional farming practices: 10 seeds m^{-2} for maize, 369 seeds m^{-2} for wheat, 44 seeds m^{-2} for faba bean, and 83 seeds m^{-2} for pea. Pea, wheat, and faba bean were sown on April 1 and harvested on July 29, August 8, and August 14, respectively. Maize was sown on May 7 and harvested on September 18. The row orientation was approximately north-south. The plots were arranged as a randomised complete block design with four blocks; see Chapter 2 for more details.

Prior to sowing wheat, pea, and faba bean, potassium (K) and phosphorus (P) were evenly applied across the entire field, at rates of 87 kg K ha^{-1} and 34 kg P ha^{-1}. Each species received N fertilisation tailored to maintain a good production with reduced environmental impact: 170 kg N ha^{-1} for maize (80 kg at sowing and 90 kg at stem elongation), 125 kg N ha^{-1} for wheat (80 kg two weeks after sowing and 45 kg at stem elongation), and 20 kg N ha^{-1} for the legumes (two weeks after sowing). Irrigation was applied every week from June to August; see Chapter 2 for more details.

4.2.2 Above-ground biomass measurements

Above-ground biomass was measured six times (five intermediate harvests and the final harvest) for wheat, faba bean, and pea, and five times (four intermediate harvests and the final harvest) for maize (Table S4.2). Intermediate harvests were done in one intercrop strip comprising two species strips in the middle of an intercropping plot, and in one species strip in the middle of a monocropping plot. Plants within a 1.6 m length in each row were harvested. In maize, we distinguished between border and inner rows in the strip, whereas in the other three species, we distinguished border rows, inner rows I, and inner rows II. Samples belonging to different row types were kept separate, but samples of the same type were pooled. During the final harvests, plants within a 4 m length in each row were harvested, and samples from each row were processed separately. The fresh weight of each sample was taken. Then, a subsample was randomly taken from each sample and weighed. Subsamples were dried at 105 °C for 48 h and used to convert sample fresh weights to dry weights.

4.2.3 Estimation of light capture and calculation of light use efficiency (LUE)

Cumulative light capture was calculated as the accumulation of daily light capture. For each row type (border and inner), the daily light capture was determined by multiplying the light capture fraction (f_{cap}) by the incoming PAR. The daily incoming PAR was estimated as 50% of the global radiation recorded at the Wageningen University weather station ‘De Veenkampen’, located 4 km west of the experimental site.

f_{cap} was calculated using a random ray tracing model. This model was initially developed to calculate light capture fraction of row crops, considering light transmission between adjacent plant rows with heterogeneous canopies (Gijzen and Goudriaan, 1989; Schnieders, 1999; Tsubo et al., 2001). It has been modified for the calculation of light capture by plant rows in strip intercropping (Wang et al., 2017). In this study, the modified model of Wang et al. (2017) was recoded based on the published equations. LUE was then estimated by the regression between measured above-ground biomass and estimated cumulative light capture. Light capture and LUE of intercropped species were compared between intercrop border rows and inner rows, and between monocrops.

In a strip comprising several plant rows, the radiation energy of a light beam attenuates while it is traversing from one row to the next. Therefore, f_{cap} of a specific row i is calculated by Lambert-Beer's Law:

$$f_{\mathrm{cap}\,i} = \exp\left(-\sum_{j=1}^{i-1} g_j \mathrm{LAD}_j p_j\right)\left[1 - \exp\left(-g_i \mathrm{LAD}_i p_i\right)\right] \qquad \text{(Eq. 4.1)}$$

where g is the canopy light extinction coefficient; LAD is the leaf area density; p is the path length of the beam when it traverses the row. No adaptations were made to the model except for the light sources, and details on calculating g, LAD, and p can be found in Wang et al. (2017) and Method S4.1.

Light sources were determined by solar positions calculated by astronomical and geographical data in the initial model (Wang et al., 2017). In the current study, a hemispherical dome with 500 random light sources was specified to mimic a uniform sky. The light sources were generated by combining 100 random solar elevation angles with 5 random solar azimuth angles (relative to the south) for each solar elevation (Fig. S4.3).

As input to the model, the daily plant height and leaf area index (LAI; green leaves, on the row level) of each species in different row types were measured (Methods S4.2 and S4.4) and linearly interpolated (Fig. S4.7). The linear interpolation was conducted in R (R Core Team, 2022), using the 'approx' function. Parallel programming was conducted for the light model using the package 'future.apply' (Bengtsson, 2021).

The model was validated by comparing the simulated f_{cap} with field measurements presented in Chapter 3. As the measured f_{cap} was determined at the strip level, the comparison was conducted after calculating the simulated f_{cap} as the sum of all row-low f_{cap} values within each strip. Root Mean Square Error (RMSE) was used to evaluate the agreement between the estimates from the light model and field measurements.

$$\mathrm{RMSE} = \sqrt{\frac{1}{N} \times \sum_{i}^{N} \left(f_{\mathrm{cap}_{\mathrm{S}\,i}} - f_{\mathrm{cap}_{\mathrm{M}\,i}}\right)^2} \qquad \text{(Eq. 4.2)}$$

where $f_{\mathrm{cap}_{\mathrm{S}\,i}}$ and $f_{\mathrm{cap}_{\mathrm{M}\,i}}$ are the light capture fractions simulated by the model and measured in the field, receptively. N is the number of measurements, which ranged from 9 to 13 depending on treatments.

Moreover, we made a comparison of the daily PAR captured by each species in different treatments, estimated using the random ray tracing model, and results of the intercrop light capture model of Gou et al. (2017a), as presented in Chapter 3.

4.2.4 Data analyses

Intercropping row effects on above-ground biomass and cumulative light capture

Data analyses were conducted in R (R Core Team, 2022). For each species, linear mixed effects models were specified to evaluate the effects of intercropping rows on above-ground biomass and cumulative light capture. A categorical variable 'Treatment_Row' was defined as a fixed effect to represent a specific row position: Border and Inner for maize, and Border, Inner I and Inner II for the other species. Block was included in the analyses as a random effect.

Comparisons of above-ground biomass and cumulative light capture in rows of monocrop strips showed that there were mostly no row position effects in monocrops (Figs S4.10 and S4.11). Therefore, monocrop rows were not differentiated for subsequent analyses for each species. Inner rows I and II in the intercrops of wheat, faba bean, and pea within the same treatment were also not differentiated because there were hardly any differences (Figs S4.12 and S4.13).

The models were fitted using the 'lmer' function from the 'lme4' package (Bates et al., 2015).

Multiple comparisons of the means were conducted using the ‘emmeans’ function from the ‘emmeans’ package (Lenth, 2021).

Regression between above-ground biomass and cumulative light capture

For each species, linear mixed effects models were specified for the regressions between above-ground biomass as the response variable and cumulative light capture as a numeric explanatory variable. Block was specified as a random effect. The regression lines were forced through the origin and the slopes obtained were the light use efficiencies (LUE in g biomass per MJ PAR). Categorical covariables were introduced to assess whether LUE of a species differed between treatments (companion species × row type), or between the monocrop, relay, and simultaneous intercrops, or between the monocrop, cereal/legume, and non-cereal/legume intercrops. Within each type of intercropping group, row effects on LUE were also examined. All models were compared with the simplest model in which the species had identical LUE across all treatments and rows (Table 4.1). The optimal model was selected using Akaike’s information criterion in the ‘anova’ function (Akaike, 1998). Among models with AIC values differing by less than two, the simpler model was chosen to avoid overfitting (Burnham and Anderson, 2004).

Table 4.1 Model specification for determining light use efficiency (LUE). j and k represent treatment ID and block ID. b_k is a random block effect. ϵ_{jk} is a random error on the plot level. Definitions of the categorical covariables: Treatment: all treatments of the species including one monocrop and three intercrops; Treatment_Row: the monocrop and the border and inner rows in the intercrops; Relay vs. Simultaneous: the monocrop, and the relay and simultaneous intercrops; Relay vs. Simultaneous_Row: the monocrop and the border and inner rows in the relay and simultaneous intercrops; Cereal.Legume: the monocrop, and the cereal/legume and non-cereal/legume intercrops; Cereal.Legume_Row: the monocrop, and the border and inner rows in the cereal/legume and non-cereal/legume intercrops.

Models	Equations
1	$\text{Biomass}_{jk} = \beta_1 * \text{Cum. PAR}_{jk} + b_k + \epsilon_{jk}$
2	$\text{Biomass}_{jk} = \beta_1 * \text{Cum. PAR}_{jk} * \text{Treatment}_{jk} + b_k + \epsilon_{jk}$
3	$\text{Biomass}_{jk} = \beta_1 * \text{Cum. PAR}_{jk} * \text{Treatment\_Row}_{jk} + b_k + \epsilon_{jk}$
4	$\text{Biomass}_{jk} = \beta_1 * \text{Cum. PAR}_{jk} * \text{Relay vs. Simultaneous}_{jk} + b_k + \epsilon_{jk}$
5	$\text{Biomass}_{jk} = \beta_1 * \text{Cum. PAR}_{jk} * \text{Relay vs. Simultaneous\_Row}_{jk} + b_k + \epsilon_{jk}$
6	$\text{Biomass}_{jk} = \beta_1 * \text{Cum. PAR}_{jk} * \text{Cereal. Legume}_{jk} + b_k + \epsilon_{jk}$
7	$\text{Biomass}_{jk} = \beta_1 * \text{Cum. PAR}_{jk} * \text{Cereal. Legume\_Row}_{jk} + b_k + \epsilon_{jk}$

4.3 Results

4.3.1 Above-ground biomass

In relay intercrops, border row maize initially had lower biomass than monocropped maize (Fig. 4.1 i). From approximately DOY 235 (maize grain filling), border row maize with wheat and pea started to have higher biomass than monocropped maize, reaching significantly higher total biomass at the final harvest. Border row maize with faba bean had similar biomass as monocropped maize at harvest. Inner row maize also began to show higher biomass than monocropped maize at maize grain filling, maintaining this advantage until harvest across all intercrops. Border rows of early-sown species initially had similar biomass as the monocrops (Fig. 4.1 ii–iv). Starting approximately on DOY 168 (wheat stem elongation, faba bean flowering, and pea pod filling), border rows of early-sown species showed higher biomass, achieving significantly higher total biomass at the final harvest than the monocrops. Inner rows showed a similar pattern with smaller differences compared to monocrops.

In the intercrops involving faba bean, intercropped wheat and pea had significantly lower biomass than monocrops in both border and inner rows, and these reductions persisted at harvest. Intercropped faba bean only showed higher biomass in border rows compared to the monocrop. In the wheat/pea intercrop, border row wheat had higher biomass after DOY 182 (wheat flowering), whereas inner row wheat remained similar to the monocrop. No intercropping row effects were found on pea biomass with wheat.

4.3.2 Light capture

The RMSE ranged from 0.067 (faba bean/wheat intercrop) to 0.125 (maize monocrop), demonstrating good agreement with the field measurements (Fig. S4.8). The results also showed good agreement with the light estimates in Chapter 3 (Fig. S4.9).

In relay intercrops, border row maize initially captured less light than monocropped maize (Fig. 4.2 i). Border row maize with wheat and pea started showing higher daily light capture from approximately DOY 195 (maize tasselling), and the total light capture was higher than monocropped maize at harvest. Border row maize with faba bean started showing higher daily light capture from approximately DOY 215 (maize grain filling), and the total light capture was similar to monocropped maize at harvest. Inner row maize started showing higher daily light capture than monocropped maize earlier than border row maize in all intercrops, reaching increased light capture at harvest. Border rows of early-sown species started showing higher daily light capture all in the early vegetative growth phase, ultimately resulting in higher total light capture than the monocrops, even in the presence of maize shading during the late season (Fig. 4.2 ii–iv). Such light capture advantages did not show in inner rows. In the intercrops involving faba bean, intercropped wheat and pea captured significantly less light capture than the monocrops in both border and inner rows. Intercropped faba bean captured more light in the border rows, whereas the increases in the inner rows were not substantial. In the wheat/pea intercrop, border row pea captured more light than monocropped pea. Border row wheat had an increase in light capture after pea was harvested.

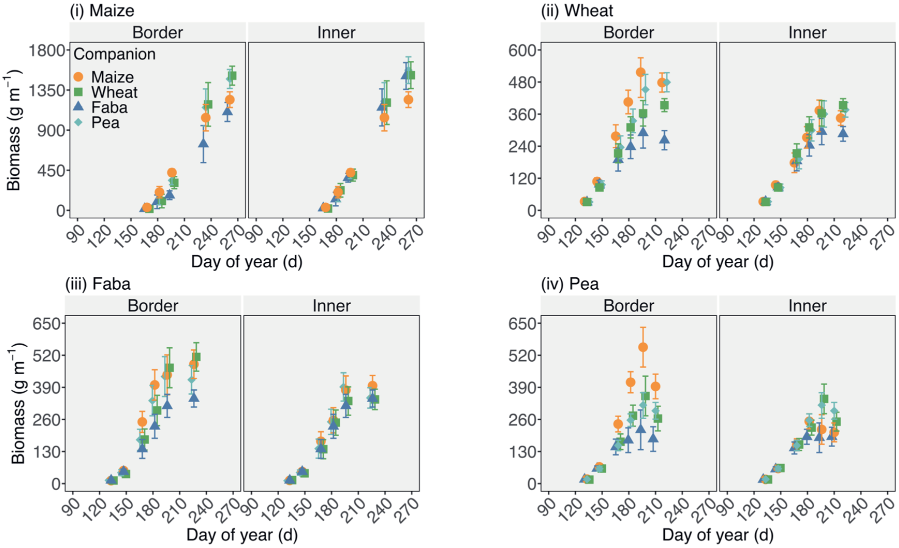

Fig. 4.1 Above-ground biomass through the growing season for maize (i), wheat (ii), faba bean (iii), and pea (iv). Biomass is expressed per metre row. For each focal species, the coloured symbols represent focal species biomass with different companion species: maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond). For each focal species, biomass in the intercrops is presented separately for the border and inner rows, whereas in the monocrop (companion species equals focal species in each panel) is presented as the average across all rows. Error bars represent the 95% confidence intervals of the means.

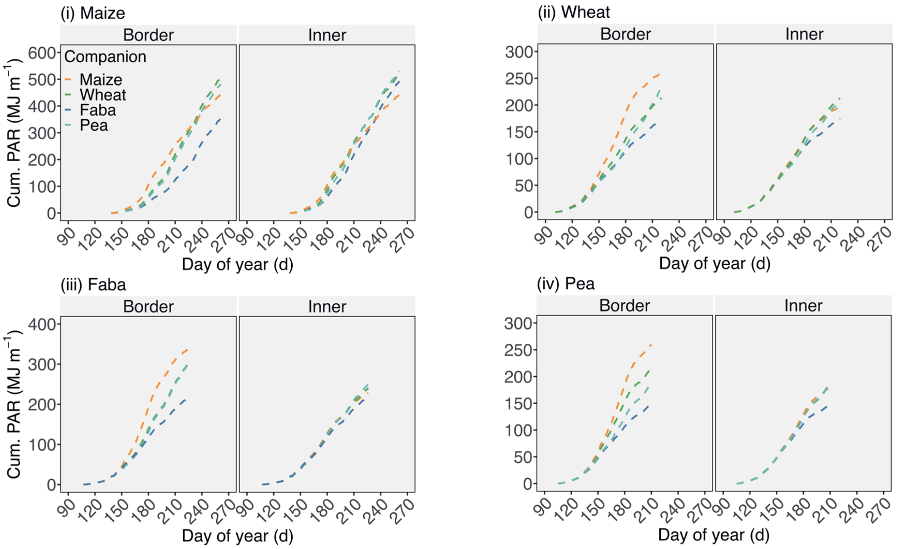

Fig. 4.2 Daily cumulative PAR captured (Cum. PAR) through the growing season for maize (i), wheat (ii), faba bean (iii), and pea (iv). Cumulative PAR captured is expressed in MJ per metre row. For each focal species, the colors represent its cumulative PAR captured when it was with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). For each focal species, cumulative PAR captured in the intercrops is presented separately for the border and inner rows, whereas in the monocrop (companion species equals focal species in each panel) is presented as the average across all rows. The comparison for total PAR captured over the whole season is presented in Fig. S4.14.

4.3.3 Light use efficiency (LUE)

Model 4 (Relay vs. Simultaneous) was selected for maize, Model 5 (Relay vs. Simultaneous_Row) was selected for faba bean, and Model 3 (Treatment_Row) was selected for wheat and pea according to AIC (Table S4.3).

In relay intercrops, intercropped maize had an 8% higher LUE than monocropped maize in both border and inner rows (Fig. 4.3; Table 4.2; $P < 0.001$). No differences were found between rows in any intercrops. Compared to the corresponding monocrops, LUE of border rows of the early-sown species remained unchanged. However, inner rows of wheat and pea had decreased LUE, with reductions of 8% for wheat and 19% for pea ($P < 0.001$). Inner row of faba bean had an 11% higher LUE than monocropped faba bean ($P < 0.001$)

Faba bean significantly reduced LUE of intercropped wheat and pea in both border and inner rows. Compared to monocropped faba bean, LUE of intercropped faba bean remained unchanged in border row, whereas it was 7% lower in inner row ($P = 0.006$). In the wheat/pea intercrop, wheat had a higher LUE in the border row, whereas it had a similar LUE in the inner rows compared with monocropped wheat. Intercropped pea had lower LUE in both border and inner rows than monocropped pea.

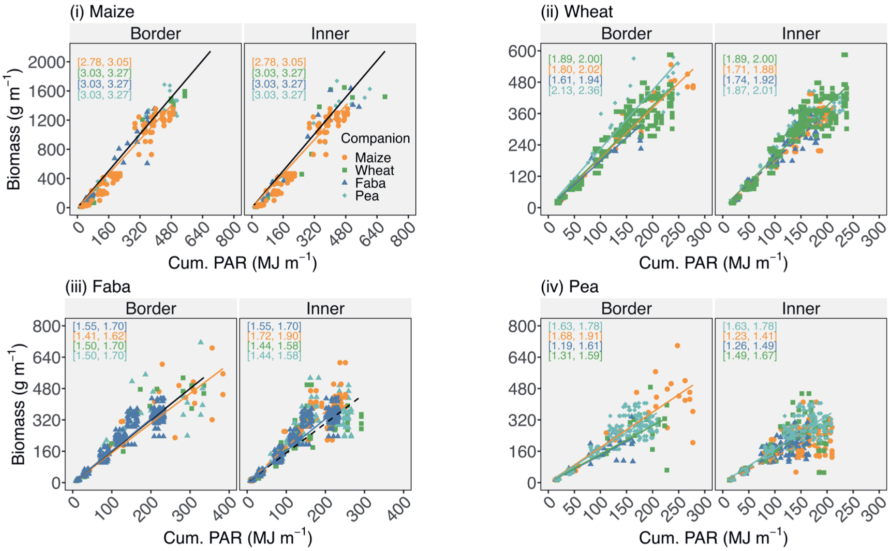

Fig. 4.3 Regressions between above-ground biomass and cumulative PAR captured (Cum. PAR) for maize (i), wheat (ii), faba bean (iii), and pea (iv). Biomass and cumulative PAR captured are expressed in the amounts per metre. For each focal species, the coloured symbols represent its biomass and cumulative PAR captured when it was with different companion species: maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond). For each focal species, biomass and cumulative PAR captured in the intercrops are presented separately for the border and inner rows, whereas in the monocrops (companion species equals focal species in each panel) are presented as the averages across all rows. Coloured numbers in the square brackets are the 95% confidence intervals of LUE of the focal species in the corresponding treatments marked by the same colours.

Table 4.2 Biomass, cumulative PAR captured (Cum. PAR) at harvest, and light use efficiency (LUE) of each focal species (presented in rows) when it was intercropped with different companion species (presented in columns). The numbers in the square brackets are the 95% confidence intervals of the means.

Focal species	Companion species	Border row			Inner row		
		Biomass (g m^{-1})	Cum. PAR (MJ m^{-1})	LUE (g MJ^{-1})	Biomass (g m^{-1})	Cum. PAR (MJ m^{-1})	LUE (g MJ^{-1})
Maize	Maize	1242 [1154, 1330]	442 [396, 488]	2.91 [2.78, 3.05]	1242 [1154, 1330]	442 [396, 488]	2.91 [2.78, 3.05]
	Wheat	1511 [1405, 1618]	506 [431, 582]	3.15 [3.03, 3.27]	1517 [1367, 1667]	519 [443, 595]	3.15 [3.03, 3.27]
	Faba bean	1104 [997, 1210]	353 [289, 418]	3.15 [3.03, 3.27]	1508 [1358, 1658]	493 [429, 557]	3.15 [3.03, 3.27]
	Pea	1474 [1368, 1581]	482 [418, 546]	3.15 [3.03, 3.27]	1573 [1423, 1723]	531 [467, 595]	3.15 [3.03, 3.27]
Wheat	Wheat	393 [369, 418]	213 [198, 228]	1.95 [1.89, 2.00]	393 [369, 418]	213 [198, 228]	1.95 [1.89, 2.00]
	Maize	478 [442, 514]	260 [242, 278]	1.91 [1.80, 2.02]	345 [318, 373]	197 [181, 212]	1.80 [1.71, 1.88]
	Faba bean	262 [227, 298]	173 [158, 195]	1.78 [1.61, 1.94]	286 [259, 313]	174 [162, 194]	1.83 [1.74, 1.92]
	Pea	479 [443, 515]	235 [218, 251]	2.25 [2.13, 2.36]	376 [349, 404]	209 [194, 224]	1.94 [1.87, 2.01]
Faba bean	Faba bean	345 [310, 379]	220 [207, 232]	1.62 [1.55, 1.70]	345 [310, 379]	220 [207, 232]	1.62 [1.55, 1.70]
	Maize	484 [426, 541]	340 [320, 360]	1.51 [1.41, 1.62]	397 [355, 438]	229 [214, 243]	1.81 [1.72, 1.90]
	Wheat	513 [456, 571]	307 [284, 331]	1.60 [1.50, 1.70]	341 [300, 383]	241 [224, 258]	1.51 [1.44, 1.58]
	Pea	421 [363, 479]	309 [289, 329]	1.60 [1.50, 1.70]	347 [306, 389]	250 [235, 265]	1.51 [1.44, 1.58]
Pea	Pea	295 [261, 329]	187 [177, 197]	1.71 [1.63, 1.78]	295 [261, 329]	187 [177, 197]	1.71 [1.63, 1.78]
	Maize	394 [344, 444]	260 [243, 276]	1.79 [1.68, 1.91]	208 [170, 246]	180 [168, 192]	1.32 [1.23, 1.41]
	Faba bean	181 [131, 230]	149 [133, 166]	1.40 [1.19, 1.61]	190 [152, 228]	148 [136, 160]	1.38 [1.26, 1.49]
	Wheat	264 [214, 314]	215 [199, 232]	1.45 [1.31, 1.59]	251 [213, 289]	185 [174, 198]	1.58 [1.49, 1.67]

4.4 Discussion

In the relay intercrops, all three early-sown species had increased biomass in border rows compared to their monocrops (Fig. 4.1), due to increased light capture with unchanged light use efficiency (LUE) (Figs 4.2 and 4.3; Table 4.2). Only faba bean had increased biomass in inner rows in relay intercropping with maize due to an increased LUE with unchanged light capture compared to monocropped faba bean. Inner rows of wheat and pea had decreased LUE and biomass compared to their monocrops. In spite of the increased LUE in border row maize in all three relay intercrops, it only had increased biomass with short-statured wheat and pea with which it captured more light than monocropped maize. Inner row maize had increased biomass in all three intercrops due to the increased LUE and increased light capture. In simultaneous intercrops, intercropping with faba bean substantially reduced the biomass in all rows of wheat and pea by decreasing both light capture and LUE. Faba bean, on the other hand, had increased biomass in border rows due to increased light capture and unchanged LUE. Inner rows of faba bean had similar biomass to monocropped faba bean, as increased light capture was offset by decreased LUE. In the wheat/pea intercrop, border row wheat had increased biomass due to increases in both light capture and LUE, whereas border row pea showed similar biomass to monocropped pea because the increase in light capture were offset by decrease in LUE. No significant responses of light capture and conversion were found in the inner rows of the wheat/pea intercrop.

4.4.1 Temporal complementarity in C_3/C_4 combinations benefits light capture and conversion

In strip intercropping, border rows have the greatest potential for interspecific interaction that results in an increase or decrease of light capture (Zhu et al., 2015). In relay intercrops, border rows of the three early-sown species had prior light access, reducing competition, and boosting border row LAI (Fig. S4.7). However, light capture of border row maize was only modestly increased in relay intercrops with wheat or pea and reduced in relay intercrops with faba bean (Fig. 4.2 i; Fig. S4.14 i). Reduced LAI went along with decreased light capture (Fig. S4.7). Similar reductions occurred in other relay intercrops, resulting from shading and resource competition by early-sown companions (Wang et al., 2015; Wu et al., 2022; Zhang et al., 2008b). While maize benefited in the late season, it only partially compensated for light loss in the early season (Wang et al., 2017).

There are variable reports in the literature on the effect of intercropping on LUE, as photosynthesis is influenced by various factors such as light quantity and quality, water and nutrient availability, and species photosynthetic capacity (Fernández-Marín et al., 2020; Herrmann et al., 2020; Niinemets, 2023; Wolf and Blankenship, 2019). We found intercropped maize had an increased LUE in both border and inner rows (Fig. 4.3; Table 4.2). In this experiment, intercropped maize overtopped wheat and pea by the ten-leaf stage and faba bean around tasselling, improving light condition, especially in its middle to upper leaf layers. Considering the species-tailored N strategy, we did not expect much N stress for maize in both intercrops and the monocrop. Therefore, the enhanced LUE of intercropped maize could be due to its C_4 photosynthesis being exploited under high-light conditions with an N availability that did not constrain growth.

The early-sown species exhibited LUE values comparable to those of monocrops (Fig. 4.3; Table 4.2), contrary to increased LUE in short C_3 species in previous studies (Gou et al., 2017a; Liu et al., 2017; Wang et al., 2021). In those studies, enhanced LUE was inferred to be attributed to the high proportion of diffuse light under the shading of taller C_4 plants. This is because diffuse light penetrates deeper and more uniformly into the canopy, stimulating photosynthesis (Emmel et al., 2020; Li and Yang, 2015). In the current experiment, the early-sown species were taller than maize until their late grain filling, and, therefore, they should not have received more diffuse light than monocrops for most of the season when the majority of biomass was determined. Moreover, the hotter summer than normal during the experimental season favoured C_4 photosynthesis more than C_3 photosynthesis (Sage and Kubien, 2007).

Simultaneous intercrops had increased light capture only in the border rows of the tall species, which did not compensate for the loss in light capture and conversion it caused in all rows of the short species, especially in intercrops involving faba bean (Figs 4.2 and 4.3). Intercropped wheat and pea received tailored fertiliser. Therefore, their photosynthesis might be mainly constrained by light limitation. Compared to the relay intercrops, we conclude that combining two C_3 species differing much in stature but lacking temporal complementarity, was not efficient in light use because the tall species did not have the potential to efficiently utilise the high light it acquired at the expense of the shorter species. One could argue that increasing N input would facilitate the light conversion of faba bean because a high leaf N concentration at high N availability could improve the photosynthesis of legumes (Adams et al., 2016). However, agronomically, it is not advisable to apply much mineral N to a legume because that will inhibit its N fixation (Coskun et al., 2017). Moreover, excessive vegetative growth promoted by N input might create an even worse light condition for the short companions.

4.4.2 Cereal/legume combinations do not have added benefits on light capture and conversion under species-tailored nitrogen strategy

Previous studies have highlighted the benefits of cereal-legume N complementarity in reducing N competition, supporting a more robust cereal canopy and enhancing light use (Bedoussac and Justes, 2010a). Legumes, although often shaded by cereals, can adapt with morphological changes and N fixation, contributing to light use (Liu et al., 2017). In this study, legumes did not show significant benefits, as seen in similar light capture and LUE of cereals in both cereal/legume and non-cereal/legume intercrops and the fact that the covariable 'Cereal.Legume' did not contribute to explaining LUE of all species (Table S4.3). Tailored fertilisation and strip design might limit N complementarity. The increased light capture and LUE in border row wheat with pea may be attributed to earlier pea harvesting rather than specific legume-related benefits. The absence of cereal/legume N complementarity has also been found in terms of the production effect in this experiment (Chapter 2). Nevertheless, in relay intercrops with maize, legumes showed comparable light capture and conversion advantages with the maize/wheat intercrop, significantly saving N fertiliser.

4.4.3 Implications about the modelling approach

Our study, along with previous research on simultaneous row intercropping and relay strip intercropping, supports the effectiveness of this random ray tracing model in estimating light capture, considering temporal and spatial heterogeneity in rows of crop mixtures (Tsubo and Walker, 2002; Wang et al., 2017). The 'uniform sky', generated by random light sources, may limit exploration of diurnal and seasonal light variations, compared to previous studies using this model in which solar positions and the corresponding direct and diffuse radiation are estimated based on astronomical and geographical inputs (Wang et al., 2017). However, the 'uniform sky' suffices and is more straightforward in agronomic research as the current study, where cumulative light capture on a crop and periodical level is needed, because the heterogeneity of plants is the key determinant of intercropping effects, rather than the characteristic of the light sources. In our model, LAI and plant height were linearly interpolated using measured data, assuming a constant growth rate between each pair of measurements (Fig. S4.7). This oversimplification, deviating from the non-linear reality of plant growth, likely led to the model overestimating light capture early in the season (Fig. S4.8), because plant growth usually follows sigmoid patterns and starts at a relatively low growth rate at the beginning (Yin et al., 2003). However, as this overestimation was consistent across all species in both intercrops and monocrops, its impact on our conclusions is judged to be small.

Plasticity plays an important role in light capture in intercropping (Li et al., 2021; Zhu et al., 2015). In the current study, plasticity in leaf area and height was part of the input. These plastic responses included the increased border row LAI of early-sown species due to reduced competition, the decreased border row LAI of maize due to increased early competition, and the taller heights of maize and faba bean in monocrops compared to intercrops due to self-shading (Fig. S4.7). There are still many plant traits especially the architectural traits affecting light capture, such as leaf shape and leaf angle, can be accounted for in this model by altering light extinction coefficients, though they have not been included yet. These factors can make a difference in light distribution within the local row and between different rows. A plant-level model that can consider more detailed plastic responses, such as functional structural plant models (Evers et al., 2019), would allow to adjust specific plant architectural and physiological traits and quantify their relevance for light capture (Barillot et al., 2019; Sarlikioti et al., 2011; Zhu et al., 2015).

Row configuration and strip width design are crucial for strip intercropping in modern agriculture due to the need for machinery adaptation (van Oort et al., 2020). Therefore, quantifying border row effects is essential for determining the appropriate species combinations and row configurations for local production. Through the modelling approach, we have quantified intercropping effects on light capture and conversion at the strip level, and shown they are primarily driven by border rows (Fig. S4.15). This method provides a more direct assessment of row differences compared to previous studies on row effects, which examined the strip-level performance of various row configurations with different proportions of border rows (van Oort et al., 2020; Wang et al., 2020; Wang et al., 2021). It also provides opportunities to assess border row effects on other resources, such as nutrients and water, by incorporating above- and below-ground feedback as previously exemplified on the strip level (Berghuijs et al., 2020; Tan et al., 2020).

4.5 Conclusion

We found that in relay intercrops, all three early-sown species obtained increased biomass in border rows due to enhanced light capture and unchanged light use efficiency (LUE). Faba bean, uniquely, had increased biomass in inner rows due to increased LUE with unchanged light capture compared to the monocrop. Despite the increased LUE in border row maize in all three relay intercrops, biomass was increased only in the intercrops with shorter-statured wheat and pea when it captured more light than monocropped maize. Inner row maize, however, had increased biomass with all three companion species due to increased light capture and increased LUE. Simultaneous intercrops, particularly those involving faba bean, had substantially reduced biomass in all rows of wheat and pea, highlighting the importance of competition for light in intercrops lacking temporal complementarity. C_3/C_4 combinations, in which the component species often have different growth cycles, provide a better chance of increasing light capture and boosting light conversion than C_3/C_3 combinations, where interspecific competition for light is more intense due to greater temporal overlap of the species' growing periods. However, such temporal overlap between species may be of less concern or even advantageous if other factors than light are driving species complementarity. Simultaneous intercrops remain promising when water and nutrients are limiting and species complementarity and facilitation are possible, e.g., for nutrients, while relay intercrops are promising particularly when other growth constraints have been overcome by management.

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Chapter 5

Relay strip intercropping increases nitrogen uptake and fertiliser nitrogen use efficiency

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Abstract

Nitrogen (N) fertilisation strategy in intercropping varies depending on the production purpose and production situation. There is limited information on N uptake when species receive tailored N fertilisation in strip intercropping. Here we determined N uptake of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.) in six bi-specific intercrops and the corresponding monocrops when the species received locally recommended fertiliser amounts for conventional agriculture. We also determined fertiliser N use efficiency of different intercrops compared to the respective monocrops, using fertiliser N equivalent ratio (FNER). In intercrops, the fertiliser was applied to the 1.5 m-wide strip of the species at a rate (kg ha^{-1}) equal to that in the monocrop. In relay intercrops involving maize, the early-sown wheat, faba bean, and pea had higher N uptake than the respective monocrops, especially in the border rows of the strips. N uptake in maize intercropped with wheat and pea was increased in the year with six weeks sowing delay compared to companion species but not in the other year, in which the sowing delay was only five weeks. Intercropping with faba bean did not result in increases in N uptake of the two cereals. Relay intercrops involving maize had land equivalent ratios for N uptake (LER$_N$) mostly higher than one, whereas simultaneous intercrops not involving maize had LER$_N$ values mostly similar to one. Relay intercrops had FNER values mostly higher than one, whereas simultaneous intercrops had FNER values mostly similar to one. N uptake and fertiliser N use efficiency of intercrops increased with temporal complementarity. Relay systems had a higher N uptake than expected based on corresponding monocrops, largely because of higher N uptake by the early-sown species. Intercrops with faba bean did not result in increases in N uptake for either cereals or other legumes compared to monocrops. While inclusion of legumes was not required for achieving complementarity for N capture, inclusion of legumes does allow a reduction in N input. Relay intercrops achieved yield advantages with a moderate N fertiliser rate compared to monocrops, indicating that relay intercropping with recommended fertiliser N input is a pathway towards more sustainable N use in agriculture.

Keywords: Conventional agriculture; Tailored nitrogen fertilisation; Nitrogen uptake; Fertiliser nitrogen equivalent ratio; Cereal/legume intercropping; Relay intercropping

5.1 Introduction

Intercropping is the mixed cultivation of multiple crop species, growing on the same field and coexisting for a time (Willey, 1990). Intercropping is gaining adoption as an agricultural intensification strategy worldwide, aiming at achieving a balance between productivity and resource inputs (Bedoussac et al., 2015; Brooker et al., 2015). It has advantages in improved use efficiencies in land, light, water, and nutrients (Li et al., 2023; Stomph et al., 2020; Xu et al., 2020; Zhang et al., 2022).

Intercropping can be done using conventional inputs such as artificial nitrogen (N) fertiliser and biocides, or it can be done at low-input levels or in organic agriculture. High land equivalent ratios (LER) have been found in both situations, but the yield increases are higher when higher inputs are used (Li et al., 2020b). Intercropping systems with conventional inputs are often strip intercrops, to allow tailored inputs to each species comprised in the mixtures (Gou et al., 2017a). On the other hand, systems without such inputs are often within-row or alternate row mixtures, allowing management of the whole field with conventional machinery with a working width of at least 3 m (Bedoussac et al., 2015). In Western Europe, ample experience has been gained with application of such within-row or alternate row mixtures under organic growing conditions (Bedoussac et al., 2015; Fischer et al., 2020; Hauggaard-Nielsen et al., 2009), but less experience has been gained with intercropping with inputs that are used by conventional farmers such as artificial N fertiliser and biocides. There is therefore a lack of knowledge on the potential of strip intercropping systems with conventional inputs to enhance productivity and resource use efficiency under Western-European conditions.

Complementarity in resource capture between component species that explore different niches is a cornerstone of overyielding in intercropping (Brooker et al., 2015; Homulle et al., 2021). For instance, most grain legumes need limited N from the soil because 60%–80% of their final plant N is derived from N fixation (Giller, 2001). Combining cereals with legumes in intercropping can decrease the competition for soil N experienced by the cereal, resulting in increased N uptake by cereals compared to their monocrops (Rodriguez et al., 2020). At the same time, legumes may not be affected much by the strong competition for soil N from the cereal because they can capture N from the atmosphere (Iannetta et al., 2016).

Another important complementarity in intercropping is complementarity in growing periods (Yu et al., 2015). When two species are combined in a relay sequence, the early-sown species experiences relaxed competition during its early growth, whereas the late-sown species may experience relaxed competition during its later growth. This results in a potential for complementarity for all resources, including light, water, and nutrients (Gou et al., 2017a; Liu et al., 2020; Zhu et al., 2015). Such temporal complementarity is relevant particularly in regions with a growing season that is longer than the growth duration of the main crops, but shorter than the growth duration of two crops grown in a double cropping sequence. In such climate conditions, relay intercropping has potential to increase the efficiency of land use and the productivity per unit area substantially (Li et al., 2020b).

N is an essential element for plant development and growth, and is a main limiting nutrient for crop production (Leghari et al., 2016). The effects of intercropping on N uptake have been studied under various N input strategies for different production objectives (Jensen et al., 2020; Rodriguez et al., 2020; Xu et al., 2020). In regions such as China, where the primary aim is to maximise absolute production, N fertiliser is often applied at high rates to prevent N limitation (Li et al., 2020b). Under this strategy, N rates for intercrops are established either at a specific high dose, as the total N rate for the entire system (Li et al., 2011; Xing et al., 2023), or determined as the weighted average of the respective N doses of the component species grown as monocrops, based on their land proportions in the intercrop (Gao et al., 2022). Another N fertilisation strategy involves setting the intercrop N fertilisation rate as the sum of those in the corresponding monocrops (Du et al., 2018; Feng et al., 2020; Yang et al., 2017). This approach is often used in additive design intercrops, ensuring a consistent N rate per plant, and maximising intercropping yield advantages (Yang et al., 2017).

Increased N uptake per unit land area is found in these high-input intercrops on both species and system levels (Li et al., 2011; Xing et al., 2023), due to various mechanisms leading to reduced interspecific N competition. For instance, reduced N competition can arise from temporal differences in growing periods, spatial differences in root distribution, functional differences in N acquisition, and complementary use of light and water, all of which stimulate enhanced N capture (Li et al., 2006; Liu et al., 2020, 2015). Moreover, fertiliser N was found to be used more efficiently in these intercrops, which is indicated by a fertiliser N equivalent ratio (FNER) greater than one (Li et al., 2020b; Xu et al., 2020). This is primarily due to the increased yield produced per unit land area, with an intercrop N fertiliser rate that falls between those used for monocrops (Xu et al., 2020). However, the application of large amounts of N fertiliser has drawbacks, particularly in cereal/legume intercropping. On the one hand, high N input can discourage N fixation of legumes (Coskun et al., 2017). On the other hand, cereals tend to become overly competitive, leading to a situation where the yield gain of cereals is offset by the yield loss they cause in legumes, resulting in no overall yield advantage for the entire intercrop (Yu et al., 2016). Finally, there is an increased possibility for leaching under this high N fertilisation (Wang et al., 2022).

Western-European intercrops, which are typically cereal/legume combinations, have shown increased N uptake with low or zero N fertilisation. In conditions of low soil mineral N, legume N fixation is exploited, allowing cereals to access more soil N than in their monocrops (Bedoussac et al., 2015; Bedoussac and Justes, 2010b; Ghaley et al., 2005). These intercrops offer advantages such as increased land productivity, enhanced cereal seed protein content, and improved resilience to weeds, pests, and diseases in comparison to equally fertilised monocrops (Bedoussac et al., 2015). They can also improve fertiliser N use efficiency compared to the corresponding monocrops under low inputs (Li et al., 2020b). Species in these intercrops are usually grown as full mixtures or alternating rows, allowing intimate rhizosphere interactions and easy mechanised management (Bedoussac et al., 2015). However, due to the limited N input, especially for cereal components, the absolute yield can be unstable and constrained (Hauggaard-Nielsen et al., 2008; Li et al., 2020b).

In addition to the typical high-input and low-input intercrops, intercropping can also be practiced at moderate fertilisation levels consistent with European standards for Good Agricultural Practices (Baghasa, 2008; FAO, 2003). In this case, species receive tailored N fertilisation at moderate levels that align with their growth needs. As a result, at the system level, the rate of fertiliser N in the intercrop is intermediate between that in the two respective monocrops. The aim of this fertilisation strategy is to minimise environmental costs while maintaining stable intercropping advantages. Yet, it is unclear whether intercropped species can benefit in their N uptake from intercropping under this species-tailored N strategy, and whether the entire intercropping system can achieve improved fertiliser N use efficiency.

Tailoring fertiliser input to species in intercropping is facilitated by using a strip design, with species grown in alternating strips consisting of several plant rows. Such strip intercropping systems are widely used in China (Li et al., 2020b). The strips are usually between 1.5 and 3 m, which is wide enough to facilitate management whereas narrow enough to ensure interspecific interaction, especially at the border rows of adjacent species strips (van Oort et al., 2020). In a strip intercrop, the border rows of the species strips experience stronger interspecific interactions compared to the adjacent inner rows (Wang et al., 2020), which may result in different N uptake in plants from different rows within a species strip.

In this study, we aim to investigate the effects of strip intercropping on N uptake and fertiliser N use efficiency when species are fertilised in accordance with recommendations for conventional agriculture in the Netherlands. We aim to quantify the responses of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.) in six bi-specific intercrops, where strips are 1.5 m wide with three (maize) or six (wheat, faba bean, and pea) rows per strip. Here the three C_3 species have the same sowing date and similar harvest dates, whereas while maize as a C_4 species is sown and harvested later than the C_3 species. The three relay intercrops (involving maize) and three simultaneous intercrops (not involving maize) exemplify differences in temporal complementarity. We study whether C_3 cereals benefit from growing with a legume in a simultaneous intercrop and compare this to growing a legume or cereal with maize in relay intercrops. We explore the responses of legumes in simultaneous intercrops with C_3 cereals and compare these responses to growing as early-sown species in relay intercrops, as well as growing the two legumes together. We study the responses of late-sown maize when relay intercropped with a cereal or a legume. Furthermore, we distinguish the responses of each species in border rows and inner rows in the intercrop strips. Finally, we determine fertiliser N use efficiency of all intercrops.

