



Temporal complementarity drives nitrogen uptake in strip intercropping with or without legumes

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Abstract

Cereal/legume intercropping enables complementary nitrogen (N) uptake, whereas relay intercropping allows temporal complementarity. However, how these mechanisms contribute to N uptake under moderate, species-tailored N fertilization remains unclear, and clarifying this could inform intercropping practices aligned with Good Agricultural Practices in Europe. We therefore 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 strip intercrops and corresponding monocrops. We compared relay intercrops involving maize (late sown) with simultaneous intercrops without maize, across cereal/legume, cereal/cereal, and legume/legume combinations. All species received locally recommended fertilizer amounts for conventional agriculture in the Netherlands. In relay strip intercrops, the early-sown wheat, faba bean, and pea had higher N uptake than the respective monocrops, especially in the border rows of strips. Maize N uptake increased when intercropped with wheat or pea in a year with substantial temporal complementarity. Intercropping with faba bean did not result in increased N uptake for either cereals or pea. Relay intercrops showed land equivalent ratios for N uptake and fertilizer N equivalent ratios mostly above one, while for simultaneous intercrops these were mostly close to one. Therefore, relay intercrops used land more efficiently for N uptake and saved fertilizer N for yield compared to monocrops, whereas simultaneous intercrops did not. We investigated, for the first time, the relative importance of temporal complementarity and cereal-legume N acquisition complementarity for N uptake in strip intercropping under conventional European agriculture, showing that complementary N uptake was strongly associated with temporal complementarity. While inclusion of legumes in intercropping was not required to achieve complementary N capture, it allowed for reduced N input. Relay strip intercropping with species-tailored N input is a pathway toward more sustainable N use in agriculture that can complement cereal-legume complementarity.

Keywords Conventional agriculture · Strip intercropping · Moderate input · Species-tailored nitrogen fertilization · Nitrogen uptake · Land equivalent ratio for nitrogen uptake · Fertilizer nitrogen equivalent ratio

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 (Brooker et al. 2015; Stomph et al. 2020). Nitrogen (N) is an essential element for plant development and growth and is a main limiting nutrient for crop production (Leghari et al. 2016). Currently, N uptake and N fertilizer use efficiency have been studied mostly under two intercropping patterns that differ in production objectives and, consequently, in synthetic N input levels (Li et al. 2020b). In regions such as China, where the primary aim is to maximize absolute production, N fertilizer is often applied at high rates to prevent N limitation (Li et al. 2020b). These intercrops show substantial positive net intercropping effects on yield, based on the land-sharing of component species, i.e., large absolute yield increases compared to monocrops (Li et al. 2020b). In regions outside China, like

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Western Europe, where minimizing anthropogenic inputs is key, synthetic N fertilizer is applied at low rates (low-input agriculture) or not at all (organic agriculture) (Bedoussac et al. 2015; Vonzun et al. 2024).

Increases in N uptake and fertilizer use efficiency have been observed in both high- and low-input/organic intercrops due to reduced interspecific N competition (Bedoussac et al. 2015; Xu et al. 2020). However, the mechanisms may differ. High N fertilization studies showed land equivalent ratios for N uptake (LER_N) greater than one, indicating that intercrops take up more N per unit land than monocrops (Li et al. 2011). High-input intercrops are often relay intercrops where component species are grown in alternating strips that are usually between 1.5 and 3 m wide (van Oort et al. 2020). In these intercrops, temporal complementarity and canopy plasticity enhance light capture, maximizing yield under non-N-constrained conditions, whereas monocrops experience strong intraspecific competition for all resources (Liu et al. 2017). The extended period that a crop is in the field if a relay intercrop is grown further increases the overall capture of resources, such as light (Gou et al. 2017), water (Tan et al. 2020), and N (Li et al. 2011) compared to monocrops. Moreover, high-input intercrops use fertilizer N more efficiently than monocrops, as indicated by a fertilizer N equivalent ratio (FNER) greater than one (Li et al. 2020b; Xu et al. 2020). Low-input/organic intercrops are often cereal-legume combinations, grown in full mixtures or alternating rows. These systems benefit from strong rhizosphere interactions and easy mechanized management (Bedoussac et al. 2015). The advantages in N uptake of such systems mainly result from cereal species capturing more soil N per plant in intercrops than in monocrops, due to N fixation by legumes, provided that other growth factors are not limiting (Rodriguez et al. 2020).

Although both high-input and low-input/organic intercropping have been found to bring N savings, there is potential to improve the N fertilization strategy. Under the high-input strategy, intercrop N rates are either established as a specific total high dose (Li et al. 2011; Xing et al. 2023), or as the weighted average of monocrop N doses based on land proportions (Gao et al. 2022). Alternatively, the total intercrop N rate is the sum of monocrop rates, often used in additive design intercrops to maximize yield (Yang et al. 2017). These high-N-strategies supply up to 300 kg N fertilizer ha^{-1} (e.g., Xu et al. 2023) but often ignore species-specific needs, particularly in cereal/legume intercropping. High N input can down-regulate N fixation in legumes (Coskun et al. 2017), while cereals may become overly competitive, offsetting their yield gain with losses in legumes, leading to limited intercrop advantage (Yu et al. 2016). Additionally, high N fertilization increases the risk of leaching (Wang et al. 2022). Under the low-input strategy, crop species rely on initial mineral soil N and N released from organic matter and applied manure throughout the season (Hauggaard-Nielsen et al. 2009;

Bedoussac et al. 2015). The limited N input is not usually an issue for seedling establishment and early growth, but it can lead to unstable and constrained absolute yield gains of species mixtures (Hauggaard-Nielsen et al. 2008; Li et al. 2020b). The limitations of current N strategies in intercrops emphasize the need for species-specific fertilization at moderate input levels to balance productivity and environmental costs.

Complementarity enhances N uptake by allowing species to access N through different pathways, whereas competition limits N uptake when dominant species suppress others. The balance between complementarity and competition, influenced by species traits such as growth cycle, root architecture, and N-fixing ability, governs N acquisition at both species and system levels (Rodriguez et al. 2020; Yu et al. 2015; Zhang et al. 2022). In Western-European regions, most intercropping studies to date have focused on cereal-legume combinations under low-input or organic conditions (Hadir et al. 2024; Homulle et al. 2024), while only a few have been conducted under conventional input levels and only with limited species combinations, such as maize/wheat and wheat/soybean (Gou et al. 2016; Wang et al. 2023; Thompson et al. 2025). It remains unclear, across various species combinations, whether temporal complementarity or cereal-legume complementarity contributes more to efficient N use when N fertilizer is applied at moderate levels tailored to species-specific needs. Such information could advance our understanding of intercropping under agronomic practices aligned with Good Agricultural Practices guidelines (Baghasa 2008; FAO 2003) in Western-European regions.

In this study, we aim to investigate the effects of strip intercropping on N uptake when species are fertilized in accordance with species-specific recommendations for conventional agriculture in the Netherlands (Ministerie van Landbouw, Natuur en Voedselkwaliteit 2019). Our fertilization level is classified as “moderate” because it falls between high-input levels, as practiced in China (Li et al. 2011; Li et al. 2025), and low-input or organic levels, as practiced in sub-Saharan Africa and Europe (Bedoussac and Justes 2010; Namatsheve et al. 2020; Mugi-Ngenga et al. 2022; Hadir et al. 2024). We examine the advantages of intercropping for land savings in N uptake and fertilizer N savings for grain yield (Fig. 1). The study quantifies responses of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), and pea (*Pisum sativum* L.) in six bi-specific strip intercrops. The three C_3 species have the same sowing and similar harvest dates, whereas maize (C_4) is sown and harvested later than the other three species. We compare three relay intercrops (with maize) and three simultaneous intercrops (without maize) to assess temporal complementarity. We investigate the benefits of C_3 cereals with legumes in simultaneous and relay intercrops, as well as legume responses in both types. Late-sown maize responses in relay intercrops with cereals or legumes are also studied. Furthermore, we distinguish the responses

