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Resource acquisition and interactions in spring wheat/faba bean intercropping under diverse environments

Dereje T. Demie [a,*], Sabine J. Seidel [a,b], Daniel Wallach [a], Thomas F. Döring [c], Frank Ewert [a,d], Thomas Gaiser [a], Madhuri Paul [c], Ixchel M. Hernández-Ochoa [a]

[a] Crop Science Group, Institute of Crop Science and Resource Conservation, University of Bonn, Germany
[b] Institute of Organic Farming, Department of Agricultural Sciences, University of Natural Resources and Life Sciences, 1180 Vienna, Austria
[c] Agroecology and Organic Farming Group, Institute of Crop Science and Resource Conservation, University of Bonn, Germany
[d] Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany

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ABSTRACT

Context: Cereal/legume intercropping offers numerous advantages over monocultures, often attributed to complementary resource use of soil water, soil nitrogen (N), and radiation.
Objective: This study explores how the dynamics of crop resource (radiation, water, soil N) demand and use drive productivity in intercropping systems under different environmental conditions.
Methods: We used a process-based intercrop simulation model and field experimental data obtained from three contrasting environments with differing soil N and precipitation levels. Spring wheat and faba bean were sown as monocultures and intercropped in a 1:1 replacement design.
Results: The simulations and field experiments revealed no considerable differences in total water uptake and light interception between intercrops and the average of monocultures across environments. Intercrops acquired more soil N than the average of monocultures in all environments. Spring wheat in intercrop systems consistently acquired more soil water and N compared to spring wheat in monocultures. Faba bean resource acquisition and use efficiency depended on the environmental conditions. Resource use efficiency of intercropping was comparable to that of the monocultures, except for N use efficiency, which was 22 % higher, and water use efficiency which was 12 % higher under low N and the low precipitation environment. There was a slightly enhanced water use efficiency in the intercropping system compared to monoculture under high N and high precipitation environment. In environments with limited water, intercropped faba bean suffered considerably from drought stress, particularly during flowering compared to the monoculture of faba bean.
Conclusions: Soil water availability is a key determinant for faba bean productivity in intercropping, while mainly soil N availability influenced spring wheat productivity compared to its corresponding monocultures. Overall, there was small (high precipitation) or no (low precipitation) increase in radiation and water acquisition in the intercrops but there was a large increase in N uptake in all cases.
Significance: Designing site specific spring wheat/faba bean intercropping systems enhances the availability of N and use efficiency, which helps to minimize N input.

1. Introduction

Making agriculture more sustainable depends on reducing the input of chemical fertilizers and pesticides to mitigate the negative impact of farming on the environment, while boosting crop production has gained interest among researchers, policy makers, and farmers (Altieri, 1999; Füsun Tatlidil et al., 2009; Timpanaro et al., 2023; Ewert et al., 2023). Cereal/legume intercropping has been shown to increase production per unit area of land, by making more efficient use of the available resources compared to monocultures (Demie et al., 2022; Yu et al., 2016; Martin-Guay et al., 2018). Intercropping cereals with legumes is considered as a more sustainable form of crop production and can be a suitable alternative (Li et al., 2020; Lithourgidis et al., 2011; Martin-Guay et al., 2018, Bedoussac et al., 2015), with several ecological processes

* Correspondence to: Institute of Crop Science & Resource Conservation (INRES), Crop Science group, University of Bonn, Katzenburgweg 5, Bonn, NRW 53115, Germany.
E-mail address: dereje.demie@uni-bonn.de (D.T. Demie).

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occurring at the temporal and spatial scale that contribute to improved resource use in intercropping systems. Benefits include the complementary use of solar radiation (Gou et al., 2017), soil nitrogen (N) (Jensen et al., 2020; Hauggaard-Nielsen et al. (2001); Peoples et al., (2009); Jensen, (1996), and water (Mao et al., 2012). Therefore, understanding these ecological mechanisms and optimizing spatio-temporal diversity in terms of delivery of ecosystem services and productivity are key to obtaining the most benefits from such systems (Hauggaard-Nielsen et al., 2008). Meta-analyses of different studies showed that in intercropping systems, cereals take up more than their proportional share of soil N sources due to competitive interactions (Pelzer et al., 2014; Rodriguez et al., 2020; Jensen et al., 2020). In the case of wheat/soybean intercropping systems, Raza et al. (2023) reported that significantly more N was taken up compared to the respective monoculture systems. Hauggaard-Nielsen et al. (2001) reported that a pea/barley intercrop took up slightly more soil N compared to the barley monocrop but significantly more than the pea monoculture, resulting in 25–38 % higher land use efficiency for grain yield. Taking advantage of the fact that intercropped legumes get more of their N from the atmosphere than monocultures, intercropping could reduce N chemical fertilizer inputs by about 26 % on a global scale (Jensen et al., 2020). However, soil N-dynamics are also affected by the availability of other resources, such as soil water; therefore, it is important to consider the combined effect of water and N together (Bahia et al., 2024). Past research reported improved water use when combining cereals and legumes, for example, the relay maize/pea strip intercropping resulted in improved total water uptake and water use efficiency compared to their respective monocultures (Mao et al., 2012).

