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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 fertilized 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.

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., 2017; 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, 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).

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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, while 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., 2017; 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 fertilizer 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 solubilize 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 neighbors, 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, while 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 fertilization 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 fertilized in their strips in accordance with recommendations for the species under conventional farming, i.e., with the use of industrial N fertilizer. 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. Materials and methods

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 (Supplementary Fig. S1). 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 (Supplementary Table S1).

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. 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.

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). 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 (Supplementary Fig. S1). 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. 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 randomized complete block designs with six (2018) or four (2019) replicates. The row orientation was approximately north-south.

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):

$$\mathrm{TND} = 1 - \frac{T_{\mathrm{overlap}}}{T_{\mathrm{system}}} \tag{1}$$

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) fertilizer 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 105 kg K_2O ha^{-1} in both years, while P fertilizer was applied at a rate of 67.5 kg ha^{-1} P_2O_5 in 2018 and 78.75 kg ha^{-1} P_2O_5 in 2019 (Supplementary Table S2). The amount of N fertilizer for each species was based on recommendations for arable crop fertilization 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 (Supplementary Table S2). Fertilizer input in wheat and maize was given in two splits. All N fertilizer in monocrops and intercrops was applied next to the rows by a machine (ENTI Co., the Netherlands), except the N fertilizer of the second split in maize, which was applied by hand. Species strips in intercrops received the same fertilization 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 (Supplementary Fig. S1).

2.2. Measurements: final harvest

All species were harvested at maturity. Two neighboring 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

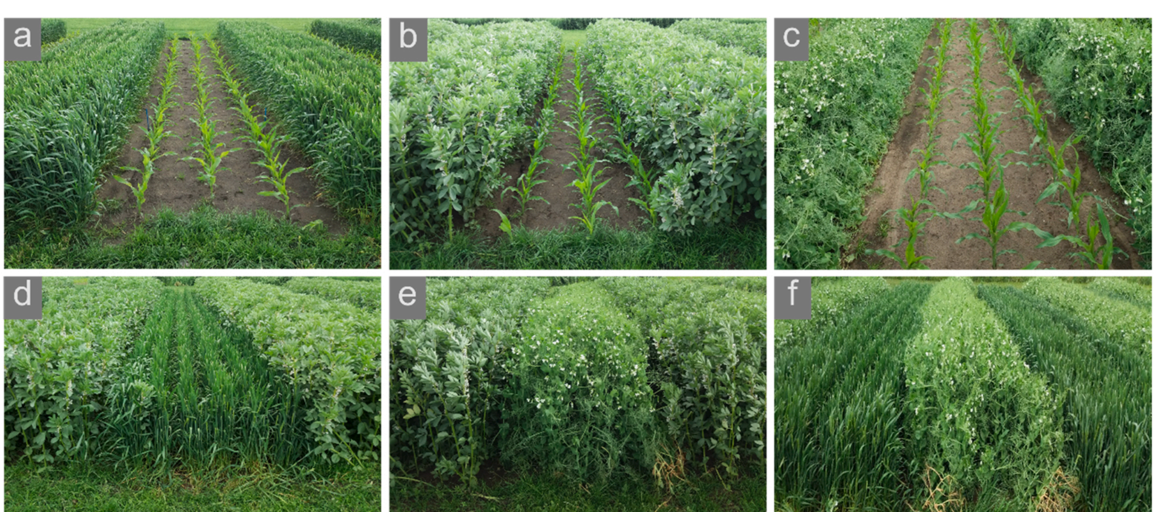

Fig. 1. Six intercrops on June 15, 2019: a. maize/wheat; b. maize/faba bean; c. maize/pea; d. faba bean/wheat; e. faba bean/pea; f. wheat/pea.