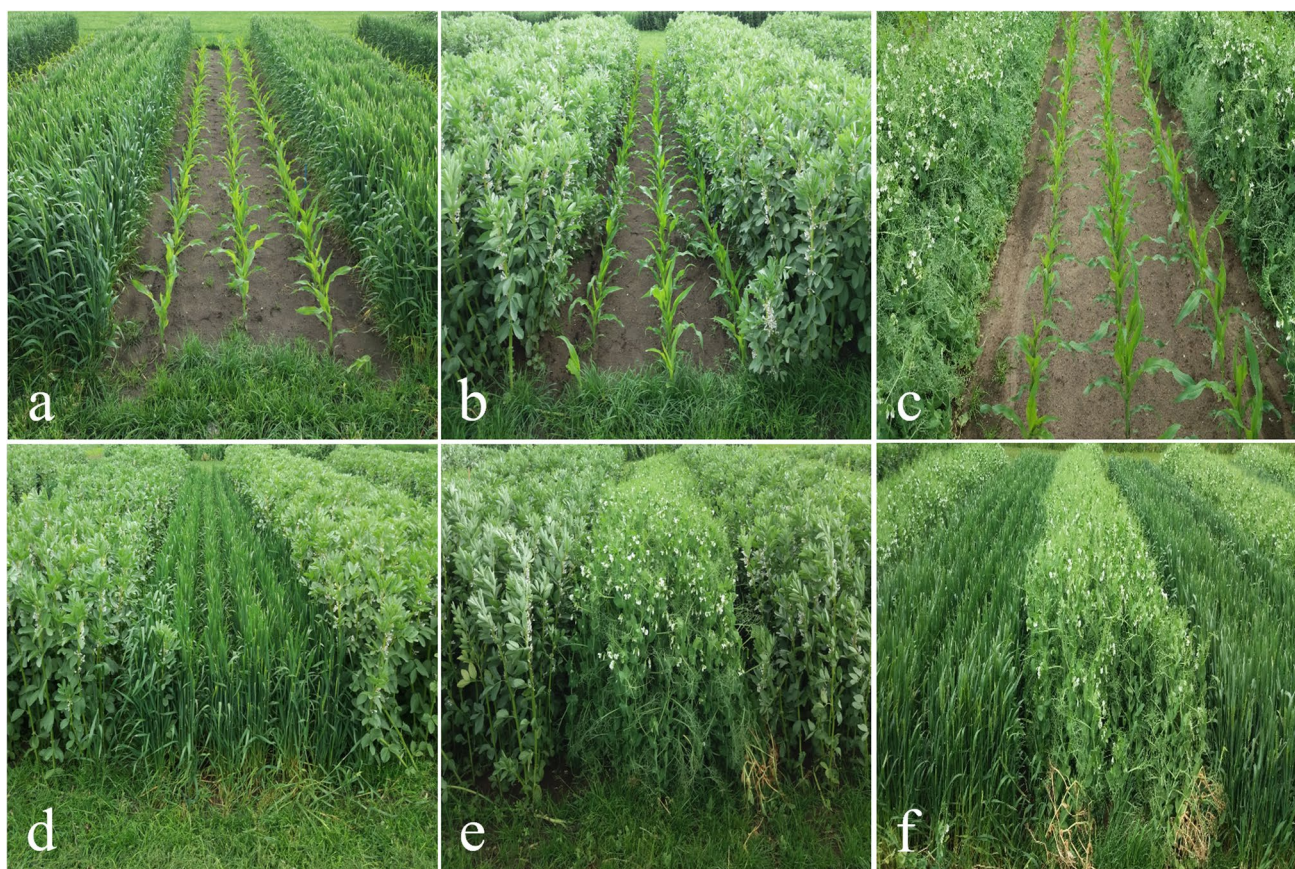


Fig. 1 Six intercropping treatments: **a** Maize/Wheat, **b** Maize/Faba bean, **c** Maize/Pea, **d** Faba bean/Wheat, **e** Faba bean/Pea, and **f** Wheat/Pea, as studied in two field experiments (2018 and 2019) in Wageningen, the Netherlands. We investigated the effects of strip intercropping on N uptake when species are fertilized in accordance with recommendations for arable crop fertilization in the Netherlands for non-organic agriculture. Intercrops with maize were relay inter-

crops with temporal complementarity between species. Four of the systems were a cereal/legume combination with high potential for complementarity for N uptake, while one system was cereal/cereal and one system was legume/legume. Photos originally published in Wang et al. (2023) under CC BY 4.0 licence. Composite image assembled by the authors. Photo credit: Zishen Wang.

of each species in border rows and inner rows in the intercrop strips, because the border rows of the species strips experience stronger interspecific interactions compared to the adjacent inner rows (Wang et al. 2020). Overall, our aim is to determine the relative importance of temporal complementarity as compared to cereal-legume complementarity as drivers of efficient N use in strip intercropping under Dutch growing conditions when the N input is tailored to the species demand.

2 Materials and methods

2.1 Site description

A 2-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 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. 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. The N released from soil organic matter during the growing season was estimated at 90 kg N ha⁻¹ in both years.

2.2 Experimental design

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. “Astronoute”)—were combined in six bi-specific intercrops: maize/wheat, maize/faba bean, maize/pea, faba bean/wheat, faba bean/pea, and wheat/pea. In total, ten cropping systems were compared, including six intercrops and the four corresponding monocrops.

Supplementary N was applied in the form of $\text{NH}_4\text{NO}_3\cdot\text{CaMg}(\text{CO}_3)_2$, and in accordance with the recommendations for arable crop fertilization in the Netherlands for non-organic agriculture (Ministerie van Landbouw, Natuur en Voedselkwaliteit 2019). In both years, faba bean and pea received 20 kg N ha^{-1} at emergence as a starter N fertilization. Wheat received 125 kg N ha^{-1} in both years, with the first dose (80 kg N ha^{-1}) at emergence and the second dose (45 kg N ha^{-1}) during stem elongation. Maize received 170 kg N ha^{-1} in both years, with the first dose (80 kg N ha^{-1}) at sowing and the second dose (90 kg N ha^{-1}) during stem elongation. All N fertilizer was applied as top dressing next to rows within the species strips, ensuring that species strips in both monocrops and intercrops received the same amount of N fertilizer. At the whole intercrop level, the N fertilizer rate input was the average of that in the monocrops of the component species, but each species was fertilized according to its recommendation for monocropping. The N fertilizer was applied using a tractor-driven machine (ENTI Co., the Netherlands), with an exception of the second dose in maize, which was applied manually to prevent fertilizer from entering the maize whorl.

Pea, wheat, and faba bean were sown on March 21 in 2018, and April 1 in 2019. Pea was harvested on July 10 in 2018, and July 29 in 2019. Wheat was harvested on July 17 in 2018, and August 8 in 2019. Faba bean was harvested on July 30 in 2018, and August 14 in 2019. Maize was sown and harvested later than the other three species, with a sowing date of May 4 in 2018 and May 7 in 2019 and a harvesting date of September 10 in 2018 and September 18 in 2019. The three intercrops involving maize were relay intercrops, whereas the other three intercrops were nearly simultaneous. Due to the cool and wet spring of 2019, the sowing of the C_3 species was delayed. Accordingly, the delay of maize compared to the early-sown species was smaller in 2019 (37 days) than in 2018 (45 days), leading to reduced temporal complementarity in 2019.

Species strips were 1.5 m wide in all plots, comprising three rows of maize or six rows of wheat, faba bean, or pea (Fig. 1). In each strip of maize, rows 1 and 3 were border rows, and row 2 was an inner row. In each strip of wheat, faba bean, and pea, rows 1 and 6 were border rows, rows 2 and 5 were inner row I, and 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 neighboring inner rows within the strip, which was 20 cm to allow the wheels of the tractor to span the six rows (Supplementary Fig. S1). 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 in which each component species shared half of the intercropping land area, and the relative density (i.e., density in the intercrop relative to the monocrop) of each species was 0.5.

In 2018, the plot size was 9 m in east-west direction $\times$ 11 m in north-south direction, comprising six species strips. In 2019, the plot size was 12 m in east-west direction $\times$ 11 m in north-south direction for monocrops, comprising eight species strips. For intercrops, the plot size was 15 m in east-west direction $\times$ 11 m in north-south direction, comprising ten species strips. The row orientation was approximately north-south in both years. The experiment had a randomized 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 $\text{K}_2\text{SO}_4\cdot\text{MgSO}_4$ and phosphorus (P) in the form of $\text{Ca}(\text{H}_2\text{PO}_4)_2\cdot\text{H}_2\text{O}$ 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.

2.3 Above-ground biomass and N concentration

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 of each species. Specifically, the plants were harvested separately for each row within one strip. These measurements were made in both intercrops and monocrops. In 2018, one intermediate harvest was made in wheat, faba bean, and pea, and two were made in maize. A 2 m row segment was harvested for wheat, faba bean, and pea. Maize plants were harvested over a 4 m row length in each harvested row in the first harvest, and a 3 m row segment in the second harvest. To gain a better insight into within-season growth dynamics, the number of intermediate harvests in 2019 was increased to five times in wheat, faba bean, and pea and four times in maize. A 1.6 m row segment was harvested per row at intermediate harvests for all species. In both years, all species were 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. Above-ground biomass was determined after drying at $105\text{ }^\circ\text{C}$ for 48 h . N concentration

was determined after drying 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 based on the Micro-Dumas combustion method using an element C/N analyzer TruMac CN (LECO Corporation, Saint Joseph, Michigan USA), which was conducted at the School of Biosciences, University of Nottingham, UK. N uptake was determined as the product of N concentration and biomass for each row.

2.4 Data analysis

2.4.1 Above-ground biomass, N uptake, and N concentration

We compared the above-ground biomass (Mg ha^{-1}), N uptake (kg ha^{-1}), and N concentration (mg g^{-1}) per species strip in intercrops and monocrops. Comparisons were made at each harvest in each year. Data were analyzed per species, using linear mixed effects models in which the species combination was specified as a fixed effect and block was a random effect. We also compared the above-ground

N uptake per row (g m^{-2}) in different row positions in intercrops with that in monocrops. We considered border row and inner row for intercropped maize, and border row, inner row I, and inner row II for intercropped wheat, faba bean, and pea. Comparisons were made at the final harvest and in each year for each species. Linear mixed effects models were used, with “species combination_row position” as a fixed effect and block as a random effect. No differentiation was made between monocrop rows. The function “lmer” from the “lme4” package (Bates et al. 2015) in R (R Core Team 2023) 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).