5.2 Materials and methods

5.2.1 Site description

A two-year field experiment was conducted at Droevendaal Experimental Farm of Wageningen University & Research, Wageningen, the Netherlands (51°59'20"N, 5°39'16"E). Experiments were conducted in one field in 2018 and a nearby field in 2019. Both fields had a sandy soil with a pH of 5.7, containing 3.4% organic matter with a C/N ratio of 11 in the top 30 cm. The climate is temperate oceanic. Prior to the 2018 experiment, the field was cultivated with winter wheat (*Triticum aestivum* L.) in 2017, followed by a green manure crop mixture of bristle oat (*Avena strigosa* Schreb.) and fodder radish (*Raphanus sativus* L.). Prior to the 2019 experiment, the field was cultivated with sugar beet (*Beta vulgaris* L.), after which it remained an uncropped fallow during late autumn and winter; see Chapter 2 for details.

5.2.2 Experimental design

Ten cropping systems were compared, including all six bi-specific intercrops of four crop species: maize (*Zea mays* L. cv. 'LG30.223'), wheat (*Triticum aestivum* L. cv. 'Nobless'), faba bean (*Vicia faba* L. cv. 'Fanfare'), and pea (*Pisum sativum* L. cv. 'Astronaute'), and their corresponding monocrops. The three intercrops involving maize were relay intercrops, with maize being sown and harvested later than wheat, faba bean, or pea. The other three intercrops were nearly simultaneous, with the same sowing date and similar harvesting dates for the component species, and the latter based on species maturity. Due to the cool and wet spring of 2019, the sowing dates of the four species were later than in 2018, with a larger delay for the early-sown species leading to a reduced temporal complementarity; see Chapter 2 for details.

Species strips were 1.5 m wide in all plots, comprising three rows of maize or six rows of wheat, faba bean, or pea. For maize, rows 1 and 3 were border rows, and row 2 were an inner row. For other three species, rows 1 and 6 were border rows, rows 2 and 5 were inner row I, rows 3 and 4 were inner row II. A narrow sowing machine (Belt Cone Seeder, Haldrup Co., Germany) and a tractor with a track width of 133 cm (Fendt 207, Fendt Co., Germany) were used for sowing. The row distance of maize was 50 cm, and that of the other three species was 25 cm, except for the distance between the border rows and the neighbouring inner rows within the strip, which was 20 cm to allow the wheels of the tractor to span the six rows. The sowing density was 10 seeds m^{-2} for maize, 44 seeds m^{-2} for faba bean, and 83 seeds m^{-2} for pea in both years. Wheat was sown at a density of 383 seeds m^{-2} in 2018 and 369 seeds m^{-2} in 2019. For each species, the sowing density was the same within species strips in both intercrops and monocrops. The intercrops followed a replacement design, and the relative density (density in the intercrop relative to the monocrop) of each species was 0.5; see Chapter 2 for details.

In 2018, the plot size was 9 m in east-west direction × 11 m in north-south direction, comprising six species strips. In 2019, the plot size was 12 m in east-west direction × 11 m in north-south direction for monocrops, comprising eight species strips. For intercrops, the plot size was 15 m in east-west direction × 11 m in north-south direction, comprising ten species strips. The row orientation was approximately north-south in both years. The experiment had a randomised complete block design with six blocks in 2018 and four blocks in 2019.

From June to August in both years, sprinkler irrigation was applied whenever the water storage in the top 25 cm soil approached 25 mm. Weeds were controlled manually and chemically. Diseases and pests were controlled chemically. Potassium (K) in the form of $K_2SO_4 \cdot MgSO_4$ and phosphorus (P) in the form of $Ca(H_2PO_4)_2 \cdot H_2O$ were applied homogeneously throughout the field before sowing wheat, faba bean, and pea. The rate of K was 87 kg K ha^{-1} in both years. The rate of P was 29 kg P ha^{-1} in 2018 and 34 kg P ha^{-1} in 2019.

In the top 30 cm soil, the residual mineral N was 22 kg N ha^{-1} in 2018 and 12 kg N ha^{-1} in 2019, and the N released from soil organic matter during the growing season was estimated at 90 kg N ha^{-1} in both years. Supplementary N was applied in the form of $NH_4NO_3 \cdot CaMg\ (CO_3)_2$, and in accordance with the recommendations for arable crop fertilisation in the Netherlands for non-organic agriculture (Ministerie van Landbouw, Natuur en Voedselkwaliteit, 2019) (Table 5.1). In both years, faba bean and pea received 20 kg N ha^{-1} at emergence as a starter N fertilisation. Wheat received 125 kg N ha^{-1} in both years, with the first dose (80 kg) at emergence and the second dose (45 kg) during stem elongation. Maize received 170 kg N ha^{-1} in both years, with the first dose (80 kg) at sowing and the second dose (90 kg) during stem elongation. All N fertiliser was applied as top dressing between rows within the species strips, ensuring that species strips in both monocrops and intercrops received the same amount of N fertiliser. The first dose of N fertiliser in maize was applied using a tractor driven machine (ENTI Co., the Netherlands), whereas the second dose was applied manually to avoid fertiliser from entering the maize whorl. The N fertiliser was applied to other species using the machine.

Table 5.1. Sowing and harvesting date, application date and rate of top dressing fertiliser N.

Year	Species	Sowing	Harvesting	First top dressing N	Second top dressing N
2018	Pea	Mar 21	Jul 10	Apr 11, 20 kg ha^{-1}	-
	Faba bean	Mar 21	Jul 30	Apr 11, 20 kg ha^{-1}	-
	Wheat	Mar 21	Jul 17	Apr 11, 80 kg ha^{-1}	May 4, 45 kg ha^{-1}
	Maize	May 04	Sep 10	May 4, 80 kg ha^{-1}	Jun 11, 90 kg ha^{-1}
2019	Pea	Apr 01	Jul 29	Apr 15, 20 kg ha^{-1}	-
	Faba bean	Apr 01	Aug 14	Apr 15, 20 kg ha^{-1}	-
	Wheat	Apr 01	Aug 08	Apr 15, 80 kg ha^{-1}	May 6, 45 kg ha^{-1}
	Maize	May 07	Sep 18	May 6, 80 kg ha^{-1}	Jun 14, 90 kg ha^{-1}

5.2.3 Above-ground biomass and N concentration measurements

Measurements were conducted during the growing season and at the final harvest. In both years, the harvests were conducted within one species strip in each plot for each species. Specifically, the plants were harvested separately for each row within one strip. These measurements were made in both intercrops and monocrops.

In 2019, intermediate harvests were conducted five times in wheat, faba bean, and pea and four times in maize. In 2018, one intermediate harvest was made in wheat, faba bean, and pea, and two were made in maize. In 2018, a 2 m row segment was harvested for wheat, faba bean, and pea. Maize plants were harvested over a 4 m row segment in the first harvest, and a 3 m row segment in the second harvest. In 2019, for all species, a 1.6 m segment of each row was harvested. All species were also harvested at maturity. A 4 m row segment was harvested, except for pea in 2018, for which a 3 m row segment was harvested.

In both intermediate and final harvests, plants were harvested and cut at ground level. Samples of intermediate harvests were analysed without distinguishing organs, but plants were disassembled into organs at the final harvest. We measured biomass of the shoot samples from intermediate harvests and organ samples from the final harvest after drying at 105 °C for 48 h. N concentration of these samples was determined. The samples were dried at 70 °C for 48 h. After that, samples were ground to coarse particles by a laboratory mill (Peppink Mills 200 AN, Olst, the Netherlands), and then to a fine powder using a ball mill (Mixer Mill 200, Retsch). N concentration was determined using an element C/N analyser based on the Micro-Dumas combustion method, which was conducted at the School of Biosciences, University of Nottingham, UK.

5.2.4 Data analysis

We compared the above-ground biomass (Mg ha^{-1}), N uptake (kg ha^{-1}), and N concentration (mg g^{-1}) of each species in intercrops and monocrops. The above-ground N uptake was calculated as the product of shoot biomass and shoot N concentration. For intercrops, these calculations were made for each component species, by using total biomass per square metre species strip and N concentration in the calculations, and also per row, by using the biomass per metre row of a species in the intercrop. The latter enables analysing differences in N uptake between border and inner rows. Comparisons were made at each harvest in each year.

Data were analysed per species, using linear mixed effects models in which the treatment, or row position (border, inner I, inner II) was specified as a fixed effect and block was a random effect. The function ‘lmer’ from the ‘lme4’ package (Bates et al., 2015) in R (R Core Team, 2022) was used to fit the models. Multiple comparisons of means were conducted using Fisher's Least Significant Difference (LSD) in the ‘emmeans’ package (Lenth, 2021).

We assessed whether plant N concentration limited the growth of maize and wheat by comparing the N dilution curves estimated in our experiment to the critical N dilution curves reported in the literature. This analysis was made using the 2019 data because of the greater number of intermediate harvests. The critical N dilution curve of maize is (Plénet and Lemaire, 1999):

$$\text{If } B_{\mathrm{m}} < 1\ \mathrm{Mg\ ha^{-1}}, \%N_{\mathrm{c,m}} = 3.4; \text{If } 1 \leq B_{\mathrm{m}} \leq 22\ \mathrm{Mg\ ha^{-1}}, \%N_{\mathrm{c,m}} = 3.4 \times {B_{\mathrm{m}}}^{-0.37} \quad \text{(Eq. 5.1)}$$

where B_{m} is the maize above-ground biomass per unit area of the species strip in monocrops and the species strip in intercrops, and $\%N_{\mathrm{c,m}}$ is the critical N concentration in maize shoots.

We used the following equation to represent the critical curve for spring wheat (Ziadi et al., 2010):

$$\text{If } B_{\mathrm{w}} < 1\ \mathrm{Mg\ ha^{-1}}, \%N_{\mathrm{c,w}} = 3.85; \text{If } B_{\mathrm{w}} \geq 1\ \mathrm{Mg\ ha^{-1}}, \%N_{\mathrm{c,w}} = 3.85 \times {B_{\mathrm{w}}}^{-0.57} \quad \text{(Eq. 5.2)}$$

where B_{w} is the wheat above-ground biomass per unit area of the species strip in monocrops and the species strip in intercrops, and $\%N_{\mathrm{c,w}}$ is the critical N concentration in wheat shoots.

A power equation was used to fit the actual N dilution curves of maize and wheat in our experiment:

$$\%N_i = a_i \times B_i^{-b_i} \quad \text{(Eq. 5.3)}$$

where i is m for maize and w for wheat, a_i and $b_i$are two parameters, and $\%N_i$ and B_i are the above-ground N concentration and biomass per species strip, respectively. When fitting models, data for maize with biomass within the range of $1 \leq B_{\mathrm{m}} \leq 22$ Mg ha^{-1}, and data for wheat with biomass $B_{\mathrm{w}} \geq 1$ Mg ha^{-1} were used.

Interactions between component species in intercrops may affect N uptake and the N dilution curve. To assess this, we estimated dilution curves for each treatment in which a species occurred, through model selection, which grouping of treatments best characterised the treatment effects on N dilution. We fitted Eq. 5.3 for maize and wheat receptively using: (i) the data of each treatment, resulting in four fitted curves; (ii) the combined data from two of the four treatments, and separately fitted to the remaining two, resulting in three curves; (iii) the combined data from three of the four treatments, and separately fitted to the remaining one, resulting in two curves; (iv) the combined data of all the four treatments, resulting in one curve. Under each of model version (i), (ii), and (iii), we also tested the combination of the two parameters differing between groups of data. There were three cases for each of them: firstly, both parameters a_i and b_i differed between groups; secondly, parameter a_i differed between groups, whereas parameter b_i was the common value; thirdly, parameter b_i differed, whereas parameter a_i was common.

The *Akaike Information Criterion* (Akaike, 1998) was used to select the best model, i.e., the model with the optimal balance between goodness of fit and number of parameters. We selected the model with the lowest AIC value. Models with AIC values within 2 units of each other (ΔAIC < 2) were considered similar, in which case the simpler model was selected (Bolker, 2008). We calculated the AIC value of each model by obtaining maximum likelihood estimates of the parameters using the mle2's formula interface in the 'bbmle' package (Bolker, 2022) of R (R Core Team, 2022). All variables were assumed normally distributed. Optimisation algorithm 'Nelder-Mead' was used when estimating parameters. Details showing the AIC values of all models are given in Table S5.1.

The land equivalent ratio for N uptake (LER$_{\mathrm{N}}$) was used to assess intercropping advantages on N uptake as compared to monocrops (Bedoussac and Justes, 2010b; Li et al., 2011):

$$\mathrm{LER_N} = \frac{N_{\mathrm{I},1}}{N_{\mathrm{M},1}} + \frac{N_{\mathrm{I},2}}{N_{\mathrm{M},2}} = \mathrm{pLER_{N,1}} + \mathrm{pLER_{N,2}} \qquad \text{(Eq. 5.4)}$$

where $N_{\mathrm{I},i}$ is the N uptake of species i in an intercrop at final harvest, expressed at per unit of total area of the intercrop, $N_{\mathrm{M},i}$ is the N uptake of species i in its monocrop at final harvest, expressed at per unit area of the monocrop, and $\mathrm{pLER}_{\mathrm{N},i}$ is the partial land equivalent ratio for N uptake of species i. An $\mathrm{LER_N}$ greater than one indicates that the combined monocrops need more land than their intercrop for the same N uptake, so the intercrop uses land more effienctly for N uptake than the combined monocrops. In a replacement design, a $\mathrm{pLER}_{\mathrm{N},i}$ greater than the relative density of species i (0.5 for all species in our experiment) indicates that N uptake per plant in the intercrop of species i is greater than in its monocrop.

To test if values differed from one for $\mathrm{LER_N}$ values and from 0.5 for $\mathrm{pLER_N}$ values, we assessed if one (or 0.5) fell outside the 95% confidence interval of $\mathrm{LER_N}$ (or $\mathrm{pLER_N}$). The 95% confidence interval was obtained using linear mixed effects models in which species combination was a fixed effect and block was a random effect. The analysis was conducted separately for each year.

Relationships between $\mathrm{LER_N}$ and temporal niche differentiation (TND; Yu et al., 2015) were estimated using linear mixed effects models. To do so, TND was calculated as:

$$\mathrm{TND} = 1 - \frac{T_{\mathrm{overlap}}}{T_{\mathrm{system}}} \qquad \text{(Eq. 5.5)}$$

where T_{overlap} is the co-growth duration of the intercropped species, and T_{system} is the duration of the intercropping system, from sowing of the first species until the harvest of the last species.

We tested whether the relationship between $\mathrm{LER_N}$ and TND differed between intercrops with maize in a relay design and intercrops without maize in a simultaneous design, between intercrops that were a cereal/legume combination and intercrops that were a cereal/cereal or a legume/legume combination, and between all different species combinations. Seven models were compared (Table 5.2), including the simplest model in which the relationship was the same for all intercrops. The R function ‘anova’ was used to compare AIC values of all models. The AIC values are given in Table S5.2.

The fertiliser N equivelant ratio (FNER) was used to assess intercropping advantages on saving fertiliser N inputs for grain yields as compared to monocrops (Xu et al., 2020):

$$\mathrm{FNER} = \left(\frac{Y_{\mathrm{I},1}}{Y_{\mathrm{M},1}} \times \frac{F_{\mathrm{M},1}}{F_{\mathrm{IC}}}\right) + \left(\frac{Y_{\mathrm{I},2}}{Y_{\mathrm{M},2}} \times \frac{F_{\mathrm{M},2}}{F_{\mathrm{IC}}}\right) \qquad \text{(Eq. 5.6)}$$

where $Y_{I,i}$ is the grain yield (per unit of total area of an intercrop) of species i in the intercrop, $Y_{M,i}$ is the grain yield (per unit area of a monocrop) of species i in the monocrop, $F_{M,i}$ is the rates of fertiliser N applied per unit area of the monocrop of species i, and F_{IC} is the fertiliser N input per unit area of the whole intercrop. The results of grain yield have been presented in Chapter 2.

In this study, all species received tailored fertiliser N applied within their species strips in both intercrops and monocrops. As the intercrop comprised 50% of the land area for component species, F_{IC} of an intercrop was therefore calculated as the average of fertiliser inputs in the respective monocrops. An FNER greater than one indicates that the combined monocrops need more fertiliser N inputs to obtain the same grain yield as the intercrop. To assess if the value of FNER was significantly different from one, linear mixed effects models were used to calculate the 95% confidence interval of FNER. This analysis was conducted within each year, with species combination as a fixed effect and block as a random effect.

Table 5.2 Models used to quantify the relationships between $\mathrm{LER_N}$ and TND. In the equations, i, j, and k represent year ID, species combination ID, and block ID, respectively. In all equations, b_{ik} is the block effect nested in year, and ε_{ijk} is the residual random error. Meaning of covariables: Relay: an intercrop was a relay system or not; Cereal.Legume: an intercrop was a cereal/legume combination or not; Comb.: all six species combinations as levels.

Model	Equations
1	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + b_{ik} + \varepsilon_{ijk}$
2	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Relay}_{ijk} + b_{ik} + \varepsilon_{ijk}$
3	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Cereal.Legume}_{ijk} + b_{ik} + \varepsilon_{ijk}$
4	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Relay}_{ijk} + \beta_3 * \mathrm{TND}_{ijk} * \mathrm{Relay}_{ijk} + b_{ik} + \varepsilon_{ijk}$
5	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Cereal.Legume}_{ijk} + \beta_3 * \mathrm{TND}_{ijk} * \mathrm{Cereal.Legume}_{ijk} + b_{ik} + \varepsilon_{ijk}$
6	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Comb.}_{ijk} + b_{ik} + \varepsilon_{ijk}$
7	$\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + \beta_2 * \mathrm{Comb.}_{ijk} + \beta_3 * \mathrm{TND}_{ijk} * \mathrm{Comb.}_{ijk} + b_{ik} + \varepsilon_{ijk}$

5.3 Results

5.3.1 Above-ground N uptake per species strip at final harvest

Maize intercropped with wheat or pea had higher N uptake than its monocrop in 2018 but no differences were found in 2019 or between maize intercropped with faba bean and the monocropped maize in both years (Fig. 5.1 i). Wheat and faba bean had higher N uptake than in their monocrops if they were intercropped with maize; the same was found for pea in 2018, but not in 2019 (Fig. 5.1 ii–iv). In the simultaneous intercrops, faba bean had increased N uptake when intercropped with pea in 2018 (Fig. 5.1 iii), and pea that was intercropped with faba bean had in both years lower N uptake than monocropped pea (Fig. 5.1 iv). No other effects of simultaneous intercropping on N uptake were found.

The N uptake by monocropped maize and intercropped maize was in the order of 250 to 300 kg ha^{-1}, highly similar to the available soil N (the purple line in Fig. 5.1 i), whereas N uptake by wheat in the simultaneous intercrops (about 50 kg N ha^{-1}) was substantially lower than the available quantity of soil N, except in the relay intercrop with maize (Fig. 5.1 ii). N uptake by faba bean was even greater than that of maize in all intercrop combinations, and far exceeded the available soil N, indicating substantial biological N fixation, of about 250 kg ha^{-1}. N uptake by pea exceeded the soil available N by about 150 to 250 kg ha^{-1} with the lowest N uptake in the intercrop with faba bean.

5.3.2 Above-ground N uptake of different rows in intercrops at final harvest

The effects of intercropping on different rows within species strips were consistent with those observed at the species strip level (Fig. 5.2). N uptake was higher in the border rows of wheat, faba bean, and pea in relay intercrops than in the neighbouring inner rows and in the corresponding monocrops (Fig. 5.2 ii–iv). Border row maize in the intercrop with faba bean had decreased N uptake compared to the adjacent inner row maize and monocrop maize in 2019 (Fig. 5.2 i-b). Border row faba bean had increased N uptake in all intercrops compared to its monocrop (Fig. 5.2 iii).

5.3.3 Above-ground N concentration per species strip at final harvest

In relay intercrops, the early-sown species had higher or similar N concentration compared to corresponding monocrops (Fig. 5.3 ii–iv). Intercropped maize had consistently lower N concentration than monocropped maize, though the difference was not significant in the maize/faba bean intercrop in 2019 ($P = 0.225$; Fig. 5.3 i). Wheat intercropped with faba bean had significantly higher N concentration than its monocrop in both years and also when intercropped with maize in 2019 (Fig. 5.3 ii). N concentration of intercropped faba bean and pea was similar among treatments and similar to that in the monocrops (Fig. 5.3 iii and iv).

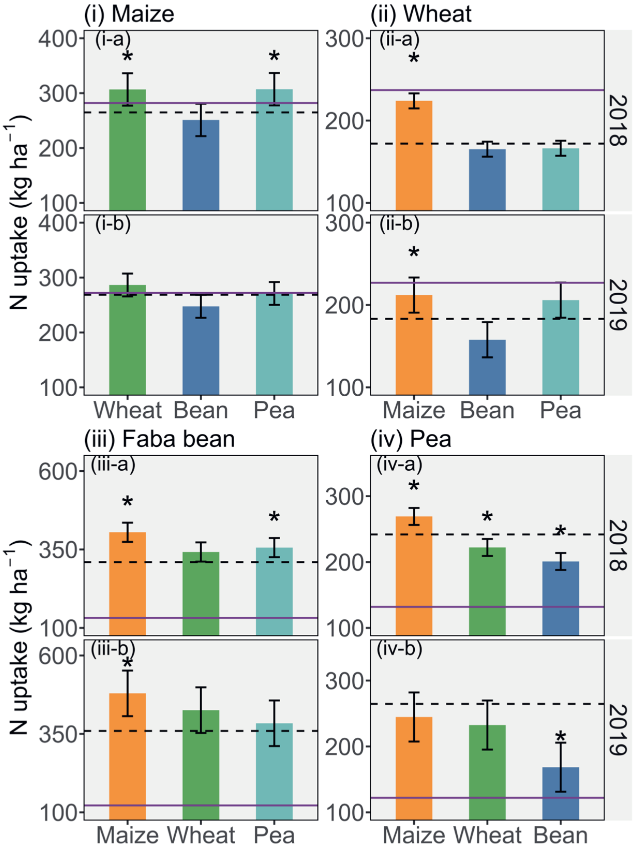

Fig. 5.1 Above-ground N uptake per species strip at final harvest of maize (i), wheat (ii), faba bean (iii), and pea (iv) when grown with different companion species in 2018 (a) and 2019 (b). The X-axis represents the companion species in intercrops. Purple solid lines represent the total estimated available soil N in species strips, comprising residual mineral N in the top 30 cm soil, N released from soil organic matter during the growing season, and fertiliser N. Black dashed lines represent N uptake of the monocrops of the focal species in each panel. Coloured bars represent N uptake of the focal species when it was with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Multiple comparisons of means were conducted within each year. Asterisks indicate significant differences between the intercrops and the monocrops at $P < 0.05$ according to Fisher's Least Significant Difference (LSD) test. Error bars indicate the 95% confidence intervals of the means. Details showing the multiple comparisons are presented in Table S5.3.

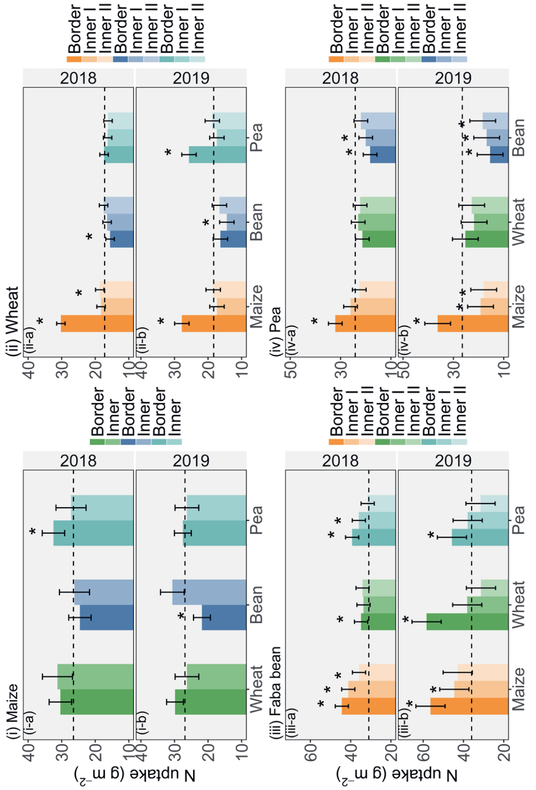

Fig. 5.2 Above-ground N uptake of different rows of intercropped maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a) and 2019 (b). Companion species are indicated along the X-axis. Dashed lines indicate N uptake of the monocrops of the focal species in each panel. Coloured bars represent N uptake of the focal species when it was with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Each colour intensity represents a different row. Multiple comparisons of means were conducted within each year with 'Species Combination_ Row' as the fixed effect. Asterisks indicate significant differences between the intercrop rows and the monocrops at $P < 0.05$ according to Fisher's Least Significant Difference (LSD) test. Error bars indicate the 95% confidence intervals of the means. Details showing the multiple comparisons are presented in Table S5.4.

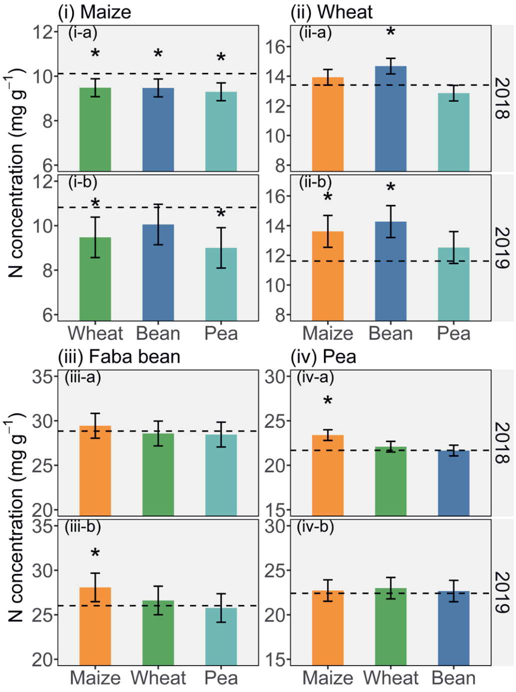

Fig. 5.3 Above-ground N concentration per species strip at final harvest for maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a) and 2019 (b). Companion species are indicated along the X-axis. Dashed lines indicate N concentration of the monocrops of the focal species in each panel. Coloured bars represent N concentration of the focal species when it was with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Multiple comparisons of means were conducted within each year. Asterisks indicate significant differences between the intercrops and the monocrops at $P < 0.05$ according to Fisher's Least Significant Difference (LSD) test. Error bars indicate the 95% confidence intervals. Details showing the multiple comparisons are presented in Table S5.5.

5.3.4 Dynamics of above-ground biomass and N uptake per species strip

Measurements were made at more times in 2019 than in 2018. The 2019 data are presented in Fig. 5.4 first. The 2018 data are given in Table 5.3 thereafter to evaluate consistency of effects between seasons.

Relay intercrops

In both years, when maize and the early-sown species were grown together as relay intercrops, the intercropped maize had lower biomass and N uptake than its monocrop (Fig. 5.4 i; Table 5.3). The negative effect was largest for maize intercropped with faba bean, both for biomass and N uptake. At maize maturity, maize in all intercrops had recovered to some extent in both biomass and N uptake. The recovery was substantial for maize biomass in the intercrops with wheat and pea in both years, as well as for maize N uptake in the intercrops with wheat and pea in 2018.

In both years from flowering onwards, wheat had higher N uptake in the relay intercrop with maize than in its monocrop (approx. DOY 196 in 2019 and DOY 155 in 2018) (Fig. 5.4 ii; Table 5.3). Intercropped wheat had a higher biomass than monocropped wheat at maturity in 2018 (Table 5.3). A consistent pattern was observed for faba bean in the relay intercrop with maize in both years; from flowering onwards, the intercropped faba bean had higher biomass and N uptake than the monocropped faba bean (approx. DOY 168 in 2019 and DOY 155 in 2018) (Fig. 5.4 iii; Table 5.3). In both years, pea intercropped with maize had higher biomass and N uptake than the monocropped pea at flowering only (approx. DOY 168 in 2019 and DOY 155 in 2018) (Fig. 5.4 iv; Table 5.3). Thus, the early-sown species in relay intercrops had increases in biomass and N uptake during the intermediate stages of growth.

Simultaneous intercrops

Wheat intercropped with pea had similar biomass and N uptake as its monocrop (Fig. 5.4 ii; Table 5.3). Intercropped pea with wheat had lower biomass and N uptake than the monocropped pea at maturity in 2018 (Table 5.3). Wheat intercropped with faba bean had lower biomass than the monocropped wheat from flowering onwards (approx. DOY 182 in 2019 and DOY 155 in 2018), whereas N uptake by the intercropped wheat was not substantially decreased. As for the faba bean intercropped with wheat, no differences in biomass and N uptake compared with monocropped faba bean were found (Fig. 5.4 iii; Table 5.3).

Around flowering intercropped faba bean with pea had increased biomass and N uptake compared to its monocrop (approx. DOY 182 in 2019 and DOY 155 in 2018), and these increased values were also observed at maturity in 2018 (Fig. 5.4 iii; Table 5.3). Simultaneously, intercropping with faba bean led to decreased biomass and N uptake of pea after flowering in 2019 (approx. DOY 182), as well as at maturity in both years (Fig. 5.4 iv; Table 5.3).

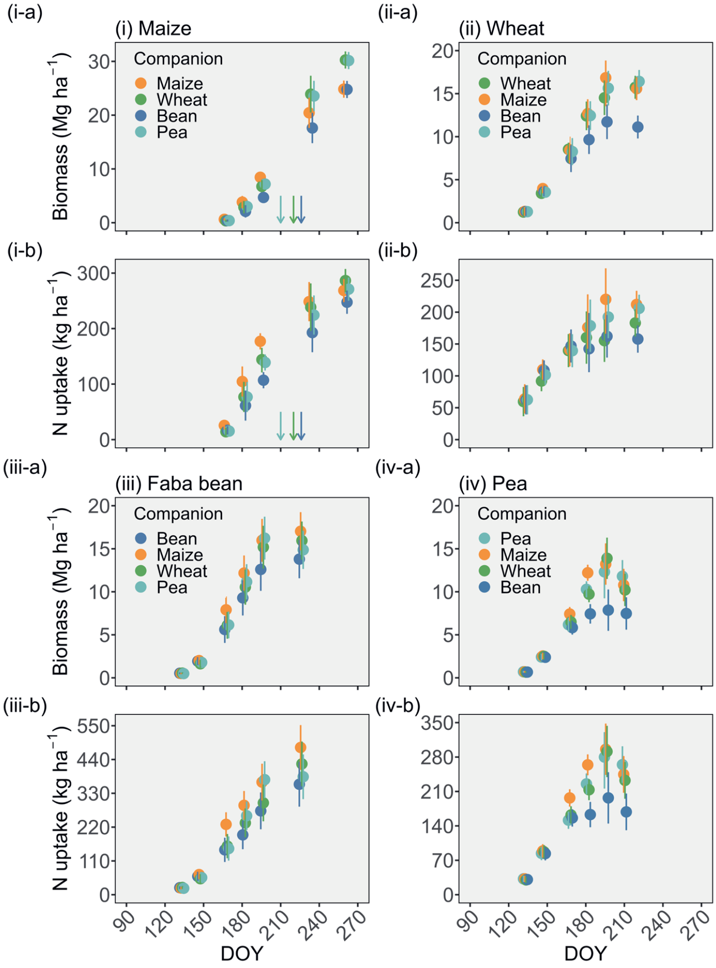

Fig. 5.4 Dynamics of above-ground biomass (a) and N uptake (b) per species strip for maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2019. Colours within each panel represent biomass and N uptake of the focal species when it was with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Arrows in panels (i-a) and (i-b) indicate the final harvest of pea (cyan), wheat (green), and faba bean (blue). Multiple comparisons of means were conducted within an individual harvest at $P < 0.05$ according to Fisher's Least Significant Difference (LSD) test. Error bars indicate the 95% confidence intervals of the means. Details showing the multiple comparisons are presented in Table S5.6.

Table. 5.3 Above-ground biomass and N uptake per species strip of maize, wheat, faba bean, and pea in 2018. Multiple comparisons of means were conducted within an individual harvest at $P < 0.05$ according to Fisher's Least Significant Difference (LSD) test. Shared letters denote non-significant differences between treatments.

		Biomass (Mg ha^{-1})			N uptake (kg ha^{-1})		
Species	Companion	DOY 155	DOY 197	Final Harvest	DOY 155	DOY 197	Final Harvest
Maize	Maize	0.825 a	7.98 a	26.3 b	34.7 a	140 a	265 b
	Wheat	0.571 a	7.15 a	32.4 a	23.8 a	104 a	307 a
	Faba	0.541 a	5.51 a	26.5 b	23.6 a	88.5 a	251 b
	Pea	0.472 a	6.99 a	33.1 a	19.9 a	105 a	307 a
Wheat	Wheat	7.04 ab	-	12.8 b	151 b	-	172 b
	Maize	8.06 a	-	16.1 a	185 a	-	224 a
	Faba	6.22 b	-	11.3 c	139 b	-	165 b
	Pea	7.28 ab	-	12.9 b	154 ab	-	166 b
Faba	Faba	4.29 a	-	10.7 c	121 a	-	310 c
	Maize	5.26 a	-	13.8 a	150 a	-	405 a
	Wheat	3.79 a	-	12.0 bc	102 a	-	342 bc
	Pea	4.90 a	-	12.5 ab	135 a	-	356 b
Pea	Pea	4.50 b	-	11.1 a	118 b	-	242 b
	Maize	5.40 a	-	11.5 a	146 a	-	269 a
	Wheat	4.77 b	-	10.1 b	124 b	-	222 c
	Faba	4.70 b	-	9.29 c	123 b	-	201 d

5.3.5 N dilution curves of maize and wheat

Maize

We compared the N dilution curves estimated from our experiment with the maize critical N dilution curve (Fig. 5.5 i). The above-ground N concentration decreased with biomass, following a slope (determined by the parameter b_{m}) (Eq. 5.3) similar to the published critical dilution curve (Eq. 5.1). We observed a higher value for the intercept parameter a_{m} (Eq. 5.3), resulting in an increase in N concentration in our experiment compared to the critical N concentration at the same biomass level. The results indicate that the plant N was sufficient during maize early growth in both the intercrops and monocrop. However, we observed a lower N concentration of maize in all intercrops than in the monocrop at the same biomass level.

Later during the growth process, at grain filling and with biomass values above approx. 20 Mg ha^{-1}, the measured N concentration of intercropped maize tended to be below the critical curve (Fig. 5.5 i), indicating that plant N likely reduced productive capacity in maize in all intercrops during the later phase.

Wheat

We compared N dilution curves estimated from our experiment with the wheat critical N dilution curve (Fig. 5.5 ii). We observed higher values of above-ground N concentration in both the intercrops and monocrop compared to the critical N concentration at the same biomass level. When comparing N dilution curves between wheat in the intercrops and monocrop, a higher N concentration in intercropped than monocropped wheat at the same biomass level was observed. This phenomenon was particularly observed after wheat produced approx. 8 Mg ha^{-1} biomass at the heading stage. Thus, the plant N was sufficient for wheat in both the intercrops and monocrop during the whole season, and in the later growth stages wheat in all intercrops had a higher N concentration than in the monocrop at per the same biomass.

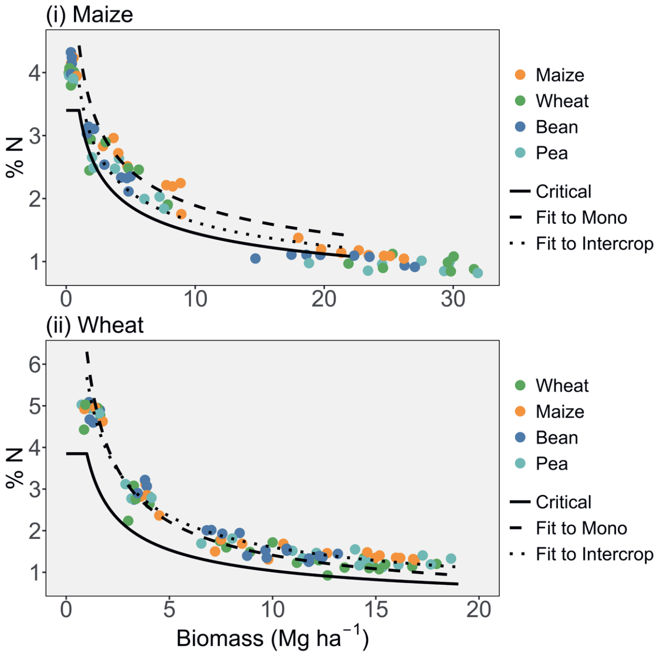

Fig. 5.5 Measured (points) and estimated (curves) N dilution for maize (i) and wheat (ii). The X-axis is the above-ground biomass per species strip. The %N is the above-ground N concentration per species strip. Coloured points represent measured %N and biomass of the focal species when it was grown with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). The solid line in each panel is the critical N dilution curve (Eq. 5.1 for maize, Eq. 5.2 for wheat). The dashed (monocrop) and dotted (intercrop) lines are the estimated N dilution curves (Eq. 5.3) for each species. For maize (i), parameter a_{m} was higher for monocrop maize than for maize in all intercrop treatments, parameter b_m was similar. Thus, two curves were drawn. For wheat (ii), the curves differed between monocrop wheat and wheat in all intercrops. Both parameters a_{m} and b_{m} are higher for the monocrop than for the intercrops; see Table S5.1 for the parameter values and their standard errors.

5.3.6 LER$_N$ and its relationship with TND

In 2018, all relay intercrops obtained LER$_N$ values larger than one, ranging from 1.14 ± 0.09 (mean ± 95% confidence interval) in the maize/faba bean intercrop to 1.24 ± 0.09 in the maize/wheat intercrop (Fig. 5.6). In 2019, only the maize/faba bean intercrop (1.13 ± 0.11) and the maize/wheat intercrop (1.12 ± 0.11) achieved LER$_N$ values larger than one. In relay intercrops, the cereal/legume combinations did not obtain larger LER$_N$ values than the cereal/cereal combination. In the maize/faba bean intercrop, the pLER$_N$ value of faba bean contributed more to the system LER$_N$ value than that of maize. In simultaneous intercrops, LER$_N$ values mostly were not different from one, ranging from 0.94 ± 0.09 in the wheat/pea intercrop to 1.04 ± 0.09 in the faba bean/wheat intercrop in 2018, and from 0.86 ± 0.11 in the faba bean/pea intercrop to 1.03 ± 0.11 in the faba bean/wheat intercrop in 2019.

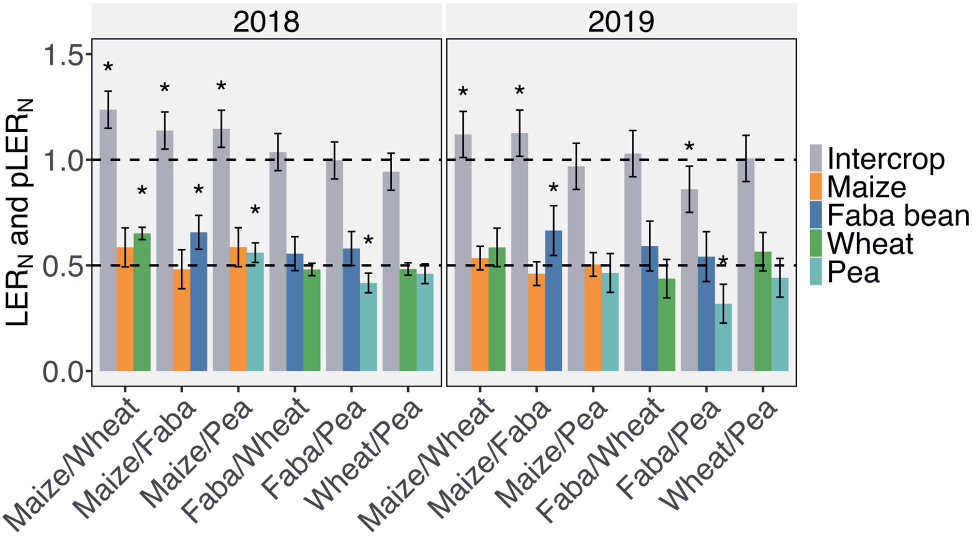

Fig. 5.6 Land equivalent ratio for N uptake (LER$_N$) of intercrops (grey bar) and partial land equivalent ratio for N uptake (pLER$_N$) of component species (coloured bar) in 2018 and 2019. Colours represent four component species in intercrops: pea (cyan), wheat (green), faba bean (blue), and maize (orange). Asterisks indicate significant differences from one for LER$_N$ values and from 0.5 for pLER$_N$ values, by testing if one (or 0.5) fell outside the 95% confidence interval of LER$_N$ (or pLER$_N$).

A positive correlation between LER$_N$ and TND was observed (Fig. 5.7). The most supported model was Model 6, which had a common slope across intercrops and species combination-specific intercepts (Table S5.2). This indicates that the positive effect of TND on LER$_N$ was consistent across species combinations, regardless of whether the intercrop systems were relay or simultaneous designs, or whether they involved a cereal/legume combination or not. Thus, both species combination and TND were key factors driving intercropping advantages in N uptake in our experiment.