However, there is limited research on water use for cereal/legume intercropping systems for small grain cereals such as wheat and barley when combined with legumes such as faba bean or pea (Bahia et al., 2024). The crop species in intercropping and their access to soil water and N resources affect the dynamics of radiation interception, ultimately influencing the overall productivity of intercropping systems. Nitrogen acquisition and radiation interception are intricately linked and influenced by the root and shoot growth dynamics, alongside the interplay between water, N uptake, and radiation interception (Dreccer et al., 2000; Ullah et al., 2019). Furthermore, it remains unclear whether the productivity in intercropping is mainly attributed to enhanced resource acquisition (absolute resources that are captured by the crop) or improved resource use efficiency (the ratio between biomass or yield and the amount of acquired resource), particularly in within-row mixtures. Consequently, there is a need for comprehensive research to investigate resource use interactions under different environments and to identify the key factors in cereal/legume intercropping, which will ultimately allow for an improved management and design. A mechanistic understanding is crucial for proposing effective and generic crop management decisions such as partner choice or N fertilizer applications in intercropping systems (Bedoussac et al., 2015).

Despite the undeniable advantages of studying resource acquisition and use efficiency in crop mixtures via field experiments, this approach also poses a challenge due to the inherent complexity of underlying mechanisms. Additionally, the results of field experiments depend heavily on the context (Jones et al., 2023) with some situations resulting in a gain or loss in productivity compared with sole crops (MacLaren et al., 2023; Martin-Guay et al., 2018). For instance, in many field experimental studies, the computation of resource use efficiency is based on the total input, overlooking losses such as soil evaporation in the case of water and leaching in the case of N. This means that not all inputs are converted into biomass or grain yield. Using calibrated and tested process-based agroecosystem model simulations offers a promising approach to separating the actual daily crop-specific consumption of different resource uses, and to explore possible interactions for resource use and acquisition under different environments (Stomph et al., 2020). A review from Gaudio et al. (2019) highlighted the potential use of process-based crop models for intercropping systems, in particular to inform the use of appropriate agronomic practices, to identify the beneficial traits involved in the performance of intercrops, and to quantify ecological processes. Previous modeling studies were mostly dedicated to evaluate intercrop model performance (Demie et al., 2025; Berghuijs et al., 2020; Gou et al., 2017; Munz et al., 2014; Githui et al., 2023; Pierre et al., 2023). Their applications included applications of models to study water use in strip intercropping (Tan et al., 2020). Further, Launay et al. (2009) applied a model to explore radiation and N use in pea-barley intercropping. Overall, process-based agroecosystem modeling, combined with comprehensive field experimental data, offers the possibility to deepen the understanding of the complex resource dynamics of intercropping systems.

In the current study, we aimed to answer the following research questions with a focus on springwheat/ faba bean: 1) Which resource (water, radiation, or N) is the main driver of the intercropping performance of faba bean and spring wheat under varying conditions? 2) Is intercropping productivity primarily associated with enhanced resource acquisition or improved resource use efficiency? 3) Which specific resource is associated with each species and impacts the grain yield of individual species as well as the overall productivity of intercropped systems? To answer these questions, we used a process-based intercrop simulation model, which was previously calibrated and evaluated with an extensive spring wheat/faba bean data set, that has been shown to be in a good agreement with the experimental results (Demie et al., 2025) as well as data from field experiments of spring wheat/faba bean intercropping collected in three contrasting environments in Germany.