2.4.2 N dilution curves of maize and wheat

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 2000):

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

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

The critical N dilution curve of maize (Eq. 1; Plénet and Lemaire 2000) applies to 0–22 Mg ha^{-1} of above-ground biomass (from emergence to 25 days after silking), beyond which the N dilution pattern changes, with an accelerated

decrease in N concentration. In our experiment, maize reached 21 Mg ha^{-1} at 37 days after silking. We restricted our analysis to biomass below 22 Mg ha^{-1} to maintain consistency with the published curve.

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

$$\text{If } B_w < 1 \text{ Mg ha}^{-1}, \%N_{c,w} = 3.85; \text{ If } B_w \geq 1 \text{ Mg ha}^{-1}, \%N_{c,w} = 3.85 \times B_w^{-0.57} \quad (2)$$

where B_w is the wheat above-ground biomass per unit area of the species strip in both monocrops and intercrops, and $\%N_{c,w}$ 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:

$$\%N_i = a_i \times B_i^{-b_i} \quad (3)$$

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 $1 \leq B_m \leq 22 \text{ Mg ha}^{-1}$, and data for wheat with biomass $B_w \geq 1 \text{ Mg ha}^{-1}$ were used.

Interactions between component species in intercrops may affect N uptake and the actual N dilution curve. We used model selection to assess whether the actual N dilution curves of maize and wheat differed when they had different companion species. We fitted Eq. 3 for maize and wheat, respectively, according to the assumption of which parameters differed among which groups of treatments. Details of all models are given in Supplementary Table S1. 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 ($\Delta\text{AIC} < 2$) 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 and R Development Core Team 2022) of R (R Core Team 2023). All variables were assumed normally distributed. The optimization algorithm “Nelder-Mead” was used when estimating parameters. Details showing the AIC values of all models are given in Supplementary Table S1.

2.4.3 Land equivalent ratio for N uptake and its relationship with temporal niche differentiation

The land equivalent ratio for N uptake (LER_N) was used to assess intercropping advantages with respect to N uptake as compared to monocrops (Bedoussac and Justes 2010; Li et al. 2011):

$$\text{LER}_N = \frac{N_{I,1}}{N_{M,1}} + \frac{N_{I,2}}{N_{M,2}} = \text{pLER}_{N,1} + \text{pLER}_{N,2} \quad (4)$$

where $N_{I,i}$ is the N uptake of species i in an intercrop at final harvest, expressed at per unit of total area of the intercrop, $N_{M,i}$ is the N uptake of species i in its monocrop at final harvest, expressed per unit area of the monocrop, and $\text{pLER}_{N,i}$ is the partial land equivalent ratio for N uptake of species i . An 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 efficiently for N uptake than the combined monocrops. In a replacement design, a $\text{pLER}_{N,i}$ 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 LER_N values and from 0.5 for pLER_N values, we assessed if one

(or 0.5) fell outside the 95% confidence interval of LER_N (or 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 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:

$$\text{TND} = 1 - \frac{T_{\text{overlap}}}{T_{\text{system}}} \quad (5)$$

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 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. Altogether seven models were compared (Table 1), 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 Supplementary Table S2.

2.4.4 Fertilizer N equivalent ratio

The fertilizer N equivalent ratio (FNER) was used to assess intercropping advantages with respect to saving fertilizer N inputs for grain yields as compared to monocrops (Xu et al. 2020):

$$\text{FNER} = \left(\frac{Y_{I,1}}{Y_{M,1}} \times \frac{F_{M,1}}{F_{IC}} \right) + \left(\frac{Y_{I,2}}{Y_{M,2}} \times \frac{F_{M,2}}{F_{IC}} \right) \quad (6)$$

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

Table 1 Models used to quantify the relationships between 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

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

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.

unit area of a monocrop) of species i in the monocrop, $F_{M,i}$ is the rate of fertilizer N applied per unit area of the monocrop of species i , and F_{IC} is the fertilizer N input per unit area of the whole intercrop. The results of grain yield have been presented in Wang et al. (2025); see Supplementary Fig. S7 for details.

In this study, all species received tailored fertilizer 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 fertilizer inputs in the respective monocrops. An FNER greater than one indicates that the combined monocrops need greater total fertilizer N input than the intercrop to obtain the same grain yields of the two species. To assess if the value of FNER was significantly different from one, linear mixed effects models were used to calculate the 95% confidence

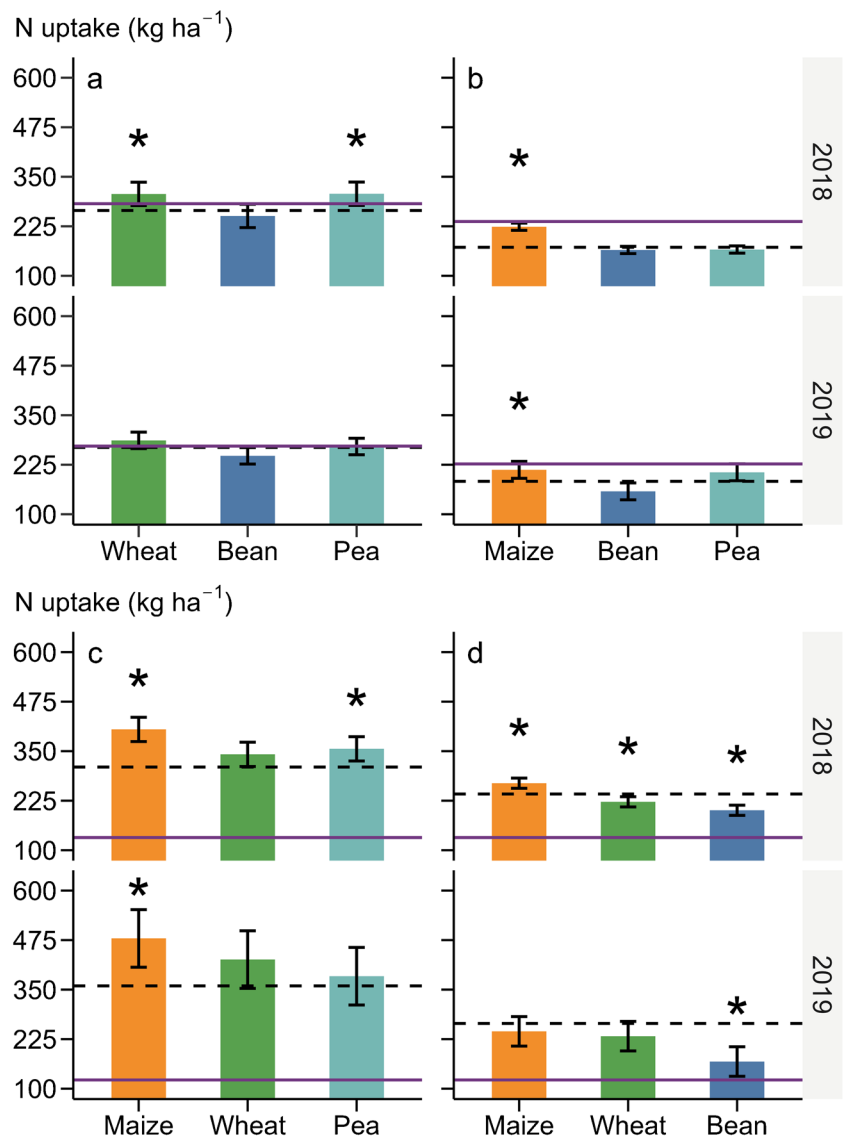
interval of FNER. This analysis was conducted within each year, with species combination as a fixed effect and block as a random effect.

3 Results

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. 2a). Wheat and faba bean had higher N uptake than in their monocrops if they were intercropped with maize; the same was found for pea

Fig. 2 Above-ground N uptake per species strip at final harvest of maize (a), wheat (b), faba bean (c), and pea (d) when grown with different companion species (X-axis) in 2018 and 2019. 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 fertilizer N. Black dashed lines represent N uptake of the monocrops of the focal species in each panel. Colored 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 and the comparison between N uptake and available soil N are presented in Supplementary Table S3.



in 2018, but not in 2019 (Fig. 2b–d). In the simultaneous intercrops, faba bean had increased N uptake when intercropped with pea in 2018 (Fig. 2c), and pea that was intercropped with faba bean had in both years lower N uptake than monocropped pea (Fig. 2d). No other effects of simultaneous intercropping on N uptake were found.

N uptake by monocropped maize and intercropped maize was in the order of 250 to 300 kg ha⁻¹, similar to the available soil N (the purple line in Fig. 2a), except for maize intercropped with faba bean, which captured less N than the available soil N in both years (Supplementary Table S3). N uptake by wheat in both monocrops and simultaneous intercrops was substantially lower than the available quantity of soil N, except in the relay intercrop with maize (Fig. 2b). N uptake by both faba bean and pea in all treatments was greater than the available soil N (Fig. 2c–d), indicating substantial biological N fixation. The largest uptake occurred in the faba bean intercropped with maize, exceeding the available soil N by about 270 kg ha⁻¹ in 2018 and 360 kg ha⁻¹ in 2019 (Fig. 2c).