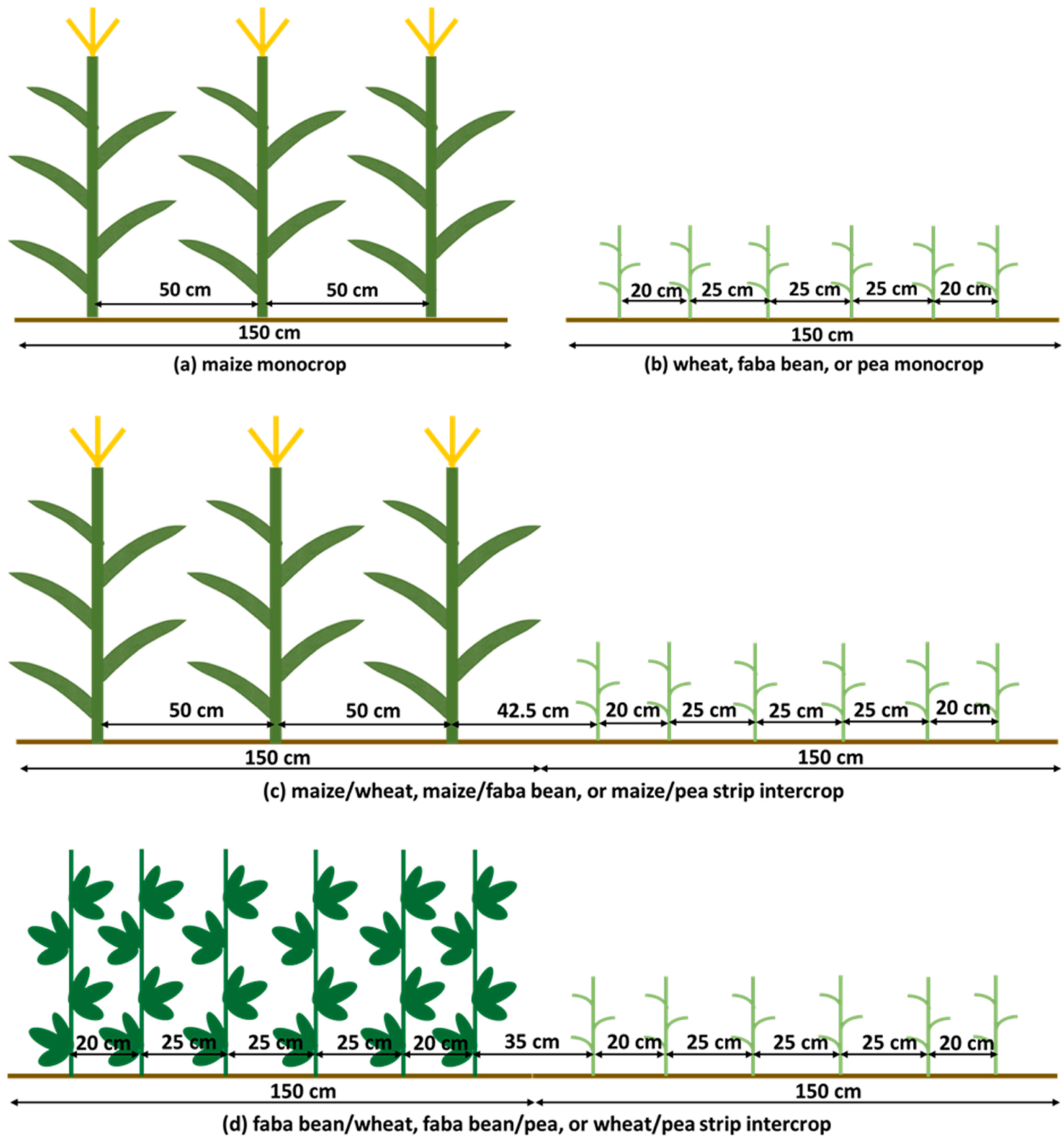

Fig. 2. Row configuration in the monocrops and intercrops. Sowing was done with a narrow sowing machine (Belt Cone Seeder, Haldrup Co., Germany) and a small tractor with 133 cm space between the wheel tracks (Fendt 207, Fendt Co., Germany). (a) monocrop of maize with a 50 cm row distance; (b) monocrop 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 1, and rows 3 and 4 were inner row 2. In intercrops, the maize strip had a border row proportion of 2/3, while the strips of wheat, faba bean, and pea had a border row proportion of 1/3.

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.