2. Materials and methods

The field experimental data presented in this study is part of already published research (Paul et al., 2023, 2024; Demie et al., 2025). These studies tested multiple spring wheat (*Triticum aestivum* L.) and faba bean (*Vicia faba* L.) cultivars under diverse intercropping systems and conditions. Part of the observed data was used to calibrate and evaluate the intercrop model applied in the current study (Demie et al., 2025). Here, the study focuses on understanding how resource uptake and use efficiency affect the performance of spring wheat/faba bean intercropping systems in three contrasting environments using one spring wheat cultivar, (Lennox) and one faba bean cultivar, (Mallory), growing as monocultures and in intercropping systems. Additionally, the model was further improved from the previous version with regards to biological N fixation by using a new approach in which biological N fixation is a function of the plant development stage, soil N content, soil depth, soil moisture content, field capacity, and wilting point (Williams and Izaurralde, 2005). This modification has a negligible effect on plant growth and development such as grain yield, shoot biomass, leaf area, or plant height but influenced the proportions of soil N uptake and biological N fixation of faba bean.

2.1. Characteristics of the experimental data and environmental conditions

The field experiments were conducted at two research facilities in two and one year, respectively, (i.e. three environments). The experiments were conducted in 2020 and 2021 at Campus Klein-Altendorf (CKA), the research facility of the University of Bonn located in Rheinbach near Bonn, Germany (50° 37' N, 6° 59' E), at 186 m above see level. The soil at the experimental station is classified as Haplic Luvisol (hypereutric, siltic) derived from loess (IUSS Working Group WRB, 2006) and characterized by a silty-loamy texture with a clay accumulation in the subsoil between about 45 and 95 cm soil depth. In 2020, an experiment was also conducted at the organically managed Wiesengut (WG), research facility of the University of Bonn (50° 47' N, 7°15' E) at 63 m above see level. The soil is characterized by a silt-loamy texture with Haplic Fluvisol (IUSS Working Group WRB, 2006) soil type. The three environments were contrasting in terms of soil N and precipitation

(CKA2020: high soil N but low precipitation; CKA2021: high soil N and high precipitation; and WG2020: low soil N, and low precipitation). In comparison to CKA, the WG organically managed field exhibited higher concentrations of total soil organic carbon (C) with a high mineralization potential in the topsoil, while at the field site CKA, higher initial topsoil mineral N (N_{min}) levels were observed (Table S1). The total precipitation during the growth period (March-August) at CKA2021 (458.5 mm) considerably exceeded that of 2020 (CKA2020: 266 mm, WG2020: 287 mm). April and May, crucial for early crop development, received less precipitation in 2020 than in 2021. Similarly, June and July, critical for flowering and grain filling, experienced significantly lower precipitation in 2020 compared to 2021 at both sites. Therefore, 2020 was classified as a dry season, while 2021 was considered a wet season (Fig. S1).

2.2. Field experimental setup and cultivars

The field experiments were performed as a randomized complete block design with four replicates, except in CKA 2021, where the intended field design was not implemented due to a sowing error, and often fewer than four field replicates were available. Spring wheat and faba bean, cultivars were grown, as monocultures and intercropped in replacement design. Spring wheat and faba bean were mixed in a 1:1 ratio, which means 50 % of seeds of each species from the respective monoculture crops were mixed in the intercrop (Paul et al., 2023). The plot size and the row distance were 1.5×10 m and 21 cm, respectively (Table S2). During the growth periods, there were no fertilizers, pesticides, or irrigation water applied. For further details about the field experiments in 2020, refer to Paul et al. (2023), and Demie et al. (2025) for CKA2021. For the current study, we selected the cultivars Lennox (spring wheat) and Mallory (faba bean), growing under sole and intercropped systems, because data availability was highest for these two cultivars and their treatment combinations.

2.3. Field data collection

Crop development was observed based on the BBCH-scale (Biologische Bundesanstalt, Bundessortenamt and CHemical industry), a decimal system for uniform coding of phenology of various mono- and dicotyledonous plant species (Meier, 2001). Agronomic data such as shoot and root biomass, plant height, volumetric soil water content, leaf area index (LAI), and grain yield were measured. The grain yield and biomass presented in this study are on dry matter (DM) basis. For details on the experimental results, including grain yield, refer to Paul et al. (2024) and Demie et al. (2025). The photosynthetically active radiation (PAR) was measured two times in 2020 and three times in 2021 with an SS1 Sunscan canopy analysis system (Delta T- T-devices Cambridge, UK). The fraction of intercepted photosynthetically active radiation (fIPAR) was calculated as the difference between PAR measured below the canopy and global PAR, divided by global PAR measured above the canopy. FDR moisture sensors HH2 with ML3 Theta Probe (ecoTech Umwelt-Meßsysteme GmbH, Bonn, Germany) were used to measure volumetric soil water content at different soil depths 30 cm, 45 cm, 60 cm, and 90 cm. The soil moisture content was measured four times on different days after sowing (DAS) during the growth period in 2020 and three times in 2021; for the details, see Demie et al. (2025). Soil nitrate-N and ammonium-N were determined photometrically using a continuous flow analyzer (Seal QuAAtro 39, Norderstedt, Germany) after K_2SO_4 extraction of the soil sample. The soil samples were taken at 0–30, 30–60, and 60–90 cm soil depths using a Pürckhauer auger by collecting a composite from three random points within each plot, for the details see Hadir et al. (2024).