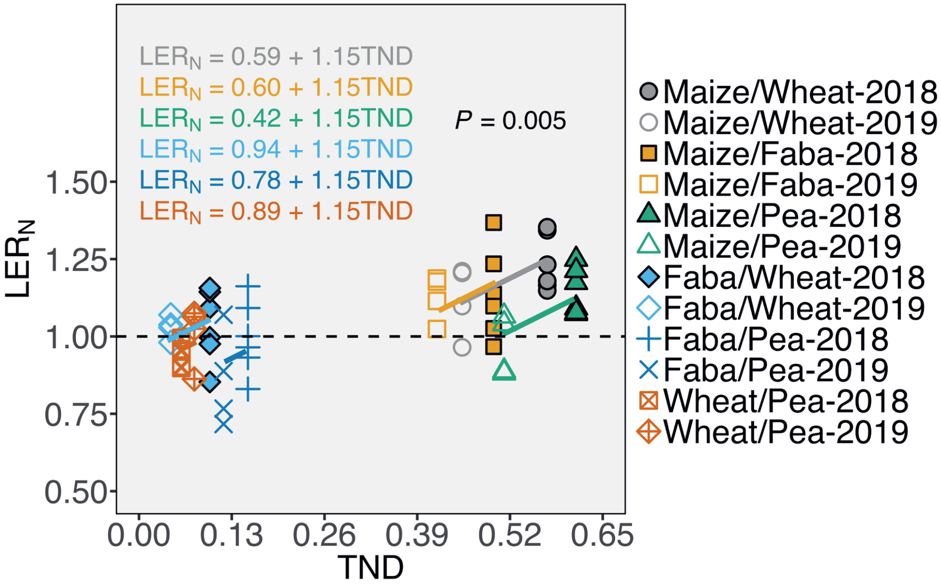

Fig. 5.7 Relationships between LER_N and TND. After comparing AIC values, Model 6 was the most supported model to describe the data (Table S5.2). This model indicates that regressions had a common slope and different intercepts across intercrops. The *P*-value is related to the slope (Student's t-test).

5.3.7 Fertiliser N equivalent ratio (FNER)

FNER ranged from 0.76 ± 0.05 (the faba bean/wheat intercrop) to 1.24 ± 0.07 (the maize/pea intercrop) in 2018, and it ranged from 0.64 ± 0.06 (the faba bean/wheat intercrop) to 1.13 ± 0.03 (the maize/pea) in 2019 (Fig. 5.8). Despite the inter-year variances within the same treatment, relay intercrops, on average, were more efficient in using fertiliser N compared to simultaneous intercrops. The average FNER over two years was 1.14 ± 0.03 for relay intercrops, whereas it was 0.85 ± 0.03 for simultaneous intercrops.

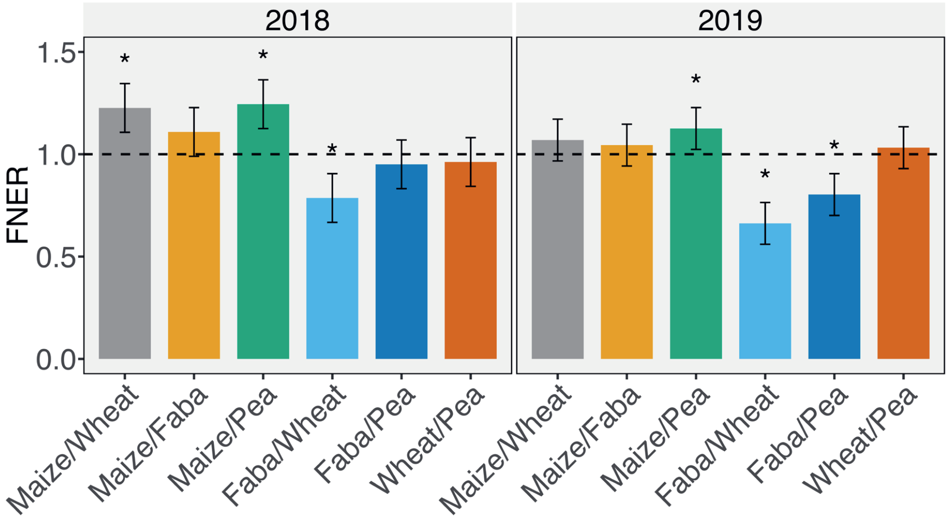

Fig. 5.8 Fertiliser N equivalent ratio (FNER) of intercrops in 2018 and 2019. X-axis is the abbreviation for the intercrops, in which WM for wheat/maize, BM for faba bean/maize, PM for pea/maize, WB for wheat/faba bean, PB for pea/faba bean, and PW for pea/wheat. Asterisks indicate significant differences from one for FNER, by testing if one fell outside the 95% confidence interval of FNER.

5.4 Discussion

Here we found that C_3 cereals had increased N uptake when grown as early-sown species in relay intercrops with maize, as compared to monocropped cereals, but they did not have increased N uptake when grown with a legume in simultaneous intercrops (Fig. 5.1). Legumes, i.e., faba bean and pea, had higher N uptake in intercrops than in monocrops when grown with maize in relay intercrops but not when grown simultaneously with wheat. N uptake by maize was increased only when relay intercropped with wheat or pea in a year with a larger temporal niche differentiation. Despite inter-year differences, the relay intercrops had land equivalent ratios for N uptake (LER_N) and fertiliser N equivalent ratios (FNER) mostly higher than one, whereas the simultaneous intercrops had LER_N and FNER values mostly similar to one. The results thus show that the relay intercrops were more efficient in capturing N and using fertiliser N than the simultaneous intercrops. These results suggest that temporal complementarity between species is a key driver for complementary N uptake and efficient fertiliser N use under the conditions of the study, whereas complementarity in N uptake mechanisms in relation to the capacity for biological N fixation was not.

Temporal complementarity is known to be important for increasing resource capture and promoting production in intercropping because it allows the component species to grow alone for a period, reducing competition compared to monocrops (Yu et al., 2015). Thus, species grow better during the 'grow alone' period when the companion species is absent, due to reduced competition for all growth resources, including light primarily, but also water and nutrients. Temporal complementarity drives land productivity, absolute yield increases, and utilisation of water and nutrients (Li et al., 2020b; Ma et al., 2022; Raza et al., 2020; Wang et al., 2023). In the present study, we found that temporal complementarity is also enhancing N uptake in strip intercropping under a species-tailored N strategy (Fig. 5.7).

A 'win-win' situation has been reported in relay intercrops, in which both early- and late-sown species achieved increased biomass and N uptake compared to the monocrops (Li et al., 2001a, 2001b; Xu et al., 2023). In relay intercrops, the early-sown species has better light conditions during early growth than the same species grown as a monocrop (Gou et al., 2017a; Zhu et al., 2015), which could stimulate their biomass accumulation (Fig. 5.4 ii–iv; Table 5.3). Biological N fixation of legumes is known to be positively affected by light capture and above-ground biomass (Carvalho et al., 2019). The higher N uptake of the two legumes, especially faba bean, that we found in the relay intercrops could be due to the better light conditions and increased biomass growth, which is likely to increase root growth and nutrient demand. Intercropped wheat had higher %N than monocrop wheat at per the same biomass (Fig. 5.5 ii), indicating that the relative increase in N uptake due to intercropping was greater than the relative biomass increase. This may be due to better access to soil N. Given that each species had identical N fertilisation within its species strips in the intercrops and monocrop, it is likely that wheat foraged for N from the neighbouring maize strips via lateral root extensions, as previously reported (Li et al., 2006; Liu et al., 2015).

Previous studies on relay intercrops, conducted under high N fertilisation strategies in which both intercrops and monocrops received the same rate of fertiliser N (N > 225 kg ha^{-1}) at the system level, indicated that N uptake of late-sown maize was higher than that of monocrop maize at maturity; these studies includes both maize relay intercropped with wheat and soybean (Li et al., 2001b, 2001a) and maize grown with faba bean (Li et al., 2011). In our experiment, the higher N uptake of maize was only observed in the relay intercrop with wheat or pea in one year, but not with faba bean (Fig. 5.1). We applied a moderate N rate for maize, with the second topdressing applied at the onset of maize stem elongation. Consequently, the mineral N was largely taken up before maize entered grain filling, reflected by the %N that gradually dropped below the critical level from grain filling in both the intercrops and monocrop (Fig. 5.5 i). Our N application strategy did not result in significantly increased N uptake by maize, possibly due to low N availability during maize reproductive growth.

The simultaneous intercrops involving faba bean were relatively inefficient in capturing N because the increased N uptake of faba bean did not compensate for the N uptake loss in the accompanying species (Fig. 5.6). The tall-statured cultivar ‘Fanfare’ of faba bean has a rapidly developing and dense canopy (Andersen et al., 2020), which severely shaded wheat and pea (Chapters 3 and 4), resulting in substantial biomass decreases in these companion species (Fig. 5.4 ii and iv; Table 5.3). In contrast to previous studies in which cereals were mostly the taller species in cereal/legume intercrops, e.g., maize/soybean intercrop in Liu et al. (2018, 2017), wheat in our experiment experienced shading when grown with faba bean (Chapters 3 and 4). Nevertheless, the wheat intercropped with faba bean captured sufficient soil N in comparison to its biomass production (Fig. 5.5 ii), indicating that the reduced N uptake was due to decreased biomass caused by light competition, rather than N competition. Maize also experienced substantial reductions in biomass and N uptake in the early stage in the intercrop with faba bean (Fig. 5.4 i). We therefore conclude that combining a cereal with a vigorous legume decreases N uptake by the cereal as a consequence of reduced crop need related to lower biomass accumulation, either in simultaneous or relay systems.

We did not detect N limitations in wheat throughout the entire season in 2019 in any of the treatments (Fig. 5.5 ii). Maize in the intercrops or monocrop did not experience N limitation until maize grain filling began (Fig. 5.5 i). The intercropped legumes maintained %N at levels no lower than their monocrops (Fig. S5.1). Given the same N and water application strategy, identical soil conditions, and similar weather conditions, we can infer that N availability should have been similar in 2018 as it was in 2019 for each species. Therefore, we conclude that the species-tailored N strategy ensured non-limiting N conditions for both cereals for most of the season in both years.

Relay intercrops showed generally substantial N capture complementarity, as evidenced by value of LER_N greater than one (with one exception; the maize/pea intercrop in 2019). However, the combination of a cereal and a legume was not a key factor driving this complementarity, as strong complementarity (high value of LER_N) was found in an intercrop comprising two cereals, wheat and maize. The LER_N of this combination was similar to that of maize/faba bean and higher than that of maize/pea. The lack of response to presence of a legume does seem to be a direct consequence of the N fertilisation strategy satisfying needs of combined species. In previous studies, the mineral N applied to legumes in the high-input intercrops, e.g., Li et al. (2001a, 2001b), or the stored soil N in the low-input intercrops, e.g., Bedoussac et al. (2015) and Rodriguez et al. (2020), largely acted as additional N for cereals because of N fixation of legumes. However, in the current study, when cereals can be satisfied by the N fertiliser applied within their own strips, and rhizosphere interactions, especially at the early stages, were limited by the strip design, N fixation by legumes contributed little, if anything, to the N uptake of the cereals. The main contribution to complementary N uptake in our systems was likely the temporal complementarity, which caused increased biomass growth, which in turn may have driven increased root proliferation and N uptake in relay-intercropped species, compared to the monocrops.

The two cereals captured almost all available mineral N in relay intercrops, and the small quantity of ‘starter’ N fertiliser also required the two legumes to thoroughly exploit N fixation, as reflected by their final N uptake that far exceeded the quantity that was applied (Fig. 5.1). Compared with the high-input N strategy where N surplus, N leaching, and inhibition of legume N fixation have been observed (Wang et al., 2022; Yu et al., 2021), we suggest that a species-tailored N strategy is good for intercropping to reduce environmental costs and make full use of N fixation. Moreover, the species-tailored N strategy does also allow for a higher cereal production compared with the low or unstable yield and N uptake found in low-input intercrops (Hauggaard-Nielsen et al., 2008; Li et al., 2020b; Wang et al., 2023).

Despite the finding that N fixation by legumes was not a key driver of complementary N uptake, combining legumes with maize in relay intercropping still allowed a reduction in N inputs compared with the maize/wheat intercrop (Fig. 5.6). An exception was the maize/pea intercrop in 2019. In 2019, pea lodged due to heavy rains, and this lodging was more severe in the relay intercrop than in the pea monocrop because the neighbouring young maize plants failed to support the lodging pea as other species did (Fig. 2.1). Thus, combining maize with a firm-stem species in relay strip intercropping is a recommended practice to ensure N uptake advantages.

Species with a weak stem are more appropriate for intercropped with firm-stem companion species in full mixtures (Barillot et al., 2012).

Fertiliser N saving effects were observed previously in both the high-input and low-input intercrops (Li et al., 2020b; Xu et al., 2020). In the current study when tailored N fertilisation was used, on average over the two years, relay intercrops had an FNER of 1.14 ± 0.03, indicating a 14% saving in fertiliser N compared to monocrops for the same grain yield. In contrast, simultaneous intercrops did not show such a fertiliser saving effect. In essence, combination of temporal complementarity and an intercrop N rate being intermediate to monocrop N rates enabled each species to capture more light, N, and probably also other resources, leading to increased yield per unit land area compared to monocrops and thus enhancing fertiliser N use efficiency.

Our findings align with meta-analyses that show that intercrop performance increases more from temporal complementarity if the N nutrition is higher (Li et al., 2020b; Yu et al., 2015). Our research seems to indicate that it is advisable to combine species with only partially overlapping growth seasons and apply N tailored to the individual species demands. The advantages in light capture offer opportunities to increase biomass with non-limiting N availability and accordingly promote the capacity of the plants to acquire N from the soil. Nevertheless, there could be potential for increasing N uptake and production advantages in late-sown maize because N limitation became evident during the late maize growth stage in the current study. (Fig. 5.5 i). Applying an additional N dose to maize when harvesting the early companions has been shown to significantly facilitate N uptake recovery in maize (Hu et al., 2016). In our species-tailored fertilisation approach, to boost a 'win-win' situation in relay intercrops, an additional N input after maize tasselling might be a recommendation; however, it remains uncertain whether this approach would be sustainable in terms of N uptake efficiency during this late growth phase. Postponing the second N fertilisation could also be an option, but it could also lead to N limitation in maize around flowering. There seems to be room for additional experimentation before making recommendations to practice. Choosing the appropriate early companions is also important. Overyielding of the late-sown maize in relay intercrops increased with a longer recovery time after harvest of the early-sown species (Chapter 2). Given the cool climate in the Netherlands, a recommendation would be to use winter-sown rather than spring-sown cereals or legumes as the early-sown species, so they may be harvested earlier than in the current experiment, leaving a longer recovery time for maize to boost its production and take up the soil N.

5.5 Conclusion

Our study investigated the effects of strip intercropping on nitrogen (N) uptake of maize, wheat, faba bean, and pea and intercropping fertiliser N use efficiency under a species-tailored N strategy in the Netherlands. Relay intercrops used land more effienctly for N uptake than the combined monocrops, whereas such intercropping advantages were not observed in simultaneous intercrops. In relay intercrops, early-sown species captured more N than their monocrops, and late-sown maize maintained comparable N uptake to the monocrop. Temporal complementarity between species was the main driver of complementary N uptake in intercrops, irrespective of the presence of a legume. Combining cereals with legumes, however, did allow a reduction in N input to the system. Under the species-tailored N fertilisation, relay intercrops used fertiliser N more efficiently than the combined monocrops and simultaneous intercrops. To enhance maize N uptake and likely production, applying additional N after maize tasselling could be required, although analysis of long-term sustainability is to be made first. Proper selection of early companion species is crucial. The species-tailored N strategy effectively ensures the complete capture of available mineral N for cereals, enables and requires legumes to exploit N fixation, and reduces environmental costs in intercropping.

Acknowledgements

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Chapter 6

General discussion

The aim of this thesis is to explore to what extent strip intercropping can contribute to improved crop production efficiency in conventional agriculture under Western-European growing conditions. I conducted a two-year field experiment in Wageningen, the Netherlands to study the productive performance of six intercropping systems involving four crop species. Species received locally recommended nitrogen (N) fertiliser amounts within their respective strips, with the expectation that cereals would not experience significant N stress, and legumes would mainly exploit N fixation to fulfil their needs. Employing this species-tailored N strategy aligns with the standards of Good Agricultural Practices (FAO, 2003), ensuring that all species benefit from N fertiliser at agronomically meaningful levels, thereby balancing production and environmental goals.

In Section 6.1 of this general discussion, I first summarise the main findings of the preceding four research chapters. Then, in Sections 6.2 to 6.5, I reflect on the insights that these findings may give in production, resource capture and resource conversion in strip intercropping. After reflecting on the content, I proceed in Section 6.6 to provide suggestions on how to adopt strip intercropping for conventional agriculture in Western Europe and how to adopt and evaluate intercropping for different production objectives. In Section 6.7, I examine and discuss limitations of this thesis and suggest opportunities for future research. Section 6.8 contains the concluding remarks for the whole thesis.

6.1 Main findings of this thesis

6.1.1 What are the land use and yield responses in different species combinations?

In Chapter 2, I explored land use and yield increases of strip intercrops involving various species combinations. I used land equivalent ratio (LER; Willey and Rao, 1980) to assess land use efficiency and net effect (NE; Loreau and Hector, 2001) to assess absolute yield increases. The relay intercrops with maize mostly showed LER values above one and positive NE values, whereas the simultaneous intercrops without maize mostly showed LER values similar to one and NE values around zero. These findings suggest that when combined with locally recommended water and nutrient inputs, temporal complementarity can enhance land use efficiency and lead to yield increases in intercrops compared to the combined monocrops, but without temporal complementarity, no productive benefits are achieved.

6.1.2 What are the yield component responses to light capture in different species combinations?

In Chapter 3, I found that grain yield had a stronger correlation with total grain number per unit land area (GN) than with thousand-grain weight (TGW) in all species in monocrops and intercrops. Exploring the correlation between yield components and light capture, I deduced that enhanced pre-grain-filling light availability promoted increased GN in all early-sown species in relay intercrops. Maize gained light capture advantages over shorter-statured wheat and pea from cob initiation, due to overtopping. This led to more grains and adequate filling thereafter, facilitated by improved light availability after the early companions were harvested. The findings of this chapter suggest a significant role of temporal complementarity in improving yield components of intercropped species. Simultaneous intercrops lacking temporal complementarity either had minimal effects on yield components for similar-statured species (wheat and pea). Alternatively, when short-statured wheat and pea were combined with tall-statured faba bean, shading of faba bean resulted in substantial reductions in both GN and TGW of wheat and pea, whereas faba bean only obtained increases in GN but not TGW.

6.1.3 What are the border and inner row contributions to light capture and conversion in different species combinations?

In Chapter 4, I used a random ray tracing model to calculate the light capture in border rows and inner rows of strips in the strip intercrops. I used the results to analyse the contribution of different row types (border and inner) to light capture and conversion. In relay intercrops, all early-sown species had higher biomass in the border rows compared to the monocrops, as a result of increased light capture, whereas their light use efficiencies (LUE) remained unchanged. Faba bean, unlike the other early-sown species, had increased biomass in inner rows due to increased LUE, but light capture remained unchanged. Both border and inner rows of intercropped maize had higher LUE in all relay intercrops. Increases in biomass occurred only when maize captured more light, which happened in the intercrops with wheat and pea, but not with faba bean. In simultaneous intercrops, faba bean significantly reduced both light capture and LUE of wheat and pea in all rows. Compared to relay intercrops, light utilisation in simultaneous intercrops was not efficient because faba bean, with increased light capture and unchanged LUE, did not compensate for the reductions in biomass production resulting from reduced light capture and light conversion in all rows of wheat and pea.

6.1.4 What are the N uptake and fertiliser N use responses in different species combinations?

In Chapter 5, I discovered that the species-tailored N strategy not only prevented cereals from experiencing significant N stress but also facilitated and necessitated legumes to exploit N fixation. Under this N strategy, relay intercrops captured more N than simultaneous intercrops. In relay intercrops, early-sown species had increased N uptake, especially in border rows. Maize showed enhanced N uptake in intercrops with wheat and pea only in 2018 with a larger temporal complementarity, but not with faba bean in either year. Analyses of the fertiliser N equivalent ratio (FNER; Xu et al., 2020) indicated that relay intercrops were also efficient than monocrops in utilising applied fertiliser N to produce grain yield.

6.2 Temporal complementarity is pivotal for productivity in strip intercropping under conventional management in the Netherlands

6.2.1 Positive effects of temporal complementarity on land use and absolute yield gain also hold in the Netherlands

Temporal complementarity enables each component species in an intercrop to undergo a phase of reduced interspecific competition due to absence or low competitiveness of the companion species (Yu et al., 2015). Temporal complementarity can be characterised using a simple index for temporal niche differentiation (TND), which represents the proportion of non-overlapping growth duration between component species in the total season length (Yu et al., 2015). Previous researchers have demonstrated the yield advantages of maize/wheat relay strip intercropping in the Netherlands (Gou et al., 2016; Zhu et al., 2015). In Chapter 2, I found that on average over two years, the land equivalent ratio for grain yield (LER) was 1.14 ± 0.02 in relay intercrops, compared to 0.92 ± 0.02 in simultaneous intercrops. The net effect for grain yield (NE) was 1.25 ± 0.20 Mg ha^{-1} in relay intercrops, compared to −0.52 ± 0.10 Mg ha^{-1} in simultaneous intercrops. The results suggest that land saving and yield increasing effects of relay intercrops hold for combinations involving maize and various companion species, including both cereals (wheat) and legumes (faba bean and pea). They also align with the globally positive effects of TND on land use and absolute yield increases (Li et al., 2020b; Yu et al., 2015).

According to a recent meta-analysis, intercrops with maize, most often cultivated in relay successions, on average had an LER of 1.29 ± 0.02 and an NE of 2.1 ± 0.1 Mg ha^{-1} worldwide

(Li et al., 2020b). These values are higher than those obtained in this thesis. The differences in TND might be a reason. Notably, most of the maize-based intercrops in the meta-analysis of Li et al. (2020b) were carried out in China, with N fertiliser rates of 155 ± 10 kg N ha^{-1} on average, which are higher than the current N rates (112 kg N ha^{-1} on average over the three relay intercrops). Across different species, cultivars, weather, soil, the positive effects of TND on LER and NE can be promoted by increasing N inputs (Yu et al., 2015), and there thus might be potential to enhance the performance of relay intercrops in the Netherlands through higher N rates. However, given that the current N fertiliser rates were efficient in promoting non-N-limiting growth for cereals and facilitating legumes to exploit N fixation, effectively avoiding N surpluses (Chapter 5), the chosen fertiliser strategy may already strike a near-optimal balance between the aims of productivity and a clean environment with low N emissions from agriculture. Nevertheless, the optimisation of N input in intercropping is a topic of great relevance and may be further studied.

6.2.2 Designing optimal temporal complementarity requires appropriate species and cultivar selection in sync with the local climate

In Chapter 2, comparing the same relay intercrop in 2018 with a larger TND and in 2019 with a smaller TND, I found that the lower LER and NE values in 2019 predominantly resulted from decreases in the less competitive species (wheat and pea in the intercrops with maize; maize in the intercrop with faba bean), whereas the more competitive species (maize in the intercrops with wheat and pea; faba bean in the intercrop with maize) were minimally impacted. This suggests that when designing a beneficial intercrop, challenges arise in establishing a sufficient TND that will enable the less competitive species to achieve a significant advantage, ensuring either yield increases in both component species or that the dominant species achieves a yield gain greater than the yield loss caused in the dominated species. Options for a larger TND exist, e.g., using winter-sown cultivars for the early-sown species or late-maturing cultivars for the late-sown species (Ma et al., 2020; Mohammed et al., 2022), but local growing degree-days (GDD) may limit practical implementation. In cooler climate regions, premature sowing and delayed harvesting may cause yield losses. In warmer climate regions, an extended season length in a relay intercrop may interfere with the cultivation of preceding and subsequent crops; in these regions when the total GDD allows, double cropping may offer larger yield increases than relay intercropping (Liang et al., 2022). Additionally, it is important to consider weather variability, as the sowing and harvesting of the chosen species and cultivars may be affected by adverse weather conditions, as exemplified by the delayed sowing of the three early species in 2019 in this thesis (Chapter 2).

6.2.3 Species employ different strategies in determining yield components in response to temporal complementarity

In Chapter 3, I found that maize and the early-sown species both had increased total grain number per unit land area (GN), but maize thoroughly took advantage of the more grains that had been determined early on, by efficiently filling all grains due to recovery growth. However, the early-sown species could not avoid a grain number-grain weight trade-off because they did not have improved light availability, owing to maize overtopping them during grain filling (Chapter 3).

The observed increases in GN of wheat, faba bean, and pea align with the finding in previous studies that relay intercropping benefits early-sown species during their early growth when grain number is determined, due to the increased access to light and other resources (Gou et al., 2016; Li et al., 2020; Zhu et al., 2016). The increased GN of intercropped maize was achieved through more cobs initiated after maize overtopped its companions around the ten-leaf stage. At this stage, intercropped maize had lower above-ground biomass than monocropped maize, suggesting there was more biomass allocation to cobs in intercropped maize under improved light conditions, compared to monocropped maize (Chapter 4). This may be linked to enhanced photosynthesis by cob leaves under high light in the non-N-limiting condition at that time (Chapters 4 and 5). These findings suggest that, in terms of grain production, maize established advantages much earlier than when the companion species were harvested in the current experiment. Nevertheless, recovery growth after harvest of companion species contributed to yield increases in maize, as light capture per grain increased, allowing maize to avoid the grain number-grain weight trade-off as observed in the three early species.

According to the results of Yu et al. (2015), the performance of relay intercrops is strongly related to the ‘grow alone’ period of the component species during which species experience reduced competition for resources because the companion species is not there. However, results of the current experiment indicate that a late-sown species with tall stature, as maize, can start gaining advantages once it overtops a short-statured early-sown companions. Therefore, TND alone may not be a sufficient indicator for assessing per-species performance in intercropping, or at least it needs to be used with a good understanding of plant-plant interactions, e.g., the time when a species takes dominance in resource capture, under specific environmental conditions.

6.3 Relay intercrops promote efficient light use

6.3.1 C_3/C_4 relay intercrops enable component species to use light efficiently, and studying row differences provides insights in species interactions

C_3/C_4 relay intercrops are considered more efficient in light use than C_3/C_3 simultaneous intercrops due to greater light capture through temporal and spatial complementarity, and efficient light conversion through functional complementarity (Stomph et al., 2020). On the one hand, the short C_3 species dominate light capture in the early season, and the tall C_4 species take over in the late season after overtopping, resulting in complementary light capture (Gou et al., 2017a; Zhu et al., 2015). On the other hand, C_4 species can photosynthesize at high light once they overtop C_3 species, and C_3 species can utilise moderate or low light. This makes in theory good use of the greater photosynthetic capacity of C_4 species at high light intensity, and the slightly higher light use efficiency of C_3 species at low light intensity (Gou et al., 2018, 2017a). In Chapter 4, efficient light use in relay intercrops was evident. The three C_3 species utilised the increased captured light with LUEs similar to their monocrops, whereas C_4 maize had increased LUE and an increased amount of captured light (with wheat and pea), or a light capture similar to monocropped maize (with faba bean). In contrast, C_3/C_3 simultaneous intercrops mainly exhibited competition in light use (Chapter 4).

Examining row differences through the random ray tracing model revealed that light capture in early-sown C_3 species was increased due to border row advantages that are related to direct exposure to sunlight in the early season. At the border row position, early-sown species had larger light capture increases than maize (Chapter 4). This was due to shading in spring of the early companion species on maize. Despite varying light environments during the early season in different species combinations, intercropped maize showed an identical increase in LUE in both border and inner rows across all three intercrops, suggesting that the improved LUE of intercropped maize was likely associated with interactions during the late season rather than early season. These increases may be attributed to the exploitation of C_4 photosynthesis under high-light conditions at the non-limiting N availability after maize overtopping (Chapters 4 and 5). In simultaneous intercrops, especially with faba bean, light capture and LUE of wheat and pea were substantially reduced in all rows. This highlights that in intercrops lacking temporal complementarity, the negative impact of a highly competitive species on less competitive companions persists throughout the strip with a narrow width design and is not alleviated by being away from the strip border.

Taken together, the row-level analysis indicates that border rows are crucial because they have the greatest niche differentiation and, consequently, the greatest interspecific complementarity and competition (Stomph et al., 2020; Zhu et al., 2015). Compared to previous studies in which the contribution of border rows to light capture and conversion in the whole system was inferred by comparing the performance of systems with varying border row proportions (van Oort et al., 2020; Wang et al., 2021), using the random ray tracing model allows sorting out effects at the level of each row. This provides a more direct and convincing assessment by evaluating the actual changes in light capture for each row.

6.3.2 Increasing light capture or increasing light conversion? Which is more achievable by growing intercrops?

In relay intercrops, the three early-sown species did not show increases in LUE. Although intercropped maize experienced an 8% increase in LUE, it only achieved higher biomass when capturing more light with wheat and pea (Chapter 4). In other words, the increased LUE only played a role conditional upon increased light capture. This raises the question: *Compared to monocrops, is increasing light capture and conversion equally achievable in intercrops, or is it more feasible for intercrops to enhance light capture?*

As a resource challenging to supplement in field crops, increasing light capture for crop species should be achieved by considering the extension of the growing season for the entire system. Using relay intercrops, a longer season for light capture can be achieved by combing early-season and late-season species in a relay succession, provided the local GDD allows and without hindering the cultivation of preceding and subsequent crops (Section 6.2.2). Optimising row configuration and sowing density can also promote efficient light capture between the component species and the whole system (Mao et al., 2016; Zhang et al., 2008a). Furthermore, species can express plasticity in leaf growth in response to enhanced light availability, amplifying light capture in addition to the intercropping design (Li et al., 2021; Zhu et al., 2015). This was also evident in the current study from the increased leaf area index (LAI) observed in border rows of early-sown species in relay intercrops (Chapter 4). All the above-mentioned methods are feasible by adopting appropriate intercrops, and one can easily employ them with a good understanding of how to reconcile specific species combinations with the local climate to serve their specific production purposes.

Higher LUE may be attained by increasing canopy photosynthesis (Slattery and Ort, 2021). Intercrops combining short-statured and early-sown C_3 species with tall-statured and late-sown C_4 species are often considered to have the potential for increasing LUE, due to functional complementarity in different photosynthetic pathways (Yu, 2016). In such intercrops, increases in LUE arise from the expectation that C_3 species can enhance their photosynthesis during the early season with prior access to light, water, and nutrients. Meanwhile, C_4 species can fully exploit their high photosynthetic capacity at high light intensity and higher summer temperatures after overtopping in the summer, and C_3 species can satisfy their relatively lower photosynthetic capacity under the shading of C_4 species. There are studies inferring that C_3 species have higher LUE because their photosynthesis is improved by the high proportion of diffuse light under the shading of C_4 companions (Gou et al., 2017a; Liu et al., 2017), as diffuse light is more uniformly distributed and can penetrate deeper layers of the canopy (Emmel et al., 2020). In any case, in terms of light responses of photosynthesis (Rosati and Dejong, 2003), it appears that increasing light capture, through reduced interspecific competition and better light distribution, is important for increasing LUE. Beyond light, various environmental factors, such as availability of water, nutrients, CO_2 concentration at the carboxylation site (rubisco), and temperature, play significant roles in impacting photosynthesis (Dusenge et al., 2019; Fernández-Marín et al., 2020). Even if plants are in an optimal environment, increasing photosynthesis requires great effort in regulating internal processes such as respiration, N metabolism, and water transport (Collalti et al., 2020; Lawlor and Tezara, 2009; Zhong et al., 2017). Achieving this goal in the long term may be more feasible through methods such as genetic modification (Zhu et al., 2010), rather than solely seeking solutions through intercropping. However, acceptance of genetic modification as a method may preclude the use of this methodology, in which case complementarity between species may provide an alternative, ecologically based approach.

In essence, intercropping is more capable of increasing light capture than increasing light conversion. This is because increasing light capture through intercropping is relatively straightforward, and the effective methods are readily available in the current agronomic toolbox. Meanwhile, improved light capture has the potential to enhance light conversion according to the light responses of photosynthesis. However, increasing light conversion demands consideration of the interplay of ecophysiological factors influencing photosynthesis. This may be challenging to regulate through intercropping, which is solely an agronomic approach.

6.4 Under species-tailored N fertilisation, relay intercrops increase N uptake and enhance fertiliser N use efficiency

6.4.1 Species-tailored N fertilisation effectively meets cereal growth demands and exploits legume N fixation

According to the standards of Good Agriculture Practices (FAO, 2003), the existing low-input and high-input N strategies in intercropping are not very efficient in terms of balancing yield increases and environmental costs. In the low N strategy, prevalent in Western Europe (Bedoussac et al., 2015; Hauggaard-Nielsen et al., 2009), N fertiliser is applied at a very low level to ensure successful seedling establishment, or no N fertiliser is applied at all, relying solely on the initial mineral soil N and N released from soil organic matter and organic manure over the season, which may cause N stress for the cereal components, leading to underproduction. In the high N strategy, prevalent in China, N doses can be grouped into three application modes: 1) at a certain high dose for annual crops as the total N rate for the entire intercrop (Li et al., 2011); 2) intercrops receive the weighted average of the respective N doses of the component species grown as monocrops, based on their respective land shares in the intercrop (Gao et al., 2022); 3) intercrops receive the sum of N doses in the corresponding monocrops, a method commonly employed in additive design intercrops (Feng et al., 2020). In these three fundamentally different N use strategies, the total N input can be as high as 300 kg N ha^{-1} (e.g., Yang et al., 2023), which can easily cause N surpluses (Wang et al., 2022). Moreover, in some studies, N fertiliser was uniformly broadcast across the entire field e.g., Li et al. (2011), neglecting the different N demands of different species at different growth stages. For instance, the legume components agronomically do not need much N fertiliser (Giller, 2001).

After pre-season soil nutrient analysis, we applied appropriate N doses to cereals and legumes within their respective species strips, considering the varying N requirements among different species as identified in monocrops. In Chapter 5, I found that under the species-tailored N fertilisation, wheat achieved non-N-limiting growth for the entire season in both the monocrop and intercrops. Maize experienced minimal N stress starting only from grain filling in intercrops. Moreover, the very low starter N input allowed and necessitated the two legumes to fix substantial amounts of N from the atmosphere in relay intercrops. These outcomes are indeed what we aimed for in our efforts to reach a tailored N application strategy in intercrops.

6.4.2 Light capture is the primary factor leading to N capture differences between relay and simultaneous intercrops

Increases in N uptake can result from extra N availability, increased biomass accumulation, or both. In Chapter 5, I found that under the species-tailored N fertilisation, which facilitated non-N-limiting growth for cereals, and enabled and required legumes to extensively exploit N fixation, biomass differences due to differences in light capture are the primary factor leading to N capture differences between relay and simultaneous intercrops, rather than N availability. In relay intercrops, increases in biomass may have promoted the N capture capacity of both early-sown species and maize, due to cascading mechanisms, enabling them to capture more N than monocrops (Evers et al., 2019). In simultaneous intercrops, particularly those involving faba bean, the decreases in N uptake in wheat and pea resulted from a lower biomass production due to light competition, rather than direct competition for N with faba bean. This was reflected by the fact that wheat and pea maintained a similar N concentration (%N) per the same biomass in both intercrops and monocrops; in other words, N uptake decreased proportionally with biomass decreases caused by light capture decreases. The role of light capture in regulating N uptake was further supported by the significant border row effects on N uptake, where the species interacted the most in light capture (Chapter 4).

Nevertheless, in relay intercrops, the three early-sown species benefited not only from increased light capture but also from additional N access. I inferred this from the higher %N in intercropped wheat compared to monocropped wheat, suggesting intercropped wheat may capture additional N, possibly through the more developed root systems, for instance from deeper soil or from the adjacent maize strips when maize was absent or young, as previously reported (Li et al., 2006). Soil N may play a limited role in the two legumes, given the low amount of fertiliser N applied. The higher %N in the two legumes in intercrops than monocrops should primarily result from improved N fixation, as N fixation ability can be promoted by good light availability and increased biomass (Carvalho et al., 2019). The young maize may have had limited access to N due to the pre-emptive foraging in maize border rows by early companions. This was reflected in the lower %N in intercropped maize compared to monocropped maize, starting from the early stage of maize growth. Therefore, maize had smaller increases in N uptake than early-sown species because it did not have extra N access but only benefited from capturing more light in the late season.

In summary, my examination of light and N together leads me to conclude that light is the more limiting and dominant resource in the current experiment. Under the species-tailored N fertilisation, temporal complementarity is essential for efficient N capture. It allows increased light capture, fostering biomass accumulation, potentially increasing root growth and improving the N capture capacity of cereals, contributing to the reduction of N surpluses and losses within the system. It also allows and requires legumes to fix more N. These conclusions are partially conjectural because no measurements were made of root growth. This is clearly an opportunity for future research.

6.4.3 Relay intercrops enhance fertiliser N use efficiency, but the utilisation efficiency of captured N is hardly improved

In Chapter 5, I used fertiliser N equivalent ratio (FNER; Xu et al., 2020) to assess the relative fertiliser N use efficiency in intercrops compared to monocrops. On average over two years, relay intercrops saved 14% fertiliser N compared to monocrops to produce the same grain yield, which aligns with the positive effect of temporal complementarity on saving N input in intercropping observed on a global database (Li et al., 2020b; Xu et al., 2020). It shows that combining species-tailored N fertilisation with temporal complementarity can enhance the ability of intercropping to achieve high yields while saving N input, thereby balancing production objectives and environmental targets.

However, FNER is solely capable of assessing fertiliser N use efficiency in intercrops from an agronomic perspective; it cannot fully reflect the plant's ability to utilise the total captured N for production. Therefore, here I reanalysed N utilisation efficiency (NUtE; Moll et al., 1982) to examine how species truly utilise the captured N.

$$\mathrm{NUtE} = \frac{\text{Grain yield}}{\text{total N uptake}} \qquad \text{(Eq. 6.1)}$$

The results show that in relay intercrops, only maize had slight increases in NUtE, whereas wheat and pea showed decreases in NUtE, and faba bean had an NUtE similar to that of its monocrop (Fig. 6.1). Previous studies have indicated that among various crop species, increases in NUtE are highly dependent on improved harvest index (HI) (de Oliveira Silva et al., 2020). This is because the primary role of N uptake in plants is to support leaf and stem growth through sustained photosynthesis (Perchlik and Tegeder, 2018), and grain yield tends to increase proportionally to total biomass due to source-sink balance, i.e., the HI remains stable (Sales et al., 2021), provided that other resources, such as light and water, are not constrained. There exists a curvilinear correlation between grain yield and total N uptake, characterised by a notable increase in yield during the initial increases in total N uptake at low levels, followed by minimal or no further yield gains as total N uptake continues to rise at the non-limiting level (de Oliveira Silva et al., 2020). Compared to monocrops, crop mixtures are not capable of increasing HI (Chen et al., 2021) because achieving such an outcome requires specific breeding practices to elevate the sink/source ratio, and it has already reached the biological maximum in most modern crop species cultivars (Hay, 1995). In relay intercrops in this thesis, wheat and pea had slight decreases in their HI (Chapter 2), and they also showed decreases in TGW (Chapter 3). These results together indicate insufficient light for them to reach their full capacity of grain filling, due to maize shading. This, in turn, resulted in lower NUtE. The most limiting resource, which is light, leads to a reduction in the efficiency of other already captured resources. A change in capture is thus the predominant effect of intercropping rather than a change in the physiology of use.

In summary, the fertiliser N saving effects of relay intercrops do not result significantly from species enhancing their N utilise efficiency, but rather from the enhanced yield promoted by light capture under non-N-limiting conditions. Building upon the discourse on light in the previous sections, I suggest that increasing the capture efficiency of light and N is achievable through growing intercropping, and increased light capture and N uptake can facilitate an increased grain yield via an HI comparable to monocrops. However, intercropping seems not quite capable of enhancing resource conversion efficiency because doing so requires manipulating the related physiological processes of plants, a realm where intercropping may have limited potential.

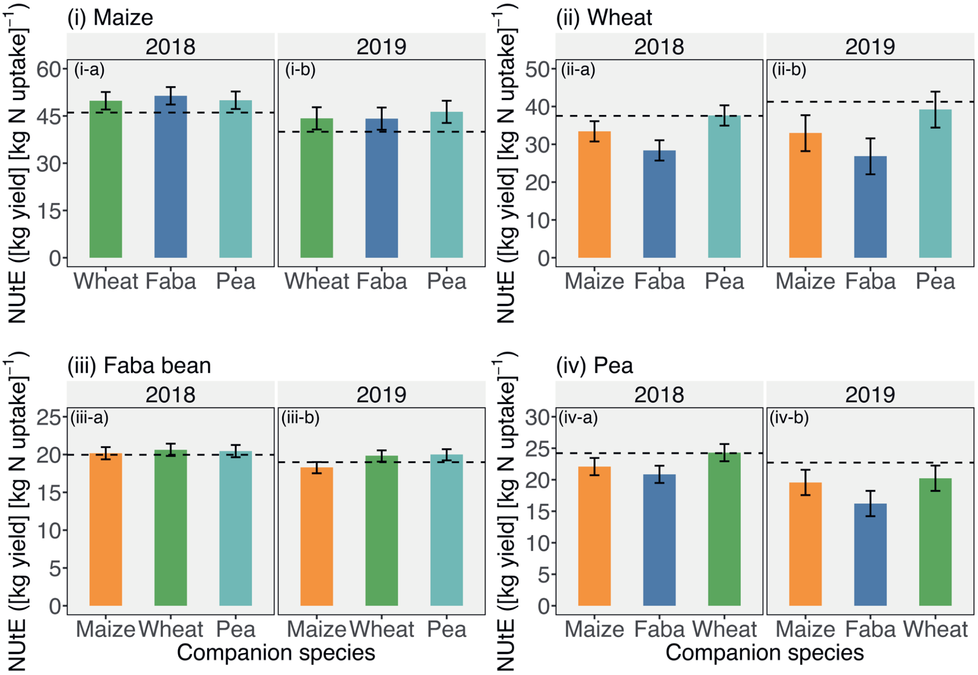

Fig. 6.1 Nitrogen unitisation efficiency (NUtE) of maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a) and 2019 (b). The bars represent NUtE of the focal species in intercrops, calculated as the ratio of yield to N uptake. Different bar colours represent different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). The dashed lines represent NUtE of the focal species in monocrops. Error bars represent the 95% confidence intervals of the means.