2.3. Data analysis

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

$$\mathrm{LER} = \mathrm{pLER}_1 + \mathrm{pLER}_2 = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \tag{2}$$

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

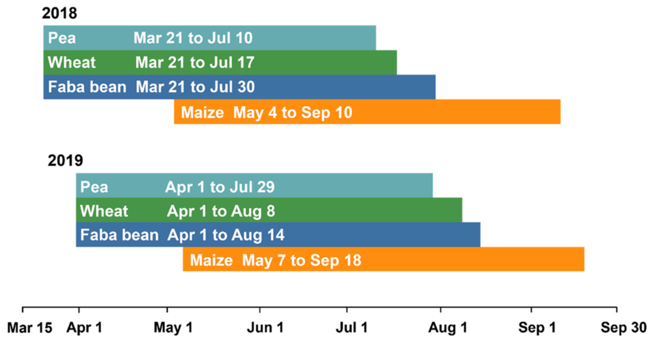

Fig. 3. Growing periods (from sowing to harvesting) of maize, wheat, faba bean, and pea in 2018 and 2019. In 2019, the later sowing of early species extended the period of co-growth, aggravated competition, and reduced temporal complementarity.

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:

$$\Delta RY_i = RY_i - RD_i \tag{3}$$

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):

$$\begin{aligned} \text{LER} &= \text{pLER}_1 + \text{pLER}_2 = (\Delta RY_1 + RD_1) + (\Delta RY_2 + RD_2) \\ &= \Delta RY_1 + \Delta RY_2 + 1 \end{aligned} \tag{4}$$

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

$$\text{CR}_1 = \frac{\text{pLER}_1}{\text{pLER}_2} \times \frac{p_2}{p_1};\ \text{CR}_2 = \frac{\text{pLER}_2}{\text{pLER}_1} \times \frac{p_1}{p_2} \tag{5}$$

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:

$$\text{CR}_1 = \frac{\text{pLER}_1}{\text{pLER}_2};\ \text{CR}_2 = \frac{\text{pLER}_2}{\text{pLER}_1} = \frac{1}{\text{CR}_1} \tag{6}$$

If $\text{CR}_i > 1$, 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:

$$\text{NE} = \text{NE}_1 + \text{NE}_2 = (Y_1 - EY_1) + (Y_2 - EY_2) \tag{7}$$

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:

$$EY_i = M_i \times p_i \tag{8}$$

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 $\text{NE} > 0$, 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 analyze 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. 9).

$$Y_{ijk} = Y + \beta_i + \tau_j + \beta\tau_{ij} + b_{ik} + \epsilon_{ijk} \tag{9}$$

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 characterized 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 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 analyze 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. 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 visualization (Wickham, 2016).

3. Results

3.1. *Grain yield, vegetative biomass, and harvest index per species strip*

3.1.1. *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. 4 i; Supplementary Table S3 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

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

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.

3.1.2. 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. 4 ii; Supplementary Table S3 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 ($P < 0.001$).

3.1.3. 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. 4 iii; Supplementary Table S3 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