2.4. Process-based intercrop model simulations

The simulations were conducted by using an agroecosystem model implemented in the modeling platform SIMPLACE (Scientific Impact Assessment and Modelling Platform for Advanced Crop Ecosystem Management, Enders et al., 2023). The model framework SIMPLACE has been developed during the last decade and allows applications for climate change impact assessments and crop management scenarios, amongst others (Enders et al., 2023). A set of SimComponents (i.e a functions that represents a crop-related process) including LINTUL5-Phenology, LINTUL5NPKDemand, SlimN, LINTUL5Biomass, SlimRoots, and SlimWater (Seidel et al., 2019), amongst others, were combined into a model solution. The intercrop sub-model implemented in the SIMPLACE platform simulates spring wheat/faba bean intercropping and their respective monocultures. The intercrop model had already been calibrated and satisfactorily tested against the field experiment dataset (Demie et al., 2025). In the current study, the tested model was applied to understand resource acquisition and plant-plant and resource-plant interaction by simulating crop growth, crop water and crop N uptake as well as radiation interception.

2.4.1. Intercrop model description

The intercrop model implemented in SIMPLACE was assembled by using all the crop-related SimComponents twice (one for each crop), using soil-related SimComponents once (one common soil), and by adding SimComponents to split radiation and water/nutrient uptake. The crop water demand per species was aggregated, and the potential transpiration of both crops was summed up and weighted by their area fraction to get field-scale data (for details, see Demie et al., 2025). Daily calculations were performed for crop water uptake (actual transpiration), N uptake, and radiation interception for each species separately for both monocultures and the intercropping systems.

2.4.1.1. Crop radiation interception and use. The radiation interception model calculates the radiation share (fraction intercepted by each species) of each species in the intercrops based on their actual plant height and LAI, the proportion of each species (the area covered by each species) in intercropping, and the canopy extinction coefficient of the species (Demie et al., 2025). The radiation use efficiency (RUE) approach was implemented in the RadiationInterception SimComponent based on the approach of Monteith and Moss (1977) in which accumulated crop biomass is linearly associated with crop intercepted radiation.

2.4.1.2. Root growth and crop water and N uptake. The below-ground allocation SimComponent calculates the root growth of each species, the water and N uptake depending on the roots presence in a specific soil layer, the resource availability in that layer, the crop water and N demand and further species-specific parameters. The below-ground allocation factor considers the root length density (RLD), the Root Restriction Factor (RRF), which is calculated by considering the RLD and root age, and the proportion of each species in intercropping. In a previous field experiment study by Hadir et al. (2024), it was observed that spring wheat rooted faster into the deeper soil layers than faba bean. Consequently, the root elongation rate was estimated to reflect these differences in the model. The SplitWaterUptake SimComponent calculates the root water and N uptake of each species per soil layer from the mobile and the retained soil water. The details of the equation are documented in Krauss (2018).

The soil profile was segmented into 40 horizontal layers each of 5 cm thickness. Crop-specific water uptake and N was computed for every layer. To facilitate the data visualization and analysis, water and N uptake were clustered into four depth layers: 0–30 cm, 30–60 cm, 60–90 cm, and 90–120 cm. The daily potential plant growth rate is driven mainly by radiation and temperature. Daily potential growth is then limited by the transpiration reduction factor (TRANRF, for water limitation) and the N nutrition index (NNI, for N limitation). TRANRF is calculated based on the ratio between actual and potential crop transpiration, which is calculated by the SimComponent SlimWater. NNI is calculated by dividing the difference between the actual N and residual N by the difference between the optimal N and the residual N.