6.4.4 Species-tailored N fertilisation and strip design minimise the contribution of cereal-legume N capture complementarity

Cereal-legume combinations are widely acknowledged for their N capture complementarity, reducing N inputs and enhancing productivity in intercropping, particularly under N-constrained growing conditions (Bedoussac et al., 2015). However, the current study did not show a large contribution of this potential complementarity mechanism to yield. The advantage of cereal-legume N capture complementarity lies in cereal components accessing additional mineral N when legume components fulfil their N requirements via N fixation (Jensen et al., 2020). In previous studies, the N fertiliser applied to legumes in the high-input intercrops, e.g., Xing et al. (2023), or the existing soil N in the low-input intercrops, e.g., Rodriguez et al. (2020) emerged as supplementary N sources for cereals. In contrast, in the current study, cereals were not anticipated to access additional N. On the one hand, the strip design limited rhizosphere interactions, relative to full mixtures and row intercrops. On the other hand, the starter N fertiliser applied to legumes should be largely consumed during their seedling stages. Thus, cereals could not have an N pool beneath legume strips, even if cereals managed to extend their roots laterally, if at all, as previously reported (Liu et al., 2020). Moreover, the extent to which N capture complementarity supports cereals ultimately depends on whether cereals experience N stress in monocrops, and accordingly, the additionally available N in the intercrop alleviates this stress. Yet, the N fertiliser applied to maize and wheat in the current study ensured non-N-limiting growth (Chapter 5), thereby making N capture complementarity, if any, less important than light capture complementarity.

6.5 Why did the simultaneous intercrops not perform under conventional management?

In this study, simultaneous intercrops were inferior to relay intercrops, evidenced by their low land productivity compared to monocrops (the average LER of 0.92 ± 0.02), low fertiliser N use efficiency compared to monocrops (the average FNER of 0.85 ± 0.03), and negative net effect (the average NE of –0.52 ± 0.10) over the two years (Chapters 2 and 5). The performance of simultaneous intercrops is even worse than the global average of simultaneous intercrops without maize, which have an LER of 1.16 ± 0.02, an FNER of 1.19 ± 0.05, and an NE of 0.5 ± 0.1 Mg ha^{-1} (Li et al., 2020b). In other words, globally, intercrops without temporal complementarity can offer some advantages in resource use and yield increases, though these benefits are not as pronounced as those in intercrops with temporal complementarity. Conversely, our simultaneous intercrops appear to have offered no benefits at all.

The input level may be the main reason for the divergence between our simultaneous intercrops and the global level. The majority of simultaneous intercrops in the meta-analysis of Li et al. (2020b) were conducted in regions outside of China, grown as full mixtures or row intercrops with low or zero resource inputs. Consequently, component species can exploit complementarity in a resource-deficit environment, according to the stress gradient hypothesis (He et al., 2013). In contrast, the resource input in the current study tends to favour interspecific competition, which prevails when the component species grow together for most of the season. The wheat/pea intercrop generally showed neither advantages nor disadvantages, as the two component species were of similar competitiveness. However, when the highly competitive faba bean was involved, the intercrops showed disadvantages. Yield losses in wheat and pea resulted from simultaneous decreases in resource capture and conversion (Chapters 4 and 5;

Fig. 6.1), indicating poor performance in the light-limited environment created by faba bean. Faba bean acquired significant amounts of light at the expense of wheat and pea, owing to its tall and vigorous canopy, and achieved higher N uptake due to enhanced N fixation under better light conditions (Chapters 4 and 5). However, it could not utilise the foraged resources with improved efficiencies, thus, faba bean failed to compensate for the yield losses it caused in wheat and pea through the yield gains it obtained. In summary, the potential for an intercrop to achieve a yield increase depends on whether the designs enable cooperation in the most limited resource, which is light in the current experiment. Unfortunately, the simultaneous systems in the current study did not succeed in this, but instead created a light environment where the advantaged species did not gain more than the disadvantaged species lost.

6.6 Practical recommendations

The above synthesis of the findings in this thesis allows some putative recommendations for adopting strip intercropping in conventional agriculture in the Netherlands, as well as in the broader Western-European regions with similar cooler and light-limited climates. Additionally, I provide recommendations on how to adopt and evaluate intercropping for various production objectives.

6.6.1 Select appropriate species combinations for effective temporal complementarity

Temporal complementarity appears crucial for boosting production and optimising resource capture in strip intercropping within conventional agriculture in the Netherlands. As shown in this thesis, combining short-statured C_3 and tall-statured C_4 species is a viable approach for achieving suitable temporal complementarity because their growth durations span different times of the agricultural season. More importantly, C_4 species typically have a tall stature, allowing them to benefit from enhanced light capture after overtopping a short companion species. This, on one hand, compensates for light losses during the early stage, and on the other hand, provides the opportunity to utilise high-light conditions through C_4 photosynthesis, facilitating thorough recovery growth. Given the decisive role of grain number in increasing grain yield, it may be advisable to consider species combinations that exhibit temporal complementarity that allows each component species to capture more resources from sowing to early grain filling, favouring a higher grain number.

6.6.2 Fertilisation of intercrops requires an intercrop mindset

The species-tailored N strategy adopted in this thesis supported species growth and reduced environmental costs associated with N surpluses, when compared to highly-fertilised intercrops as practised in some cases in China (Feng et al., 2021). While the contribution of cereal-legume N capture complementarity may be limited under species-tailored N fertilisation, it is recommended to incorporate legumes in intercropping. This practice not only aids in further reducing anthropogenic N but also contributes to the production of high-protein food stuffs suitable for human consumption. Yet, the N doses in this thesis are based on local recommendations for species cultivated as monocrops, assuming a consistent N demand when interacting with different species. However, the N demand in intercropping is likely to be affected by the interaction with the companion species. Ideally, the 'tailored' N doses should be approached with an intercrop mindset, considering possible pre-emptive N forage of early-sown species from neighbouring strips and the resultant legacy effects on the late-sown species, as I found in Chapter 5. Results obtained in this thesis suggest that one might opt for slightly below the recommended doses for early-sown species and slightly above for late-sown species. This would avoid over-fertilising the early-sown species, which may forage in the neighbouring strip, and could overcome adverse effects on the late-sown species due to such pre-emptive nutrient foraging by the early-sown companions. Ultimately, developing an effective species-tailored N strategy for intercropping requires comprehensive experiments on plant nutrient interactions within specific species combinations. Such trials may be done in the future and may help determine the N demands of species within the context of interspecific complementarity and competition. Investigating species-tailored fertilisation in intercropping for other essential nutrients such as phosphorus (P) and potassium (K) is also worthwhile.

6.6.3 Expecting from intercrops to improve resource capture than to improve resource conversion

Results of this thesis indicate that intercropping is an effective approach for enhancing resource capture without necessarily improving resource conversion. In a conventional production context in which water and nutrients meet crop demand, light is the main limiting resource. Increasing light capture efficiency can be achieved by designing appropriate temporal complementarity, optimising row configuration and sowing density, or using a combination of these approaches. Efficient light capture is expected to promote N capture efficiency, provided that N fertilisation is tailored to meet the demands of species. Not much is to be expected from intercropping in terms of improving resource conversion (Tang et al., 2021). Improving conversion efficiency might require breeding rather than growing multiple species on the same land.

6.6.4 Call for a joint effort in developing adaptive machinery

The effective management of strip intercropping poses a significant challenge due to agricultural mechanisation, which is oriented towards large and uniform cultivated areas (van Oort et al., 2020). This challenge is not exclusive to Western Europe but is also true for regions where strip intercrops are extensively cultivated, such as China (Hong et al., 2017). Widening strip width does not appear to be a solution, as the benefits of strip intercropping linked to complementary resource capture tend to diminish with increasing strip width and decreasing border row proportion (van Oort et al., 2020; Wang et al., 2021). Therefore, the effective solution lies in the development of machinery suitable for operating through narrow strips. To achieve such a goal, a joint effort among stakeholders, researchers, and manufacturers is needed (Ditzler and Driessen, 2022). To achieve a productive strip intercropping system, stakeholders and researchers can collaborate on species selection and configuration design, providing manufacturers with valuable feedback on the needs of the system, such as sowing, harvesting, fertilisation, and irrigation. In turn, manufacturers can address these insights to advance machinery. Furthermore, stakeholders and researchers can tackle the challenges faced by manufacturers, working to refine the system and minimise hurdles in evolving machinery as much as possible, without significantly impacting production. This collaborative approach can create a more conducive environment, avoiding a deadlock where stakeholders and researchers believe that the ultimate machinery for intercropping should solely result from mechanical innovations, whereas manufacturers think it is not worthwhile to invest unless stakeholders and researchers are willing to simplify intercrops as much as possible.

6.6.5 Intercropping should be adopted with clearly defined production objectives and evaluated with sound metrics

The aim of this thesis is to explore the contribution of strip intercropping to yield increases and resource use in conventional agriculture. The term ‘conventional’ means that the cropping system seeks to increase yield, employing chemical gradients such as fertilisers, pesticides, herbicides, and growth regulators to ensure that species growth is not significantly restricted, as how the field experiment was operated in this thesis. According to the findings of this thesis and a global meta-analysis (Li et al., 2020b), in term of increasing yield, relay intercropping with a strip design under conventional management appears the most effective approach. A key reason for this is that the relay design allows for the complementary capture of primarily limited resources, i.e., light, under conventional management (Chapter 3, 4). This, in turn, facilitates the capture of other less-limited resources, such as N (Chapter 5), ultimately promoting yield increases (Chapter 2). However, when the aim is to minimise anthropogenic inputs, researchers typically adopt simultaneous intercropping with a fully-mixed or alternative-rowed design under low-input or organic management (Bedoussac et al., 2015). In such intercropping systems, the primary focus is to leverage species complementarity for benefits in pest and disease control, weed suppression, improved grain quality, whereas a substantial increase in yield is not the prioritised pursuit (Bedoussac et al., 2015; Li et al., 2020b).

Through my PhD research, I observed that, in most cases, arguments about whether intercropping has advantages over monocropping arose from individuals with different production objectives and evaluation metrics. Such differences are evident in the two distinctly different intercropping syndromes I mentioned above. To compare them, LER is not an appropriate metric because it is a relative measure and may obscure the fact that under low-input management, both monocrops and intercrops have low production. NE, on the other hand, can accurately capture true production in the absolute sense and properly assess the production performance (Li et al., 2020a). Moreover, if stakeholders do not have specific requirements for crop rotation, they tend to evaluate the performance of a cropping system by considering the revenue from the total bulk yield (Li et al., 2023). In this regard, determining whether an intercrop can yield more than the highest yield of the component species grown as monocrops appears to be a fair assessment. Transgressive overyielding index (TOI; Yu, 2016) is an appropriate metric for such a purpose:

$$\mathrm{TOI} = \frac{Y_{\mathrm{I},1} + Y_{\mathrm{I},2}}{\mathrm{Max}(Y_{\mathrm{M},1}, Y_{\mathrm{M},2})} \qquad \text{(Eq. 6.2)}$$

where $Y_{\mathrm{I},i}$ is the yield of species i in the intercrop per unit land area of the intercrop; $Y_{\mathrm{M},i}$ is the yield of species i in the monocrop per unit land area of the monocrop. A TOI > 1 indicates that the intercrop yields more than the highest yield of the two monocrops.

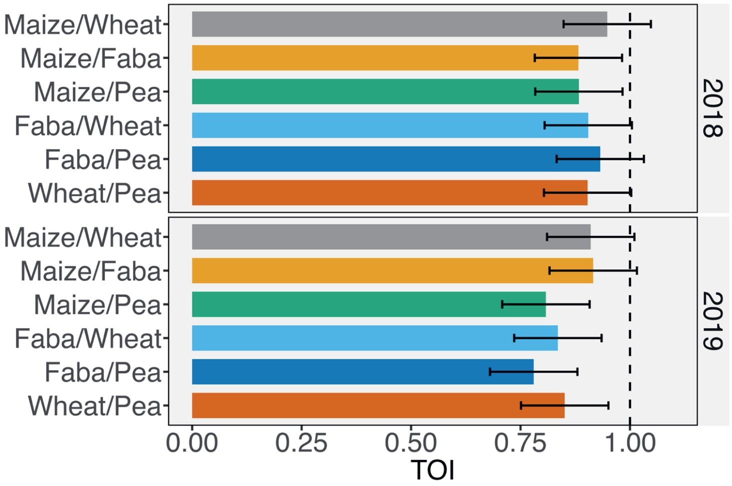

Fig. 6.2 Transgressive overyielding index (TOI) of different intercrops in 2018 and 2019. Error bars represent the 95% confidence intervals of the means.

There is no transgressive overyielding in intercrops studied in this thesis (Fig. 6.2), which is not surprising because transgressive overyielding necessitates robust complementarity to offset the replacement of a high-yielding species with lower-yielding companions (Li et al., 2023). In the end, it is important to consider the trading price per species to determine if there is an aggregate increase in total revenue. This adds complexity, when factoring in inter-year price fluctuations. More specifically, TOI can be used to assess whether an intercrop can provide transgressive overyielding in protein yield, which is relevant when stakeholders want to introduce a high-protein species into the original monocrops to gain increased revenue through improved yield quality (Li et al., 2023).

6.7 Limitations of the thesis and opportunities for further research

6.7.1 Water was not studied

When designing the field experiment for this thesis, I omitted studying water consumption due to the complexity of separating evapotranspiration among different species and further distinguishing between evaporation and transpiration, either through measurement or modelling. However, water may have significantly influenced intercropping performance in this study. The hotter-than-normal summers in both years resulted in substantial evapotranspiration. Despite regular irrigation, water stress, intra- and inter-specific competition for water were expected to persist, particularly in May and June (Fig. S3.7). Additionally, relay intercrops are known for their inefficient water use, mainly attributed to substantial water losses through evaporation from unvegetated strips (Miao et al., 2016; Yang et al., 2011). Hence, investigating water use of relay and simultaneous intercrops in comparison to monocrops may provide an opportunity for a more comprehensive evaluation.

6.7.2 In-depth crop physiological studies will be valuable

Generally speaking, I have proposed and addressed the research questions in this thesis with an agronomic mindset. In this framework, I have successfully established discourses on species selection and management for a productive strip intercropping in conventional agriculture in the Netherlands. However, considering some of the more profound questions that emerged during this study, I believe that relying solely on agronomic methods will not provide sufficiently in-depth answers. In-depth crop physiological studies, such as leaf and canopy photosynthesis, light-N canopy distribution, and shoot-root interaction, may aid in further revealing how intercropped species utilise the captured resources, and help pinpoint the underlying challenges in intercropping in improving resource conversion efficiency, as demonstrated in this thesis and other studies (Gao et al., 2010; Stomph et al., 2020; Tang et al., 2021). Conducting source-sink experiments may contribute to uncovering how intercropped species determine yield components under the altered resource availability because of interspecific interactions, presenting more detailed evidence than the regression analyses in this thesis. Crucially, these studies should account for field variability and intra- as well as inter-specific interactions at the crop level, rather than focusing solely on the plant level, enabling the outcomes to be applicable in field production.

6.7.3 A comparison between conventionally managed strip intercropping and low-input/organic intercropping in Western Europe should be conducted

The primary goal of this thesis is to examine how strip intercropping can contribute to increasing yield and efficient resource use in conventional agriculture under Western-European climate. All the intercropping systems in this thesis are conventionally managed, with the expectation that species growth and production are not (significantly) constrained. Their aim is to increase yield production with the help of species complementarity. This approach is fundamentally different from the currently prevailing full mixtures or row intercrops with low or zero inputs in Western Europe, as they aim to substantially minimise anthropogenic inputs by thoroughly exploiting species complementarity (Bedoussac et al., 2015). The yield increasing advantages of conventionally managed strip intercropping over low-input/organic intercropping have been discussed at the global level (Li et al., 2020b). In Western Europe, stakeholders might also appreciate a similar comparison locally to assist them in choosing the optimal intercropping design for their production objectives.

6.8 Concluding remarks

I conducted the work in this thesis with the aim of exploring to what extent conventionally managed strip intercropping can contribute to yield increases and efficient resource use in the Netherlands. I hope to provide some initiative for Western Europe, offering more options in crop diversification beyond the locally typical crop mixtures under low-input or organic management.

Under a species-tailored N fertilisation meeting species N demands and other anthropogenic inputs aiming at species growth are not constrained by weeds, diseases, and pests, light proved to be the primary limiting resource governing intercropping performance. The findings of this thesis highlight that relay strip intercropping increases production efficiency in conventional agriculture in the Netherlands, like it does in a global context (Li et al., 2020b). This is because temporal complementarity in relay strip intercropping allows component species to capture more light than their monocrops, thereby promoting enhanced N capture. However, according to my study, intercropping is not quite capable of enhancing the conversion efficiency of either light or N. The effective tools for increasing resource conversion efficiency may lie in more in-depth plant physiological research, but intercropping as an agronomic approach may provide limited potential to boost resource conversion efficiency.

This thesis not only provides practical guidance for integrating strip intercropping in conventional agriculture in the Netherlands and other Western-European regions with similar cooler and light-limited climates, but also contributes to a broader understanding of how interspecific interactions influence resource use and production in crop species mixtures. Yet, by no means does this thesis suggest that strip intercropping with anthropogenic inputs is superior to the currently prevalent low-input/organic crop mixtures in Western Europe and worldwide. It is the specific production objectives that determine which type of intercropping is most suited.

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Supplementary information for Chapter 2

Temporal complementarity drives species combinability in strip intercropping in the Netherlands

Fig. S2.1 Meteorological information and irrigation of experimental seasons of 2018 and 2019 in Wageningen, the Netherlands.

Fig. S2.2 Grain yield, vegetative biomass, and harvest index of different rows in the monocrop strips.

Table S2.1 Main crops and cover crops preceding the experiments in 2018 and 2019.

Table S2.2 Details on the application of fertiliser, herbicides, pesticides, fungicides, and growth regulator.

Table S2.3 Comparisons of grain yield, vegetative biomass, and harvest index per strip.

Table S2.4 Comparisons of LER per intercrop and pLER per each species for grain yield and vegetative biomass.

Table S2.5 Comparisons of NE per intercrop and NE per each species for grain yield and vegetative biomass.

Table S2.6 Model comparison output of the relationship between LER for grain yield and TND and the relationship between NE for grain yield and TND.

Table S 2.7 Comparisons of grain yield, vegetative biomass, and harvest index per metre row.

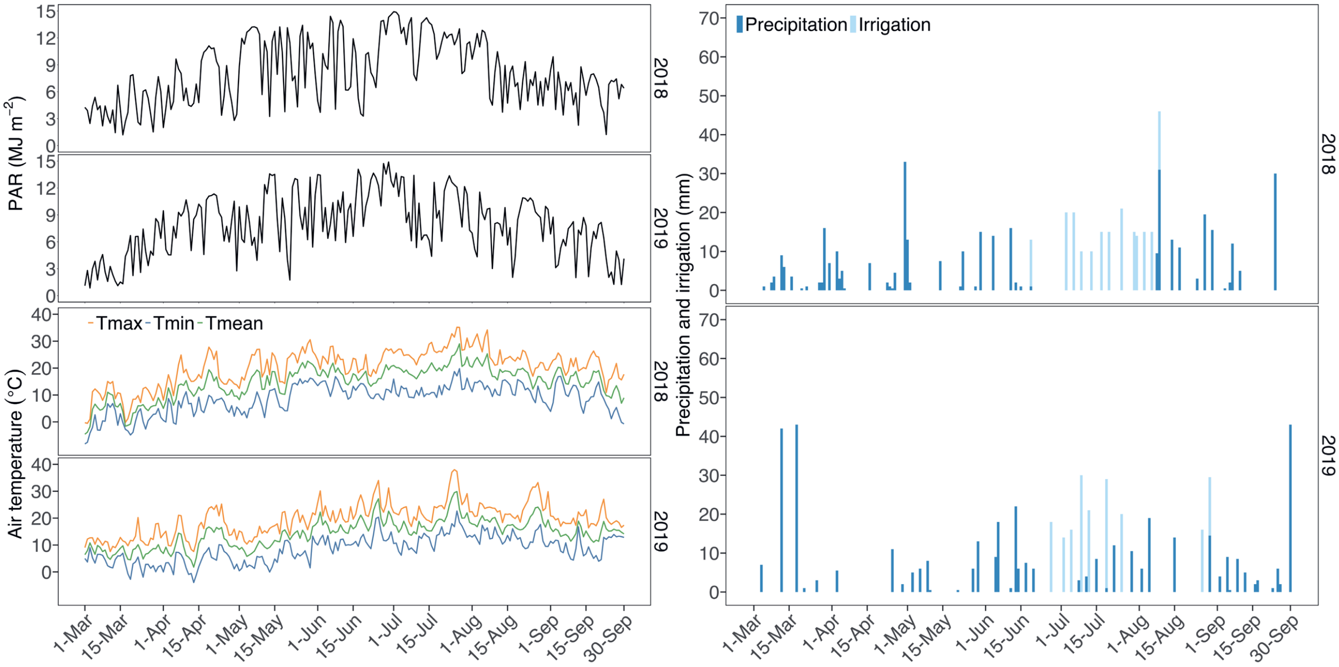


Fig. S2.1 Photosynthetically active radiation (PAR), air temperature, precipitation, and irrigation of 2018 and 2019 experimental seasons in Wageningen, the Netherlands.

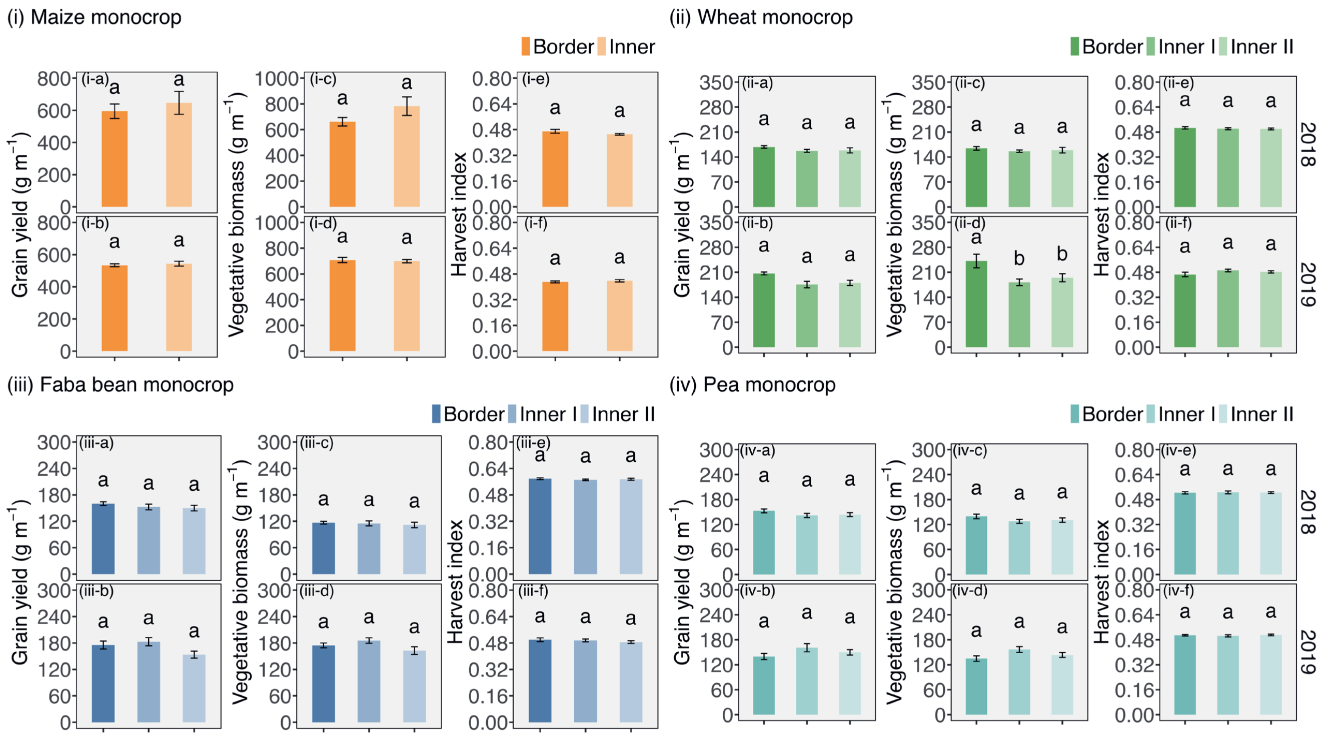


Fig. S2.2 Grain yield, vegetative biomass, and harvest index of different rows in the monocrop strips of maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a, c, e) and 2019 (b, d, f). Each colour intensity represents a row. Error bars represent standard errors of the means. Shared letters denote non-significant differences within an individual year according to Tukey's Post-Hoc Test ($P \leq 0.05$).

Table S2.1 Main crops and cover crops preceding the experiments in 2018 and 2019.

Year	Main crop	Main crop sown	Main crop harvested	Cover crop	Cover crop sown	Cover crop ploughed under
2018	Winter wheat (*Triticum aestivum* L.)	Oct 28, 2016	Jul 20, 2017	Bristle oat (*Avena strigosa* Schreb.) (50 kg seeds ha^{-1}) + Fodder radish (*Raphanus raphanistrum* L.) (10 kg seeds ha^{-1})	Jul 25, 2017	Mar 5, 2018
2019	Sugar beet (*Beta vulgaris* L.)	Apr 12, 2018	Nov 7, 2018	-	-	-

Table S2.2 Details on the application of fertiliser, herbicides, pesticides, fungicides, and growth regulator.

Year	Date	Fertiliser (kg ha^{-1})	Rate
2018	Feb 28	K_2O, P_2O_5	87 kg K ha^{-1} , 29 kg P ha^{-1}
	Apr 11	$NH_4NO_3 . CaMg(CO_3)$	296 (80 kg N ha^{-1} for wheat), 74 (20 kg N ha^{-1} for bean), 74 (20 kg N ha^{-1} for pea)
	May 04	$NH_4NO_3 . CaMg(CO_3)$	167 (45 kg N ha^{-1} for wheat), 296 (80 kg N ha^{-1} for maize)
	Jun 11	$NH_4NO_3 . CaMg(CO_3)$	333 (90 kg N ha^{-1} for maize)
2019	Feb 25	K_2O, P_2O_5	87 kg K ha^{-1}, 34 kg P ha^{-1}
	Apr 15	$NH_4NO_3 . CaMg(CO_3)$	296 (80 kg N ha^{-1} for wheat), 74 (20 kg N ha^{-1} for bean), 74 (20 kg N ha^{-1} for pea)
	May 06	$NH_4NO_3 . CaMg(CO_3)$	167 (45 kg N ha^{-1} for wheat), 296 (80 kg N ha^{-1} for maize)
	Jun 14	$NH_4NO_3 . CaMg(CO_3)$	333 (90 kg N ha^{-1} for maize)
Year	Date	Herbicide/Pesticide/Fungicide (g ha^{-1})	Dose
2018	Mar 23	Pendimethalin	800
	Apr 13	Bentazon	480
	Apr 25	Bentazon	720
	May 07	Bentazon	720
	May 31	Tebuconazole, Prothioconazole, Pirimicarb	125, 125, 250
2019	Apr 05	Pendimethalin	800
	Apr 26	Bentazon	600
	May 03	Bentazon	840
	May 13	Bentazon	720
	May 16	Pirimicarb	250
	May 23	Prohexadione Calcium, Trinexapac Ethyl	15, 22.5
	Jun 03	Tebuconazole, Prothioconazole	125, 125
	Jun 11	Deltamethrin	6.25
	Jun 25	Tebuconazole, Prothioconazole	98.82, 98.82
		Cyproconazole, Trifloxystrobin	26.35, 61.76

Table S2.3 Comparisons of grain yield, vegetative biomass, and harvest index per strip. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(i) Maize

Species		Year	Treatment	Mean ± Standard error	Comparison		
Maize	Grain yield (Mg ha^{-1})	2018	Monocrop maize	12.2 ± 0.78	b		
			Maize/wheat	15.2 ± 0.84	a		
			Maize/faba	12.9 ± 0.51	ab		*P*-value
			Maize/pea	15.4 ± 0.74	a	Treatment	0.000
		2019	Monocrop maize	10.7 ± 0.22	b	Year	0.010
			Maize/wheat	12.5 ± 0.33	ab	Treatment × Year	0.656
			Maize/faba	10.9 ± 0.51	b		
			Maize/pea	12.5 ± 0.13	ab		
	Vegetative biomass (Mg ha^{-1})	2018	Monocrop maize	14.0 ± 0.78	bd		
			Maize/wheat	17.2 ± 1.11	ac		
			Maize/faba	13.7 ± 0.81	d		*P*-value
			Maize/pea	17.8 ± 0.87	ac	Treatment	0.000
		2019	Monocrop maize	14.1 ± 0.40	abcd	Year	0.758
			Maize/wheat	17.7 ± 0.43	ab	Treatment × Year	0.973
			Maize/faba	13.8 ± 0.62	cd		
			Maize/pea	17.7 ± 0.51	ab		
	Harvest index	2018	Monocrop maize	0.465 ± 0.007	abc		
			Maize/wheat	0.471 ± 0.007	ab		
			Maize/faba	0.487 ± 0.010	a		*P*-value
			Maize/pea	0.464 ± 0.005	abc	Treatment	0.010
		2019	Monocrop maize	0.433 ± 0.006	cd	Year	0.000
			Maize/wheat	0.415 ± 0.010	d	Treatment × Year	0.434
			Maize/faba	0.441 ± 0.003	bcd		
			Maize/pea	0.414 ± 0.006	d		

Table S2.3 (continued) Comparisons of grain yield, vegetative biomass, and harvest index per strip. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(ii) Wheat

Species		Year	Treatment	Mean ± Standard error	Comparison		
Wheat	Grain yield (Mg ha^{-1})	2018	Monocrop wheat	6.45 ± 0.13	bc		
			Maize/wheat	7.48 ± 0.08	ab		
			Faba/wheat	4.70 ± 0.46	d		*P*-value
			Wheat/pea	6.25 ± 0.22	c	Treatment	0.000
		2019	Monocrop wheat	7.50 ± 0.20	abc	Year	0.059
			Maize/wheat	6.99 ± 0.06	abc	Treatment × Year	0.000
			Faba/wheat	4.24 ± 0.51	d		
			Wheat/pea	8.01 ± 0.25	a		
	Vegetative biomass (Mg ha^{-1})	2018	Monocrop wheat	6.40 ± 0.17	b		
			Maize/wheat	8.60 ± 0.14	a		
			Faba/wheat	6.61 ± 0.21	b		*P*-value
			Wheat/pea	6.67 ± 0.17	b	Treatment	0.000
		2019	Monocrop wheat	8.24 ± 0.57	a	Year	0.037
			Maize/wheat	8.59 ± 0.25	a	Treatment × Year	0.000
			Faba/wheat	6.89 ± 0.14	b		
			Wheat/pea	8.41 ± 0.44	a		
	Harvest index	2018	Monocrop wheat	0.502 ± 0.007	a		
			Maize/wheat	0.465 ± 0.002	ab		
			Faba/wheat	0.412 ± 0.028	bc		*P*-value
			Wheat/pea	0.483 ± 0.007	a	Treatment	0.000
		2019	Monocrop wheat	0.478 ± 0.011	ab	Year	0.292
			Maize/wheat	0.449 ± 0.006	ab	Treatment × Year	0.532
			Faba/wheat	0.377 ± 0.027	c		
			Wheat/pea	0.489 ± 0.006	ab		

Table S2.3 (continued) Comparisons of grain yield, vegetative biomass, and harvest index per strip. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(iii) Faba bean

Species		Year	Treatment	Mean ± Standard error	Comparison		
Faba	Grain yield (Mg ha^{-1})	2018	Monocrop faba	6.17 ± 0.11	b		
			Maize/faba	8.17 ± 0.25	a		
			Faba/wheat	7.06 ± 0.46	ab		P-value
			Faba/pea	7.28 ± 0.34	ab	Treatment	0.001
		2019	Monocrop faba	6.83 ± 0.33	ab	Year	0.032
			Maize/faba	8.72 ± 0.52	a	Treatment × Year	0.681
			Faba/wheat	8.43 ± 0.65	a		
			Faba/pea	7.69 ± 0.80	ab		
	Vegetative biomass (Mg ha^{-1})	2018	Monocrop faba	4.58 ± 0.16	d		
			Maize/faba	5.62 ± 0.28	bcd		
			Faba/wheat	4.92 ± 0.29	d		P-value
			Faba/pea	5.26 ± 0.30	cd	Treatment	0.010
		2019	Monocrop faba	6.97 ± 0.16	abc	Year	0.001
			Maize/faba	8.31 ± 0.63	a	Treatment × Year	0.637
			Faba/wheat	7.51 ± 0.36	a		
			Faba/pea	7.18 ± 0.59	ab		
	Harvest index	2018	Monocrop faba	0.574 ± 0.007	a		
			Maize/faba	0.593 ± 0.010	ab		
			Faba/wheat	0.589 ± 0.004	a		P-value
			Faba/pea	0.581 ± 0.004	a	Treatment	0.022
		2019	Monocrop faba	0.494 ± 0.012	c	Year	0.001
			Maize/faba	0.513 ± 0.010	c	Treatment × Year	0.456
			Faba/wheat	0.528 ± 0.007	bc		
			Faba/pea	0.516 ± 0.015	c		

Table S2.3 (continued) Comparisons of grain yield, vegetative biomass, and harvest index per strip. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(iv) Pea

Species		Year	Treatment	Mean ± Standard error	Comparison		
Pea	Grain yield (Mg ha^{-1})	2018	Monocrop Pea	5.84 ± 0.12	a		
			Maize/pea	5.93 ± 0.13	a		
			Faba/pea	4.18 ± 0.15	bc		*P*-value
			Wheat/pea	5.39 ± 0.09	a	Treatment	0.000
		2019	Monocrop Pea	6.01 ± 0.11	a	Year	0.085
			Maize/pea	4.85 ± 0.70	ab	Treatment × Year	0.061
			Faba/pea	2.80 ± 0.57	c		
			Wheat/pea	4.75 ± 0.57	ab		
	Vegetative biomass (Mg ha^{-1})	2018	Monocrop Pea	5.31 ± 0.19	ab		
			Maize/pea	5.57 ± 0.14	ab		
			Faba/pea	5.10 ± 0.29	ab		*P*-value
			Wheat/pea	4.66 ± 0.12	b	Treatment	0.008
		2019	Monocrop Pea	5.80 ± 0.04	ab	Year	0.127
			Maize/pea	5.94 ± 0.43	a	Treatment × Year	0.140
			Faba/pea	4.68 ± 0.32	ab		
			Wheat/pea	5.46 ± 0.47	ab		
	Harvest index	2018	Monocrop Pea	0.525 ± 0.009	a		
			Maize/pea	0.516 ± 0.005	ab		
			Faba/pea	0.452 ± 0.020	c		*P*-value
			Wheat/pea	0.536 ± 0.004	a	Treatment	0.000
		2019	Monocrop Pea	0.509 ± 0.006	abc	Year	0.012
			Maize/pea	0.445 ± 0.024	bc	Treatment × Year	0.075
			Faba/pea	0.366 ± 0.030	d		
			Wheat/pea	0.463 ± 0.011	abc		

Table S2.4 Comparisons of LER per intercrop and pLER per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(i) System

	Year	Treatment	Mean ± Standard error	Comparison		
LER for grain yield	2018	Maize/wheat	1.22 ± 0.05	a		
		Maize/faba	1.20 ± 0.06	a		
		Maize/pea	1.14 ± 0.04	abd		
		Faba/wheat	0.94 ± 0.02	cef		
		Faba/pea	0.95 ± 0.04	cef		*P*-value
		Wheat/pea	0.95 ± 0.02	cef	Treatment	0.000
	2019	Maize/wheat	1.05 ± 0.01	abcde	Year	0.045
		Maize/faba	1.15 ± 0.02	abc	Treatment × Year	0.126
		Maize/pea	0.98 ± 0.06	bcdef		
		Faba/wheat	0.90 ± 0.04	ef		
		Faba/pea	0.80 ± 0.08	f		
		Wheat/pea	0.93 ± 0.04	def		
LER for vegetative biomass	2018	Maize/wheat	1.30 ± 0.06	a		
		Maize/faba	1.11 ± 0.08	bcde		
		Maize/pea	1.17 ± 0.03	abd		
		Faba/wheat	1.05 ± 0.03	bcde		
		Faba/pea	1.06 ± 0.05	bcde		*P*-value
		Wheat/pea	0.96 ± 0.02	ce	Treatment	0.000
	2019	Maize/wheat	1.16 ± 0.04	abc	Year	0.213
		Maize/faba	1.09 ± 0.03	abcde	Treatment × Year	0.204
		Maize/pea	1.14 ± 0.04	abc		
		Faba/wheat	0.96 ± 0.02	bcde		
		Faba/pea	0.92 ± 0.06	de		
		Wheat/pea	0.99 ± 0.05	bcde		

Table S2.4 (continued) Comparisons of LER per intercrop and pLER per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between ‘Treatment_Year’ combinations (Tukey’s Post-Hoc Test, $P \leq 0.05$).

(ii) Maize

Species		Year	Treatment	Mean ± Standard error	Comparison		
Maize	pLER for grain yield	2018	Maize/wheat	0.64 ± 0.06	a		
			Maize/faba	0.54 ± 0.05	b		*P*-value
			Maize/pea	0.64 ± 0.04	a	Treatment	0.001
		2019	Maize/wheat	0.58 ± 0.01	ab	Year	0.391
			Maize/faba	0.51 ± 0.02	ab	Treatment × Year	0.869
			Maize/pea	0.58 ± 0.02	ab		
	pLER for vegetative biomass	2018	Maize/wheat	0.62 ± 0.06	ab		
			Maize/faba	0.50 ± 0.04	cd		*P*-value
			Maize/pea	0.64 ± 0.03	ab	Treatment	0.000
		2019	Maize/wheat	0.63 ± 0.02	ac	Year	0.990
			Maize/faba	0.49 ± 0.03	bd	Treatment × Year	0.945
			Maize/pea	0.63 ± 0.02	ac		

Table S2.4 (continued) Comparisons of LER per intercrop and pLER per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(iii) Wheat

Species		Year	Treatment	Mean ± Standard error	Comparison		
Wheat	pLER for grain yield	2018	Maize/wheat	0.58 ± 0.01	a		
			Faba/wheat	0.36 ± 0.03	cd		*P*-value
			Wheat/pea	0.48 ± 0.01	b	Treatment	0.000
		2019	Maize/wheat	0.47 ± 0.01	abc	Year	0.139
			Faba/wheat	0.28 ± 0.04	d	Treatment × Year	0.003
			Wheat/pea	0.54 ± 0.02	ab		
	pLER for vegetative biomass	2018	Maize/wheat	0.67 ± 0.01	a		
			Faba/wheat	0.52 ± 0.02	bc		*P*-value
			Wheat/pea	0.52 ± 0.01	bc	Treatment	0.000
		2019	Maize/wheat	0.53 ± 0.03	ab	Year	0.063
			Faba/wheat	0.42 ± 0.03	c	Treatment × Year	0.000
			Wheat/pea	0.52 ± 0.04	ab		

Table S2.4 (continued) Comparisons of LER per intercrop and pLER per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(iv) Faba bean

Species		Year	Treatment	Mean ± Standard error	Comparison		
Faba	pLER for grain yield	2018	Maize/faba	0.66 ± 0.02	a		
			Faba/wheat	0.57 ± 0.03	a		*P*-value
			Faba/pea	0.59 ± 0.03	a	Treatment	0.153
		2019	Maize/faba	0.64 ± 0.04	a	Year	1.000
			Faba/wheat	0.62 ± 0.04	a	Treatment × Year	0.558
			Faba/pea	0.57 ± 0.07	a		
	pLER for vegetative biomass	2018	Maize/faba	0.62 ± 0.04	a		
			Faba/wheat	0.54 ± 0.02	a		*P*-value
			Faba/pea	0.58 ± 0.04	a	Treatment	0.046
		2019	Maize/faba	0.59 ± 0.04	a	Year	0.404
			Faba/wheat	0.54 ± 0.02	a	Treatment × Year	0.542
			Faba/pea	0.52 ± 0.05	a		

Table S2.4 (continued) Comparisons of LER per intercrop and pLER per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(v) Pea

Species		Year	Treatment	Mean ± Standard error	Comparison		
Pea	pLER for grain yield	2018	Maize/pea	0.51 ± 0.012	a		
			Faba/pea	0.36 ± 0.014	bc		*P*-value
			Wheat/pea	0.46 ± 0.010	ab	Treatment	0.000
		2019	Maize/pea	0.40 ± 0.055	ab	Year	0.012
			Faba/pea	0.23 ± 0.047	c	Treatment × Year	0.470
			Wheat/pea	0.40 ± 0.048	ab		
	pLER for vegetative biomass	2018	Maize/pea	0.53 ± 0.027	a		
			Faba/pea	0.48 ± 0.021	a		*P*-value
			Wheat/pea	0.44 ± 0.017	a	Treatment	0.026
		2019	Maize/pea	0.51 ± 0.037	a	Year	0.410
			Faba/pea	0.40 ± 0.029	a	Treatment × Year	0.186
			Wheat/pea	0.47 ± 0.042	a		

Table S2.5 Comparisons of NE per intercrop and NE per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(i) System

	Year	Treatment	Mean ± Standard error	Comparison		
NE on grain yield (Mg ha^{-1})	2018	Maize/wheat	2.01 ± 0.54	a		
		Maize/faba	1.33 ± 0.59	ab		
		Maize/pea	1.60 ± 0.36	a		
		Faba/wheat	−0.43 ± 0.13	cde		
		Faba/pea	−0.27 ± 0.22	cde		*P*-value
		Wheat/pea	−0.33 ± 0.10	cde	Treatment	0.000
	2019	Maize/wheat	0.65 ± 0.12	abcd	Year	0.051
		Maize/faba	1.04 ± 0.14	abc	Treatment × Year	0.206
		Maize/pea	0.29 ± 0.41	abcde		
		Faba/wheat	−0.83 ± 0.27	de		
		Faba/pea	−1.17 ± 0.49	e		
		Wheat/pea	−0.37 ± 0.22	bcde		
NE on vegetative biomass (Mg ha^{-1})	2018	Maize/wheat	2.67 ± 0.75	a		
		Maize/faba	0.33 ± 0.73	cde		
		Maize/pea	2.01 ± 0.33	ab		
		Faba/wheat	0.28 ± 0.17	cde		
		Faba/pea	0.24 ± 0.25	cde		*P*-value
		Wheat/pea	−0.18 ± 0.16	cde	Treatment	0.000
	2019	Maize/wheat	1.98 ± 0.36	ac	Year	0.505
		Maize/faba	0.54 ± 0.35	abcde	Treatment × Year	0.660
		Maize/pea	1.85 ± 0.34	abcd		
		Faba/wheat	−0.40 ± 0.24	e		
		Faba/pea	−0.46 ± 0.43	e		
		Wheat/pea	−0.09 ± 0.36	bde		

Table S2.5 (continued) Comparisons of NE per intercrop and NE per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between ‘Treatment_Year’ combinations (Tukey’s Post-Hoc Test, $P \leq 0.05$).