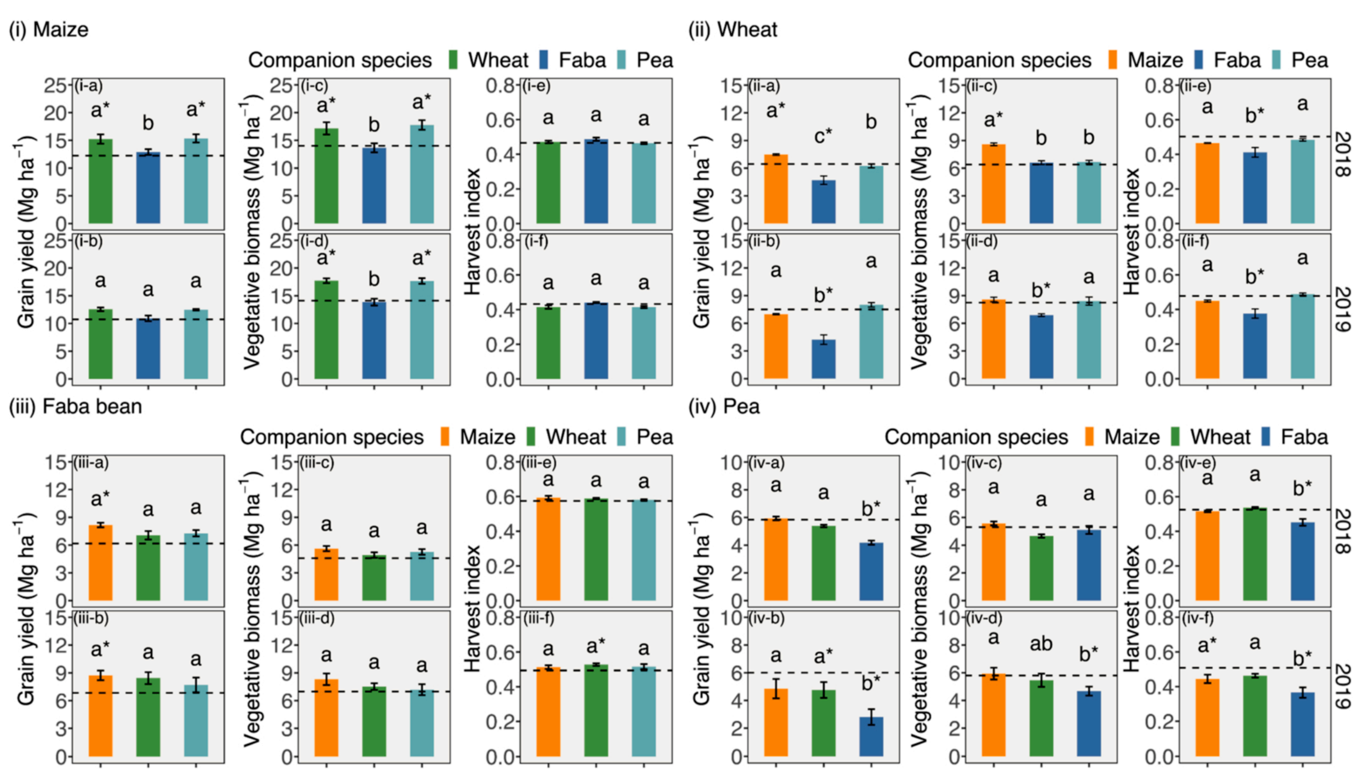

Fig. 4. Grain yield, vegetative biomass, and harvest index of maize (i), wheat (ii), faba bean (iii), and pea (iv) when growing with different companion species in 2018 (a, c, e) and 2019 (b, d, f). Grain yield and vegetative biomass are expressed per unit species area of the species to allow comparison of intercrops and monocrops. Colors 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, while 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 Supplementary Table S3.

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 ($P = 0.040$).

3.1.4. 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. 4 iv; Supplementary Table S3 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.

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. 5; Supplementary Table S4 i). In 2018, the relay systems with maize all obtained grain yield LER values significantly higher than one, while 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.

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 while 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 while 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, while 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, while the other intercrops had near zero NE on grain yield (Fig. 6; Supplementary Table S5).

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). 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.

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 (Supplementary Table S6). This model implies that LER and NE increased with TND with a common slope across all species combinations (no interaction), while the six differernt 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. 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.