The factors NNI and TRANRF range from 0 (severe N or drought stress, no increase of biomass on that day) to 1 (no stress, optimum water and N supply). Additional details of the model SimComponents are given in Demie et al. (2025) and Seidel et al. (2021).

2.5. Data processing and calculations

In this study, we used both simulated and field experimental data (Table 1). However, most of the data came from the process-based simulation model, as it was not feasible to measure certain variables in the field experiments. This was particularly true for soil-related dynamics per crop species when growing them as intercrops mixed within the same row. Table 1 summarizes the sources of the various data used in the analysis.

The primary objective was to compare resource acquisition between the two cropping systems (monocultures vs. intercrop). As a result, we compared the average of captured resources of the two monocultures to the resources captured in intercrops (the sum of resources captured by both species in intercropping systems). Additionally, to understand species and cropping system interactions, we compared the resources captured by species in intercropping to their respective monocultures. Therefore, to compare the absolute resources captured, specifically, crop water uptake (actual transpiration in mm), N uptake (kg ha^{-1}), and radiation capture (MJ m^{-2}) of the two cropping systems and the two species, we calculated the following terms:

$$SW\_mono = \text{Total resource capture of spring wheat in monocultures} * 0.5 \quad (1)$$

$$FB\_mono = \text{Total resource capture of faba bean in monocultures} * 0.5 \quad (2)$$

$$Ave\_mono = SW\_mono + FB\_mono \quad (3)$$

$$Inter = SW\_inter + FB\_inter \quad (4)$$

Where SW_mono is the resource capture of spring wheat in monoculture and FB_mono is the resource capture of faba bean in monoculture. The factor 0.5 was used to compare the performance of each species in monoculture with its performance in intercropping because when intercropped each species was grown with 50 % of their respective plant density in monoculture. Ave_mono is the average of resource capture of monocultures of the spring wheat and the faba bean; Inter is the sum of resource capture of spring wheat and faba bean in intercropping; SW_inter is resource capture of the spring wheat in intercropping; FB_inter is resource capture of the faba bean in intercropping.

A standard measure of intercrop performance is the land equivalence ratio (LER), which is the relative land area that is required for crop monocultures to produce the same grain yield as observed in the mixture (Willey and Rao, 1980). For both, observed and simulated values, the LER was calculated as follows:

$$LER = pLER_{SW} + pLER_{FB} = \frac{Y_{SW\_inter}}{Y_{SW\_mono}} + \frac{Y_{FB\_inter}}{Y_{FB\_mono}} \quad (5)$$

Where $pLER_{SW}$ is the partial land equivalent ratio of spring wheat; Y_{SW_inter} is the grain yield of spring wheat in intercropping, Y_{SW_mono} is the grain yield of spring wheat in monoculture and $pLER_{FB}$ is the partial land equivalent ratio of faba bean; Y_{FB_inter} is the grain yield of faba bean in intercropping, and Y_{FB_mono} is the grain yield of FB in monoculture.

Yield can be expressed as the product of two terms, a resource acquisition term, and an efficiency term:

$$\text{Yield} = \text{resource acquisition} \times \text{resource use efficiency} \quad (6)$$

Here, the resource use efficiency infers to resource conversion efficiency where by definition, efficiency is the ratio of yield to the resource acquired. In the present study, we were interested in three resources: intercepted radiation, water and N (soil N, and biologically fixed atmospheric N). The above equation applies to all four resources. For pLER to be greater than 0.5, resource acquisition in the intercrop must be larger than one-half of the value in the monocrop and/or resource use efficiency in the intercrop larger than in the monocrop. Thus, the analysis will allow us to identify, for each species, to what extent a value of pLER$>$ 0.5 is driven by increased acquisition in the intercrop compared to the monocrop, and to what extent it is driven by an increase in efficiency, for each resource and crop.

To understand the effect of resource use on yield and to identify if the obtained higher productivity in the intercropping system is associated with resource acquisition or use efficiency, we introduce two indices, the resource acquisition ratio (Table 2) and the resource use efficiency ratio (Table 3), which were calculated for each resource (water, N and light) and each environment. The concept is similar to common calculations of water use efficiency, N use efficiency, and radiation use efficiency (Ullah et al., 2019), where yield is divided e.g. by water uptake (or transpiration). The comparison here is between intercrop resource use efficiency and monoculture resource use efficiency (comparative use efficiency). The resource use efficiency ratio represents the relative amount of resources used in monocultures to determine the yield obtained in a unit area of intercrop. It is similar to the resource equivalent ratio (Mao et al., 2012; Werf et al., 2021).