(ii) Maize

Species		Year	Treatment	Mean ± Standard error	Comparison		
Maize	NE on grain yield (Mg ha^{-1})	2018	Maize/wheat	1.50 ± 0.59	ab		
			Maize/faba	0.33 ± 0.57	b		*P*-value
			Maize/pea	1.56 ± 0.34	a	Treatment	0.004
		2019	Maize/wheat	0.90 ± 0.12	ab	Year	0.356
			Maize/faba	0.09 ± 0.23	ab	Treatment × Year	0.726
			Maize/pea	0.87 ± 0.15	ab		
	NE on vegetative biomass (Mg ha^{-1})	2018	Maize/wheat	1.57 ± 0.77	ab		
			Maize/faba	−0.19 ± 0.60	cd		*P*-value
			Maize/pea	1.87 ± 0.37	ab	Treatment	0.000
		2019	Maize/wheat	1.81 ± 0.19	ac	Year	0.873
			Maize/faba	−0.13 ± 0.44	bd	Treatment × Year	0.887
			Maize/pea	1.78 ± 0.31	ac		

Table S2.5 (continued) Comparisons of NE per intercrop and NE per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(iii) Wheat

Species		Year	Treatment	Mean ± Standard error	Comparison		
Wheat	NE om grain yield (Mg ha^{-1})	2018	Maize/wheat	0.51 ± 0.08	a		
			Faba/wheat	−0.88 ± 0.23	cd		*P*-value
			Wheat/pea	−0.10 ± 0.08	b	Treatment	0.000
		2019	Maize/wheat	−0.25 ± 0.1	abc	Year	0.130
			Faba/wheat	−1.63 ± 0.34	d	Treatment × Year	0.002
			Wheat/pea	0.26 ± 0.14	ab		
	NE on vegetative biomass (Mg ha^{-1})	2018	Maize/wheat	1.10 ± 0.06	a		
			Faba/wheat	0.10 ± 0.10	bc		*P*-value
			Wheat/pea	0.14 ± 0.08	bc	Treatment	0.000
		2019	Maize/wheat	0.17 ± 0.23	ab	Year	0.076
			Faba/wheat	−0.68 ± 0.33	c	Treatment × Year	0.000
			Wheat/pea	0.08 ± 0.33	ab		

Table S2.5 (continued) Comparisons of NE per intercrop and NE per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between ‘Treatment_Year’ combinations (Tukey’s Post-Hoc Test, $P \leq 0.05$).

(iv) Faba bean

Species		Year	Treatment	Mean ± Standard erro	Comparison		
Faba	NE on grain yield (Mg ha^{-1})	2018	Maize/faba	1.00 ± 0.10	a		
			Faba/wheat	0.45 ± 0.22	a		*P*-value
			Faba/pea	0.56 ± 0.20	a	Treatment	0.139
		2019	Maize/faba	0.95 ± 0.23	a	Year	0.781
			Faba/wheat	0.80 ± 0.30	a	Treatment × Year	0.562
			Faba/pea	0.43 ± 0.47	a		
	NE on vegetative biomass (Mg ha^{-1})	2018	Maize/faba	0.52 ± 0.16	a		
			Faba/wheat	0.17 ± 0.11	a		*P*-value
			Faba/pea	0.34 ± 0.16	a	Treatment	0.066
		2019	Maize/faba	0.67 ± 0.26	a	Year	0.994
			Faba/wheat	0.27 ± 0.12	a	Treatment × Year	0.483
			Faba/pea	0.11 ± 0.34	a		

Table S2.5 (continued) Comparisons of NE per intercrop and NE per each species for grain yield and vegetative biomass. Shared letters denote non-significant differences between 'Treatment_Year' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(v) Pea

Species		Year	Treatment	Mean ± Standard error	Comparison		
Pea	NE on grain yield (Mg ha^{-1})	2018	Maize/pea	0.05 ± 0.07	a		
			Faba/pea	−0.83 ± 0.09	bc		*P*-value
			Wheat/pea	−0.23 ± 0.06	ab	Treatment	0.000
		2019	Maize/pea	−0.58 ± 0.33	ab	Year	0.010
			Faba/pea	−1.60 ± 0.28	c	Treatment × Year	0.447
			Wheat/pea	−0.63 ± 0.29	ab		
	NE on vegetative biomass (Mg ha^{-1})	2018	Maize/pea	0.13 ± 0.14	a		
			Faba/pea	−0.10 ± 0.11	a		*P*-value
			Wheat/pea	−0.32 ± 0.10	a	Treatment	0.031
		2019	Maize/pea	0.07 ± 0.22	a	Year	0.411
			Faba/pea	−0.56 ± 0.17	a	Treatment × Year	0.171
			Wheat/pea	−0.17 ± 0.24	a		

Table S2.6 Model comparison output of the relationship between LER for grain yield and TND and the relationship between NE for grain yield and TND. The model with the lowest AIC value was selected as the optimal model. For models with very close AIC values, the simpler model was selected to avoid overfitting because AIC is known to tend to select for over-complex models. Therefore, Model 8 was select for both LER and NE.

(i) Model comparison output for the relationship between LER and TND

Model	AIC	BIC	Negative log likelihood	Df
1	−94.627	−86.250	51.313	4
2	−93.206	−82.734	51.603	5
3	−93.724	−83.252	51.862	5
4	−99.610	−89.138	54.805	5
5	−92.612	−80.046	52.306	6
6	−97.329	−84.763	54.664	6
7	−98.022	−85.455	55.011	6
8	−108.901	−90.052	63.450	9
9	−106.447	−77.126	67.223	14

(ii) Model comparison output for the relationship between NE and TND

Model	AIC	BIC	Negative log likelihood	Df
1	148.946	157.323	70.473	4
2	149.450	159.922	69.725	5
3	150.846	161.318	70.423	5
4	150.105	160.577	70.053	5
5	149.576	162.142	68.788	6
6	147.527	160.093	67.764	6
7	151.093	163.659	69.546	6
8	147.844	166.693	64.922	9
9	153.230	182.551	62.615	14

Table S2.7 Comparisons of grain yield, vegetative biomass, and harvest index per meter row. Shared letters denote non-significant differences between 'Treatment_Row_Year ' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(i) Maize

Species		Year	Treatment	Row	Mean ± Standard error	Comparison		
Maize	Grain yield (g m^{-1})	2018	Monocrop	-	612 ± 37	bc		
			Maize/wheat	Border	749 ± 33	ab		
				Inner	787 ± 73	ab		
			Maize/faba	Border	637 ± 36	bc		
				Inner	660 ± 70	abc		
			Maize/pea	Border	802 ± 38	a		*P*-value
				Inner	699 ± 40	abc	Treatment	0.000
		2019	Monocrop	-	537 ± 8.0	c	Year	0.011
			Maize/wheat	Border	634 ± 9.0	abc	Treatment × Year	0.412
				Inner	615 ± 43	abc		
			Maize/faba	Border	498 ± 38	c		
				Inner	643 ± 24	abc		
			Maize/pea	Border	614 ± 23	abc		
				Inner	644 ± 26	abc		
	Vegetative biomass (g m^{-1})	2018	Monocrop	-	701 ± 34	bc		
			Maize/wheat	Border	819 ± 38	abc		
				Inner	935 ± 83	a		
			Maize/faba	Border	664 ± 41	bc		
				Inner	719 ± 91	abc		
			Maize/pea	Border	913 ± 46	a		*P*-value
				Inner	840 ± 42	abc	Treatment	0.000
		2019	Monocrop	-	705 ± 14	abc	Year	0.544
			Maize/wheat	Border	877 ± 27	ab	Treatment × Year	0.314
				Inner	902 ± 42	ab		
			Maize/faba	Border	606 ± 51	c		
				Inner	865 ± 49	abc		
			Maize/pea	Border	860 ± 41	ab		
				Inner	929 ± 44	ab		
	Harvest index	2018	Monocrop	-	0.463 ± 0.008	abc		
			Maize/wheat	Border	0.478 ± 0.009	ab		
				Inner	0.457 ± 0.003	abcd		
			Maize/faba	Border	0.491 ± 0.014	a		
				Inner	0.482 ± 0.006	ab		*P*-value
			Maize/pea	Border	0.468 ± 0.005	abc	Treatment	0.001
				Inner	0.454 ± 0.004	abcd	Year	0.000
		2019	Monocrop	-	0.433 ± 0.004	cd	Treatment × Year	0.638
			Maize/wheat	Border	0.420 ± 0.009	d		
				Inner	0.404 ± 0.009	d		
			Maize/faba	Border	0.453 ± 0.005	abcd		
				Inner	0.427 ± 0.010	bcd		
			Maize/pea	Border	0.417 ± 0.009	d		
				Inner	0.410 ± 0.004	d		

Table S2.7 (continued) Comparisons of grain yield, vegetative biomass, and harvest index per meter row. Shared letters denote non-significant differences between 'Treatment_Row_Year ' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(ii) Wheat

Species		Year	Treatment	Row	Mean ± Standard error	Comparison		
Wheat	Grain yield (g m^{-1})	2018	Monocrop	-	161 ± 3	bc		
			Maize/wheat	Border	229 ± 7	a		
				Inner I	165 ± 3	bc		
				Inner II	168 ± 4	bc		
			Faba/wheat	Border	98 ± 9	h		
				Inner I	123 ± 7	fgh		
				Inner II	131 ± 9	defg		
			Wheat/pea	Border	155 ± 9	cde		
				Inner I	159 ± 8	bcde		*P*-value
				Inner II	155 ± 4	cdef	Treatment	0.000
		2019	Monocrop	-	187 ± 5	bc	Year	0.159
			Maize/wheat	Border	196 ± 3	ab	Treatment × Year	0.000
				Inner I	159 ± 3	bcdef		
				Inner II	169 ± 4	bcd		
			Faba/wheat	Border	89 ± 12	h		
				Inner I	107 ± 10	gh		
				Inner II	122 ± 11	efgh		
			Wheat/pea	Border	229 ± 10	a		
				Inner I	179 ± 4	bc		
				Inner II	193 ± 4	abc		
	Vegetative biomass (g m^{-1})	2018	Monocrop	-	160 ± 3	c		
			Maize/wheat	Border	287 ± 9	a		
				Inner I	179 ± 4	bc		
				Inner II	179 ± 4	bc		
			Faba/wheat	Border	161 ± 5	c		
				Inner I	161 ± 5	c		
				Inner II	173 ± 5	bc		
			Wheat/pea	Border	186 ± 8	bc		
				Inner I	161 ± 6	bc		*P*-value
				Inner II	153 ± 6	c	Treatment	0.000
		2019	Monocrop	-	206 ± 9	b	Year	0.061
			Maize/wheat	Border	282 ± 7	a	Treatment × Year	0.000
				Inner I	169 ± 17	c		
				Inner II	193 ± 5	bc		
			Faba/wheat	Border	174 ± 7	bc		
				Inner I	163 ± 5	c		
				Inner II	180 ± 5	bc		
			Wheat/pea	Border	250 ± 16	a		
				Inner I	181 ± 4	bc		
				Inner II	199 ± 6	bc		
	Harvest index	2018	Monocrop	-	0.502 ± 0.004	ad		
			Maize/wheat	Border	0.444 ± 0.005	bcefghij		
				Inner I	0.479 ± 0.002	abcdefghij		
				Inner II	0.484 ± 0.002	abcdefghij		
			Faba/wheat	Border	0.370 ± 0.022	klmno		
				Inner I	0.431 ± 0.016	cfhjklmn		
				Inner II	0.427 ± 0.022	cfhjklmno		
			Wheat/pea	Border	0.453 ± 0.009	bcefghij		
				Inner I	0.494 ± 0.009	abdegi		*P*-value
				Inner II	0.505 ± 0.008	abde	Treatment	0.000
		2019	Monocrop	-	0.480 ± 0.006	abck	Year	0.382
			Maize/wheat	Border	0.410 ± 0.008	defghijlmn	Treatment × Year	0.085
				Inner I	0.498 ± 0.038	abc		
				Inner II	0.468 ± 0.007	abcdefghklm		
			Faba/wheat	Border	0.324 ± 0.035	o		
				Inner I	0.391 ± 0.023	ijno		
				Inner II	0.398 ± 0.021	ghijmno		
			Wheat/pea	Border	0.480 ± 0.013	abcdefkl		
				Inner I	0.496 ± 0.004	abc		
				Inner II	0.493 ± 0.005	abc		

Table S2.7 (continued) Comparisons of grain yield, vegetative biomass, and harvest index per meter row. Shared letters denote non-significant differences between 'Treatment_Row_Year ' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(iii) Faba bean

Species		Year	Treatment	Row	Mean ± Standard error	Comparison		
Faba	Grain yield (g m^{-1})	2018	Monocrop	-	154 ± 3	e		
			Maize/faba	Border	224 ± 9	abc		
				Inner I	209 ± 8	bcd		
				Inner II	180 ± 8	bcde		
			Faba/wheat	Border	181 ± 9	bcde		
				Inner I	175 ± 13	cde		
				Inner II	174 ± 9	cde		
			Faba/pea	Border	204 ± 9	bcd		
				Inner I	183 ± 9	bcde		*P*-value
				Inner II	159 ± 7	de	Treatment	0.000
		2019	Monocrop	-	171 ± 6	de	Year	0.058
			Maize/faba	Border	240 ± 23	ab	Treatment × Year	0.000
				Inner I	210 ± 17	bcde		
				Inner II	204 ± 22	bcde		
			Faba/wheat	Border	283 ± 22	a		
				Inner I	190 ± 12	bcde		
				Inner II	160 ± 10	de		
			Faba/pea	Border	225 ± 27	abc		
				Inner I	189 ± 15	bcde		
				Inner II	164 ± 13	cde		
	Vegetative biomass (gm^{-1})	2018	Monocrop	-	115 ± 3	g		
			Maize/faba	Border	156 ± 14	cdef		
				Inner I	141 ± 5	cdefg		
				Inner II	124 ± 6	fg		
			Faba/wheat	Border	121 ± 5	fg		
				Inner I	124 ± 9	fg		*P*-value
				Inner II	125 ± 6	efg	Treatment	0.000
			Faba/pea	Border	137 ± 7	defg	Year	0.001
				Inner I	136 ± 7	defg	Treatment × Year	0.002
				Inner II	123 ± 7	fg		
		2019	Monocrop	-	174 ± 4	cde		
			Maize/faba	Border	244 ± 17	a		
				Inner I	194 ± 15	abc		
				Inner II	185 ± 17	bcd		
			Faba/wheat	Border	231 ± 14	ab		
				Inner I	174 ± 10	cdef		
				Inner II	158 ± 9	cdefg		
			Faba/pea	Border	196 ± 23	abc		
				Inner I	181 ± 14	bcde		
				Inner II	161 ± 10	cdefg		
	Harvest index	2018	Monocrop	-	0.574 ± 0.003	abcd		
			Maize/faba	Border	0.596 ± 0.025	ab		
				Inner I	0.596 ± 0.004	ab		
				Inner II	0.592 ± 0.004	ab		
			Faba/wheat	Border	0.599 ± 0.004	a		
				Inner I	0.585 ± 0.003	abc		
				Inner II	0.582 ± 0.005	abcd		
			Faba/pea	Border	0.600 ± 0.005	a		
				Inner I	0.574 ± 0.005	abcde		*P*-value
				Inner II	0.566 ± 0.005	abcdef	Treatment	0.000
		2019	Monocrop	-	0.494 ± 0.005	g	Year	0.001
			Maize/faba	Border	0.492 ± 0.017	g	Treatment × Year	0.199
				Inner I	0.518 ± 0.013	defg		
				Inner II	0.520 ± 0.013	defg		
			Faba/wheat	Border	0.549 ± 0.005	abcdef		
				Inner I	0.522 ± 0.014	cdefg		
				Inner II	0.501 ± 0.007	fg		
			Faba/pea	Border	0.533 ± 0.011	bcdefg		
				Inner I	0.509 ± 0.011	efg		
				Inner II	0.501 ± 0.010	fg		

Table S2.7 (continued) Comparisons of grain yield, vegetative biomass, and harvest index per meter row. Shared letters denote non-significant differences between 'Treatment_Row_Year ' combinations (Tukey's Post-Hoc Test, $P \leq 0.05$).

(iv) Pea

Species		Year	Treatment	Row	Mean ± Standard error	Comparison		
Pea	Grain yield (g m^{-1})	2018	Monocrop	-	146 ± 3	abcde		
			Maize/pea	Border	172 ± 18	ac		
				Inner I	144 ± 7	abcdef		
				Inner II	129 ± 6	abcdefgh		
			Faba/pea	Border	88 ± 8	ghi		
				Inner I	105 ± 7	defghi		
				Inner II	121 ± 6	bdefgh		
			Wheat/pea	Border	128 ± 9	abcdefgh		
				Inner I	140 ± 6	abcdef		*P*-value
				Inner II	136 ± 4	abcdefg	Treatment	0.000
		2019	Monocrop	-	150 ± 5	abcd	Year	0.041
			Maize/pea	Border	182 ± 31	ab	Treatment × Year	0.029
				Inner I	95 ± 14	efghi		
				Inner II	87 ± 15	fghi		
			Faba/pea	Border	56 ± 16	i		
				Inner I	70 ± 8	hi		
				Inner II	84 ± 13	fghi		
			Wheat/pea	Border	121 ± 24	abcdefgh		
				Inner I	119 ± 18	cdefgh		
				Inner II	117 ± 10	cdefghi		
	Vegetative biomass (g m^{-1})	2018	Monocrop	-	133 ± 3	bc		
			Maize/pea	Border	159 ± 9	b		
				Inner I	139 ± 6	bc		
				Inner II	121 ± 5	bc		
			Faba/pea	Border	131 ± 12	bc		
				Inner I	123 ± 9	bc		
				Inner II	129 ± 6	bc		
			Wheat/pea	Border	113 ± 6	c		
				Inner I	120 ± 5	bc		*P*-value
				Inner II	117 ± 4	c	Treatment	0.000
		2019	Monocrop	-	145 ± 4	bc	Year	0.137
			Maize/pea	Border	212 ± 26	a	Treatment × Year	0.001
				Inner I	127 ± 8	bc		
				Inner II	106 ± 11	c		
			Faba/pea	Border	125 ± 13	bc		
				Inner I	111 ± 8	c		
				Inner II	115 ± 11	bc		
			Wheat/pea	Border	143 ± 14	bc		
				Inner I	129 ± 12	bc		
				Inner II	137 ± 10	bc		
	Harvest index	2018	Monocrop	-	0.525 ± 0.004	a		
			Maize/pea	Border	0.509 ± 0.017	abc		
				Inner I	0.509 ± 0.005	abc		
				Inner II	0.516 ± 0.004	abc		
			Faba/pea	Border	0.403 ± 0.024	d		
				Inner I	0.460 ± 0.012	abcd		
				Inner II	0.484 ± 0.009	abcd		
			Wheat/pea	Border	0.529 ± 0.009	ab		
				Inner I	0.539 ± 0.005	a		*P*-value
				Inner II	0.537 ± 0.005	a	Treatment	0.000
		2019	Monocrop	-	0.508 ± 0.003	ab	Year	0.001
			Maize/pea	Border	0.439 ± 0.075	abcd	Treatment × Year	0.040
				Inner I	0.414 ± 0.033	bcd		
				Inner II	0.438 ± 0.025	abcd		
			Faba/pea	Border	0.280 ± 0.039	e		
				Inner I	0.380 ± 0.020	de		
				Inner II	0.410 ± 0.017	bcd		
			Wheat/pea	Border	0.407 ± 0.053	cd		
				Inner I	0.433 ± 0.058	abcd		
				Inner II	0.458 ± 0.007	abcd		

Supplementary information for Chapter 3

On the relationship between light capture and yield components in strip intercropping

Supplementary methods

Method S3.1 Light measurements on selected days for verifying the light capture model.

Method S3.2 Principles of the model for light capture in strip canopies according to Gou et al. (2017).

Method S3.3 Plant selections for measuring plant heights of maize, wheat, faba bean, and pea in 2018 and 2019.

Method S3.4 Method for measuring LAI in 2018 and 2019 as an input of the light capture model.

Supplementary results

Fig. S3.1 Fitting Lambert-Beer's Law using the measured fraction of captured PAR (f_{cap}) in the monocrops to obtain the light extinction coefficient (k) per species.

Fig. S3.2 Linear interpolations of the LAI per species strip and the plant height; the simulated cumulative PAR captured per species strip per species.

Fig. S3.3 Relationships between thousand-grain weight and total grain number per species.

Fig. S3.4 Comparisons between treatments of total grain number, thousand-grain weight, and grain yield per species.

Fig. S3.5 Comparisons between treatments of the yield components determining total grain number per species.

Fig. S3.6 Validation of the light capture model by comparing the fractions of captured PAR (f_{cap}) measured in the field and estimated by the model.

Fig. S3.7 The reference evapotranspiration (ET0) and total water supply (precipitation + irrigation) in 2018 and 2019.

Table S3.1 Cumulative PAR captured per unit area of the species strip throughout the season, before and during grain filling per species.

Table S3.2 Marginal R^2 and R^2 for the random block effect of the relationships between yield components and the cumulative PAR captured.

Table S3.3 Model comparison outputs for the relationships of LER ~ LCER.

Supplementary methods

Method S3.1 Light measurements on selected days for verifying the light capture model.

Incident and transmitted PAR were measured in intercrops and monocrops using an SS1 SunScan Canopy Analysis System (Delta-T Devices Ltd, UK). Measurements were conducted in one whole three-metre-wide intercrop strip (comprising two adjacent 1.5 m-wide species strips) in the centre of each intercrop plot, and one 1.5 m-wide strip in the centre of each monocrop plot.

In 2018, the one-metre-long probe was placed parallel to the row direction to measure transmitted PAR ($\mathrm{PAR_{trans}}$) on the ground across the entire 3 m width of an intercrop strip (Fig. 3.2 a). The probe was placed parallel to the row direction to measure $\mathrm{PAR_{trans}}$ between or next to the plant rows (the orange square represents the cross section of the probe).

In 2019, the probe was placed perpendicular to the row direction (Fig. 3.2 b). $\mathrm{PAR_{trans}}$ was measured approximately every 20 cm along the row direction, five times in each species strip. The orange bar represents the probe, and the trapezoidal represents the probe handle. Measurements were done such that the observer held the handle and let the probe tip reach the strip edge.

In both years, a Beam Fraction sensor (BFS) was placed on a tripod at a similar height as the top of the canopy to measure incident PAR ($\mathrm{PAR_{in}}$) simultaneously with $\mathrm{PAR_{trans}}$. Measurements were taken from one hour before till one hour after solar noon, and they were taken weekly before flowering and bi-weekly thereafter. As the probe and BFS differed in their measuring of solar radiation because of the optical structures, before the measurement in each plot, the probe was placed alongside the BFS and one reading was taken to calibrate measurements for each plot. All measurements were taken either with fully clear or fully overcast sky.

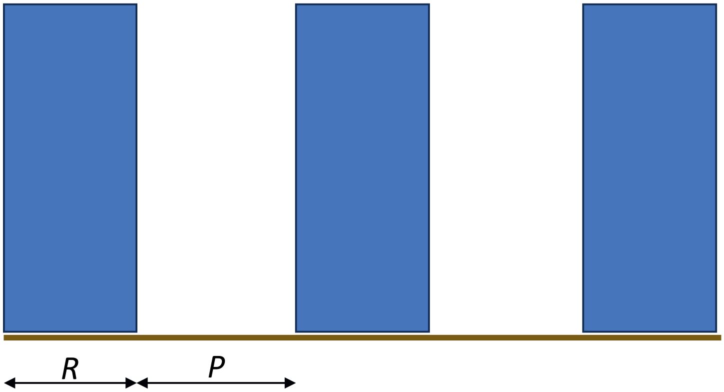
The average of all readings was taken as the $\mathrm{PAR_{trans}}$ of the intercrop or monocrop in this plot. The fractions of transmitted (f_{trans}) and captured (f_{cap}) PAR of the canopy were calculated as:

$$f_{\mathrm{cap}} = 1 - f_{\mathrm{trans}} = 1 - \frac{\mathrm{PAR_{trans}}}{\mathrm{PAR_{in}}} \qquad \text{(Eq. S3.1)}$$

Method S3.2 Principles of the model for light capture in strip canopies according to Gou et al. (2017).

Method S3.2.1 Light capture fraction of a strip crop canopy f_{strip}

A strip crop is characterised by strips of a single species with a strip width (*R*) alternating with a path with a width (*P*) where the path may be occupied by another species or not:



A strip crop comprising three strips and two paths. The strips have a width of R, and the paths have a width of P. For a strip monocrop, the paths are vacant. For a strip intercrop, the paths are occupied by a second species, i.e., the path width for species 1 is the strip width for species 2.

Considering the leaf area remains unchanged on the whole system level, light capture of a strip crop is lower than that of a homogenous canopy in which the leaves cover the entire land (Jackson and Palmer, 1979), whereas it is higher than that of a fully 'compressed' canopy in which the leaves are compressed to one side of the land, leaving no border rows to capture light as they do in the strip crop (Gou et al., 2017). Therefore, light capture fraction of the strip crop f_{strip} is calculated as the weighted average of the fractions of the homogenous canopy f_{homo} and the compressed canopy f_{compr} (Pronk et al., 2003):

$$f_{\mathrm{strip}} = f_{\mathrm{homo}} \times (1 - w) + f_{\mathrm{compr}} \times w \qquad \text{(Eq. S3.2)}$$

where f_{homo} is the light capture fraction of the homogeneous canopy calculated by Lamert-Beer's Law, f_{compr} is the light capture fraction of the compressed canopy, and w is a weight factor.

To calculate f_{compr}, LAI of the compressed canopy $\text{LAI}_{\text{compr}}$ is calculated. The compressed canopy has a bigger LAI than the whole system because the leaves that are originally distributed on a $R + P$ wide area are now compressed to a R wide area:

$$\text{LAI}_{\text{compr}} = \text{LAI} \times \frac{R+P}{R} \qquad \text{(Eq. S3.3)}$$

Therefore, f_{compr} is calculated on the whole system level as:

$$f_{\text{compr}} = \left(1 - e^{-k \times \text{LAI}_{\text{compr}}}\right) \times \frac{R}{R+P} \qquad \text{(Eq. S3.4)}$$

where the element in parentheses is the local light capture faction within the compressed canopy, and $\frac{R}{R+P}$ is used to convert the faction to the whole system, as leaves cover only this proportion of the land.

w is calculated as:

$$w = \frac{SP - SR}{1 - e^{-k \times \text{LAI}_{\text{compr}}}} \qquad \text{(Eq. S3.5)}$$

where SP and SR are the fractions of transmitted light onto the soil in the path and underneath the strip. w is used to capture how the strip crop is different from the homogenous and the compressed canopy: with $SP - SR = 0$, the strip crop is homogeneous, whereas with $SP - SR = 1 - e^{-k \times \text{LAI}_{\text{compr}}}$, the strip crop is fully compressed.

SP and SR are calculated by considering the origins of the transmitted light. SP consists of the light transmitted from right above the path and through the neighbouring strips. SR consists of the light transmitted through the strip and the neighbouring paths; see Eqs A6–A9 in Gou et al. (2017).

Method S3.2.2 Light capture fraction of a strip intercrop canopy

In strip intercropping, during the sole-growth period, when only one species is grown in the field, Eq. S3.2 is used to calculate its light capture fraction with the intermediate variables calculated by Eqs S3.3−S3.5.

During the co-growth period, when one species is taller than the other, the intercrop canopy is sectioned into two layers: an upper layer between the tops of the taller and the shorter species, and a lower layer consisting of the alternating strips of the two species with the height from the soil up to the top of the shorter species.

Light capture fraction of the taller species (f_{taller}) consists of two elements:

$$f_{\text{taller}} = f_{\text{taller, upper}} + f_{\text{taller, lower}} \qquad \text{(Eq. S3.6)}$$

where $f_{\text{taller, upper}}$ and $f_{\text{taller, lower}}$ are the fractions of light captured by the upper and lower layers of the taller species.

The upper layer of the taller species is a strip crop canopy with its height the same as the height difference between the taller and shorter species $H_{\text{difference}}$, and its leaf area index $LAI_{\text{taller, upper}}$ proportional to the total LAI of the taller species, assuming that the leaves are homogenously distributed along the height; see Eq. 1 in Gou et al. (2017). Therefore, $f_{\text{taller, upper}}$ is calculated using Eq. S3.2 with $H_{\text{difference}}$ and $LAI_{\text{taller, upper}}$ as inputs to calculate the intermediate variables in Eqs S3.3−S3.5; see Eqs A10−A19 in Gou et al. (2017).

The lower layer of the taller species is a compressed canopy because it has no border rows, as the shorter species occupies the adjacent path. It has the same height as the shorter species H_{shorter} and the leaf area index $LAI_{\text{taller, lower}}$ proportional to the total LAI of the taller species, assuming the LAI is homogeneously distributed along the plant height. Therefore, $f_{\text{taller, lower}}$ is calculated using Eq. S3.4 with H_{shorter} and $LAI_{\text{taller, lower}}$ as inputs, considering that the incident light is the light transmitted from the upper layer; see Eq. 5 in Gou et al. (2017).

The shorter species has a compressed canopy. Eq. S3.4 is used to calculate the light capture fraction with its height H_{shorter} and leaf area index LAI_{shorter} as inputs, considering that the incident light is the light transmitted through and between the taller species.

During the co-growth period, when the two species have the same height. Both species are considered to have a compressed canopy. Eq. S3.4 calculates the light capture fraction with the corresponding plant height and LAI as inputs.

Method S3.3 Plant selections for measuring plant heights of maize, wheat, faba bean, and pea in 2018 and 2019. DOY indicates day of the year in the Julian calendar.

Year	Species	DOY	Methods
2018	Maize	164, 171, 179, 185, 192, and 200	Three maize plants in each intercrop plot were selected. In each plot, one plant from each row in one maize strip was selected. The measurements were made in six blocks.
	Wheat/ Faba bean/Pea	129, 144, and 164	Six plants in each intercrop plot were selected. In each plot, one plant from each row in one species strip was selected. The measurements were made in six blocks.
	Wheat/Faba bean	177	Three plants in each intercrop plot were selected. In each plot, one plant from one border row (row 1 of the strip), the adjacent inner row I (row 2 of the strip), and the adjacent inner row II (row 3 of the strip) was selected. The measurements were made in three blocks.
	Pea	179	
2019	Maize	165	Three maize plants in each intercrop plot were selected. In each plot, one plant from each row in one maize strip was selected. The measurements were made in four blocks.
		190, 204	Two maize plants in each intercrop plot were selected. In each plot, one plant from one border row and one from the inner row of one maize strip were selected. The measurements were made in four blocks.
		220	Fifteen maize plants in each intercrop plot were selected. In each plot, five plants from each row in one maize strip were selected. The measurements were made in four blocks.
	Wheat/Faba bean	140, 155, and 176	Three plants in each intercrop plot were selected. In each plot, one plant from one border row (row 1 of the strip), the adjacent inner row I (row 2 of the strip), and the adjacent inner row II (row 3 of the strip) was selected. The measurements were made in four blocks.
	Pea	140, 155	
	Wheat/Faba bean	189	Six plants in each intercrop plot were selected. In each plot, one plant from each row in one species strip was selected. The measurements were made in four blocks.
	Pea		One plant in each intercrop plot were selected. In each plot, one plant from the border row in one species strip was selected. The measurements were made in four blocks. The measurement was only made on the border row due to lodging.

Method S3.4 Method for measuring LAI in 2018 and 2019 as an input of the light capture model. DOY indicates day of the year in the Julian calendar.

Year	Species	DOY	Harvesting	Processing
2018	Maize	155	Six blocks were classified as three meta blocks (meta block 1: blocks 1 and 2; meta block 2: blocks 3 and 4; meta block 3: blocks 5 and 6). Two adjacent intercrop strips of each intercrop plot and two adjacent species strips of each monocrop plot in each meta block were chosen to harvest. The Plants within 2 m were harvested.	1. The weight of harvested plants was taken for each sample. 2. A subsample of at least five plants for maize, and ten plants for the other three species was randomly taken and weighed. 3. Leaves were disassembled and taken the weight. Leaf area was measured using a leaf meter (LI-3100 Area Meter, LI-COR Inc., United States), and then converted to the leaf area of each sample by weight. 4. LAI on the species strip and system areas were calculated.
		197	Six blocks were classified as three meta blocks (meta block 1: blocks 1 and 2; meta block 2: blocks 3 and 4; meta block 3: blocks 5 and 6). Two adjacent intercrop strips of each intercrop plot and two adjacent species strips of each monocrop plot in each meta block were chosen to harvest. The plants within 1.5 m were harvested.	
	Wheat/ Faba bean/Pea	155	Six blocks were classified as three meta blocks (meta block 1: blocks 1 and 2; meta block 2: blocks 3 and 4; meta block 3: blocks 5 and 6). Two adjacent intercrop strips of each intercrop plot and two adjacent species strips of each monocrop plot in each meta block were chosen to harvest. The plants within 1 m were harvested.	
2019	Maize	168, 182, 196, and 234	One intercrop strip of each intercrop plot and one species strip of each monocrop plot in each block were chosen to harvest. The plants within 1.6 m were harvested. The harvests were conducted in all four blocks.	
	Wheat/ Faba bean/Pea	133, 147, 168, 182, and 196		

Supplementary results

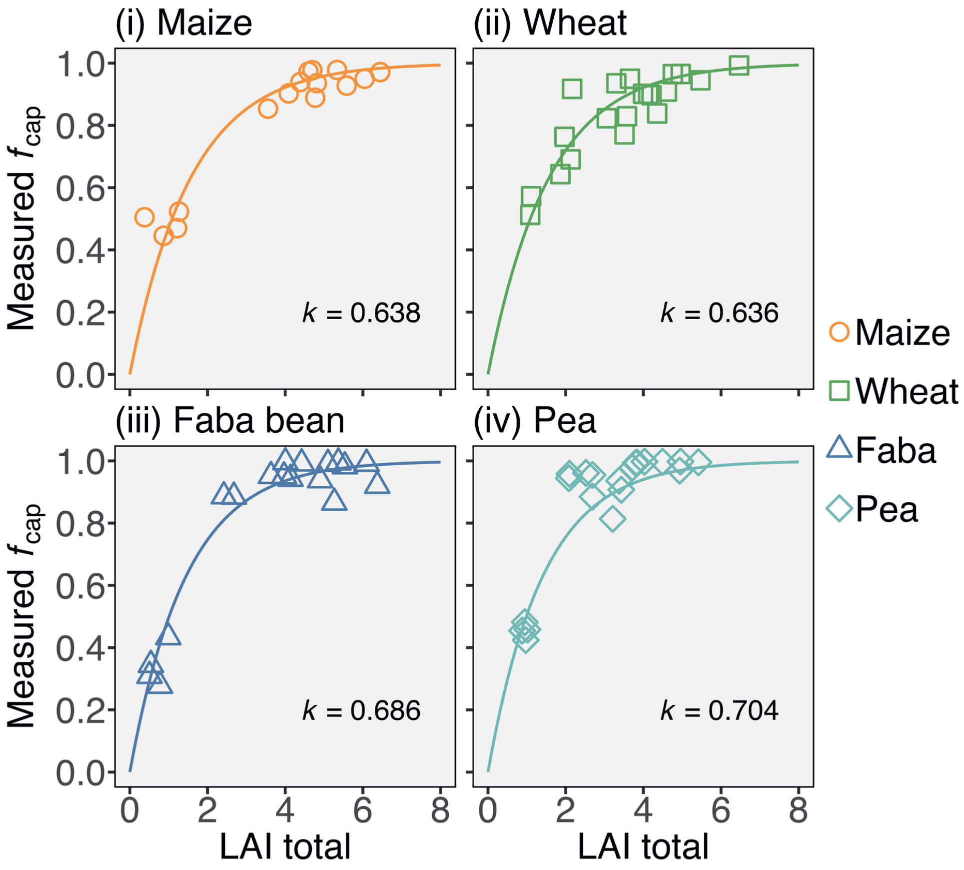


Fig. S3.1 Fitting Lambert-Beer's Law using the measured fraction of captured PAR (f_{cap}) in the monocrops of maize (i), wheat (ii), and faba bean (iii), and pea (iv) in 2019 to obtain the light extinction coefficients (k). Fitting was conducted using data from the monocrop of each species to obtain a light extinction coefficient as one of the inputs for light modelling for both the monocrop and intercrops. LAI total was the total LAI including green and yellow leaves as the measured f_{cap} was resulted from the whole canopy.

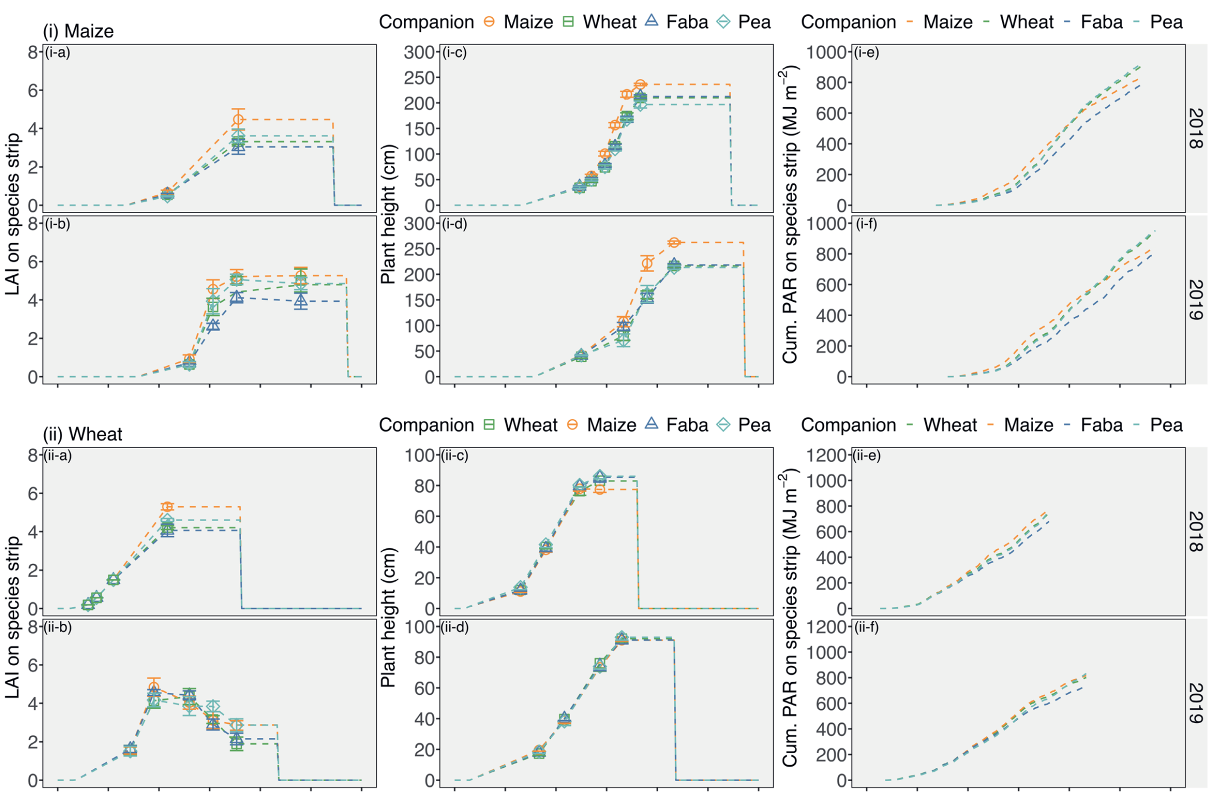


Fig. S3.2 Linear interpolations of the LAI per species strip (a, b) and the plant height (c, d); the simulated cumulative PAR captured per species strip (e, f) of maize (i), wheat (ii), faba bean (iii), and pea (iv). The dashed lines of LAI and plant height are the daily values that were linearly interpolated by the field measurements (the points). Different colours and symbols indicate that the focal species were combined with different companion species: maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond). Error bars represent standard errors of the means of field measurements. From the dates of the final measurements of LAI and plant height, the interpolations were kept as the values of the measurements. In simulation, the LAI of a species in the intercrops were expressed on the system level as one of the inputs. The LAI of green leaves was used for interpolation and modelling. Leaves with more than half of their area green were considered green leaves.