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

In relay intercrops, maize inner and border rows generally had similar N uptake as monocropped maize, with two exceptions. Border row maize growing next to pea had higher N uptake than monocropped maize in 2018, while border row maize intercropped with faba bean had lower N uptake than monocropped maize in 2019 (Fig. 3a). Border rows of wheat, faba bean, and pea in relay intercrops had higher N uptake than inner rows and monocrops (Fig. 3b–d). In simultaneous intercrops, faba bean reduced wheat N uptake in border rows in 2018 and inner row I in 2019 (Fig. 3b). It also reduced N uptake in pea in all rows of the strip in both years (Fig. 3d). Border row faba bean had increased N uptake when intercropped with wheat or pea (Fig. 3c).

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

Intercropped maize had consistently lower N concentration than monocropped maize, though the difference was not significant in the faba bean/maize intercrop in 2019 ($P = 0.225$; Fig. 4a). Wheat in the intercrop with faba bean had significantly higher N concentration than in its monocrop in both years, and the same effect was found for wheat in the wheat/maize intercrop in 2019 (Fig. 4b). N concentration of intercropped faba bean and pea was similar among treatments and comparable to that in the monocrops (Fig. 4c and d).

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. The 2018 data are given in Supplementary Table S6 to evaluate the consistency of effects between seasons.

3.4.1 Relay intercrops

Late-sown maize

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. 5a; Supplementary Table S6). 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.

Early-sown species

From flowering onwards (approx. DOY 196 in 2019 and DOY 155 in 2018), wheat had higher N uptake in the relay intercrop than in its monocrop, and a higher biomass of intercropped wheat was found at maturity in 2018 (Fig. 5b; Supplementary Table S6). A consistent pattern was observed for faba bean in the relay intercrop with maize in both years; from flowering onwards (approx. DOY 168 in 2019 and DOY 155 in 2018), the intercropped faba bean had higher biomass and N uptake than the monocropped faba bean (Fig. 5c; Supplementary Table S6). In both years, pea intercropped with maize had higher biomass and N uptake than the monocropped pea at flowering (approx. DOY 168 in 2019 and DOY 155 in 2018) (Fig. 5d; Supplementary Table S6). Thus, the early-sown species in relay intercrops showed increases in both biomass and N uptake compared to those in monocrops.

3.4.2 Simultaneous intercrops

Wheat intercropped with pea had similar biomass and N uptake as its monocrop (Fig. 5b; Supplementary Table S6). 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. Around flowering, faba bean intercropped 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

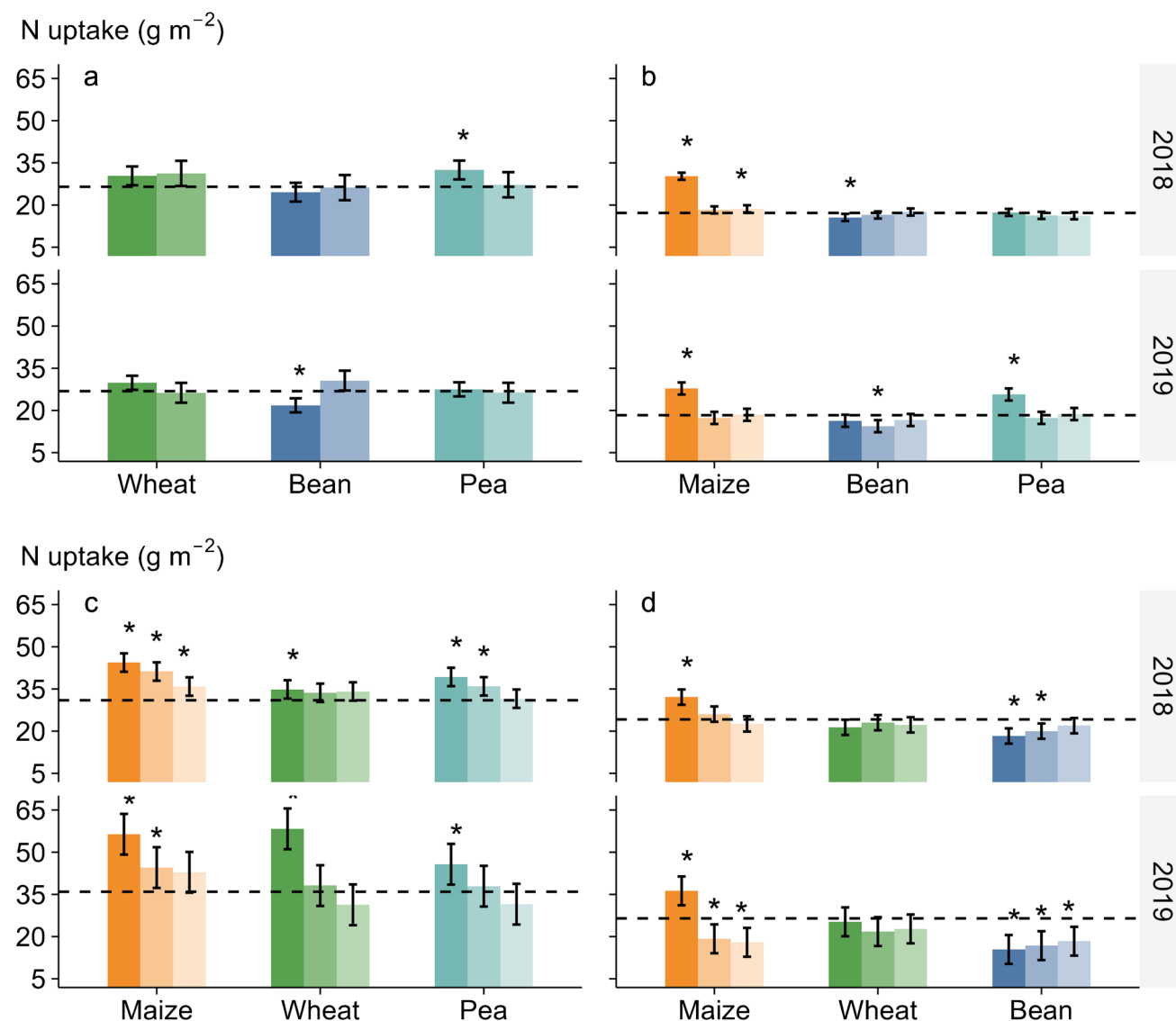


Fig. 3 Above-ground N uptake of different rows of intercropped maize (**a**), wheat (**b**), faba bean (**c**), and pea (**d**) in 2018 and 2019. Companion species are indicated along the X-axis. Dashed lines indicate N uptake of the monocrops of the focal species in each panel. Colored bars represent N uptake of the focal species when it was with different companion species: maize (orange), wheat (green), faba bean (blue), and pea (cyan). Panel **a** shows six sets of two bars, i.e., three sets (companion species) for each of two years (2018 and 2019). In each set, the left bar (darker color) represents the border row and the right bar is the inner row (lighter color). Panels **b–d**

show sets of three bars, with from left to right the border row (darkest color), inner row I (intermediate color) and inner row II (lightest color). Multiple comparisons of means were conducted within each year with “species combination_row position” as the fixed effect. No differentiation was made between monocrop rows. Asterisks indicate significant differences between the intercrop rows and the monocrops at $P < 0.05$ according to Fisher’s LSD test. Error bars indicate the 95% confidence intervals of the means. Details showing the multiple comparisons are presented in Supplementary Table S4.