Table 1
Observed and simulated data used in the current study (x stands for data available). Grain yield and biomass were in dry matter (DM) basis.

Variables	Measured		Simulated	
	Available	Measured for	Available	Simulated for
Grain yield (t ha^{-1})	×	Each species	×	Each species
Above-ground dry biomass (kg ha^{-1})			×	Each species
Crop water uptake (mm)			×	Each species
Crop N uptake (kg ha^{-1})			×	Each species
Crop radiation interception (MJ m^{-2})	×	Intercrop and monoculture	×	Each species
Transpiration reduction factor (TRANRF)			×	Each species
Nitrogen nutrition index (NNI)			×	Each species
Volumetric soil water content	×	Intercrop and monoculture	×	Each species
Soil mineral nitrogen content at sowing (kg ha^{-1})	×	Intercrop and monoculture	x	Each species

3. Results

3.1. Monoculture and intercrop grain yield under diverse environments

The observed and simulated intercropping grain yield revealed a significant increase in land use efficiency (Table 4), with both grain yield and LER being influenced by the environment (Paul et al., 2024). In all environments, spring wheat consistently showed a higher yield compared to the expected yield from spring wheat monocultures, while faba bean in the intercropping system showed less yield at CKA2020 and WG2020 but slightly higher at CKA2021 compared to the expected yield from faba bean monocultures. Observed LER, a proxy for land use efficiency, increased by about 4 %, 22 % and 20 % at CKA202, CKA2021, and WG2020. In both, CKA2020 and WG2020, the partial land use efficiency of intercropped faba bean was lower than 0.5, whereas at

Table 2
Resource acquisition ratio of intercrops compared to monocultures calculated from simulated data. An acquisition ratio (AR) > 1 indicates higher resource capture in the intercropping system compared to monocultures, and AR < 1 indicates lower resource capture in the intercropping system compared to monocultures. For a given species, if the acquisition ratio (AR) > 0.5 indicates higher resource capture in the intercropping system compared to monocultures and AR < 0.5 indicates lower resource capture in the intercropping system compared to monocultures.

Index	Acronym	Equation	Description
Water acquisition ratio of SW (FB)	$WAR_{SW (FB)}$	$\frac{WU_{SW(FB)\_inter}}{WU_{SW(FB)\_mono}}$	$WU_{SW(FB)\_inter}$: Water use of SW or FB in intercropping $WU_{SW(FB)\_mono}$: Water use of SW or FB in monoculture
Water acquisition ratio	WAR	$WAR_{SW} + WAR_{FB}$	Total water acquisition ratio
N acquisition ratio of SW (FB)	$NAR_{SW (FB)}$	$\frac{NU_{SW(FB)\_inter}}{NU_{SW(/FB)\_mono}}$	$NU_{SW(FB)\_inter}$: N use of SW or FB in intercropping $NU_{SW(FB)\_mono}$: N use of SW or FB in monoculture
N acquisition ratio	NAR	$NAR_{SW} + NAR_{FB}$	Total N acquisition ratio
N acquisition ratio including BNF	NAR_{FB_BNF}	$\frac{soil\ N + BNF\ NU_{FB\_inter}}{soil\ N + BNF\ NU_{FB\_mono}}$	BNF NU_{FB_inter}: FB N use in intercropping including BNF BNF NU_{FB_mono}: FB N use in monoculture including BNF
N acquisition ratio including BNF	NAR_{BNF}	$NAR_{SW} + NAR_{FB\,BNF}$	Total N use including BNF
Radiation acquisition ratio of SW (FB)	$RAR_{SW (FB)}$	$\frac{RU_{SW(FB)\_inter}}{RU_{SW(FB)\_mono}}$	$RU_{SW(FB)\_inter}$: Radiation use of SW or FB in intercropping $RU_{SW(FB)\_mono}$: Radiation use of SW or FB in monoculture
Radiation acquisition ratio	RAR	$RAR_{SW} + RAR_{FB}$	Total radiation acquisition ratio

SW-spring wheat; FB- faba bean; BNF- biological N fixation in kg ha^{-1}, water uptake in mm, N in kg ha^{-1}, radiation in MJ m^{-2}

CKA2021, the land use efficiency was similar in both systems. Across all environments, spring wheat demonstrated higher intercropping land use efficiency than spring wheat in monoculture (spring wheat pLER >0.5).