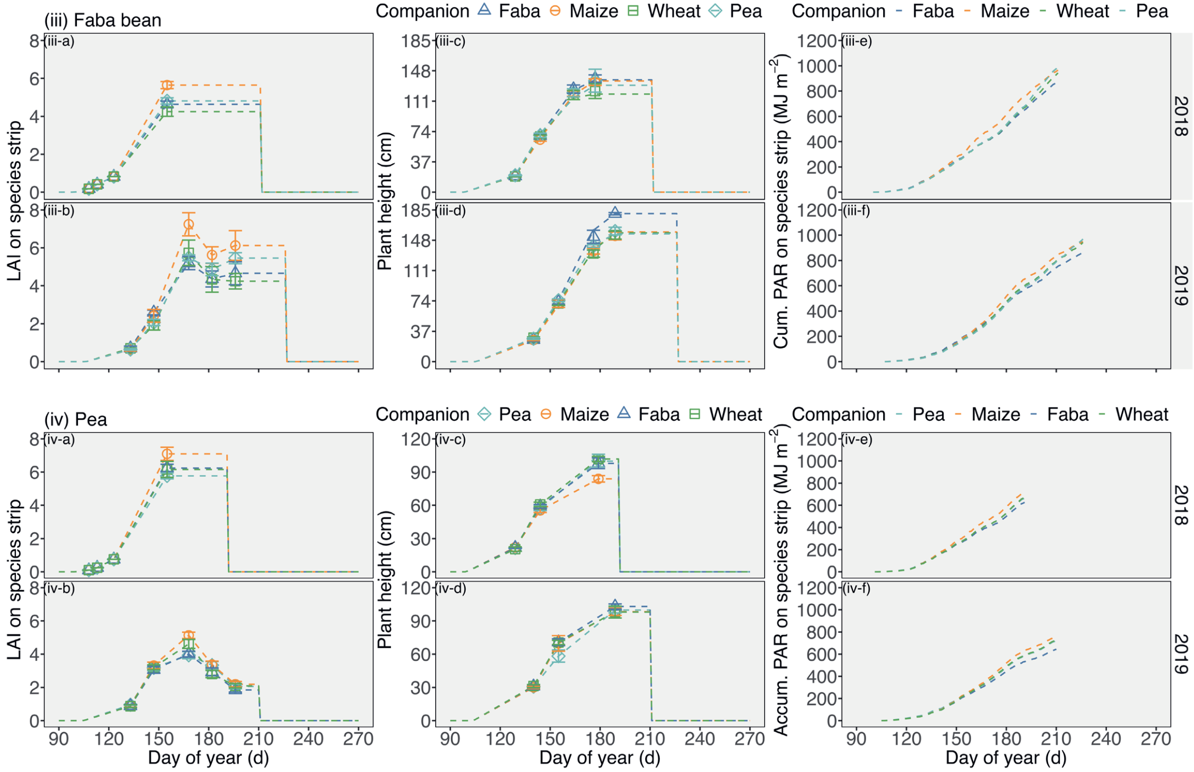


Fig. S3.2 (continued) Linear interpolations of the LAI per species strip (a, b) and the plant height (c, d); the simulated cumulative PAR captured per species strip (e, f) of maize (i), wheat (ii), faba bean (iii), and pea (iv). The dashed lines of LAI and plant height are the daily values that were linearly interpolated by the field measurements (the points). Different colours and symbols indicate that the focal species were combined with different companion species: maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond). Error bars represent standard errors of the means of field measurements. From the dates of the final measurements of LAI and plant height, the interpolations were kept as the values of the measurements. In simulation, the LAI of a species in the intercrops were expressed on the system level as one of the inputs. The LAI of green leaves was used for interpolation and modelling. Leaves with more than half of their area green were considered green leaves.

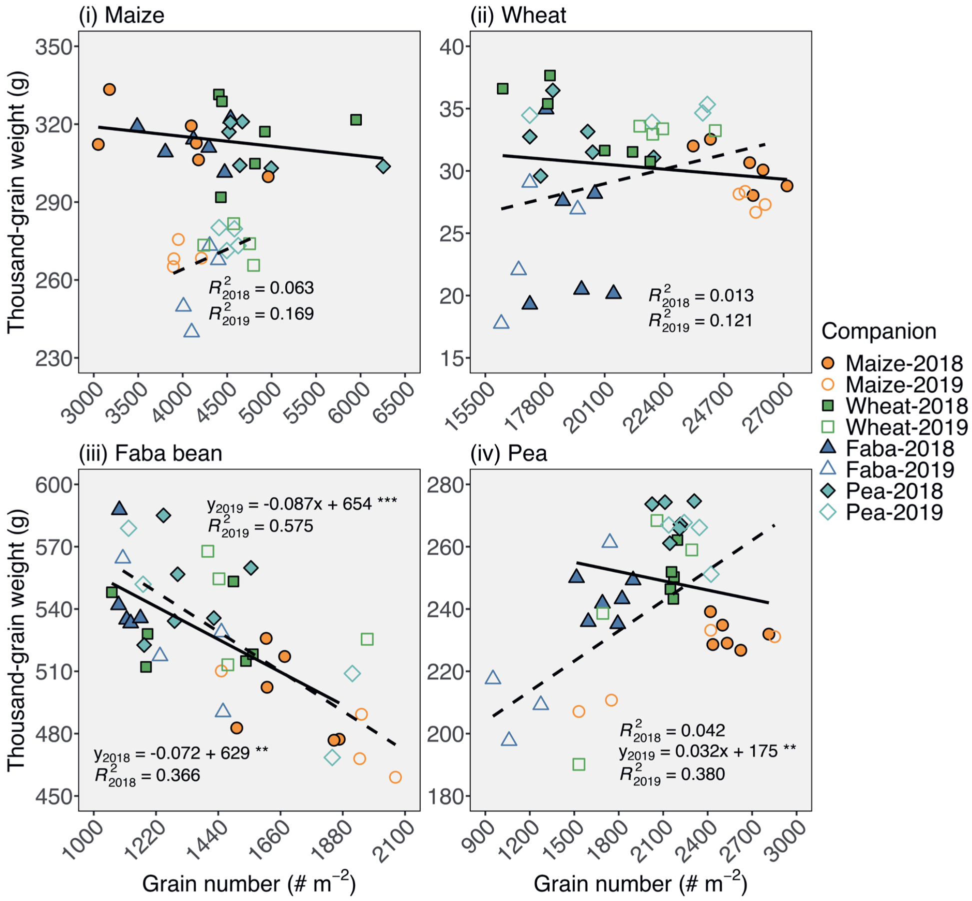


Fig. S3.3 Relationships between thousand-grain weight and grain number per unit land area of maize (i), wheat (ii), faba bean (iii), and pea (iv). Different symbols indicate that the focal species was combined with different companion species: maize (orange circle), wheat (grain square), faba bean (blue triangle), and pea (cyan diamond). Data collated in 2018 and 2019 are indicated as filled and open symbols. 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.

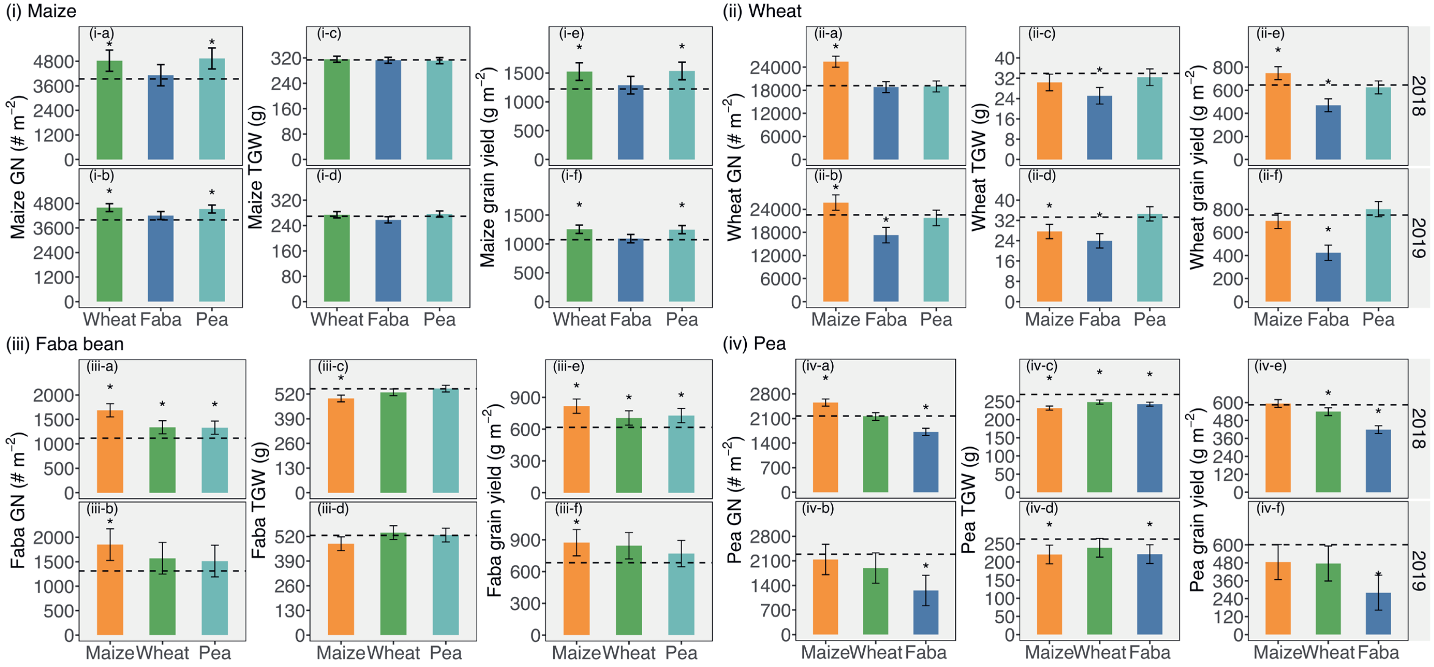


Fig. S3.4 Grain number per unit land area (GN) (a, b), thousand-grain weight (TGW) (c, d), and grain yield (e, f) of maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a, c, and e) and 2019 (b, d, and f). GN and grain yield are expressed per unit area of the species strip. The coloured bars represent the grain yield or yield components of the focal species when they were combined with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). The dashed lines represent the relevant variables of the focal species in monocrops. An Asterisk denotes significant difference between an intercrop and the monocrop. Error bars represent the 95% confidence intervals of the means.

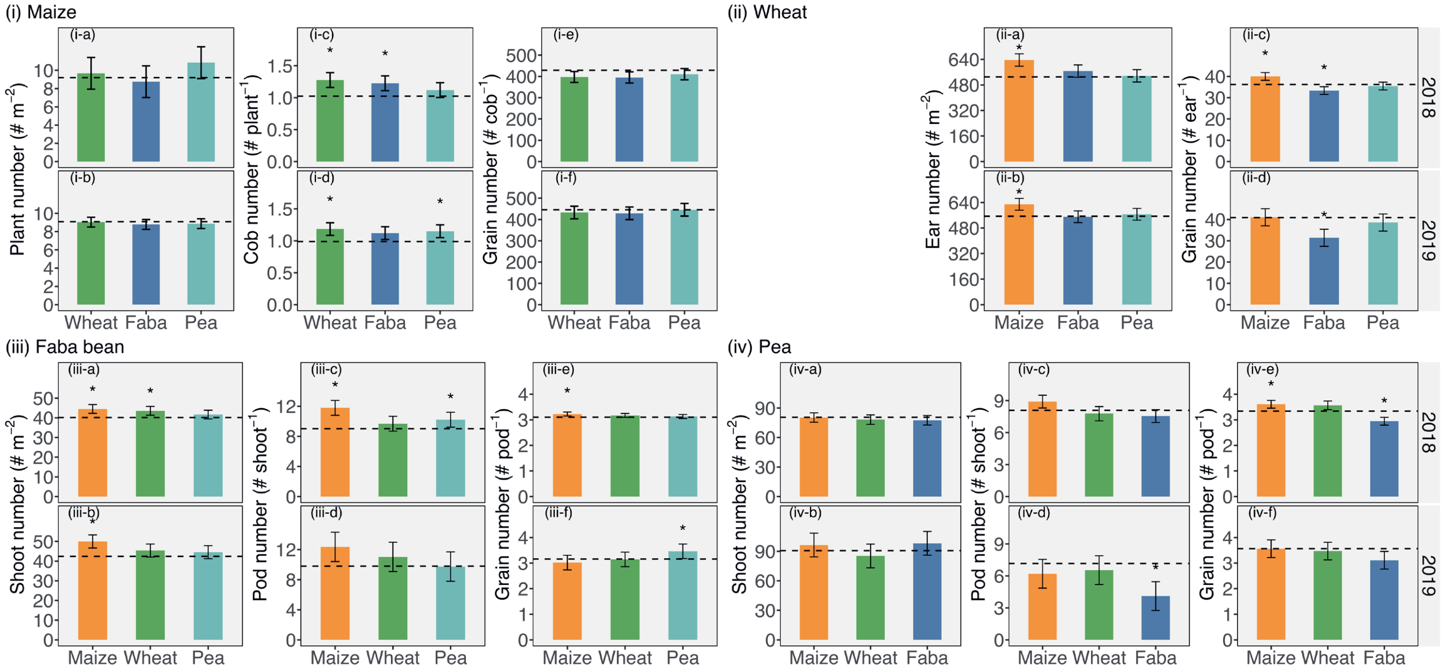


Fig. S3.5 Yield components determining the grain number per unit area of the species strip. The coloured bars represent the yield components of the focal species when they were combined with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). The dashed lines represent the metric value for the focal species in monocrops. An Asterisk denotes significant difference between an intercrop and the monocrop. Error bars represent the 95% confidence intervals of the means.

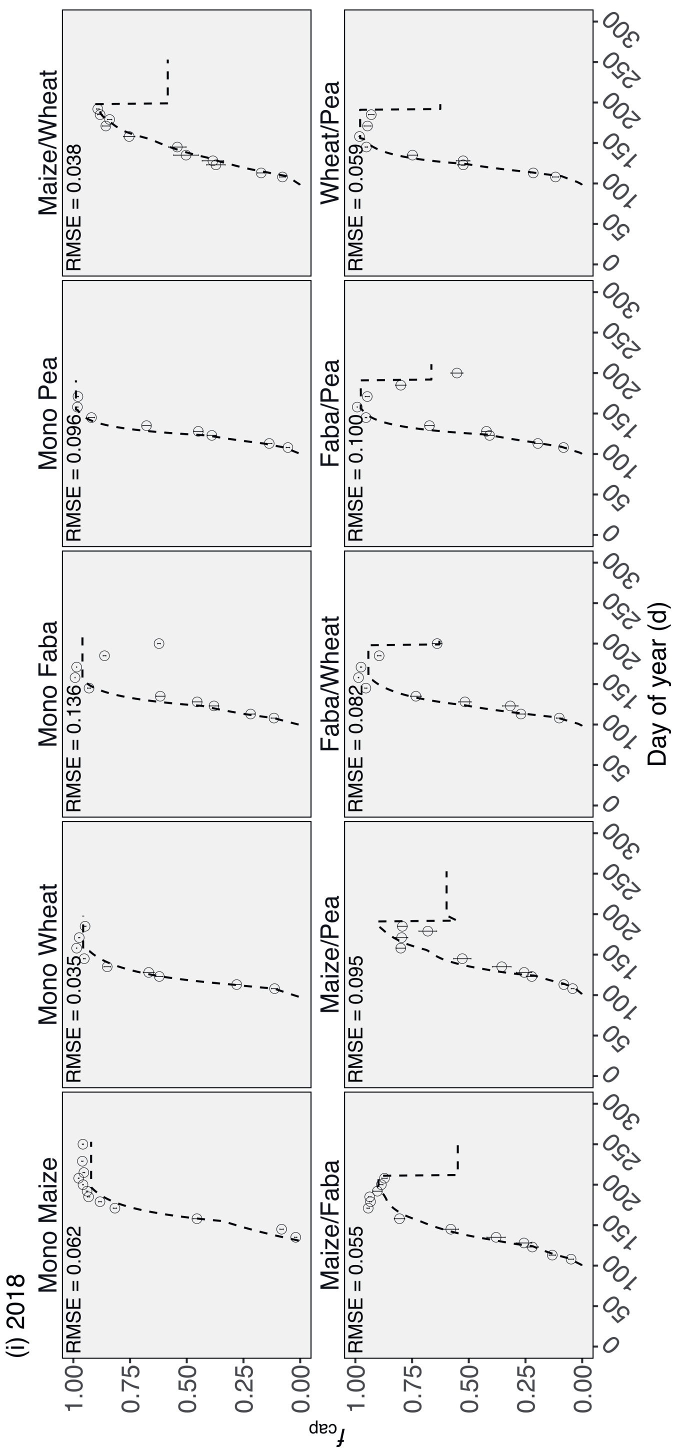


Fig. S3.6 Validation of the light capture model by comparing the fractions of captured PAR (f_{cap}) measured in the field (circle) and estimated by the model (dashed line).

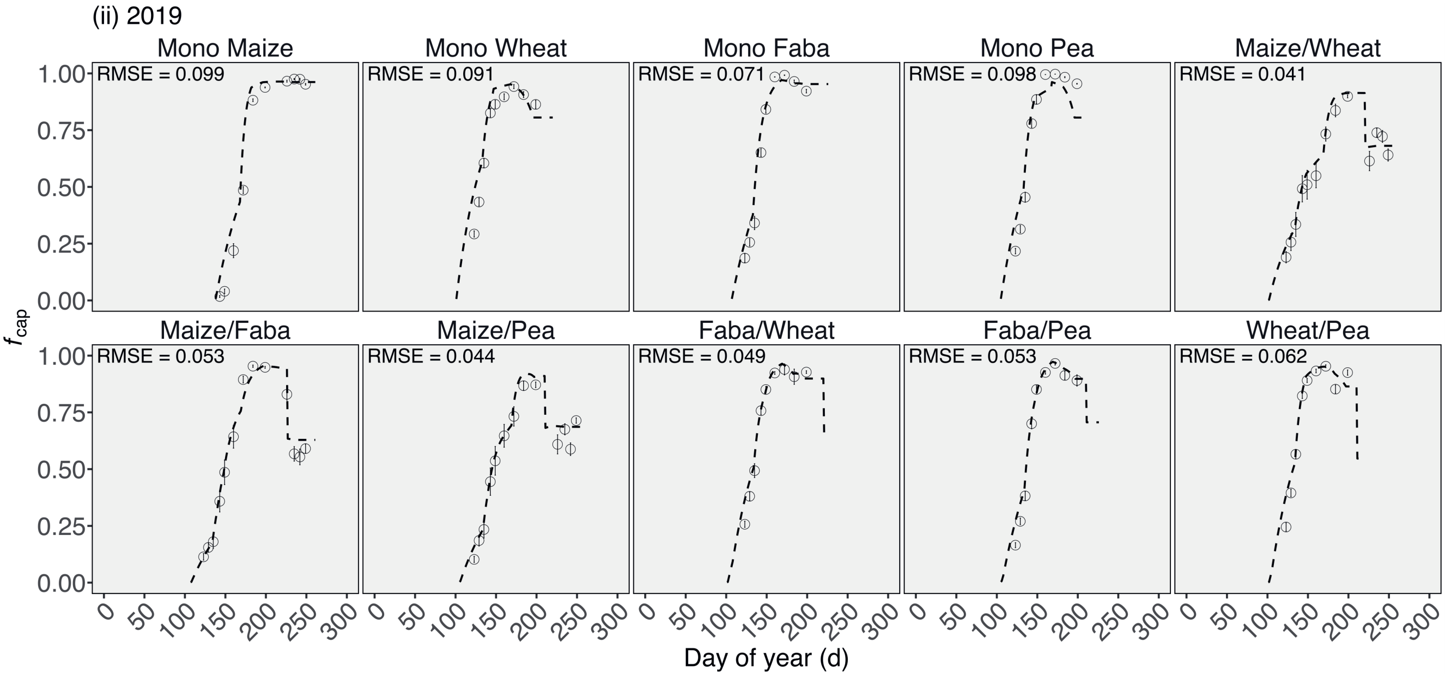


Fig. S3.6 (continued) Validation of the light capture model by comparing the fractions of captured PAR (f_{cap}) measured in the field (circle) and estimated by the model (dashed line).

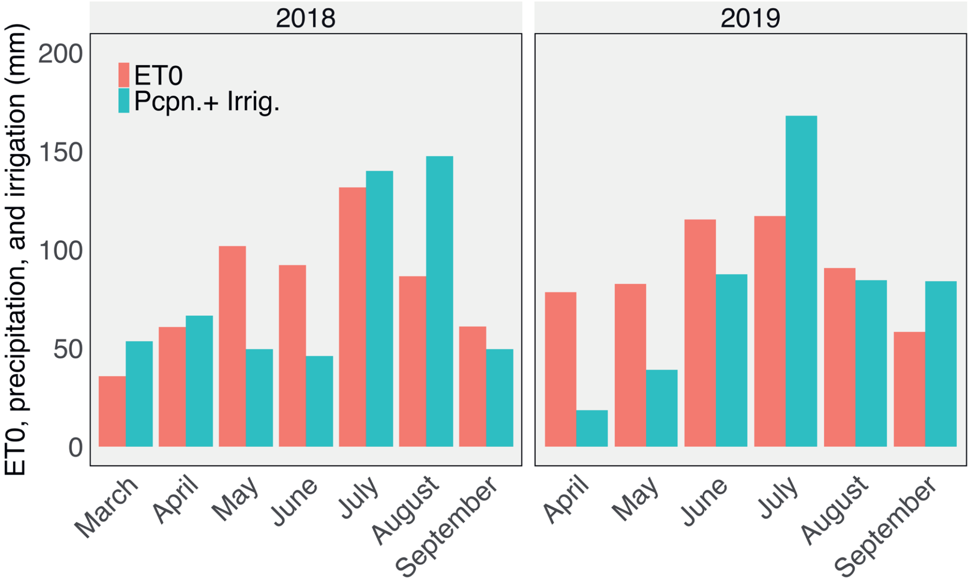


Fig. S3.7 The reference evapotranspiration (ET0) and total water supply (precipitation + irrigation) in 2018 and 2019. A higher ET0 than the total water supply indicates a possible water deficit in the experiment.

Table S3.1 Cumulative PAR captured per unit area of the species strip of maize (i), wheat (ii), faba bean (iii), and pea (iv) during the whole growth season, before and during grain filling. Asterisks denote significant differences between the intercrops and the monocrop for a focal species (Fisher's LSD): $P \leq 0.001$: ***, $P \leq 0.01$: **, $P \leq 0.05$: *, $P \leq 0.1$: (.).

(i) Maize

Year	Companion	Cum. PAR before grain fill. (MJ m^{-2})	Cum. PAR during grain fill. (MJ m^{-2})	Cum. PAR total (MJ m^{-2})
2018	Maize	512 ± 13	321 ± 9.5	833 ± 20
	Wheat	500 ± 11	406 ± 8.9 ***	906 ± 18 *
	Faba	411 ± 25 ***	376 ± 24 **	787 ± 49
	Pea	508 ± 25	415 ± 19 ***	923 ± 44 **
2019	Maize	408 ± 22	432 ± 2.7	840 ± 21
	Wheat	362 ± 23 *	578 ± 19 ***	939 ± 32 *
	Faba	295 ± 12 ***	509 ± 22 **	805 ± 28
	Pea	352 ± 23 *	600 ± 15 ***	952 ± 30 **

Table S3.1 (continued) Cumulative PAR captured per unit area of the species strip of maize (i), wheat (ii), faba bean (iii), and pea (iv) during the whole growth season, before and during grain filling. Asterisks denote significant differences between the intercrops and the monocrop for a focal species (Fisher's LSD): $P \leq 0.001$: ***, $P \leq 0.01$: **, $P \leq 0.05$: *, $P \leq 0.1$: (.).

(ii) Wheat

Year	Companion	Cum. PAR before grain fill. (MJ m^{-2})	Cum. PAR during grain fill. (MJ m^{-2})	Cum. PAR total (MJ m^{-2})
2018	Wheat	419 ± 1.9	326 ± 1.5	745 ± 3.3
	Maize	458 ± 2.1 ***	314 ± 2.8	772 ± 4.2
	Faba	386 ± 5.5 ***	294 ± 4.3 **	680 ± 9.4 ***
	Pea	411 ± 1.6	348 ± 1.4 *	759 ± 2.8
2019	Wheat	534 ± 21	269 ± 20	802 ± 38
	Maize	546 ± 15	272 ± 17	818 ± 25
	Faba	485 ± 5.9 ***	240 ± 13 *	734 ± 8.1 **
	Pea	505 ± 21 **	328 ± 11 ***	833 ± 30

(iii) Faba bean

Year	Companion	Cum. PAR before grain fill. (MJ m^{-2})	Cum. PAR during grain fill. (MJ m^{-2})	Cum. PAR total (MJ m^{-2})
2018	Faba	412 ± 2.9	465 ± 2.4	877 ±5.4
	Maize	483 ± 3.3 ***	483 ± 8.0	966 ± 11 *
	Wheat	416 ± 7.4	528 ± 12 ***	944 ± 20 *
	Pea	419 ± 4.7	573 ± 11 ***	992 ± 16 *
2019	Faba	482 ± 8.2	382 ± 6.1	864 ± 11
	Maize	546 ± 23 ***	404 ± 14	950 ± 33 ***
	Wheat	500 ± 22	443 ± 7.5 ***	942 ± 20 *
	Pea	484 ± 5.6	485 ± 11 ***	967 ± 8.5 ***

(iv) Pea

Year	Companion	Cum. PAR before grain fill. (MJ m^{-2})	Cum. PAR during grain fill. (MJ m^{-2})	Cum. PAR total (MJ m^{-2})
2018	Pea	272 ± 1.6	392 ± 0.93	665 ± 2.6
	Maize	298 ± 2.3 ***	416 ± 3.4 ***	715 ± 1.6 *
	Faba	264 ± 1.5 (.)	362 ± 7.0 ***	626 ± 6.5 *
	Wheat	271 ± 3.5	400 ± 2.3	671 ± 5.8
2019	Pea	346 ± 3.7	379 ± 7.1	725 ± 8.7
	Maize	367 ± 10 ***	391 ± 9.7 (.)	758 ± 17 **
	Faba	327 ± 7.8 ***	319 ± 1.0 ***	646 ± 7.6 ***
	Wheat	349 ± 6.4	382 ± 4.7	731 ± 10

Table S3.2 Marginal R^2 and R^2 for the random block effect of the relationships between yield components and the cumulative PAR captured during the corresponding growth phases. Marginal R^2 is the R^2 of the relationship without considering the random block effect, which has been presented in Fig. 3.5, and it indicates the proportion of the yield components variances explained by light without considering the inter-block variances. Block R^2 is the R^2 of the relationship only considering the random block effect.

Year	Species	GN ~ Cum. PAR before grain fill.		TGW ~ Cum. PAR during grain fill.	
		Marginal R^2	Block R^2	Marginal R^2	Block R^2
2018	Maize	NA	NA	NA	NA
	Wheat	0.64	0.002	0.277	0.151
	Faba bean	0.652	0.03	0.469	0
	Pea	0.625	0.083	0.037	0
2019	Maize	NA	NA	NA	NA
	Wheat	0.357	0	0.381	0.062
	Faba bean	0.327	0.08	0.644	0
	Pea	0.442	0.039	0.044	0

Table S3.3 Model comparison outputs for the relationships of LER ~ LCER. The model with the lowest AIC value was selected as the optimal model. For the models with AIC values differing less than two, the simpler model was selected to avoid overfitting (Burnham and Anderson, 2004). Therefore, Model 8 is selected.

Model	AIC	BIC	Negative log likelihood	Df
1	–59.399	–51.022	–33.700	4
2	–99.036	–88.564	–54.518	5
3	–58.036	–47.565	–34.018	5
4	–62.322	–51.851	–36.161	5
5	–100.059	–87.493	–56.030	6
6	–66.132	–53.566	–39.066	6
7	–61.174	–48.608	–36.587	6
8	–103.954	–85.105	–60.977	9
9	–102.204	–72.883	–65.102	14

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Supplementary information for Chapter 4

The contribution of border row effects to light capture and light use efficiency in strip intercropping

Supplementary methods

Method S4.1 Principles of the random ray tracing model according to Wang et al. (2017).

Fig. S4.1 Illustration for strip width w_S, designed row width w_R, and hedgerow width w_H.

Fig. S4.2 A hemispherical dome with a radius of r.

Fig. S4.3 Horizontal projections of the 500 random light sources.

Fig. S4.4 Illustration of a beam traversing two hedgerows, adjusted according to Wang et al. (2017).

Fig. S4.5 Illustration of the *xz* cross section of hedgerows, adjusted according to Wang et al. (2017).

Fig. S4.6 Illustration of the cases in which the beam enters and exits hedgerow i from different positions.

Method S4.2 Measurements of leaf area index (LAI) per row.

Method S4.3 Intermediate and final harvest dates.

Table S4.1 Dates of intermediate and final harvests of maize, wheat, faba bean, and pea.

Method S4.4 Measurements of plant height per row.

Table S4.2 Plants selected for measuring plant height per row.

Supplementary results

Fig. S4.7 Measured and interpolated plant height and leaf area index (LAI).

Fig. S4.8 Validating the random ray tracing model by comparing the fractions of PAR captured (f_cap) measured in the field and estimated by the model.

Fig. S4.9 Comparing daily captured PAR of each species on the species strip level in different treatments simulated by the block model of Gou et al. (2017) and by the random ray tracing model.

Fig. S4.10 Above-ground biomass through the growth season of the four species in their monocrop rows.

Fig. S4.11 Daily cumulative PAR captured (Cum. PAR) through the growth season of the four species in their monocrop rows.

Fig. S4.12 Above-ground biomass of inner rows I and II through the growth season of the four species in their intercrops.

Fig. S4.13 Daily cumulative PAR captured (Cum. PAR) of inner rows I and II through the growth season of the four species in their intercrops.

Fig. S4.14 Total cumulative PAR captured (Cum. PAR) in the whole growth season of the four species.

Fig. S4.15 Above-ground biomass, daily cumulative PAR captured (Cum. PAR), and regressions between above-ground biomass and cumulative PAR captured of the four species on the species strip level.

Table S4.3 Model selection outputs for determining light use efficiency (LUE).

Supplementary methods

Method S4.1 Principles of the random ray tracing model according to Wang et al. (2017).

Method S4.1.1 Hedgerow width w_H

In strip cropping, each plant row can be assumed as a hedgerow containing leaves. The width of the hedgerow w_{H}, can be different than the designed row width w_{R}, because of ground cover. Therefore, the light beam traverses the hedgerows and the atmosphere between them (Fig. S4.1).

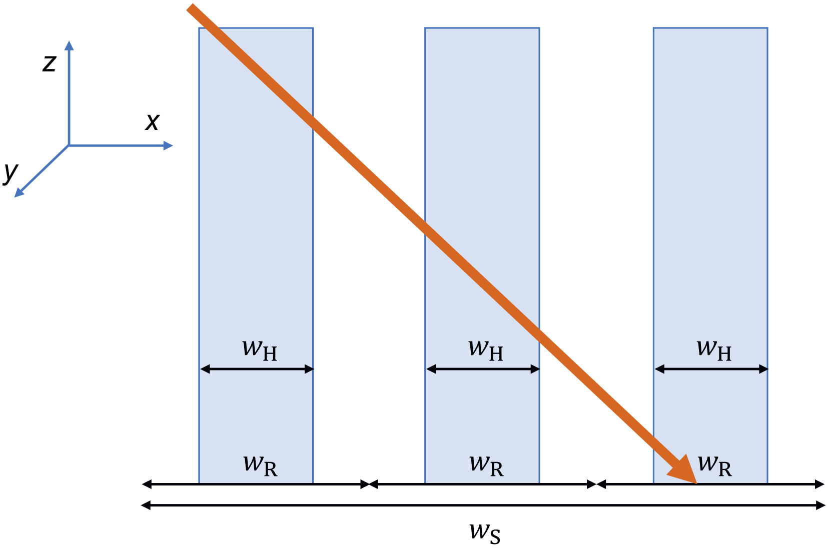


Fig. S4.1 A scenario in which a light beam traverses a strip with a strip width w_{S}. The strip comprises three plant rows with a designed row width w_{R}. Each plant row can be assumed as a hedgerow with a hedgerow width w_{H}.

In this study, w_{R} was 50 cm for maize, and 25 cm for wheat, faba bean, and pea. w_{H} is calculated as:

$$w_{\mathrm{H}} = w_{\mathrm{R}} * \tau_{\mathrm{C}} \qquad \text{(Eq. S4.1)}$$

where τ_{C} is the ground cover of the crop, and is calculated using the estimation by Christopher (2006):

$$\tau_{\mathrm{C}} = \begin{cases} \mathrm{LAI}/3, & \mathrm{LAI} < 3 \\ 1, & \mathrm{LAI} \geq 3 \end{cases} \qquad \text{(Eq. S4.2)}$$

Method S4.1.2 Leaf area density LAD

Assuming leaf areas are homogenously distributed along the plant height h, the leaf area density LAD in the hedgerow is calculated as:

$$\mathrm{LAD} = \frac{\mathrm{LAI}}{h} \times \frac{w_{\mathrm{R}}}{w_{\mathrm{H}}} \quad \text{(Eq. S4.3)}$$

where h is the plant height; LAI is the leaf area index on the w_{R} space.

Method S4.1.3 Light extinction coefficient g

The canopy light extinction coefficient g was calculated using the G-function (Campbell and Norman, 1998):

$$g = \frac{\sqrt{\chi^2 \sin^2\beta + \cos^2\beta}}{\chi + 1.774(\chi + 1.182)^{-0.773}} \quad \text{(Eq. S4.4)}$$

where β is the solar elevation angle; χ is the ratio of the average projected area of canopy elements on a horizontal surface to the projected area on a vertical surface. It describes the leaf angle distribution. A canopy with mostly horizontally oriented leaves has a χ greater than one, whereas a canopy with mostly vertically oriented leaves has a χ smaller than one. In the present study, the χ values suggested by Campbell and Norman (1998) were used: 0.8 for maize, 0.9 for wheat, 0.8 for faba bean, and 0.8 for pea.

Method S4.1.4 Solar elevation β and solar azimuth α

β was randomly generated between 0 to $\pi/2$, considering the low frequencies of β close to $\pi/2$ (the zenith) according to the spherical distribution (Fig. S4.2).

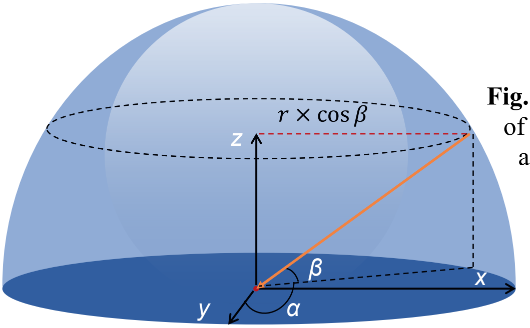


Fig. S4.2 A hemispherical dome with a radius of r. A solar position is determined by its solar azimuth α (relative to the south) and solar elevation β. The frequencies of β get lower from the ground to the zenith because the ground projection of the dome has a shorter radius $r \times \cos\beta$.

In the present study, the light sources were generated by combining 100 random β with 5 random α for each β (Fig. S4.3).

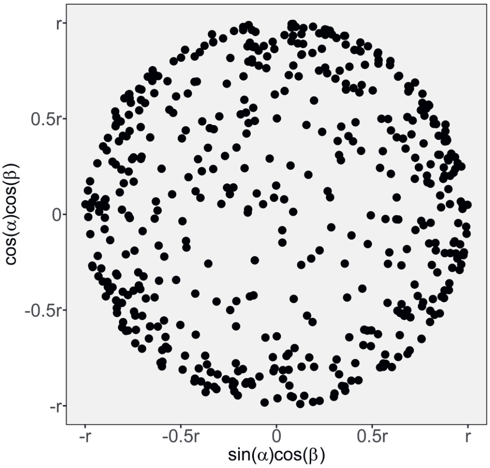


Fig. S4.3 Horizontal projections of the 500 random light sources. The 500 random light sources were generated by combining 100 random solar elevation angles β with 5 random solar azimuth angles α (relative to the south) for each solar elevation.

Method S4.1.5 Beam path length p

The beam path length traversing the hedgerows, illustrated as *AB* + *CD* in Fig. S4.4 is calculated as:

$$p = \frac{p'}{\sin\theta_\mathrm{b}\cos\theta_\mathrm{c}} \quad \text{(Eq. S4.5)}$$

where p is the beam path length, illustrated as *AB* + *CD* in Fig. S4.4; p' is the horizontal component of the *xz* projection of p, illustrated as *HI* + *JD* in Fig. S4.4; θ_b is the angle of the beam's *xz* projection against the vertical; θ_c is the angle of the beam against the *xz* plane.

θ_b and θ_c are calculated as:

$$\theta_\mathrm{c} = \arcsin(\cos(\pi - \theta_\mathrm{a})\cos\beta) \quad \text{(Eq. S4.6)}$$

$$\theta_\mathrm{b} = \arccos(\frac{\sin\beta}{\cos\theta_\mathrm{c}}) \quad \text{(Eq. S4.7)}$$

where θ_a is the difference between solar and row azimuths; β is the solar elevation angle.

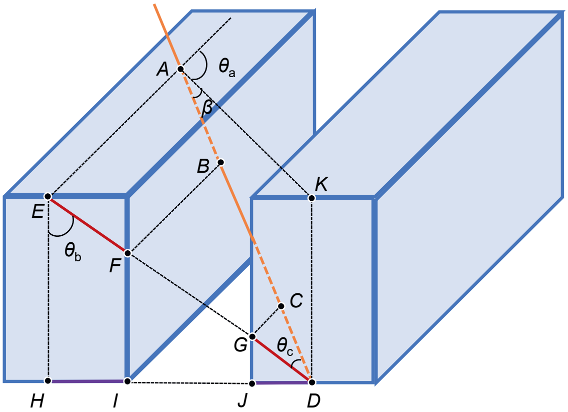


Fig. S4.4 Illustration of a beam traversing two hedgerows, adjusted according to Wang et al. (2017). *AD* (orange) is the beam. *AB* + *CD* is the path length. *EF* + *GD* (red) is path length's projection on the *xz* plane. *HI* + *JD* (purple) is the horizontal component of *EF* + *GD*. θ_a is the difference between solar and row azimuths. β is the solar elevation angle. θ_b is the angle of the beam's *xz* projection against the vertical. θ_c is the angle of the beam against the *xz* plane.

Method S4.1.6 The horizontal component of the xz projection of the path length $\mathbf{p}'$

p' depends on the number of hedgerows traversed by the beam (Fig. S4.5). For a specific beam, the number of hedgerows n it can traverse is calculated as:

$$n = Nn_\mathrm{s} + n' \tag{Eq. S4.8}$$

where N is the number of complete intercrop strips counted from the first hedgerow traversed by the beam to the edge of the last intercrop strip; n_s is the number of hedgerows in one complete intercrop strip; n' is the number of hedgerows traversed in the intercrop strip that is first traversed by the beam.

N is calculated as:

$$N = \mathrm{floor}\left(\frac{d_0 + h_\mathrm{max}\tan\theta_\mathrm{b}}{w_\mathrm{s}}\right) \tag{Eq. S4.9}$$

where d_0 is the distance from the intersection of the beam and ground to the edge of the last intercrop strip; h_max is the maximum height of the hedgerows; w_s is the intercrop strip width.

For hedgerow i, p'_i is calculated as:

$$p'_i = \begin{cases} w_{\mathrm{H}\,i} & h_{\mathrm{out}\,i} > 0, h_{\mathrm{in}\,i} > 0, h_i > h_{\mathrm{in}\,i} \\ (h_i - h_{\mathrm{out}\,i})\tan\theta_{\mathrm{b}} & h_{\mathrm{out}\,i} > 0, h_{\mathrm{in}\,i} > 0, h_{\mathrm{out}\,i} < h_i \le h_{\mathrm{in}\,i} \\ h_{\mathrm{in}\,i}\tan\theta_{\mathrm{b}} & h_{\mathrm{out}\,i} \le 0, h_{\mathrm{in}\,i} \ge 0 \\ 0 & h_{\mathrm{in}\,i} < 0 \\ 0 & h_{\mathrm{out}\,i} > 0, h_{\mathrm{in}\,i} > 0, h_i \le h_{\mathrm{out}\,i} \end{cases} \qquad \text{(Eq. S4.10)}$$

where h_i is the canopy height; $h_{\mathrm{in}\,i}$ and $h_{\mathrm{out}\,i}$ are the heights from the ground to where the beam enters and exits the hedgerow. The conditions represent cases in which the beam enters and exits hedgerow i from different positions (Fig. S4.6).

$h_{\mathrm{in}\,i}$ and $h_{\mathrm{out}\,i}$ are calculated as:

$$h_{\mathrm{in}\,i} = \frac{[\gamma w_{\mathrm{S}} + w_{\mathrm{R1}} + w_{\mathrm{R2}} + \cdots + w_{\mathrm{R}b} - 0.5(w_{\mathrm{R}\lambda} - w_{\mathrm{H}\lambda}) - d_0]}{\tan\theta_{\mathrm{b}}} \qquad \text{(Eq. S4.11)}$$

$$h_{\mathrm{out}\,i} = \frac{[\gamma w_{\mathrm{S}} + w_{\mathrm{R1}} + w_{\mathrm{R2}} + \cdots + w_{\mathrm{R}(\lambda-1)} + 0.5(w_{\mathrm{R}\lambda} - w_{\mathrm{H}\lambda}) - d_0]}{\tan\theta_{\mathrm{b}}} \qquad \text{(Eq. S4.12)}$$

where γ is the number of complete strips counted from the edge of the last intercrop strip to hedgerow i; λ is the number of hedgerows traversed by the beam in the strip where hedgerow i is, including hedgerow i.

γ and λ are calculated as:

$$\gamma = \mathrm{floor}\left(\frac{i}{n_{\mathrm{s}}}\right) \qquad \text{(Eq. S4.13)}$$

$$\lambda = i\% n_{\mathrm{s}} \qquad \text{(Eq. S4.14)}$$

where n_{s} is the number of hedgerows in an intercrop strip; γ is the integer of the division between i and n_{s}; λ is the remainder of the division between i and n_{s}.