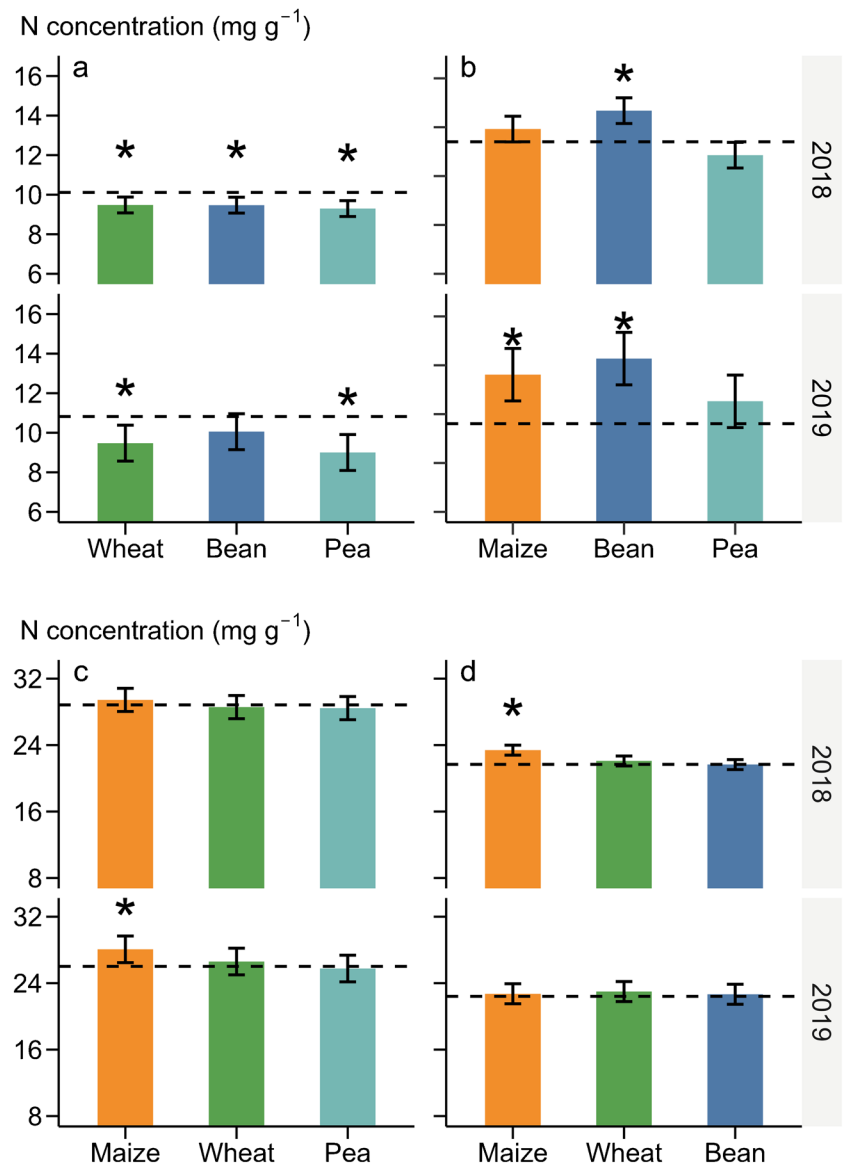
2018 (Fig. 5c; Supplementary Table S6). Simultaneously, intercropping with faba bean led to decreased biomass and N uptake of pea after flowering in 2019 (approx. DOY 182), as well as at maturity in both years (Fig. 5d; Supplementary Table S6). Thus, in simultaneous intercrops involving faba bean, the companion wheat or pea had decreased biomass compared to their monocrops.

3.5 N dilution curves of maize and wheat

3.5.1 Maize

We compared the actual N dilution curves estimated from our experiment with the maize critical N dilution curve (Fig. 6a). The above-ground N concentration decreased with biomass, following a slope (determined by the

Fig. 4 Above-ground N concentration per species strip at final harvest for maize (a), wheat (b), faba bean (c), and pea (d) in 2018 and 2019. Companion species are indicated along the X-axis. Dashed lines indicate N concentration of the monocrops of the focal species in each panel. Colored 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 LSD test. Error bars indicate the 95% confidence intervals. Details showing the multiple comparisons are presented in Supplementary Table S5.



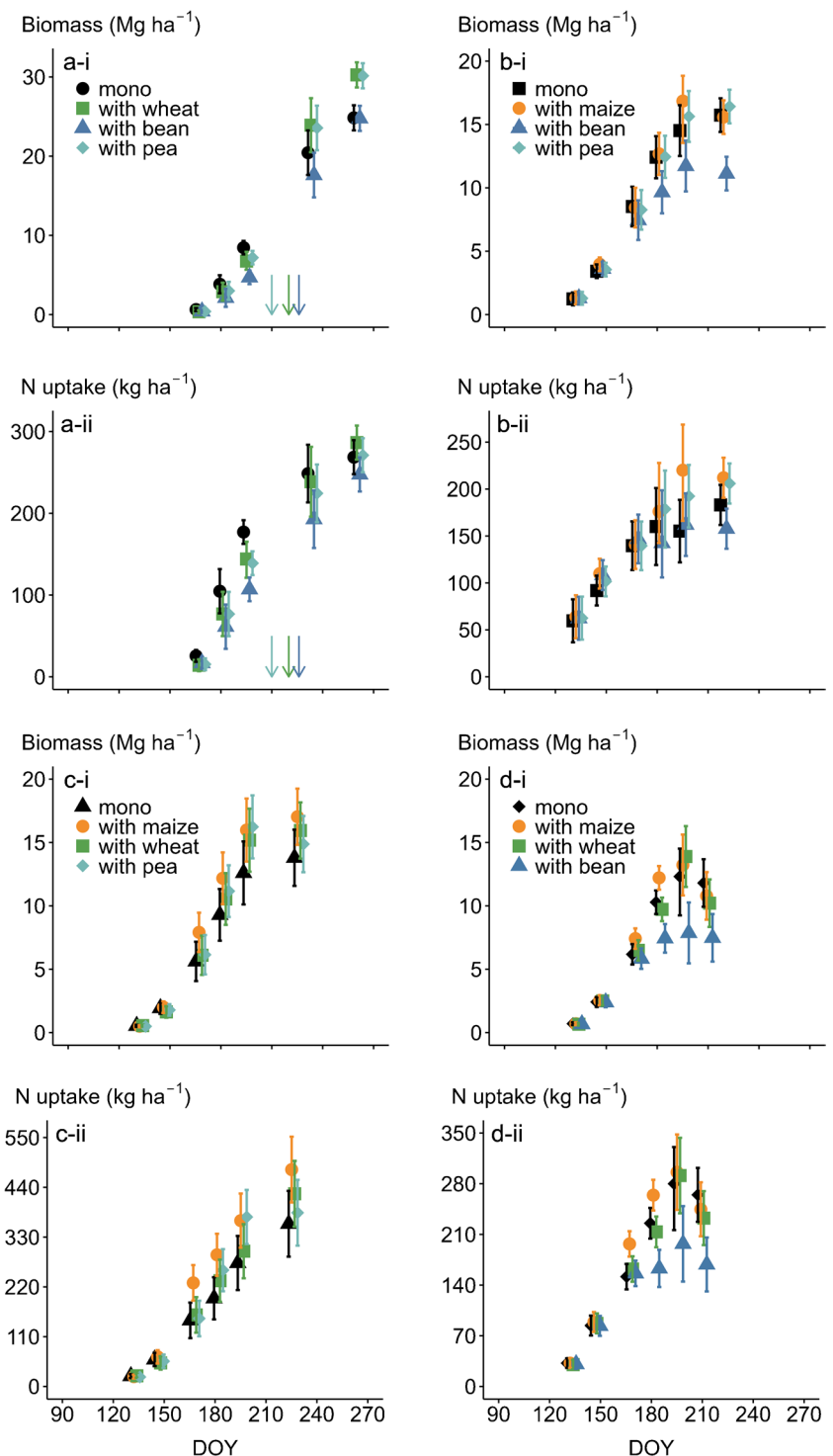
parameter b_m) (Eq. 3) comparable to the published critical dilution curve (Eq. 1). We observed a higher value for the intercept parameter a_m (Eq. 3), resulting in an N concentration in our experiment that was higher than the critical N concentration at the same biomass level. The results indicate that 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.

During the later growth process, at grain filling and with biomass values between approximately 18 and 22 Mg ha⁻¹, the measured N concentration of intercropped maize tended to be below the critical curve (Fig. 6a), and at higher biomass levels in later phases, values tended to be lower than in monocropped maize. This indicates that plant N likely reduced productive capacity in maize in all intercrops during grain filling.

3.5.2 Wheat

We compared the actual N dilution curves estimated from our experiment with the wheat critical N dilution curve (Fig. 6b). 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. We furthermore found a higher N concentration in intercropped than monocropped wheat at the same biomass level. This phenomenon was particularly observed after wheat produced approx. 8 Mg ha⁻¹ biomass at the heading stage. Thus, plant N was sufficient for wheat in both the intercrops and monocrop during the whole season, and in the later growth stages, wheat had in all intercrops a higher N concentration than in the monocrop at the same biomass.

Fig. 5 Dynamics of above-ground biomass (i) and N uptake (ii) per species strip for maize (a), wheat (b), faba bean (c), and pea (d) in 2019 over time in day of the year (DOY) in the Julian calendar. Symbols within each panel represent biomass and N uptake of the focal species when it was with different companion species: maize (orange circles), wheat (green squares), faba bean (blue triangles), and pea (cyan diamonds). The monocrops (i.e., companion species = focal species) are denoted in black. Arrows in panel a indicate the final harvest of pea (cyan), wheat (green), and faba bean (blue). Error bars indicate the 95% confidence intervals of the means. Multiple comparisons of means are conducted within an individual harvest at $P < 0.05$ according to Fisher's LSD test, which are presented in Supplementary Table S7.