3.2. Resource use in intercropping and monocultures under diverse environments

3.2.1. Observed resource use in intercrops and monocultures

The observed soil water content (Fig. S2-S3) and intercepted photosynthetically active radiation (IPAR) (Fig. S4) showed no substantial difference between the average of the monocultures and intercrops during the growth period, which suggests that crop water uptake in the mixture was comparable to the average of both monocultures. This was consistent across the studied environments and measuring dates. With regard to species, in most of the cases, the measured and simulated soil moisture content in faba bean monocultures was higher compared to wheat monocultures and intercropping. The observed soil water content at different soil depths indicated that the upper soil layers (until about 30 cm or 45 cm) generally exhibited a lower water content compared to the deeper soil layers. However, this pattern was dependent on environmental conditions. In the particularly wet season of CKA2021, in many days the soil water content at each soil layer was comparable, suggesting homogeneous water distribution across soil layers due to ample water input. Conversely, during the drier seasons at CKA2020 and WG2020, the water in the topsoil was depleted more rapidly due to crop water uptake, high soil evaporation, and limited rainfall.

3.2.2. Simulated resource acquisition and use efficiency under high N and high precipitation (CKA2021)

For all three resources the faba bean acquisition ratios, i.e WAR, NAR and RAR were close to 0.5 and resource use efficiencies WUER, NUER and RUER were > 1 (Table 5). On the other hand, all spring wheat resources acquisition ratio (WAR, NAR and RAR) were > 0.5, and WUER and RUER were > 1. Spring wheat soil N acquisition was considerably higher than for faba bean: the partial N acquisition ratio for wheat was 0.68, although the use efficiencies were lower than 1 (Table 5). Remarkably, an enhanced total N use in intercropping was due to an enhanced biological N fixation (NUE_{BNF} = 1.15) and soil N uptake (NAR = 1.17). Total light interception and water uptake were higher in the intercropping system compared to the averages of the monocultures.

3.2.2.1. Simulated resource uptake by soil depth and over time (CKA2021). Simulated total radiation and water acquisition were similar during the vegetative stage in both intercropping and monocultures, however, differences became more pronounced during the grain filling period (Fig. 1). In all cropping systems, the higher proportion of water uptake occurred in the upper soil layer (0–60 cm soil depth) with a very small proportion of water uptake occurring in the deeper soil layer (90–120 cm soil depth). Species-wise, the intercropped spring wheat water uptake was slightly higher (30 mm) than spring wheat in monoculture (Fig. 1A). The soil N uptake in intercropping surpassed the average of monocultures by 20 %, particularly, before flowering (Fig. 1B). The N acquisition in intercropping was greater compared to the monocultures, due to enhanced acquisition from the deeper soil layers (90–120 cm soil depth, Fig. 1B).

At CKA2021 the simulated daily faba bean above ground biomass increament, radiation interception, drought stress and nitrogen nutrition index (NNI) were comparable in both intercrops and monocultures. However, the simulated intercrop spring wheat showed lower water and N stress compared to the faba bean, consequently resulting in higher shoot biomass and radiation interception compared to spring wheat monoculture (Fig. 2). After flowering, the radiation interception of the spring wheat intercrop exceeded that of the spring wheat monocultures (~DAS 70, Fig. 2B), resulting in an increased above ground biomass (Fig. 2A).

3.2.3. Simulated resource acquisition and use efficiency under high N and low precipitation (CKA2020)

Simulated faba bean resource acquisition ratios (WAR, NAR and RAR) were < 0.5, while resource use efficiencies were < 1, except for the NUER and $NUER_{BNF}$ (Table 6). In contrast, for spring wheat, the resources acquisition partial ratios (WAR, NAR and RAR) were > 0.5 and the use efficiencies (WUER, NUER and RUER) were > 1. The water uptake was higher in the intercropped spring wheat, while an opposite trend was observed in faba bean, which suggests a higher competitiveness of spring wheat versus the faba bean in soil water acquisition. However, the total water uptake was similar between the intercrop and the average of the two monocultures (Fig. 3). On the other hand, there was an increase in total soil N uptake (Fig. 3). Overall, the intercrops' resource acquisitions and use efficiencies were similar to the average of monocultures, except for N, where NAR was 1.10 and NAR_{BNF} was 1.12, and water use efficiency was slightly enhanced (WUE=1.05) (Table 6). However, the LER for grain yield was only 1.04 %.