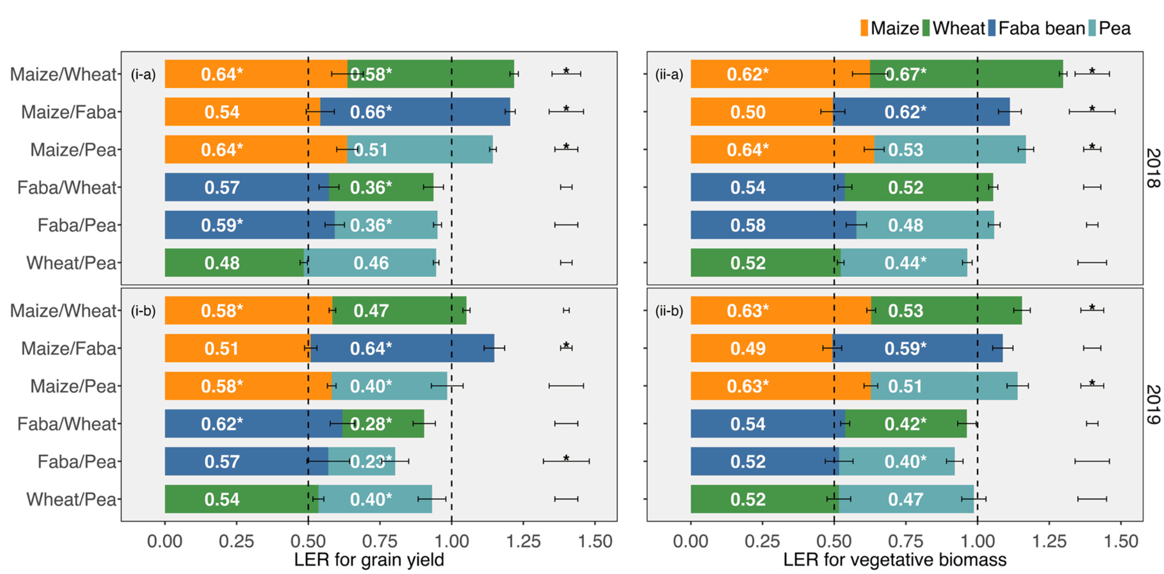

Fig. 5. Land equivalent ratio of intercrops and partial land equivalent ratio of component species for grain yield (i) and vegetative biomass (ii) in six species combinations in 2018 (a) and 2019 (b). Colors represent four different component species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Error bars attached to the bars indicate the standard errors of pLER, while 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 Supplementary Table S4.

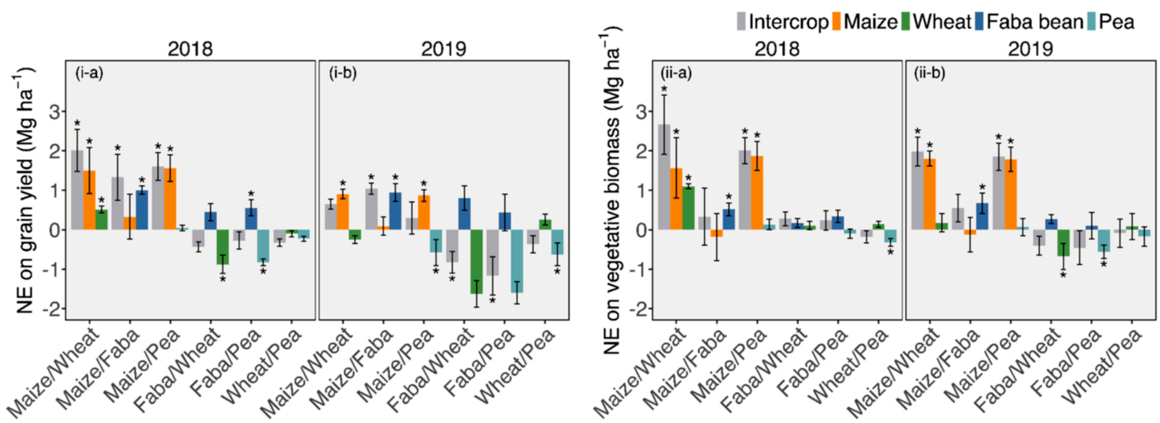

Fig. 6. Net effects on grain yield (i) and vegetative biomass (ii) in 2018 (a) and 2019 (b) of intercrops (grey) and the component species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Error bars represent standard errors of the means. The asterisks denote significant differences from zero by examining if zero was located outside the 95% confidence interval of NE. Further details are presented in Supplementary Table S5.

Table 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).

Year	Companion species	Competitive ratio for grain yield			Competitive ratio for vegetative biomass		
		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 (.)