3.6 LER_N , the relationship between LER_N and TND, and FNER

In 2018, all relay intercrops obtained LER_N values larger than one, ranging from 1.14 ± 0.09 (mean $\pm$ 95% confidence interval) in the faba bean/maize intercrop to 1.24 ± 0.09 in the wheat/maize intercrop (Fig. 7a). In 2019, only the faba

bean/maize intercrop (1.13 ± 0.11) and the wheat/maize intercrop (1.12 ± 0.11) achieved LER_N values larger than one. In relay intercrops, the cereal/legume combinations faba bean/maize and pea/maize did not obtain larger LER_N values than the cereal/cereal combination wheat/maize. In the faba bean/maize intercrop, the $pLER_N$ value of faba bean contributed more to the total LER_N value than that of maize. In

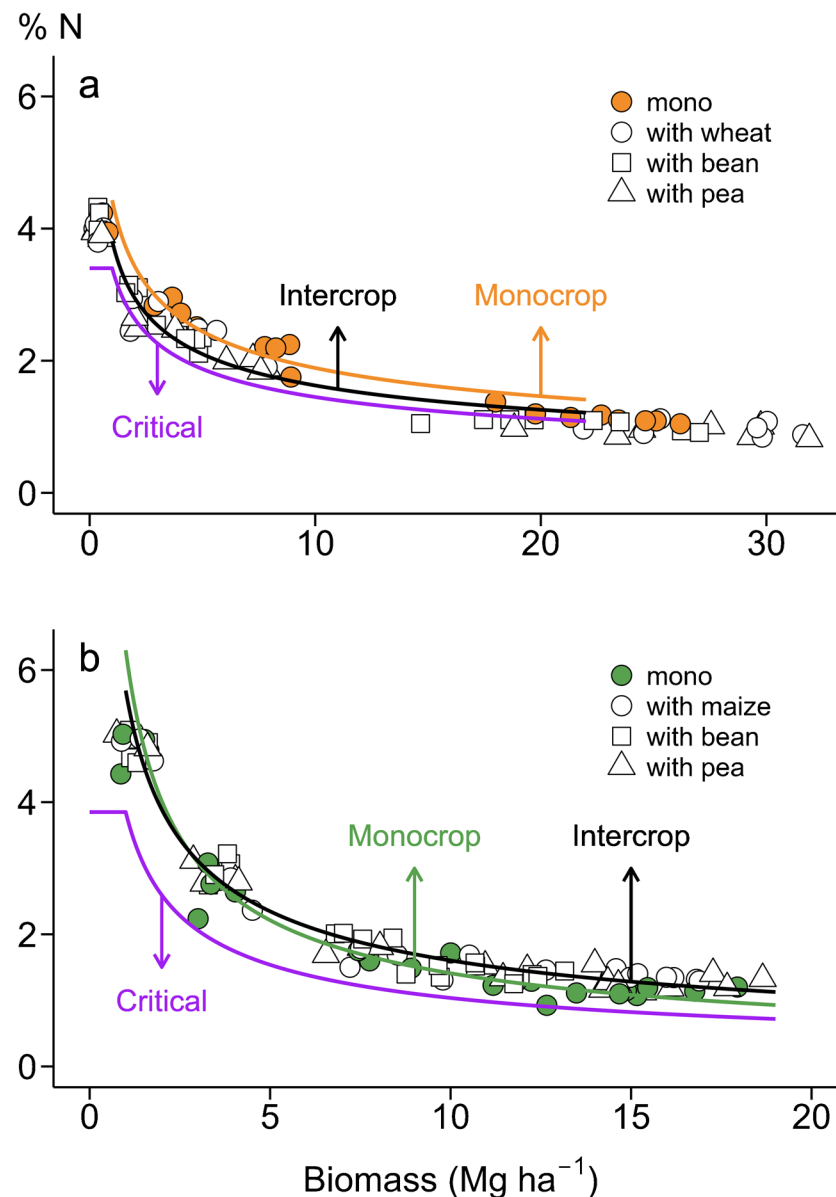


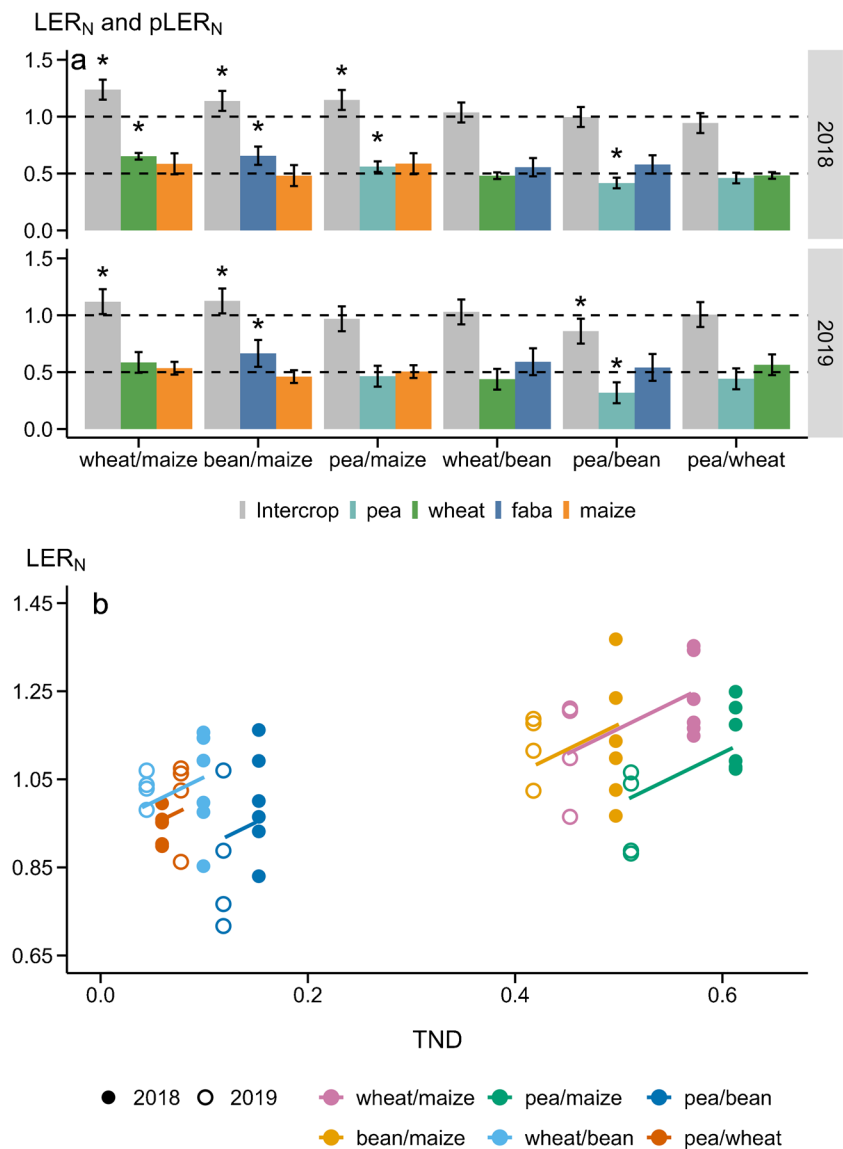
Fig. 6 N dilution curves for maize (**a**) and wheat (**b**). The X-axis is the above-ground biomass per species strip. The %N is the above-ground N concentration per species strip. Each open symbol represents measured %N and biomass of maize (**a**) or wheat (**b**) when it was grown with different companion species; colored circles represent monocrops. The purple line in each panel is the critical N dilution curve (Eq. 1 for maize, Eq. 2 for wheat). Data for both maize critical and actual N dilution curves were restricted to biomass values below 22 Mg ha⁻¹ to ensure consistency with the published critical N dilution curve (Plénet and Lemaire 2000) and avoid biases from shifts in N dilution patterns during the late reproductive stage. The optimal

model for each species, accounting for treatment effects on N dilution, was selected based on the lowest AIC value (Akaike 1998). For maize (**a**), the parameter a_m was higher for monocrop maize (4.43 ± 0.14) than for maize in intercrop treatments, but there was a common intercept in the intercrops (3.81 ± 0.25), whereas the parameter b_m was identical across all treatments (0.37 ± 0.03). Thus, two curves were drawn. For wheat (**b**), the curves differed between monocrop wheat and wheat in all intercrops. Both parameters, a_w and b_w , were higher for the monocrop ($a_w = 6.30 \pm 0.26$; $b_w = 0.65 \pm 0.03$) than for the intercrops ($a_w = 5.69 \pm 0.10$; $b_w = 0.55 \pm 0.01$); see Supplementary Table S1 for more details.

simultaneous intercrops, LER_N values mostly were not different from one, ranging from 0.94 ± 0.09 in the pea/wheat intercrop to 1.04 ± 0.09 in the wheat/faba bean intercrop in 2018, and from 0.86 ± 0.11 in the pea/faba bean intercrop to 1.03 ± 0.11 in the wheat/faba bean intercrop in 2019.

We found positive correlation between LER_N and TND (Fig. 7b). The most supported model was Model 6 (Table 1), which had a common slope across intercrops and species combination-specific intercepts. This indicates that the positive effect of TND on LER_N was consistent across

Fig. 7 Land equivalent ratio for N uptake (LER_N) of intercrops and partial land equivalent ratio for N uptake ($pLER_N$) of component species in 2018 and 2019 (a), and relationships between LER_N and temporal niche differentiation (TND) (b). In panel a, grey bars represent the LER_N of intercrops and colored bars represent the $pLER_N$ of component species. The X-axis represents species combinations. Error bars indicate the 95% confidence intervals. Asterisks in panel a 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 $pLER_N$). In panel b, all regressions had an identical slope ($P = 0.005$) and different intercepts across intercrops. Details on coefficients and their standard errors are presented in Supplementary Table S2.