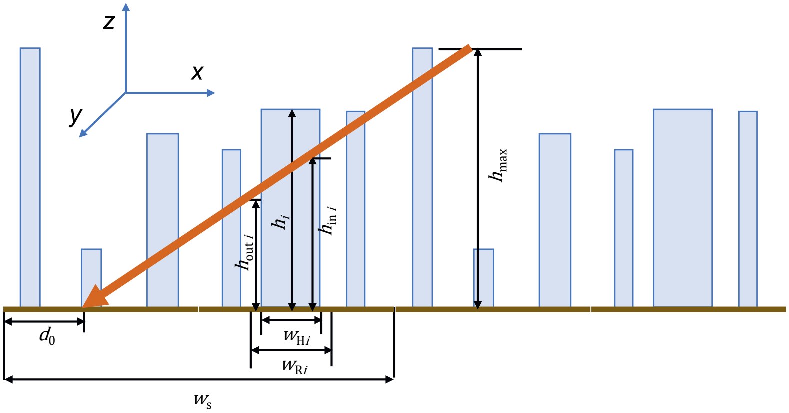
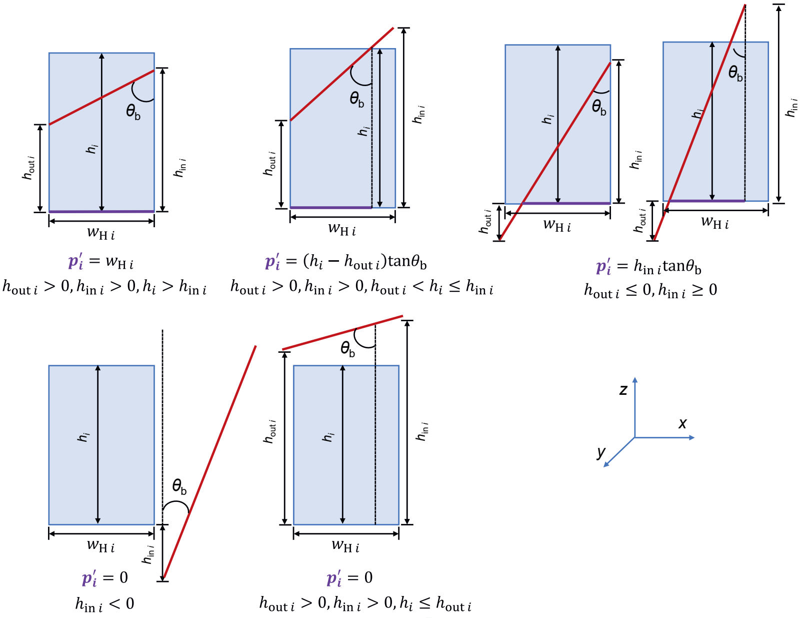


Fig. S4.5 Illustration of the *xz* cross section of hedgerows, adjusted according to Wang et al. (2017). w_s is the intercrop strip width, which is the sum of the species strip widths. In this example, the beam traverses one complete intercrop strip and the first two hedgerows in the second intercrop strip, i.e., eight rows in total. i denotes the rank of a specific hedgerow traversed by the beam, which is 5 in this example. For hedgerow i, $w_{\mathrm{R}i}$ is the designed row width; $w_{\mathrm{H}i}$ is the hedgerow width; h_i is the canopy height; $h_{\mathrm{in}\,i}$ and $h_{\mathrm{out}\,i}$ are the heights from the ground to where the beam enters and exits the hedgerow. h_{max} is the maximum height of the hedgerows. d_0 is the distance from the intersection of the beam and ground to the edge of the last intercrop strip.



$p'_i = w_{\mathrm{H}\,i}$
$h_{\mathrm{out}\,i} > 0, h_{\mathrm{in}\,i} > 0, h_i > h_{\mathrm{in}\,i}$

$p'_i = (h_i - h_{\mathrm{out}\,i})\tan\theta_\mathrm{b}$
$h_{\mathrm{out}\,i} > 0, h_{\mathrm{in}\,i} > 0, h_{\mathrm{out}\,i} < h_i \le h_{\mathrm{in}\,i}$

$p'_i = h_{\mathrm{in}\,i}\tan\theta_\mathrm{b}$
$h_{\mathrm{out}\,i} \le 0, h_{\mathrm{in}\,i} \ge 0$

$p'_i = 0$
$h_{\mathrm{in}\,i} < 0$

$p'_i = 0$
$h_{\mathrm{out}\,i} > 0, h_{\mathrm{in}\,i} > 0, h_i \le h_{\mathrm{out}\,i}$

Fig. S4.6 Illustration of the cases in which the beam enters and exits hedgerow i from different positions. The rectangle represents the *xz* cross section of hedgerow i. h_i is the canopy height. $h_{\mathrm{in}\,i}$ and $h_{\mathrm{out}\,i}$ are the heights from the ground to where the beam enters and exits the hedgerow. $w_{\mathrm{H}i}$ is the hedgerow width. The red line is path length's projection on the *xz* plane. θ_b is the angle of the path length's *xz* projection against the vertical. The purple line p' is the horizontal component of the path length's *xz* projection.

Method S4.1.7 Light capture fraction f_{cap} per certain row position

In the present study, 150 values of d_0 were taken an interval of 0.02 m from 0 to 0.98 m to evenly cover a 3 m-wide intercrop strip. A certain beam has 150 traversing scenarios depending on the d_0. In all, there are 75000 traversing scenarios for the 500 random beams.

Therefore, for a certain row position in one unit intercrop strip, its f_{cap} is calculated as:

$$f_{\text{cap}} = \sum_{i=1}^{k} \frac{f_{\text{cap}\,i} \times \sin\beta_j}{\sum_{j=1}^{75000} \sin\beta_j} \qquad \text{(Eq. S4.15)}$$

where j represents the jth ‘solar elevation × solar azimuth × d_0’ scenario; $f_{\text{cap}\,i}$ is the light capture fraction of hedgerow at a specific row position under the jth scenario. For a certain beam, the energy cast upon one unit of land is proportional to $\sin\beta$. k represents the total number of traversed hedgerows at the same row position across all scenarios.

Method S2 Measurements of leaf area index (LAI) per meter row.

LAI was measured during each intermediate harvest (Table S4.1). For maize, a subsample of at least five plants was randomly selected from each intermediate harvesting sample and weighed. For the other three species, at least ten plants were randomly chosen from each intermediate harvesting sample and weighed. Leaves were disassembled, and their weight was measured. Leaf area was measured using a leaf meter (LI-3100 Area Meter, LI-COR Inc., United States), and then converted to the leaf area of each sample based on weight. LAI per metre row was subsequently calculated. For maize, this represented LAI on a 0.5 m^2 area, and for wheat, faba bean, and pea, it was on a 0.25 m^2 area.

Method S3 Intermediate and final harvest dates.

Table S4.1 Dates of intermediate and final harvests of maize, wheat, faba bean, and pea

Species	Harvest	Date (Day of year, DOY)
Maize	Intermediate	DOY 168, 182, 196, 234
	Final	DOY 261
Wheat	Intermediate	DOY 133, 147, 168, 182, 196
	Final	DOY 220
Faba bean	Intermediate	DOY 133, 147, 168, 182, 196
	Final	DOY 226
Pea	Intermediate	DOY 133, 147, 168, 182, 196
	Final	DOY 210

Method S4 Measurements of plant height per row.

In the field, plant height was measured using a measuring stick, with the plant height defined as the distance from the bottom of the main stem to the base of the last fully developed leaf. In wheat, faba bean, and pea plants, a leaf was deemed fully developed when its blade had fully expanded. In maize, the criterion was the visibility of the leaf collar. Plants selected for measurements are presented in Table S4.2.

Table S4.2 Plants selected for measuring plant height per row. Dates are presented as day of year (DOY).

Species	DOY	Plants selection
Maize	165	Three maize plants in each monocrop plot were selected. In each intercrop plot, one plant from each row in one maize strip was selected.
	190, 204	One random maize plant in each monocrop plot was selected. In each intercrop plot, one plant from one border row and one from the inner row of one maize strip were selected.
	220	Eight random maize plants in each monocrop plot were selected. In each intercrop plot, five plants from each row in one maize strip were selected.
Wheat, Faba bean	140, 155, and 176	In each monocrop plot, one random plant was selected. In each intercrop plot, one plant from each of one border row (row 1 of the strip), the adjacent inner row I (row 2 of the strip), and the adjacent inner row II (row 3 of the strip) was selected.
Pea	140, 155	
Wheat, Faba bean	189	In each monocrop and intercrop plot, one plant from each row in one species strip was selected.
Pea		One plant in each monocrop and intercrop plot was selected. In each plot, one plant from the border row in one species strip was selected. The measurement was only made on the border row due to lodging. Plant heights in inner rows I and II were assumed the same as in the border rows as the pea rows were entangled, resulting in a rather homogeneous canopy.

Supplementary results

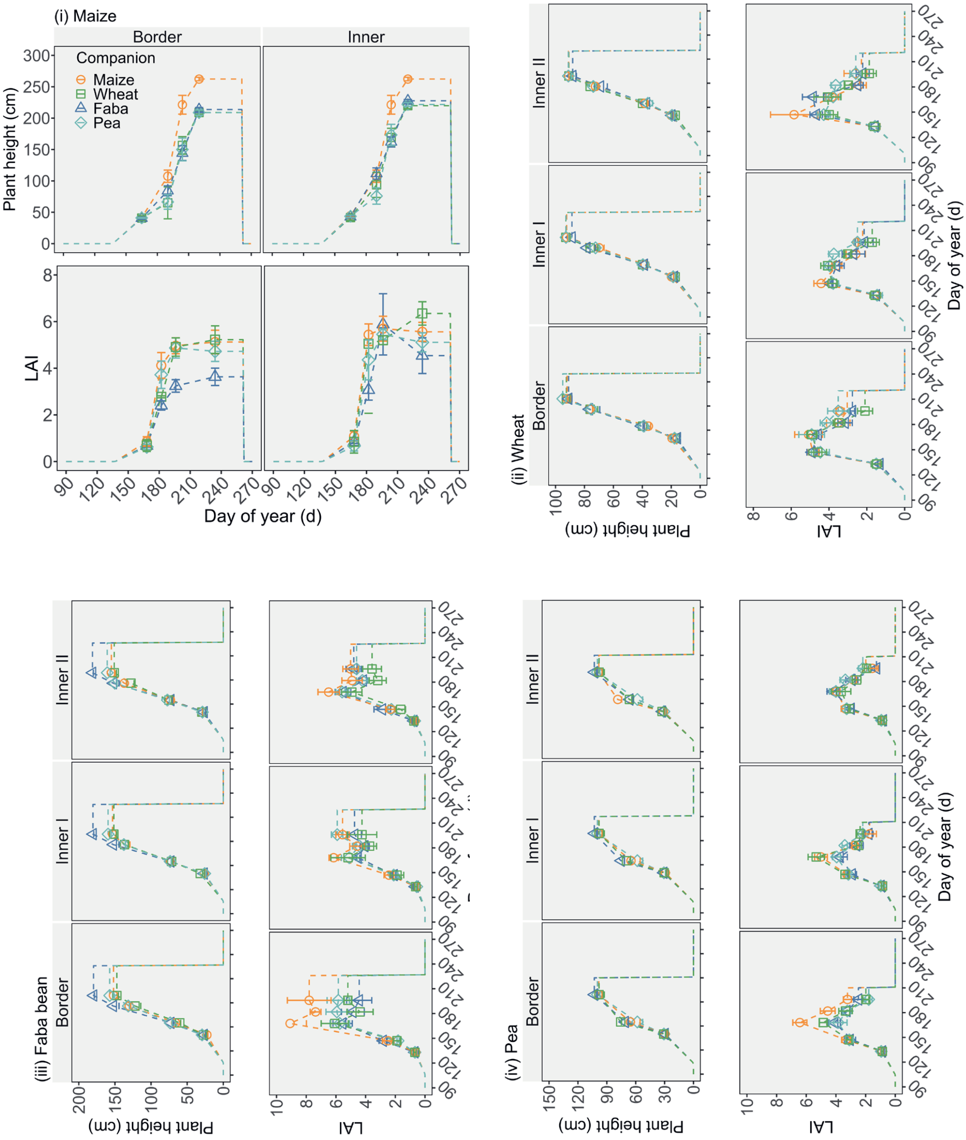


Fig. S4.7 Measured (points) and interpolated (dashed lines) plant height and leaf area index (LAI) of maize (i), wheat (ii), faba bean (iii), and pea (iv). Each panel represents a focal species. Different symbols and colours represent the plant heights and LAIs of the focal species with different companion species: maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond). LAI is the leaf area index of each row type on a 1 m × the row width area, i.e., 0.5 m^2 for maize, and 0.25 m^2 for wheat, faba bean, and pea. Error bars represent standard errors of the means.

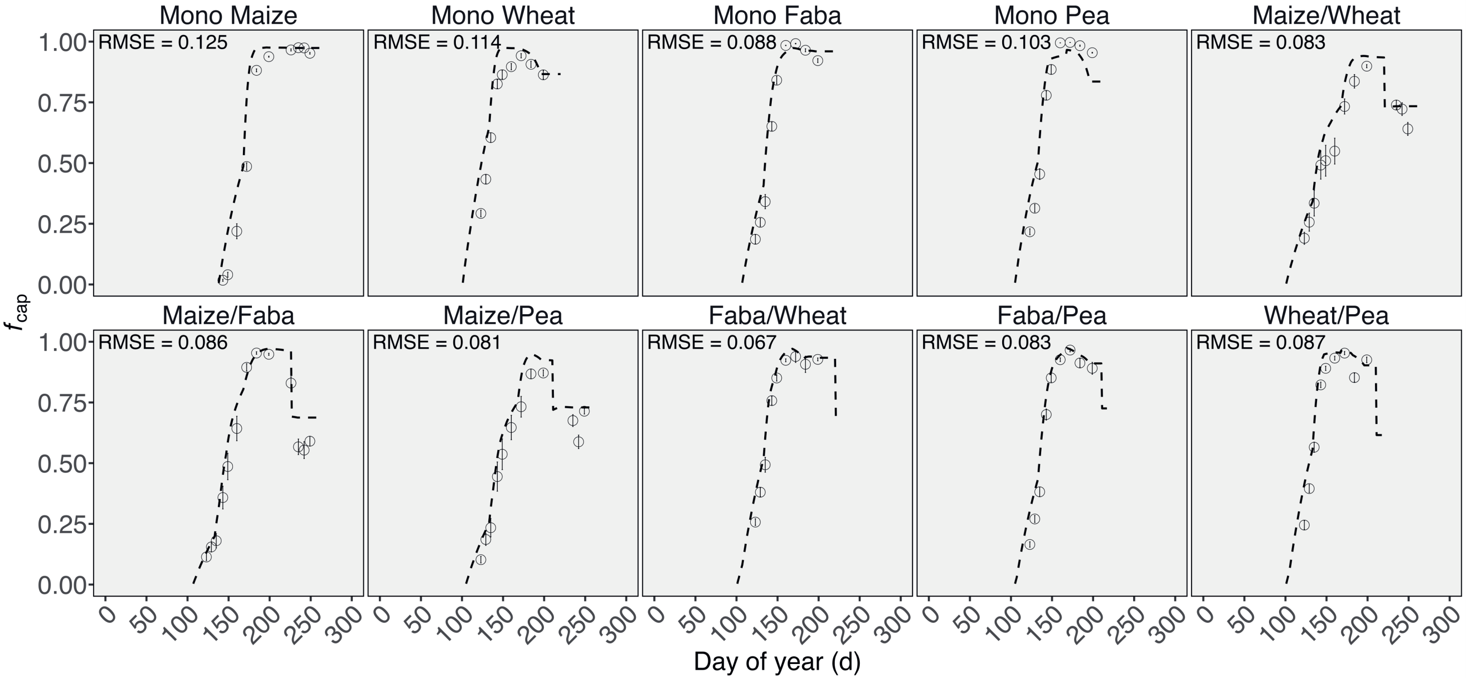


Fig. S4.8 Validating the random ray tracing model by comparing the fractions of captured PAR (f_{cap}) measured in the field (circle) and estimated by the model (dashed line). Measurements were conducted using a SS1 SunScan Canopy Analysis System (Delta-T Devices Ltd, UK) to determine the fractions of captured PAR on the strip level; see Chapter 3 for details. For a strip, the simulated f_{cap} on the strip level was the sum of f_{cap} of all rows within this strip.

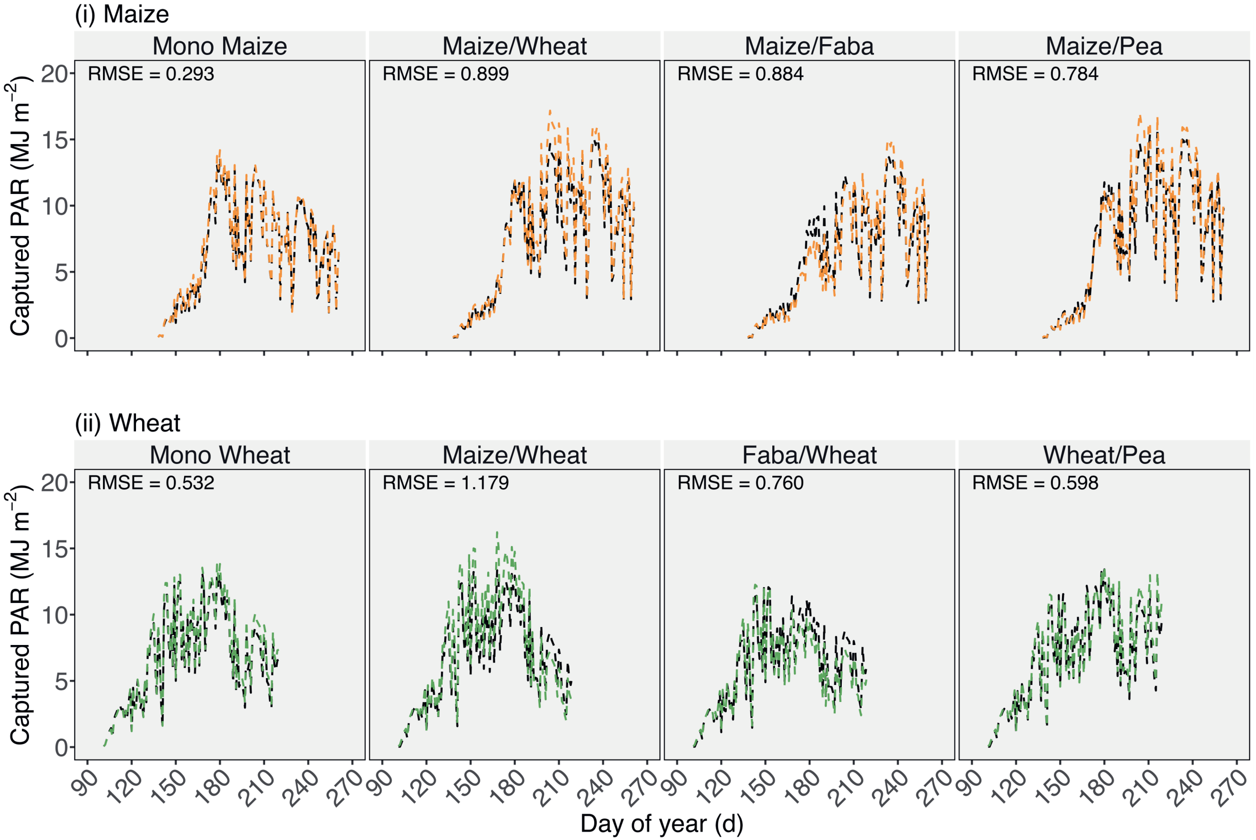
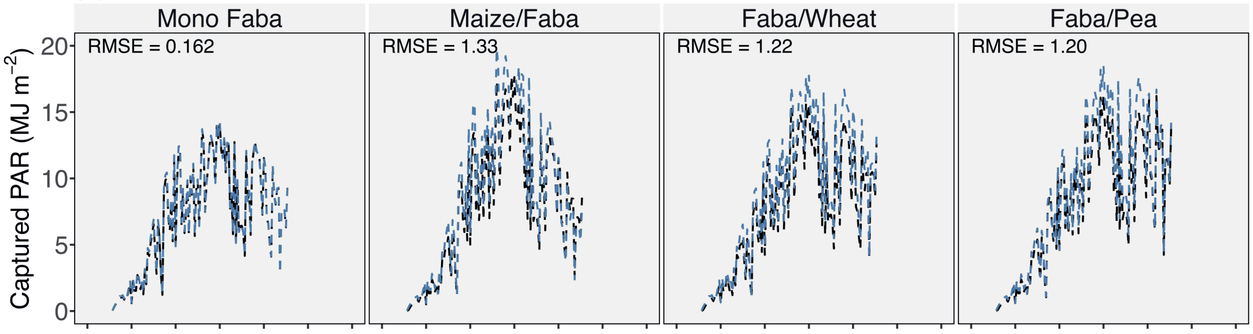


Fig. S4.9 Daily PAR captured by each species, averaged over the species strip, in different treatments simulated by the block model of Gou et al. (2017) (black dashed lines) and by the random ray tracing model (coloured dashed lines). For a species strip, the coloured lines represent the sum of fractions of captured PAR from all rows within this strip, multiplied by the total incident PAR.

(iii) Faba bean



(iv) Pea

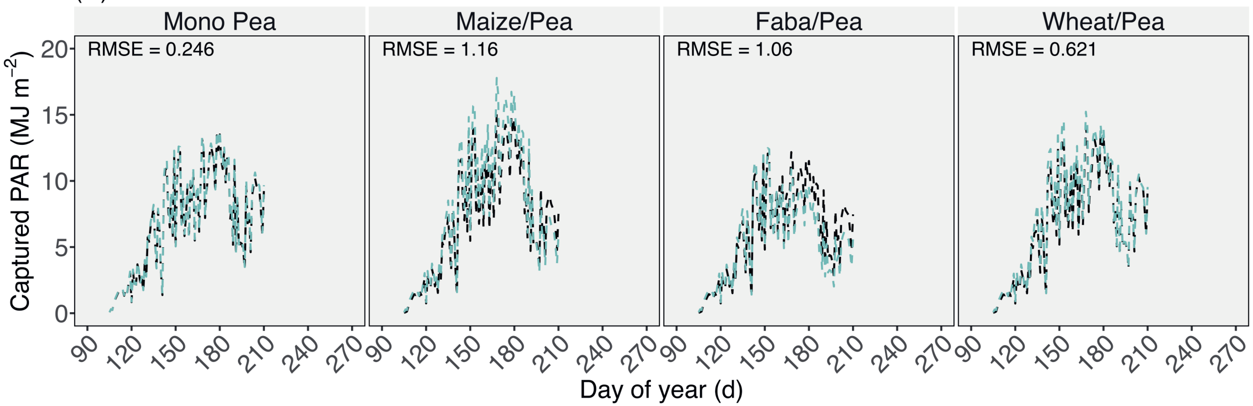


Fig. S4.9 (continued) Daily PAR captured by each species, averaged over the species strip, in different treatments simulated by the block model of Gou et al. (2017) (black dashed lines) and by the random ray tracing model (coloured dashed lines). For a species strip, the coloured lines represent the sum of fractions of captured PAR from all rows within this strip, multiplied by the total incident PAR.

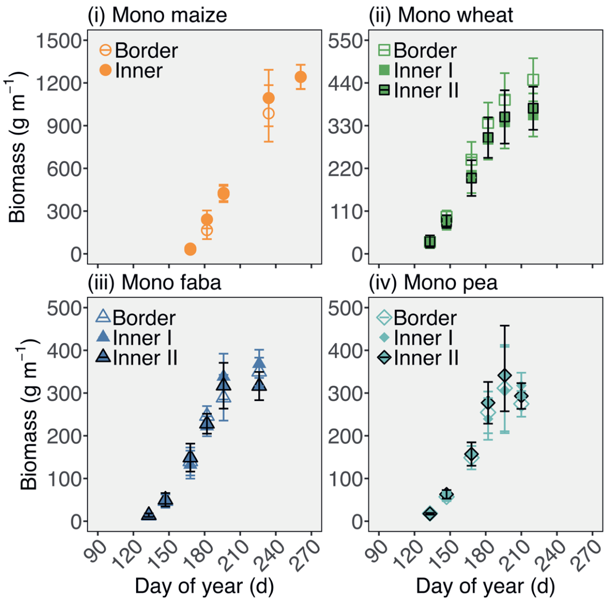


Fig. S4.10 Above-ground biomass through the growth season for maize (i), wheat (ii), faba bean (iii), and pea (iv) in their monocrops. Biomass is expressed per metre, representing the biomass on a 1 m × the row width area, which is 0.5 m^2 for maize, 0.25 m^2 for wheat, faba bean, and pea. Error bars represent the 95% confidence intervals of the means.

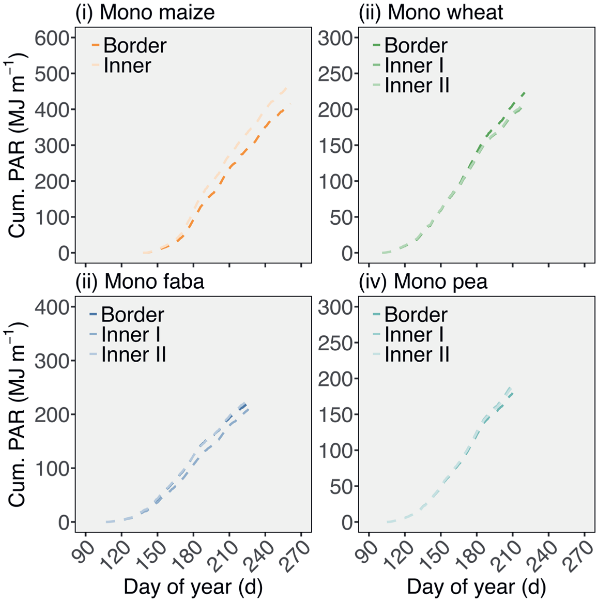


Fig. S4.11 Daily cumulative PAR captured (Cum. PAR) through the growth season for maize (i), wheat (ii), faba bean (iii), and pea (iv) in their monocrops. Cumulative PAR captured is expressed per metre, representing the amount on a 1 m × the row width rea, which is 0.5 m^2 for maize, 0.25 m^2 for wheat, faba bean, and pea.

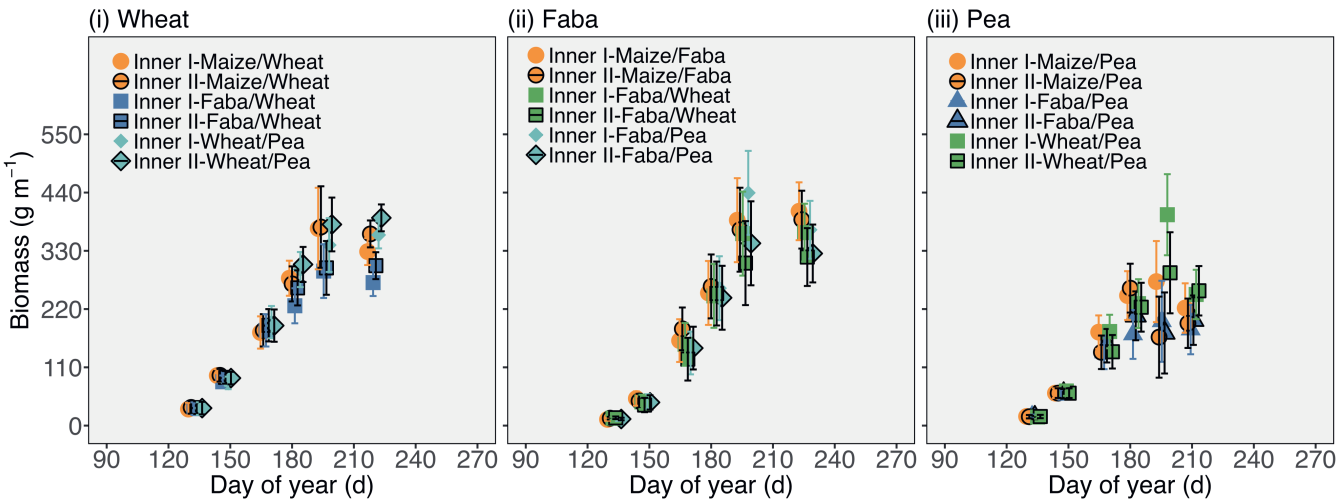


Fig. S4.12 Above-ground biomass of inner rows I and II through the growth season for wheat (i), faba bean (ii), and pea (iii) in their intercrops. Biomass is expressed per metre, representing the biomass on a 1 m × the row width area, which is 0.5 m^2 for maize, 0.25 m^2 for wheat, faba bean, and pea. Error bars represent the 95% confidence intervals of the means.

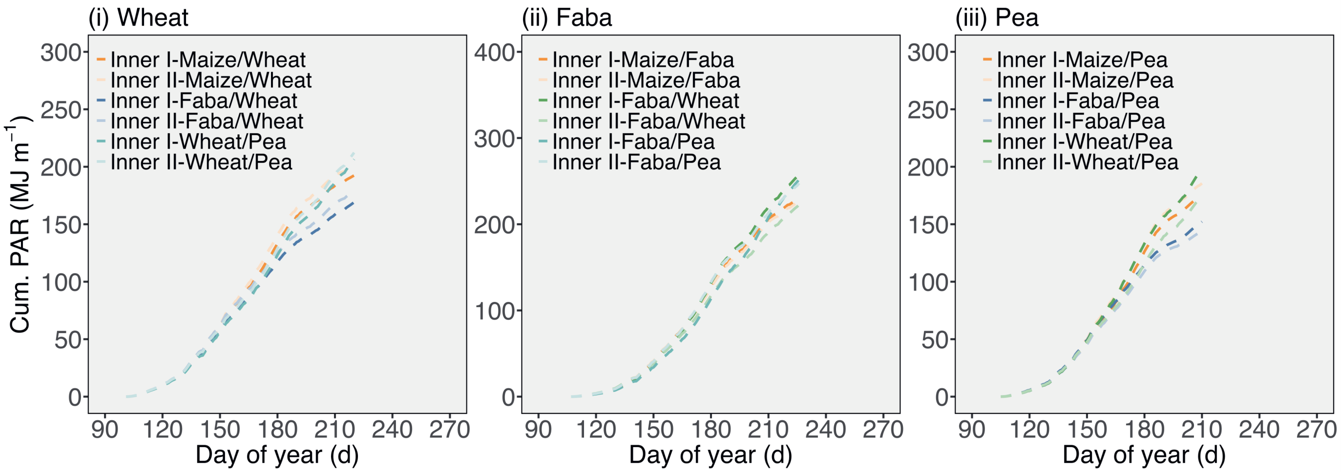


Fig. S4.13 Daily cumulative PAR captured (Cum. PAR) of inner rows I and II through the growth season for wheat (i), faba bean (ii), and pea (iii) in their intercrops. Cumulative PAR captured is expressed per metre, representing the amount on a 1 m × the row width rea, which is 0.5 m^2 for maize, 0.25 m^2 for wheat, faba bean, and pea.

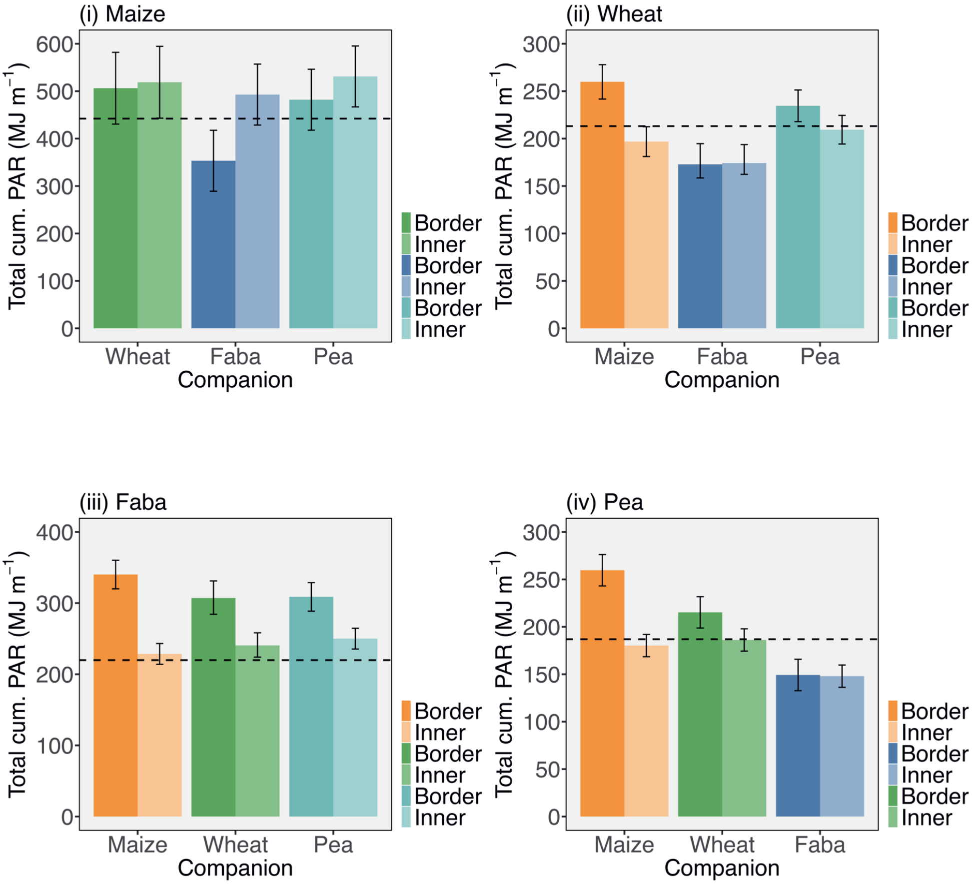
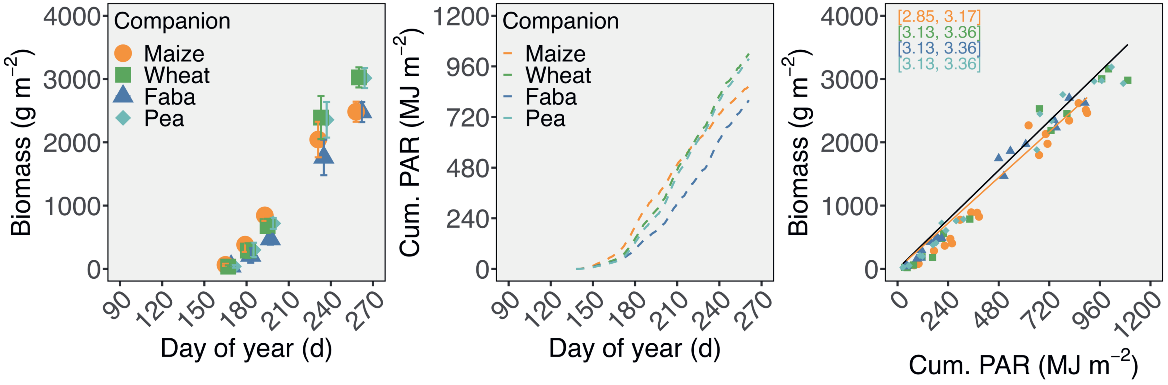


Fig. S4.14 Total cumulative PAR captured (Cum. PAR) over the whole growth season for maize (i), wheat (ii), faba bean (iii), and pea (iv). Total Cumulative PAR captured is expressed in MJ per metre row, representing the cumulative PAR on a 1 m × the row width area, which is 0.5 m^2 for maize, 0.25 m^2 for wheat, faba bean, and pea. For each species, Cumulative PAR captured in the intercrops is presented separately for the border and inner rows, whereas in the monocrop (where the companion species is the same as the focal species in each panel) it is presented as the average across all rows. For each focal species, different colours represent the cumulative PAR captured when it was grown with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). The dashed line represents the total cumulative PAR captured of the monocrop of the focal species in each panel. Error bars represent the 95% confidence intervals of the means.

(i) Maize



(ii) Wheat

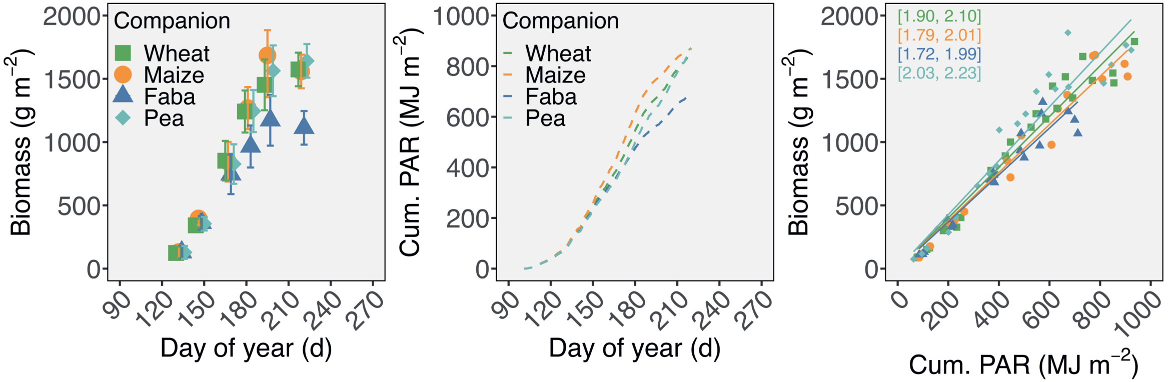


Fig. S4.15 Above-ground biomass, daily cumulative PAR captured (Cum. PAR), and regressions between above-ground biomass and cumulative PAR captured for maize (i), wheat (ii), faba bean (iii), and pea (iv) on the species strip level. For each focal species, different symbols and colours represent its biomass and cumulative PAR captured when it was with different companion species: maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond). Error bars represent the 95% confidence intervals of the biomass means.

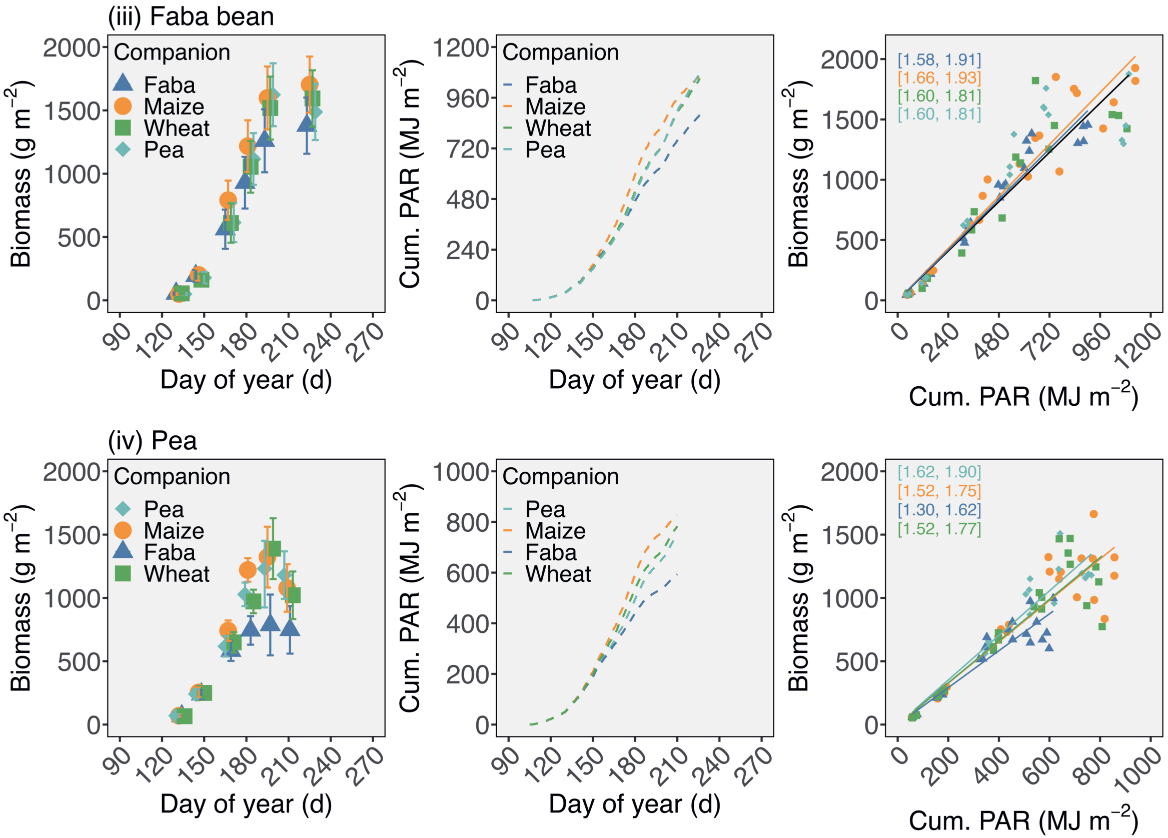


Fig. S4.15 (continued) Above-ground biomass, daily cumulative PAR captured (Cum. PAR), and regressions between above-ground biomass and cumulative PAR captured for maize (i), wheat (ii), faba bean (iii), and pea (iv) on the species strip level. For each focal species, different symbols and colours represent its biomass and cumulative PAR captured when it was with different companion species: maize (orange circle), wheat (green square), faba bean (blue triangle), and pea (cyan diamond). Error bars represent the 95% confidence intervals of the biomass means.

Table S4.3 Model selection outputs for determining light use efficiency (LUE). The model marked in bold is the most supported model for a specific species.

(i) Maize

Model	Df	AIC	BIC	Negative log likelihood
Model 1	3	2650.617	2660.615	1322.308
Model 4	**4**	**2640.020**	**2653.351**	**1316.010**
Model 5	5	2640.451	2657.115	1315.226
Model 6	5	2639.944	2656.608	1314.972
Model 2	6	2641.343	2661.339	1314.671
Model 7	7	2642.049	2665.378	1314.024
Model 3	9	2645.114	2675.108	1313.557

(ii) Wheat

Model	Df	AIC	BIC	Negative log likelihood
Model 1	3	6283.293	6296.469	3138.646
Model 4	5	6275.795	6297.755	3132.897
Model 6	5	6275.795	6297.755	3132.897
Model 2	6	6260.328	6286.680	3124.164
Model 5	7	6262.530	6293.273	3124.265
Model 7	7	6262.530	6293.273	3124.265
Model 3	**9**	**6238.682**	**6278.209**	**3110.341**

(iii) Faba bean

Model	Df	AIC	BIC	Negative log likelihood
Model 1	3	7150.916	7164.286	3572.458
Model 4	5	7138.114	7160.398	3564.057
Model 6	5	7151.271	7173.555	3570.635
Model 2	6	7139.571	7166.312	3563.786
Model 5	**7**	**7120.726**	**7151.923**	**3553.363**
Model 7	7	7152.524	7183.722	3569.262
Model 3	9	7121.568	7161.679	3551.784

(iv) Pea

Model	Df	AIC	BIC	Negative log likelihood
Model 1	3	7416.636	7430.149	–3705.318
Model 4	5	7383.994	7406.516	–3686.997
Model 6	5	7378.177	7400.699	–3684.089
Model 2	6	7378.372	7405.398	–3683.186
Model 5	7	7345.209	7376.739	–3665.605
Model 7	7	7368.498	7400.028	-3677.249
Model 3	**9**	**7339.160**	**7379.699**	**–3660.580**

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Gou, F., van Ittersum, M.K., Simon, E., Leffelaar, P.A., van der Putten, P.E.L., Zhang, L., van der Werf, W., 2017. Intercropping wheat and maize increases total radiation interception and wheat RUE but lowers maize RUE. European Journal of Agronomy 84, 125–139. https://doi.org/10.1016/J.EJA.2016.10.014

Wang, Z., Zhao, X., Wu, P., Gao, Y., Yang, Q., Shen, Y., 2017. Border row effects on light interception in wheat/maize strip intercropping systems. Field Crops Res 214, 1–13. https://doi.org/10.1016/j.fcr.2017.08.017

Supplementary information for Chapter 5

Relay strip intercropping increases nitrogen uptake and fertiliser nitrogen use efficiency

Table S5.1 AIC values of all models to estimate N dilution curves for maize and wheat, and the fitted parameter values of the selected models.