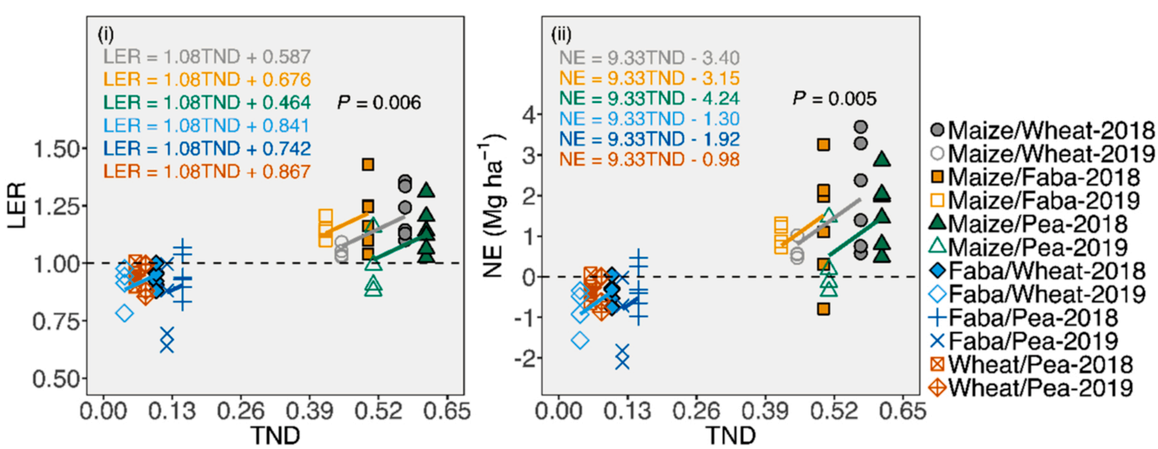

Fig. 7. Relationships between TND and LER (i) and NE (ii) for grain yield. The equations and symbols are in the same color for a particular species combination. The *P*-values are related to the slopes, indicating whether they are significantly different from zero (F-test).

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 (Supplementary Fig. S2). 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.

3.4.1. Relay intercrops

3.4.1.1. Maize. 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. 8 i; Supplementary Table S7 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.