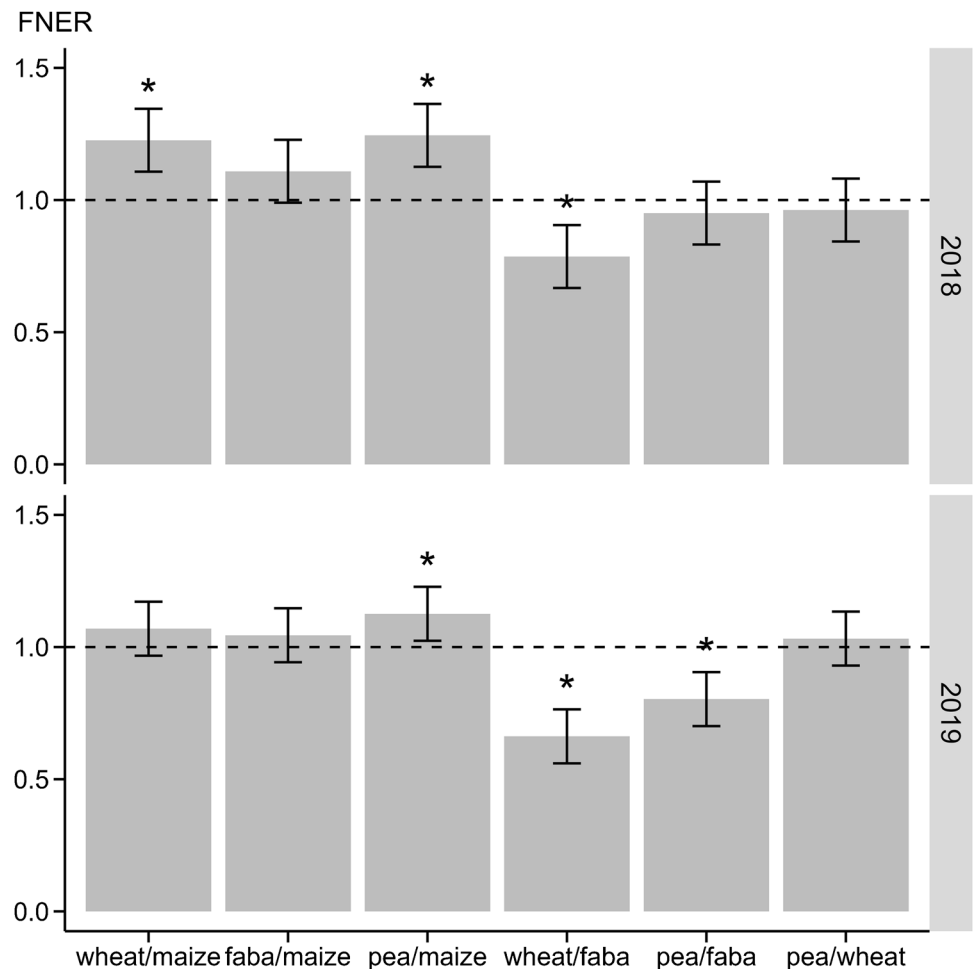
species combinations, regardless of whether the intercrop systems were relay or simultaneous designs, or whether they involved a cereal/legume combination or not. Thus, both species combination and TND were key factors driving intercropping advantages with respect to N uptake in our experiment.

FNER values ranged from 0.79 ± 0.24 (mean $\pm$ 95% confidence interval) in the wheat/faba bean intercrop to 1.24 ± 0.24 in the pea/maize intercrop in 2018, and ranged from 0.66 ± 0.20 in the wheat/faba bean intercrop to 1.13 ± 0.20 in the pea/maize intercrop in 2019 (Fig. 8). The average FNER over two years was 1.14 ± 0.03 for relay intercrops, whereas it was only 0.85 ± 0.03 for simultaneous intercrops. Despite the inter-year variances within the same treatment, relay intercrops, on average, were more efficient in using fertilizer N than simultaneous intercrops.

4 Discussion

We compared the effects of temporal complementarity and cereal-legume complementarity on nitrogen (N) uptake and fertilizer N use efficiency under a species-tailored, moderate N fertilization strategy in intercropping. We found that wheat had increased N uptake when grown as an early-sown species in the relay intercrop with maize, compared to monocropped wheat, but not when grown with a legume in simultaneous intercrops (Fig. 2). Legumes (faba bean and pea) had higher N uptake in relay intercrops with maize, but not in simultaneous intercrops with wheat. Maize had increased N uptake only when relay intercropped with wheat or pea in a year with larger temporal niche differentiation (TND). Relay intercropping benefits were most evident in border rows of earlier-sown species (Fig. 3). Competition occurred

Fig. 8 Fertilizer N equivalent ratio (FNER) of intercrops in 2018 and 2019. The X-axis represents species combinations. Asterisks indicate significant differences from one for FNER, by testing if one fell outside the 95% confidence interval of FNER.



between border row faba bean and its companion species, shown by increased N uptake in border row faba bean and decreased N uptake in companion maize, wheat, or pea. Despite inter-year differences, relay intercrops had favourable land equivalent ratios for N uptake (LER_N) (Fig. 7) and fertilizer N equivalent ratios (FNER) (Fig. 8), mostly higher than one, whereas simultaneous intercrops had both values mostly similar to one. The results indicate that under the conditions of the study relay intercrops were more efficient in capturing N and using fertilizer N than simultaneous intercrops. Temporal complementarity between species was a key driver for complementary N uptake and efficient fertilizer N use, whereas cereal-legume N uptake complementarity related to biological N fixation was not.

4.1 Species-tailored N fertilization prevents N stress in cereals and enhances legume N fixation

Using N dilution curves, we detected no N limitation in wheat throughout the season (Fig. 6b). Maize only experienced N limitation during grain filling (Fig. 6a). Legumes in intercrops maintained N concentration similar to those

in monocrops (Supplementary Fig. S6). The cereals captured nearly all available soil N, and the small “starter” N fertilizer enabled legumes to fully exploit N fixation (Fig. 2). Compared to high-input N strategies, which cause N surplus, leaching, and inhibit legume N fixation (Yu et al. 2021; Wang et al. 2022), the species-tailored moderate N strategy minimizes environmental costs and enhances N fixation. Furthermore, such an N strategy supports cereal production (Supplementary Fig. S7; Wang et al. 2025) avoiding low or unstable yield and N uptake found in low-input intercrops (Hauggaard-Nielsen et al. 2008; Li et al. 2020b). Our results show that species-tailored and moderate N fertilization effectively sustains cereal N supply and enhances legume N fixation, supporting both productivity and sustainability.

4.2 N uptake is enhanced by temporal complementarity through increased biomass

Compared to monocropped maize, intercropped maize showed no increase in N concentration for the same biomass, indicating all extra uptake was used for additional biomass (Fig. 6a). Like other relay intercrops with a replacement

design in the Netherlands (Zhu et al. 2015; Gou et al. 2017), we observed that the early-sown species had better light conditions during early growth than the same species grown as a monocrop (Wang et al. 2025), which likely stimulated their biomass accumulation, and therefore N uptake (Fig. 5). Biological N fixation in legumes benefits from light capture and biomass production (Carvalho et al. 2019). The higher N uptake in relay intercrops, especially faba bean, likely resulted from better light and increased biomass, boosting root growth and N demand as well as energy available for biological fixation. Intercropped wheat had higher N concentration than monocropped wheat for the same biomass (Fig. 6b), especially at later growth stage when light competition may have been limiting biomass more than tissue N. Since N fertilization was identical within species strips in the intercrops and monocrop, wheat may have foraged for N from the neighboring maize strips via lateral root extensions (Li et al. 2006; Liu et al. 2015). The marginal increase in N concentration is secondary to the primary role of increased biomass in enhancing N uptake (Fig. 6b). Maize in relay intercrops also benefited from improved light capture and biomass accumulation, except when intercropped with faba bean, which resulted in no substantial biomass increase compared to monocrop maize. In summary, temporal complementarity in relay intercropping enhanced N uptake mainly by promoting biomass production, driving greater nutrient demand and acquisition.

The study highlights the importance of temporal complementarity in strip intercropping by comparing relay systems with simultaneous systems involving different species combinations. The effect of temporal lag within the same species combination can be assessed experimentally by modifying relative sowing times of the mixed crop species provided that the growing season is sufficiently long to allow maturation of the later sown species, such as in tropical climates (Meirelles et al. 2024). Functional-structural plant models also offer an option to simulate different temporal arrangements in intercrops *in silico* (Yu 2016; Evers et al. 2019).

4.3 Inefficient N uptake in simultaneous intercrops is driven by decreased biomass rather than direct N competition

Simultaneous intercrops, especially those involving faba bean, were inefficient in capturing N, as increased faba bean N uptake did not offset losses in wheat and pea (Fig. 7a). Unlike typical cereal/legume intercrops, where cereals are the more competitive species (Bedoussac et al. 2015; Yu et al. 2016), the tall faba bean cultivar “Fanfare” has a rapidly developing and dense canopy (Andersen et al. 2020), severely shading wheat and pea (Wang et al. 2025) and reducing their biomass (Fig. 5). Nevertheless, wheat still

captured sufficient soil N relative to its biomass (Fig. 6b), in fact ending up at slightly increased N concentration, suggesting the reduced N uptake was due to decreased biomass, not N competition. Unlike cereal/legume intercrops in low-input/organic systems (Hadir et al. 2024; Vonzun et al. 2024), where mixed or alternating row designs allow close interactions between component species, a strip design enhances interactions among conspecifics, limiting allospecific rhizosphere interactions (Li et al. 2016). In simultaneous intercrops with species-tailored fertilization, inefficient N uptake is driven by decreased biomass, with more vigorous species suppressing weaker ones, reducing N uptake.