Table S5.2 AIC values of all models used to quantify the relationships between LER_N and TND.

Table S5.3 Comparisons of above-ground N uptake per species strip.

Table S5.4 Comparisons of above-ground N uptake in each row for each species.

Table S5.5 Comparisons of above-ground N concentration per species strip.

Table S5.6 Comparisons of above-ground biomass and N uptake per species strip during the intermediate harvests and at the final harvest in 2019.

Fig. S5.1 Above-ground N concentration per species strip compared with above-ground biomass per species strip for faba bean and pea in 2019.

Table S5.1 AIC values of all models used to estimate N dilution curves, and the fitted parameter values of the selected model for maize (i) and wheat (ii). The AIC value of each model version was calculated based on negative log-likelihood and a penalty term for the number of parameters: $\mathrm{AIC} = -2\log(L) + 2k$, where $\log(L)$ is the log-likelihood of the fit, and k is the number of parameters. The **bold** AIC value represents the selected model. ΔAIC is the difference of a model compared to the selected model.

(i) Maize. AIC values of all models:

Model	Groups of data used to fit model	Parameter differing among groups	Parameter number (k)	-2log(L)	AIC	ΔAIC
1	Monocrop, Wheat-Maize, Bean-Maize, Pea-Maize	a and b	9	–5.16	12.8	3.84
2		a	6	0.82	12.8	3.81
3		b	6	3.99	16.0	6.98
4	(Monocrop, Wheat-Maize), Bean-Maize, Pea-Maize	a and b	7	3.35	17.3	8.35
5		a	5	6.96	17.0	7.96
6		b	5	5.31	15.3	6.30
7	(Monocrop, Bean-Maize), Wheat-Maize, Pea-Maize	a and b	7	7.19	21.2	12.2
8		a	5	9.28	19.3	10.3
9		b	5	10.9	20.9	11.9
10	(Monocrop, Pea-Maize), Wheat-Maize, Bean-Maize	a and b	7	6.18	20.2	11.2
11		a	5	9.69	19.7	10.7
12		b	5	8.09	18.1	9.08
13	(Wheat-Maize, Bean-Maize), Monocrop, Pea-Maize	a and b	7	–1.26	12.7	3.74
14		a	5	0.85	10.9	1.85
15		b	5	5.15	15.1	6.14
16	(Wheat-Maize, Pea-Maize), Monocrop, Bean-Maize	a and b	7	–4.53	9.47	0.46
17		a	5	1.00	11.0	2.00
18		b	5	4.40	14.4	5.39
19	(Bean-Maize, Pea-Maize), Monocrop, Wheat-Maize	a and b	7	–2.51	11.5	2.49
20		a	5	0.89	10.9	1.89
21		b	5	4.20	14.2	5.19
22	(Wheat-Maize, Bean-Maize, Pea-Maize), Monocrop	a and b	5	–0.14	9.86	0.86
23		a	4	1.00	**9.00**	0.00
24		b	4	5.15	13.1	4.14
25	(Monocrop, Bean-Maize, Pea-Maize), Wheat-Maize	a and b	5	10.4	20.4	11.4
26		a	4	11.5	19.5	10.5
27		b	4	11.6	19.6	10.6
28	(Monocrop, Wheat-Maize, Pea-Maize), Bean-Maize	a and b	5	6.99	17.0	7.99
29		a	4	10.6	18.6	9.56
30		b	4	8.24	16.2	7.24
31	(Monocrop, Wheat-Maize, Bean-Maize), Pea-Maize	a and b	5	9.68	19.7	10.7
32		a	4	10.0	18.0	9.03
33		b	4	10.9	18.9	9.88
34	All data combined	None	3	11.7	17.7	8.67

Fitted parameter values (standard errors in brackets) of the selected model for **maize** (i.e., Model 23). Identical values of a parameter across treatments indicates that the parameter was not different among those treatments.

Parameter	Monocrop	Wheat-Maize	Bean-Maize	Pea-Maize
a_{m}	4.43 (0.14)	3.81 (0.25)	3.81 (0.25)	3.81 (0.25)
b_{m}	0.37 (0.03)	0.37 (0.03)	0.37 (0.03)	0.37 (0.03)

Table S5.1 (continued)

(ii) Wheat. The AIC values of all models:

Model	Groups of data used to fit model	Parameter differing among groups	Parameter number (k)	-2log(L)	AIC	ΔAIC
1	Monocrop, Wheat-Maize, Wheat-Bean, Pea-Wheat	a and b	9	–13.9	4.06	3.27
2		a	6	–2.58	9.42	8.64
3		b	6	–4.78	7.22	6.44
4	(Monocrop, Wheat-Maize), Wheat-Bean, Pea-Wheat	a and b	7	–6.83	7.17	6.38
5		a	5	–0.30	9.70	8.91
6		b	5	0.91	10.9	10.1
7	(Monocrop, Wheat-Bean), Wheat-Maize, Pea-Wheat	a and b	7	–2.62	11.4	10.6
8		a	5	–2.56	7.44	6.66
9		b	5	–1.61	8.39	7.60
10	(Monocrop, Pea-Wheat), Wheat-Maize, Wheat-Bean	a and b	7	–8.40	5.60	4.81
11		a	5	–1.67	8.33	7.54
12		b	5	–1.30	8.70	7.91
13	(Wheat-Maize, Wheat-Bean), Monocrop, Pea-Wheat	a and b	7	–8.63	5.37	4.59
14		a	5	0.83	10.8	10.0
15		b	5	–4.34	5.66	4.88
16	(Wheat-Maize, Pea-Wheat), Monocrop, Wheat-Bean	a and b	7	–13.9	0.09	-0.69
17		a	5	–2.19	7.81	7.02
18		b	5	–4.41	5.59	4.80
19	(Wheat-Bean, Pea-Wheat), Monocrop, Wheat-Maize	a and b	7	–10.8	3.24	2.45
20		a	5	–1.07	8.93	8.14
21		b	5	–4.77	5.23	4.44
22	(Wheat-Maize, Wheat-Bean, Pea-Wheat), Monocrop	a and b	5	–9.21	**0.79**	0.00
23		a	4	1.04	9.04	8.25
24		b	4	–4.25	3.75	2.96
25	(Monocrop, Wheat-Bean, Pea-Wheat), Wheat-Maize	a and b	5	–1.01	8.99	8.20
26		a	4	–0.91	7.09	6.31
27		b	4	–0.36	7.64	6.86
28	(Monocrop, Wheat-Maize, Pea-Wheat), Wheat-Bean	a and b	5	–5.31	4.69	3.90
29		a	4	–0.28	7.72	6.93
30		b	4	1.53	9.53	8.74
31	(Monocrop, Wheat-Maize, Wheat-Bean), Pea-Wheat	a and b	5	1.26	11.3	10.5
32		a	4	1.27	9.27	8.48
33		b	4	1.40	9.40	8.61
34	All data combined	None	3	1.74	7.74	6.95

Fitted parameter values (standard errors in brackets) of the selected model for **wheat** (i.e., Model 22). Identical values of a parameter across treatments indicates that the parameter was not different among those treatments.

Parameter	Monocrop	Wheat-Maize	Wheat-Bean	Pea-Wheat
a_w	6.30 (0.26)	5.69 (0.10)	5.69 (0.10)	5.69 (0.10)
b_w	0.65 (0.03)	0.55 (0.01)	0.55 (0.01)	0.55 (0.01)

Table S5.2 AIC values of all models used to quantify the relationships between LER_N and TND. The bold AIC value represents the selected model. ΔAIC is the difference of a model compared to the selected model.

Model	Degrees of freedom	log-likelihood	AIC	ΔAIC
1	4	46.253	–84.5	10.3
2	5	46.664	–83.3	11.5
3	5	46.254	–82.5	12.3
4	6	47.087	–82.2	12.7
5	6	51.543	–91.1	3.8
6	9	56.428	**–94.9**	0.0
7	14	60.578	–93.2	1.7

Table S5.3 Comparisons of above-ground N uptake per species strip (kg ha^{-1}) for maize, wheat, faba bean, and pea at final harvest. Mean values and their 95% confidence intervals in brackets are presented for each focal species when it was with the conspecific in the monocrop and with other species in intercrops. The 95% confidence interval was obtained separately for each year, with the treatment as the fixed effect and the block as the random effect. Shared letters denote non-significant differences between treatments within each year according to Fisher's LSD test at $P < 0.05$. To allow a direct comparison between monocrops and intercrops, N uptake in intercrops is expressed per unit area (kg ha^{-1}) of the 1.5 m-wide strip of a species.

Species	Year	Companion	N uptake (kg ha^{-1})	Species	Year	Companion	N uptake (kg ha^{-1})
Maize	2018	Maize	265 [235, 294] b	Wheat	2018	Wheat	172 [163, 181] b
		Wheat	307 [277, 336] a			Maize	224 [215, 233] a
		Faba bean	251 [222, 281] b			Faba bean	165 [156, 174] b
		Pea	307 [278, 337] a			Pea	166 [157, 175] b
	2019	Maize	269 [248, 289] ab		2019	Wheat	183 [162, 204] bc
		Wheat	286 [266, 307] a			Maize	212 [191, 233] a
		Faba bean	248 [227, 268] b			Faba bean	158 [136, 179] c
		Pea	271 [250, 292] ab			Pea	206 [185, 227] ab
Faba bean	2018	Faba bean	310 [279, 341] c	Pea	2018	Pea	242 [229, 255] b
		Maize	405 [374, 436] a			Maize	269 [256, 282] a
		Wheat	342 [311, 373] bc			Wheat	222 [209, 235] c
		Pea	356 [325, 387] b			Faba bean	201 [188, 214] d
	2019	Faba bean	359 [287, 432] b		2019	Pea	265 [227, 302] a
		Maize	479 [407, 552] a			Maize	245 [207, 282] a
		Wheat	426 [353, 498] ab			Wheat	232 [195, 270] a
		Pea	384 [311, 457] ab			Faba bean	168 [131, 206] b

Table S5.4 Comparisons of above-ground N uptake in each row (g m^{-2}) for maize (i), wheat (ii), faba bean (iii), and pea (iv) at final harvest. Means values and their 95% confidence intervals in brackets are presented for each focal species. The 95% confidence interval was obtained in each year, with 'Species Combination_ Row' as the fixed effect and block as the random effect. Shared letters denote non-significant differences between 'Species Combination_ Row's within each year according to Fisher's LSD test at $P < 0.05$.

(i) Maize

Species	Year	Companion	Row	N uptake (g m^{-2})
Maize	2018	Maize	-	26.5 [23.6, 29.4] bc
		Wheat	Border	30.4 [27.0, 33.7] ab
			Inner	31.3 [26.8, 35.7] ab
		Faba bean	Border	24.6 [21.2, 27.9] c
			Inner	26.2 [21.7, 30.7] bc
		Pea	Border	32.5 [29.1, 35.8] a
			Inner	27.2 [22.7, 31.7] bc
	2019	Maize	-	26.9 [24.8, 28.9] a
		Wheat	Border	29.8 [27.3, 32.3] a
			Inner	26.3 [22.7, 29.8] a
		Faba bean	Border	21.8 [19.3, 24.3] b
			Inner	30.6 [27.1, 34.2] a
		Pea	Border	27.5 [25.0, 30.0] a
			Inner	26.3 [22.8, 29.8] a

(ii) Wheat

Species	Year	Companion	Row	N uptake (g m^{-2})
Wheat	2018	Wheat	-	17.2 [16.4, 18.0] cd
		Maize	Border	30.2 [29.0, 31.5] a
			Inner I	18.3 [17.0, 19.5] bc
			Inner II	18.7 [17.4, 19.9] b
		Faba bean	Border	15.6 [14.3, 16.9] e
			Inner I	16.5 [15.2, 17.7] de
			Inner II	17.5 [16.3, 18.8] bcd
		Pea	Border	17.4 [16.1, 18.6] bcd
			Inner I	16.3 [15.1, 17.6] de
			Inner II	16.2 [14.9, 17.5] de
	2019	Wheat	-	18.3 [16.6, 20.0] b
		Maize	Border	27.8 [25.7, 30.0] a
			Inner I	17.3 [15.2, 19.5] b
			Inner II	18.5 [16.3, 20.6] b
		Faba bean	Border	16.3 [14.2, 18.5] bc
			Inner I	14.4 [12.2, 16.6] c
			Inner II	16.6 [14.5, 18.8] bc
		Pea	Border	25.7 [23.5, 27.8] a
			Inner I	17.4 [15.2, 19.5] b
			Inner II	18.7 [16.6, 20.9] b

Table S5.4 (continued)

(iii) Faba bean

Species	Year	Companion	Row	N uptake (g m^{-2})
Faba bean	2018	Faba bean	-	31.0 [28.8, 33.2] f
		Maize	Border	44.4 [41.1, 47.7] a
			Inner I	41.2 [37.9, 44.5] ab
			Inner II	35.9 [32.6, 39.1] cd
		Wheat	Border	34.8 [31.6, 38.1] de
			Inner I	33.6 [30.4, 36.9] def
			Inner II	34.1 [30.8, 37.4] def
		Pea	Border	39.3 [36.0, 42.5] bc
			Inner I	35.9 [32.7, 39.2] cd
			Inner II	31.6 [28.3, 34.8] ef
	2019	Faba bean	-	35.9 [31.1, 40.8] cd
		Maize	Border	56.4 [49.1, 63.6] a
			Inner I	44.5 [37.3, 51.8] b
			Inner II	42.9 [35.6, 50.1] bc
		Wheat	Border	58.3 [51.1, 65.5] a
			Inner I	38.1 [30.9, 45.4] bcd
			Inner II	31.3 [24.1, 38.5] d
		Pea	Border	45.7 [38.5, 53.0] b
			Inner I	37.9 [30.7, 45.2] bcd
			Inner II	31.5 [24.3, 38.8] d

(iv) Pea

Species	Year	Companion	Row	N uptake (g m^{-2})
Pea	2018	Pea	-	24.2 [22.6, 25.8] bc
		Maize	Border	32.1 [29.4, 34.8] a
			Inner I	26.1 [23.3, 28.8] b
			Inner II	22.6 [19.9, 25.3] bcd
		Wheat	Border	21.4 [18.6, 24.1] cde
			Inner I	23.0 [20.3, 25.7] bcd
			Inner II	22.2 [19.5, 25.0] bcd
		Faba bean	Border	18.3 [15.6, 21.0] e
			Inner I	20.0 [17.3, 22.7] de
			Inner II	22.0 [19.2, 24.7] cde
	2019	Pea	-	26.5 [23.4, 29.6] b
		Maize	Border	36.2 [31.1, 41.4] a
			Inner I	19.2 [14.1, 24.3] cde
			Inner II	18.0 [12.8, 23.1] de
		Wheat	Border	25.2 [20.1, 30.4] bc
			Inner I	21.8 [16.7, 26.9] bcde
			Inner II	22.7 [17.6, 27.8] bcd
		Faba bean	Border	15.4 [10.3, 20.5] e
			Inner I	16.8 [11.6, 21.9] de
			Inner II	18.3 [13.2, 23.5] cde

Table S5.5 Comparisons of above-ground N concentration per species (mg g^{-1}) for maize, wheat, faba bean, and pea at final harvest. Mean values and their 95% confidence intervals in brackets are presented for each focal species when it was with the conspecific in the monocrop and with other species in intercrops. The 95% confidence interval was obtained in each year, with the treatment as the fixed effect and the block as the random effect. Shared letters denote non-significant differences between treatments within each year according to Fisher's LSD test at $P < 0.05$.

Species	Year	Companion	N concentration (mg g^{-1})	Species	Year	Companion	N concentration (mg g^{-1})
Maize	2018	Maize	10.1 [9.71, 10.5] a	Wheat	2018	Wheat	13.4 [12.9, 13.9] bc
		Wheat	9.48 [9.08, 9.88] b			Maize	13.9 [13.4, 14.4] ab
		Faba bean	9.47 [9.07, 9.87] b			Faba bean	14.7 [14.2, 15.2] a
		Pea	9.30 [8.90, 9.70] b			Pea	12.9 [12.3, 13.4] c
	2019	Maize	10.8 [9.91, 11.7] a		2019	Wheat	11.6 [10.5, 12.7] c
		Wheat	9.47 [8.57, 10.4] b			Maize	13.6 [12.5, 14.7] ab
		Faba bean	10.1 [9.14, 11.0] ab			Faba bean	14.3 [13.2, 15.3] a
		Pea	9.00 [8.09, 9.91] b			Pea	12.5 [11.5, 13.6] bc
Faba bean	2018	Faba bean	28.8 [27.4, 30.2] a	Pea	2018	Pea	21.7 [21.1, 22.3] b
		Maize	29.4 [28.0, 30.8] a			Maize	23.4 [22.8, 24.0] a
		Wheat	28.6 [27.2, 30.0] a			Wheat	22.1 [21.5, 22.7] b
		Pea	28.5 [27.1, 29.8] a			Faba bean	21.7 [21.1, 22.3] b
	2019	Faba bean	26.0 [24.4, 27.6] b		2019	Pea	22.4 [21.2, 23.6] a
		Maize	28.1 [26.5, 29.7] a			Maize	22.7 [21.5, 23.9] a
		Wheat	26.6 [25.0, 28.2] b			Wheat	23.0 [21.8, 24.2] a
		Pea	25.8 [24.2, 27.4] b			Faba bean	22.7 [21.5, 23.9] a

Table S5.6 Comparisons of above-ground biomass and N uptake per species strip for maize (i), wheat (ii), faba bean (iii), and pea (iv) at each intermediate harvest and the final harvest in 2019. Mean values and their 95% confident intervals in brackets are presented for each focal species. The 95% confidence interval was obtained at each individual harvest, with the treatment as the fixed effect and the block as the random effect. Shared letters denote non-significant differences between treatments within an individual harvest according to Fisher's LSD test at $P < 0.05$.

(i) Maize. DOY 261 was the final harvest.

Species	DOY	Companion	Biomass (Mg ha^{-1})	N uptake (kg ha^{-1})
Maize	168	Maize	0.632 [0.440, 0.825] a	25.6 [18.3, 32.8] a
		Wheat	0.356 [0.164, 0.548] b	14.1 [6.84, 21.4] b
		Faba bean	0.401 [0.209, 0.594] b	16.7 [9.47, 24.0] b
		Pea	0.392 [0.200, 0.584] b	15.3 [8.05, 22.6] b
	182	Maize	3.83 [2.69, 4.97] a	105 [77.6, 132] a
		Wheat	2.89 [1.75, 4.03] ab	76.9 [49.8, 104] ab
		Faba bean	2.11 [0.97, 3.25] b	61.3 [34.2, 88.4] b
		Pea	3.00 [1.86, 4.14] ab	76.8 [49.7, 104] ab
	196	Maize	8.45 [7.60, 9.30] a	177 [163, 192] a
		Wheat	6.75 [5.66, 7.92] b	144 [121, 165] b
		Faba bean	4.70 [3.84, 5.55] c	107 [92.5, 122] c
		Pea	7.19 [6.33, 8.04] b	139 [124, 153] b
	234	Maize	20.4 [17.6, 23.3] ab	249 [213, 284] a
		Wheat	23.9 [20.5, 27.3] a	239 [196, 281] ab
		Faba bean	17.6 [14.8, 20.4] b	193 [158, 228] b
		Pea	23.6 [20.7, 26.4] a	224 [189, 260] ab
	261	Maize	24.8 [23.3, 26.4] b	269 [248, 289] ab
		Wheat	30.3 [28.7, 31.8] a	286 [266, 307] a
		Faba bean	24.8 [23.2, 26.4] b	248 [227, 268] b
		Pea	30.1 [28.6, 31.7] a	271 [250, 292] ab

(ii) Wheat. DOY 220 was the final harvest.

Species	DOY	Companion	Biomass (Mg ha^{-1})	N uptake (kg ha^{-1})
Wheat	133	Wheat	1.24 [0.73, 1.75] a	59.7 [36.8, 82.6] a
		Maize	1.31 [0.81, 1.82] a	64.0 [41.1, 86.9] a
		Faba bean	1.30 [0.79, 1.80] a	62.4 [39.5, 85.2] a
		Pea	1.28 [0.77, 1.79] a	62.5 [39.6, 85.4] a
	147	Wheat	3.42 [2.88, 3.96] b	91.9 [76.0, 108] a
		Maize	3.97 [3.43, 4.50] a	110 [94.0, 126] a
		Faba bean	3.62 [3.08, 4.16] ab	108 [92.5, 124] a
		Pea	3.55 [3.01, 4.09] ab	102 [85.7, 117] a
	168	Wheat	8.53 [6.96, 10.1] a	140 [114, 166] a
		Maize	8.44 [6.88, 10.0] a	141 [115, 167] a
		Faba bean	7.45 [5.89, 9.01] a	147 [121, 173] a
		Pea	8.27 [6.70, 9.83] a	140 [114, 165] a
	182	Wheat	12.4 [10.8, 14.1] a	160 [119, 201] a
		Maize	12.7 [11.0, 14.3] a	176 [143, 228] a
		Faba bean	9.65 [7.99, 11.3] b	142 [106, 199] a
		Pea	12.4 [10.8, 14.1] a	179 [138, 220] a
	196	Wheat	14.5 [12.5, 16.5] a	155 [122, 189] b
		Maize	16.8 [13.5, 18.8] a	220 [166, 269] a
		Faba bean	11.7 [9.72, 13.7] b	162 [129, 195] ab
		Pea	15.6 [13.6, 17.6] a	192 [159, 226] ab
	220	Wheat	15.7 [14.4, 17.1] a	183 [162, 204] bc
		Maize	15.6 [14.3, 16.9] a	212 [191, 233] a
		Faba bean	11.1 [9.80, 12.5] b	158 [136, 179] c
		Pea	16.4 [15.1, 17.7] a	206 [185, 227] ab

(iii) Faba bean. DOY 226 was the final harvest. (**Table S5.6 continued**)

Species	DOY	Companion	Biomass (Mg ha^{-1})	N uptake (kg ha^{-1})
Faba bean	133	Faba bean	0.534 [0.450, 0.617] a	22.9 [18.6, 27.3] a
		Maize	0.501 [0.418, 0.584] a	21.7 [17.4, 26.1] a
		Wheat	0.548 [0.465, 0.631] a	23.6 [19.2, 27.9] a
		Pea	0.490 [0.407, 0.573] a	21.0 [16.6, 25.4] a
	147	Faba bean	1.93 [1.48, 2.39] a	59.7 [45.0, 74.5] a
		Maize	2.00 [1.55, 2.46] a	65.5 [50.8, 80.2] a
		Wheat	1.63 [1.17, 2.09] a	52.0 [37.3, 66.8] a
		Pea	1.78 [1.33, 2.24] a	55.8 [41.1, 70.5] a
	168	Faba bean	5.62 [4.06, 7.17] b	146 [107, 185] b
		Maize	7.91 [6.35, 9.46] a	229 [190, 268] a
		Wheat	6.10 [4.55, 7.65] b	158 [119, 197] b
		Pea	6.14 [4.59, 7.70] b	150 [111, 190] b
	182	Faba bean	9.29 [7.25, 11.3] b	195 [148, 241] c
		Maize	12.2 [10.1, 14.2] a	291 [244, 337] a
		Wheat	10.5 [8.50, 12.6] ab	234 [187, 280] bc
		Pea	11.2 [9.12, 13.2] ab	257 [210, 303] ab
	196	Faba bean	12.6 [10.1, 15.1] a	273 [213, 333] b
		Maize	16.0 [13.5, 18.5] a	366 [307, 426] a
		Wheat	15.2 [12.7, 17.7] a	299 [239, 359] ab
		Pea	16.2 [13.7, 18.7] a	375 [315, 434] a
	226	Faba bean	13.8 [11.6, 16.0] a	359 [287, 432] b
		Maize	17.0 [14.8, 19.2] a	479 [407, 552] a
		Wheat	15.9 [13.7, 18.2] a	426 [353, 498] ab
		Pea	14.9 [12.7, 17.1] a	384 [311, 457] ab

(iv) Pea. DOY 210 was the final harvest. (**Table S5.6 continued**)

Species	DOY	Companion	Biomass (Mg ha^{-1})	N uptake (kg ha^{-1})
Pea	133	Pea	0.703 [0.593, 0.812] a	32.2 [25.6, 38.9] a
		Maize	0.695 [0.586, 0.805] a	32.2 [25.6, 38.8] a
		Wheat	0.659 [0.550, 0.768] a	30.1 [23.5, 36.8] a
		Faba bean	0.666 [0.557, 0.775] a	30.8 [24.2, 37.5] a
	147	Pea	2.41 [2.02, 2.80] a	84.1 [70.4, 97.9] a
		Maize	2.54 [2.15, 2.93] a	89.0 [75.3, 103] a
		Wheat	2.50 [2.11, 2.89] a	87.1 [73.4, 101] a
		Faba bean	2.39 [2.00, 2.78] a	83.7 [69.9, 97.4] a
	168	Pea	6.18 [5.37, 6.98] bc	152 [134, 169] b
		Maize	7.42 [6.61, 8.22] a	197 [179, 214] a
		Wheat	6.49 [5.68, 7.29] b	162 [145, 180] b
		Faba bean	5.83 [5.03, 6.64] c	156 [139, 174] b
	182	Pea	10.3 [9.35, 11.2] b	225 [204, 247] b
		Maize	12.2 [11.3, 13.1] a	264 [243, 285] a
		Wheat	9.72 [8.79, 10.7] b	213 [192, 235] b
		Faba bean	7.44 [6.31, 8.56] c	163 [137, 189] c
	196	Pea	12.3 [9.25, 14.5] a	280 [216, 331] a
		Maize	13.2 [10.8, 15.6] a	296 [244, 348] a
		Wheat	13.9 [11.5, 16.3] a	291 [239, 343] a
		Faba bean	7.86 [5.46, 10.3] b	197 [145, 249] b
	210	Pea	11.8 [9.93, 13.7] a	265 [227, 302] a
		Maize	10.8 [8.91, 12.7] a	245 [207, 282] a
		Wheat	10.2 [8.33, 12.1] ab	232 [195, 270] a
		Faba bean	7.48 [5.60, 9.36] b	168 [131, 206] b

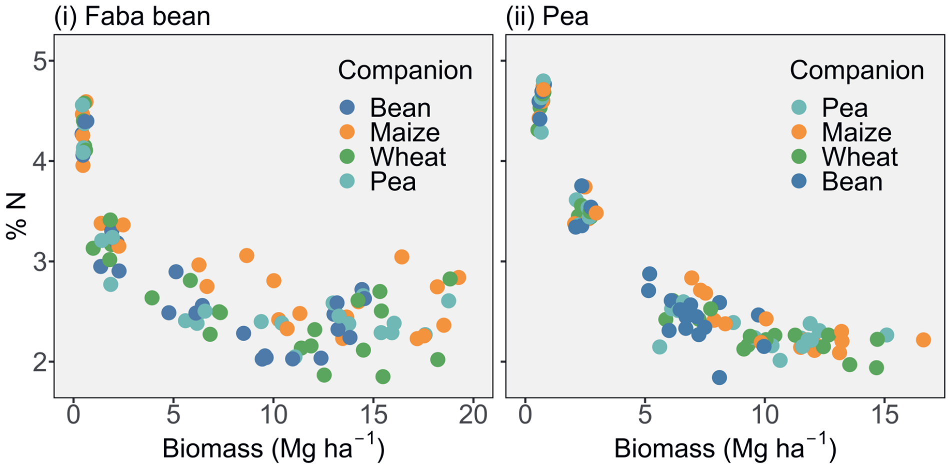

Fig. S5.1 Above-ground N concentration (%N) per species strip compared with above-ground biomass per species strip for faba bean (i) and pea (ii) in 2019. Colours within each panel represent %N and biomass of the focal species when it was with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Points are the measurements from different blocks.

Summary

There is a vast literature documenting that intercropping has higher land productivity and resource use efficiency than monocropping, mainly due to interspecific complementarity, but information is scarce on the potential of strip intercropping under Western-European conditions with moderate inputs of fertiliser, due to a shortage of experimental studies. Therefore, the potential of strip intercropping under Western-European production conditions is unclear.

The aim of this thesis is to determine the yield responses, resource capture and resource conversion efficiency of strip intercropping with different species combinations under conventional management in the Netherlands. I studied the growth and resource use efficiency of six bi-specific strip intercrops based on four crop species with different functional traits: maize, *Zea mays* L.; wheat, *Triticum aestivum* L.; faba bean, *Vicia faba* L.; and pea, *Pisum sativum* L. Maize is a C_4 species with later sowing and harvesting than the other three species, which have C_3 photosynthesis and are better adapted to growth under cool conditions in spring. Maize and wheat are cereals, whereas faba bean and pea are legumes which have the potential to fix atmospheric nitrogen (N) through symbiosis with *Rhziobium* bacteria. Different species combinations represent different potential mechanisms for complementarity. I used a species-tailored N fertilisation for each species with agronomically meaningful N doses in their species strips in intercrops. I explored how intercropped species captured and utilised resources differently compared to monocropped species and identified the complementarity mechanisms driving yield gains in intercropping.

In Chapter 2, I compared yield performance of the six intercrops at both the system level and the species level. Relay intercrops involving late-sown maize on average achieved increased land use efficiency (i.e., land equivalent ratio [LER] > 1) and absolute yield increases (i.e., net effect [NE] > 0) compared to the respective monocrops. In contrast, simultaneous intercrops, i.e., those species combinations not involving maize, on average did not show such advantages. The distinction between relay and simultaneous intercrops held for systems with and without legumes. This finding suggests that temporal complementarity is the key for obtaining yield advantages in strip intercropping when the cereals receive moderate fertiliser inputs to meet their demands. Cereal-legume N capture complementarity appears to have limited contribution in this situation. The importance of temporal complementarity was further supported by the results of regression analysis, indicating that temporal niche differentiation (TND) had positive effects on LER and NE across all species combinations. However, whether or not the intercrop was a cereal/legume combination did not explain the variation in LER and NE. Faba bean emerged as a dominant species in all species combinations due to its tall and rapidly growing canopy. In the maize/faba bean intercrop, maize did not achieve yield increases as observed in the intercrops with wheat and pea. In simultaneous intercrops, faba bean significantly reduced the yields of the companion species wheat and pea. The diminished performance in land productivity and yield increases of relay intercrops in 2019, compared to 2018, can be attributed to the later sowing of the three early-sown species, as a result of adverse spring weather. This highlights the importance of designing adequate temporal complementarity to ensure increased yields for both early- and late-sown species. The results of Chapter 2 show that temporal complementarity positively affects land use efficiency and yield gains in strip intercropping in the Netherlands. Both cereal/cereal and cereal/legume mixtures can be designed as relay intercrops by combining early- and late-sown species. But combinations with a legume will require lower N input.

Nutrients and water were supplied to meet species demand. Hence, I expected that light would be the main limiting resource in my experiments. In Chapter 3, I tried to figure out whether yield advantages in a species were caused mainly during early or late growth. I did an analysis of yield components, and explored how light capture before and during grain filling affected total grain number per unit land area (GN) and thousand-grain weight (TGW) of the four species in all treatments, and how these yield components were related to species and intercrop productivity. The results showed that in both monocrops and intercrops, grain yield was more strongly associated with GN than with TGW. In relay intercrops, early-sown species achieved increased GN, correlating with enhanced pre-grain filling light capture compared to monocrops. The increased GN in intercropped maize could be attributed to improved light availability once maize overtopped the companion species (only with wheat and pea, but not with faba bean). Maize then efficiently capitalised on the initially determined GN, sufficiently filling all grains due to increased per-grain light availability after companion species were harvested. In contrast, the early-sown species did not have improved light availability during grain filling, and as a result, they were unable to completely fill all grains and thus showed a grain number-grain weight trade-off. In simultaneous intercrops lacking temporal complementarity, presence of faba bean caused substantial reductions in both GN and TGW in companion species wheat and pea, presumably due to faba bean shading. The results in this chapter underscore the importance of temporal complementarity for intercropped species to achieve yield gains. In relay intercrops, the increased light availability when the total grain number is determined enables component species to increase the number of grains per unit land area, compared to monocrops. The late-sown species may have greater opportunity to fully utilise the increased grain number by adequately filling all grains. This occurs under enhanced light availability after the early-sown companions are harvested.

In Chapter 4, I further explored intercropping effects on light capture and conversion. In light of the significance of border rows in strip intercropping, I used a random ray tracing model to distinguish light capture between border and inner rows of each species in intercrops. The results showed that in relay intercrops all three early-sown species obtained higher biomass in the border rows than the corresponding monocrops, due to increased light capture, but not increased light use efficiency (LUE). Intercropped maize, both in the border and inner rows, had higher LUE in all relay intercrops. Increased biomass was observed when maize captured more light in intercrops with wheat and pea, but not with faba bean. In simultaneous intercrops, faba bean significantly reduced both light capture and LUE of wheat and pea across all rows. Compared to relay intercrops, simultaneous intercrops did not have efficient light capture and conversion. Faba bean created a light environment in which wheat and pea were negatively affected in both light capture and conversion. However, the advantaged faba bean did not compensate for these losses merely by capturing more light, as its LUE remained unchanged. The findings of this chapter suggest that C_3/C_4 combinations, featuring temporal complementarity between species, are more likely to enhance light use than C_3/C_3 combinations in which species grow together for most of the season. By distinguishing light capture between border and inner rows, the analysis provides a compelling evaluation of how different rows contribute to the effects of strip intercropping on light capture. This approach can aid in deciding the optimal row configuration for a particular combination of species in a given production situation.

In Chapter 5, I explored N uptake and fertiliser N use efficiency of the six intercrops. I found that the species-tailored N fertilisation not only prevented cereals from experiencing significant N stress but also facilitated and necessitated legumes to exploit N fixation to meet most of their N demands. Within this N strategy, relay intercrops used land more efficiently to capture N than simultaneous intercrops and monocrops. In relay intercrops, early-sown species achieved increased N uptake compared to monocrops, particularly in the border rows. Maize had increased N uptake in intercrops with wheat and pea, though not with faba bean, and the N uptake advantage of maize was not as pronounced as that of the early-sown companions. Furthermore, relay intercrops on average saved 14% fertiliser N compared to monocrops for the same product output. In simultaneous intercrops lacking temporal complementarity, faba bean substantially reduced N uptake of wheat and pea. The findings of this chapter indicates that temporal complementarity between species is a crucial factor for increasing N uptake and efficient use of fertiliser N under a species-tailored N strategy. However, there is a lack of evidence supporting that cereal-legume N capture complementarity played a decisive role under the conditions of this study.

In Chapter 6, I reflect on the intercropping effects on light and N use presented in the preceding four research chapters. I found that light was indeed the main limiting resource in this study. The pivotal role of temporal complementarity in relay intercrops was based on its ability to increase light capture of intercropped species, subsequently promoting N capture efficiency under a species-tailored N fertilisation. Simultaneous intercrops, in contrast, created a light environment in which the advantaged species markedly reduced the light capture of the disadvantaged species, thereby diminishing N capture as well. However, the advantaged species (i.e., faba bean) did not gain more than the disadvantaged species lost. By synthesising the intercropping effects on the capture and conversion efficiencies of light and N, I concluded that intercropping has greater effects on resource capture than on resource conversion. In the end, I emphasised that one should determine the desired intercropping patterns, species, and management based on clearly defined production objectives and evaluate the performance using appropriate metrics.

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Zishen Wang
王子申
April 11, 2024, at home on Haarweg

About the author

Zishen Wang was born in February 1991 in Hequ, Shanxi, China, a town situated along the Yellow River, where he spent his first fourteen years and received primary and junior high education. After that, he moved to Taiyuan, the capital of the province, continuing his senior high education. From 2009, he majored in agricultural hydraulic engineering at Shanxi Agricultural University in Taigu, a town one hour's drive from the provincial capital. In 2013, after earning his Bachelor's degree, he started his master's study at Northwest Agriculture & Forestry University in Yangling, China. His master thesis was about winter wheat water consumption in the arid region of Northwestern China and the relevant irrigation regime redesign based on that. Since then, his interest gradually shifted from agricultural engineering to the crops themselves. In 2016, after earning his Master's degree, he moved to Xi'an and started his junior engineer career at Shaanxi Land Engineering Group Co., Ltd., where he was engaged in agricultural land-use planning, helping farmers in underdeveloped regions improve their arable land. In 2017, he decided to return to academia and started his research as a PhD candidate at the Centre for Crop Systems Analysis, Wageningen University & Research, the Netherlands. His PhD project was part of the European Union's Horizon 2020 Research and Innovation Programme, project ReMIX: Redesigning European cropping systems based on species MIXtures. He was under the supervision of Dr. Wopke van der Werf, Dr. Tjeerd Jan Stomph, and Prof. Dr. Jochem Evers. His project focused on productivity and resource efficiency in strip intercropping in the Netherlands, aiming to provide an option for crop diversification for the country and possibly broader Western-European regions. The outcomes of his project have been presented in this thesis.

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List of publications

Wang, Z., Dong, B., Stomph, T.J., Evers, J.B., L. van der Putten, P.E., Ma, H., Missale, R., van der Werf, W., 2023. Temporal complementarity drives species combinability in strip intercropping in the Netherlands. Field Crops Res 291, 108757. https://doi.org/10.1016/J.FCR.2022.108757

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Dong, B., **Wang, Z.**, Evers, J.B., Jan Stomph, T., van der Putten, P.E.L., Yin, X., Wang, J.L., Sprangers, T., Hang, X., van der Werf, W., 2024. Competition for light and nitrogen with an earlier-sown species negatively affects leaf traits and leaf photosynthetic capacity of maize in relay intercropping. European Journal of Agronomy 155, 127119. https://doi.org/10.1016/J.EJA.2024.127119

Stomph, T.J., Dordas, C., Baranger, A., de Rijk, J., Dong, B., Evers, J., Gu, C., Li, L., Simon, J., Jensen, E.S., Wang, Q., Wang, Y., **Wang, Z.**, Xu, H., Zhang, C., Zhang, L., Zhang, W.P., Bedoussac, L., van der Werf, W., 2020. Designing intercrops for high yield, yield stability and efficient use of resources: Are there principles?, in: Advances in Agronomy. Academic Press Inc., pp. 1–50. https://doi.org/10.1016/bs.agron.2019.10.002

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review/project proposal (10.5 ECTS)

- Effects of plant-plant interactions on light and nitrogen use in intercropping
- Designing resource use-efficient intercrops of cereals and legumes for Europe by combining meta-analysis, experiments, and plant models

Post-graduate courses (6.8 ECTS)

- Introduction to R for statistical analysis; PE&RC and SENSE (2017)
- Structural equation modelling; PE&RC (2020)
- Generalised linear models; PE&RC and WIMEK (2021)
- Mixed linear models; PE&RC and WIMEK (2021)
- Advances in intercropping: principles and implementation; PE&RC (2021)
- Crop physiology and climate change: understanding fundamental processes to counter the challenge; PE&RC and University of Florida (2022)

Invited review of journal manuscripts (8 ECTS)

- Biological agriculture & horticulture: impact of millet, soybean, and Moldavian balm intercropping on organic sugar beet yield and quality (2019)
- Plant and soil: faba bean yield responses to interspecific interactions in intercropping (2021)
- Soil and tillage research: enhanced productivity and nitrogen fixation in maize/faba bean intercropping with rhizobial inoculation in reclaimed desert soil (2021)
- Journal of integrative agriculture: improving N uptake efficiency in maize/legume intercropping through enhanced root distribution and soil nitrogen cycle (2021)
- South African journal of plant and soil: impact of cassava sowing dates on yield performance and species competitiveness of voandzou-cassava intercropping (2021)
- Agricultural systems: light use in paddy cropping systems (2021)
- Food and energy security: kernel number responses of maize to light stress (2022)
- Annals of agricultural sciences: wheat/tomato intercropping responses to chilling stress (2022)

Deficiency, refresh, brush-up courses (24 ECTS)

- Advanced statistics; Biometrics, WUR (2017)
- Systems analysis, simulation, and systems management; PPS, WUR (2017)
- Functional diversity for sustainable crop production; CSA, WUR (2018)
- Ecological modelling and data analysis in R; CSA, WUR (2018)

Competence, skills, and career-oriented activities (5.9 ECTS)

- Scientific writing; Wageningen in'to Language (2020)
- Presenting with impact; Wageningen in'to Language (2020)
- Tidy data transformation and visualisation with R; PE&RC (2020)
- Ethics in plant and environmental sciences; WGS (2022)
- Career orientation; WGS (2023)
- Scientific integrity; WGS (2023)

PE&RC annual meetings, seminars, and PE&RC weekend/retreat (1.5 ECTS)

- PE&RC Weekend for first years (2017)
- PE&RC Day (2021)
- PE&RC Symposium: Crop diversification - new perspectives beyond agronomy (2022)

Discussion groups/local seminars or scientific meetings (9 ECTS)

- ReMIX thesis ring (2017-2018)
- Modelling plant form and function discussion group (2018-2020)
- Statistical rethinking (2019)
- Automating agroecology: how to make an ecofeminist robot (2019)
- Journal club CSA (2022)

International symposia, workshops, and conferences (8.1 ECTS)

- Crop mixture and mechanisation workshop with China Agricultural University; oral presentation; Wageningen (2019)
- ReMIX annual meeting; oral presentation; online (2020)
- Crop mixture workshop with University of Bonn; oral presentation (2020)
- Intercropping for sustainability conference; oral presentation; online (2021)
- Netherlands annual ecology meeting; poster presentation; online (2021)
- Agricultural green development workshop; oral presentation; Wageningen (2023)

Lecturing/supervision of practicals/tutorials (0.6 ECTS)

- Functional diversity for sustainable crop production (2022)
- Research methods in crop science (2022)

BSc/MSc thesis supervision (13.5 ECTS)

- The border row effect on light interception and radiation use efficiency in wheat-maize strip intercropping
- Interception and use efficiency of light in simultaneous and relay intercrops
- Wheat yield responses to light capture in strip intercropping: competition and complementarity
- Yield response of faba bean in strip intercropping
- Comparing yield and yield components of species in different strip intercropping systems
- Light distribution in strip intercrops

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