3.4.1.2. Faba bean, wheat, and pea. Positive border row effects were

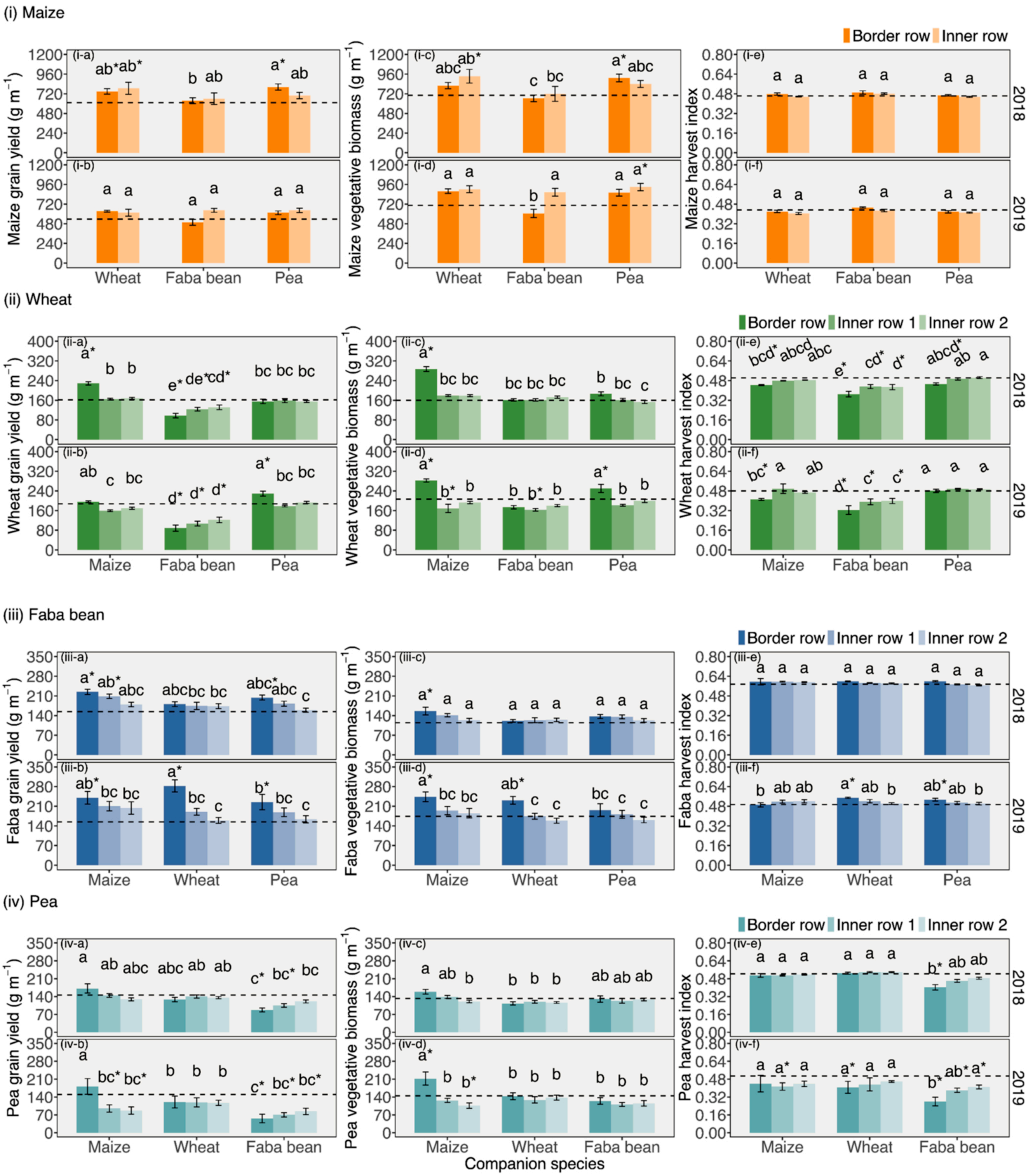

Fig. 8. Grain yield, vegetative biomass, and harvest index of different rows in intercrops for maize (i), wheat (ii), faba bean (iii), and pea (iv) in 2018 (a, c, e) and 2019 (b, d, f). Companion species are indicated along the X-axis. Dashed lines represent grain yield, vegetative biomass, and harvest index of the monocrop of the focal species indicated along the Y-axis (these monocrop values represent the expected values of intercrop rows). Each color 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, while 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 Supplementary Table S7.

observed for faba bean grain yield in the maize/faba bean intercrop in both years (Fig. 8 iii; Supplementary Table S7 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. 8 ii; Supplementary Table S7 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. 8 iv; Supplementary Table S7 iv).

3.4.2. *Simultaneous intercrops*

3.4.2.1. Faba bean/wheat, faba bean/pea. 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. 8 iii; Supplementary Table S7 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. 8 ii and iv; Supplementary Table S7 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.

3.4.2.2. Wheat/pea. In the wheat/pea intercrop in 2019, border row wheat had a 22% higher grain yield and a 22% higher vegetative biomass than expected ($P < 0.001$), while no such increases were found in 2018 (Fig. 8 ii; Supplementary Table S7 ii). The harvest index of wheat was 10% lower in border row wheat in the wheat/pea intercrop than expected in 2018 ($P = 0.015$), while 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 ($P = 0.014$), while no such a decrease was found in 2018 (Fig. 8 iv; Supplementary Table S7 iv).

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. 5 and 6). The positive effects of TND on LER and NE were significant in all intercrops (Fig. 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. 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., 2017; 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., 2017, 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 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 harvest 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. 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 fertilization 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 fertilization 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 fertilization strategy applied in this study, the cereals received moderate N fertilization, and the legumes received low starter N fertilization. This strategy differs from the high-input strategy giving full fertilization 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, 2009). We adopted this species-specific fertilization strategy to avoid over-fertilization of the legumes, and achieve policy targets of lowering N application in agriculture, while at the same time avoiding under-fertilization 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 neighboring strips can occur (Zhang et al., 2022) and could affect species access to the designed N fertilizer 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 neighboring strip as earlier reported for fully fertilized 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 neighboring cereal. On the other hand, it is entirely possible that legumes acquired N from the neighboring 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 fertilization 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 while maize plants remained erect. The lodging resulted in large grain yield decreases in inner rows 1 and 2 of pea (Fig. 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. 5 and 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 fertilizer 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. 4 ii and iv). The border rows suffered the most due to the close proximity (Fig. 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. 8 ii, iii, and iv). In contrast, faba bean with maize produced substantially higher grain yield at only a slight penalty for maize (Fig. 4 i and iii; Fig. 8 i and iii), leading to overall gains of the system (Figs. 5 and 6). The largest intercepts of the LER $\sim$ TND and the NE $\sim$ 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. 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 fertilizer 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 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 fertilization 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 optimized 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 mechanization 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 mechanization options need to be explored to benefit from the application of intercropping with narrower strips.

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.

CRediT authorship contribution statement

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

Declaration of Competing Interest

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

Data Availability

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2022.108757.

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