Competition for N was not entirely absent. In relay intercrops, maize contributed minimally to the N uptake advantage, with its $pLER_N$ values similar to or lower than earlier-sown species (Fig. 7a). Maize only showed increased N uptake in 2018 when temporal complementarity allowed for enough recovery growth but not in 2019 when there was less temporal complementarity due to late sowing and late harvesting of wheat, pea, and faba bean. These observations align with a meta-analysis showing that yield gains of intercropping shift from the competitive dominance of high-yielding species to the complementarity effect as temporal niche differentiation increases (Li et al. 2020a). Previous studies on relay intercrops in which both intercrops and monocrops received the same rate of fertilizer N (e.g., $N > 225 \text{ kg ha}^{-1}$) at the system level, indicated that N uptake of late-sown maize was higher than that of monocrop maize at maturity; these studies include both maize relay intercropped with wheat and soybean (Li et al. 2001a, b) and maize grown with faba bean (Li et al. 2011). We applied a moderate N rate for maize, with the second topdressing applied at the onset of maize stem elongation while in the intercrop we provided only starter N to the legume strip. Consequently, the soil N was largely taken up before maize entered grain filling, leading to N deficit, as reflected by the N concentration that gradually dropped below the critical level from grain filling in intercrops (Fig. 6a). Our N application strategy did not result in significantly increased N uptake by maize, possibly due to low N availability during maize reproductive growth.

4.4 Cereal-legume N capture complementarity is not influential with species-tailored N input

Relay intercrops showed generally substantial N capture complementarity, with LER_N values greater than one (except pea/maize in 2019) (Fig. 7a). However, the cereal-legume combination was not a key factor driving this complementarity, as high LER_N values were also found in wheat/maize. The LER_N of this combination was similar to that of faba bean/maize and higher than that of pea/maize. The lack of response to legumes seems to result from the N fertilization strategy satisfying the needs of both species. In previous

studies, mineral N applied to legumes in high-input intercrops (Li et al. 2001a, b), or soil-stored N in low-input intercrops (Bedoussac et al. 2015; Rodriguez et al. 2020), largely acted as additional N for cereals. However, in the current study, cereals were sufficiently supplied with N from their own strips, and rhizosphere interactions, especially at the early stages, were limited by the strip design, so N fixation by legumes contributed little to the cereal N uptake. The main contribution to complementary N uptake was likely temporal complementarity, which enhanced biomass growth, which in turn may have driven increased root proliferation and N uptake in relay-intercropped species, compared to the monocrops. Thus, the contribution of cereal-legume N capture complementarity to cereals depends on the N stress in monocrops and whether intercropping alleviates it. Here, species-tailored fertilization minimized N limitation (Fig. 6), reducing its influence. Instead, temporal complementarity drove biomass growth, enhancing root proliferation and N uptake in relay intercrops.

Although N fixation by legumes was not a key driver of complementary N uptake in this study, combining legumes with maize in relay intercropping still reduced N inputs compared to the wheat/maize intercrop, except for the pea/maize intercrop in 2019 (Fig. 7a). In 2019, heavy rains caused pea lodging, which was more severe in the relay intercrop than in the monocrop because the young maize plants could not support the pea (Fig. 1). Therefore, combining maize with a firm-stem species in relay strip intercropping is recommended for N uptake advantages, whereas species with weak stems are more suited for full mixtures with firm-stem companions (Barillot et al. 2012).

4.5 Practical implications

This study investigated intercropping under conventional practices, where the focus is on maximizing yield with fertilizers, pesticides, and herbicides. The species-tailored N fertilization aims to balance high yields with efficient N use. Our findings suggest that strip intercropping with species-tailored N fertilization efficiently increases N uptake and improves fertilizer use efficiency. In the current study, on average over the two years, relay intercrops had an FNER of 1.14 ± 0.03 , indicating a 14% saving in fertilizer N compared to monocrops for the same yield (Fig. 8).

However, the species-tailored N strategy was not the sole contributor to the increases in N uptake and fertilizer N use efficiency, as N availability was hardly improved in intercrops compared to monocrops. The benefits are attributed to a combination of temporal complementarity and intercrop N rates being intermediate to monocrop N rates enabled each species to capture more light (Wang et al. 2025), and probably also other resources, leading to increased yield per unit land area compared to monocrops and thus enhancing fertilizer N use efficiency. Therefore, our research indicates

that it is advisable to combine species with only partially overlapping growing 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.

The comparison of relay intercrops between 2018 and 2019 emphasizes the importance of sufficient temporal complementarity. C₃ and C₄ species, with different growth peaks, can provide a large TND (Yu et al. 2015). Additionally, weather variability should be considered to maintain intercrop stability, as shown by the reduced benefits caused by the late sowing of wheat, faba bean, and pea due to heavy rain in late March 2019. Other options also exist to fully use the growing season and avoid bare fallow periods, such as strip cropping rotations and cover crop mixtures recently studied in the Netherlands (Elhakeem et al. 2019; Juventia et al. 2022). In regions where degree days allow successive main crops (e.g., double cropping; Liang et al. 2022), double cropping is likely to give higher total yields than relay intercropping. The choice of cropping system should depend on objectives, species selection, management, and climate. The evaluation may also focus on comparing different cropping systems over the whole season, rather than solely between inter- and monocropping.

Late-sown maize had increased N uptake, with potential for further gains as N limitation emerged late in growth (Fig. 6a). Applying an additional N dose after harvesting early companions has been shown to significantly facilitate N uptake recovery in maize (Hu et al. 2016). In our species-tailored and moderate fertilization approach, adding additional N after maize tasseling could improve N uptake, but its long-term sustainability remains uncertain. Postponing the second N fertilization might also help (Xu et al. 2023), but could lead to N limitation in maize around stem elongation. There seems to be room for additional experimentation before making recommendations to practice. Choosing the appropriate early companions is also crucial. Overyielding of the late-sown maize increased with longer recovery times after harvest of the early-sown species (Wang et al. 2023; Zhao et al. 2023). Given the cool climate in the Netherlands, a potential 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.

This study does not suggest that strip intercropping with species-tailored fertilization is inherently superior to fully mixed or alternating row intercropping in organic or low-input cereal/legume systems in Western Europe. These intercropping patterns differ in their primary objectives: while strip intercropping with species-tailored fertilization improves N uptake and fertilizer N use efficiency under

conventional management, low-input/organic intercropping prioritizes reducing anthropogenic fertilizer use while delivering additional agroecological benefits, such as improved weed suppression, disease control, and enhanced cereal grain quality for better marketability (Bedoussac et al. 2015). The choice of intercropping strategy should therefore be guided by production goals and management priorities. Further research is needed on strip intercropping with species-tailored fertilization under organic conditions to determine if the N benefits found in conventional systems are applicable to organic systems, where N sources and dynamics differ. Additionally, comparing species-tailored fertilization with a uniform low-input strategy across crops may help to further disentangle the effects of fertilization from those of intercropping design and temporal complementarity.

5 Conclusion

Here we showed, for the first time, the effects of strip intercropping on nitrogen (N) uptake under a species-tailored N strategy in Western Europe. Relay strip intercropping with sufficient temporal complementarity allowed for improved N uptake compared to monocrops, whereas simultaneous intercropping did not. 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. The species-tailored and moderate N strategy ensured the complete capture of available soil N for cereals in relay intercrops and enabled legumes to exploit N fixation. Relay strip intercropping combined with such a N fertilization is advisable for sustainable agriculture due to its advantages in efficient land utilization for N uptake and fertilizer N savings for productivity compared to monocrops. To enhance maize N uptake and likely production, applying additional N after maize tasseling could be required, although an analysis of long-term sustainability is to be made first. Proper selection of early companion species is crucial.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13593-025-01052-z>.

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Authors' contributions Bei Dong and Zishen Wang jointly contributed to: conceptualization, methodology, formal analysis, investigation, data curation, visualization, writing—original draft, writing—review and editing. Tjeerd Jan Stomph: conceptualization, methodology,

supervision, writing—review and editing. Jochem B. Evers: conceptualization, methodology, supervision, writing—review and editing. Peter E. L. van der Putten: methodology, investigation, resources. Wopke van der Werf: Conceptualization, Methodology, Supervision, Project administration, Writing—review and editing. Bei Dong and Zishen Wang jointly led this work and contributed equally across all major aspects of the research.

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Data availability The data of this study are available at <https://doi.org/10.17026/PT/IFLWWZ>.

Code availability The codes for analysis during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval Not applicable

Consent to participate Not applicable

Consent for publication Not applicable

Conflict of interest The authors declare no competing interests.

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