3.2.3.1. Simulated resource uptake by soil depth and over time (CKA2020). The simulation results showed no considerable differences in total seasonal water uptake between intercropping and monocultures

Table 3
Resource use efficiency ratio of intercrops compared to monocultures calculated from simulated data. A resource use efficiency ratio (ER) > 1 indicates higher resource use efficiency in the intercropping system compared to monocultures, and a resource use efficiency ratio (ER) < 1 indicates lower resource use efficiency, i.e. lower yield per unit of resource used.

Indice	Acrom	Equation	Description
Water use efficiency ratio of SW (FB)	$WUER_{SW(FB)}$	$pLER_{SW(FB)} \times \frac{WU_{SW(FB)\_mono}}{WU_{SW(FB)\_inter}}$	$WU_{SW(FB)\_inter}$: Water use of SW or FB in intercropping $WU_{SW(FB)\_mono}$: Water use of SW or FB in monoculture
Water use efficiency ratio	$WUER$	$pLER_{SW} \frac{WU_{SW\_mono}}{WU_{inter}} + pLER_{FB} \frac{WU_{FB\_mono}}{WU_{inter}}$	Total water use efficiency ratio WU_{inter}: total water use in intercrop
N use efficiency ratio of SW	$NUER_{SW(FB)}$	$pLER_{SW(FB)} \times \frac{NU_{SW(FB)\_mono}}{NU_{SW(FB)\_inter}}$	NU_{SW_inter}: N use of SW or FB in intercropping NU_{SW_mono}: N use of SW or FB in monoculture
N use efficiency ratio	$NUER$	$pLER_{SW} \frac{NU_{SW\_mono}}{NU_{inter}} + pLER_{FB} \frac{NU_{FB\_mono}}{NU_{inter}}$	Total N use efficiency ratio NU_{inter}: total N use in intercrop
N use efficiency ratio including BNF	$NUER_{FB\_BNF}$	$pLER_{FB} \times \frac{soil\ N + BNF\ NU_{FB\_mono}}{soil\ N + BNF\ NU_{FB\_inter}}$	BNF NU_{FB_inter}: N use of FB in intercropping and BNF BNF NU_{FB_mono}: N use of FB in monoculture and BNF
N use efficiency ratio including BNF	$NUER_{BNF}$	$pLER_{SW} \frac{NU_{SW\_mono}}{soil\ N + BNF\ NU_{inter}} + pLER_{FB} \frac{soil + BNF\ NU_{FB\_mono}}{soil + BNF\ NU_{inter}}$	Total N use efficiency ratio including BNF
Radiation use efficiency ratio of SW	$RUER_{SW(FB)}$	$pLER_{SW(FB)} \times \frac{RU_{SW(FB)\_mono}}{RU_{SW(FB)\_inter}}$	RU_{SW_inter}: Radiation use of SW or FB in intercropping RU_{SW_mono}: Radiation use of SW or FB in monoculture
Radiation use efficiency ratio	$RUER$	$pLER_{SW} \frac{RU_{SW\_mono}}{RU_{inter}} + pLER_{FB} \frac{RU_{FB\_mono}}{RU_{inter}}$	Total radiation use efficiency ratio RU_{inter}: total radiation use in intercrop

SW-spring wheat; FB- faba bean; $pLER_{FB}$ is the partial land equivalent ratio of faba bean and $pLER_{SW}$ is the partial land equivalent ratio of spring wheat; with regard to grain yield; BNF- biological N fixation. The water use is similar to accumulated actual crop transpiration (mm), N use is similar to accumulated soil N uptake including biologically fixed N (kg ha^{-1}) and radiation is similar to accumulated intercepted radiation (MJ m^{-2}) over the whole growing cycle. Water uptake in mm, N in kg ha^{-1}, radiation in MJ m^{-2}

Table 4
Simulated and observed grain yield and land equivalent ratios (LER) in three environments (CKA2020, CKA2021 and WG2020).

Environment	Grain yield (t ha^{-1})				LER			Source
	Spring wheat		Faba bean		$pLER_{SW}$ [c]	$pLER_{FB}$ [d]	LER [e]	
	mono. [a]	inter [b].	mono.	inter.				
CKA2020	3.46	2.69	4.10	1.07	0.78	0.26	1.04	obs [f]
CKA2021	5.23	3.20	3.63	2.20	0.61	0.61	1.22	obs
WG2020	2.68	2.07	1.19	0.50	0.77	0.42	1.20	obs
CKA2020	3.75	2.65	3.02	1.00	0.71	0.33	1.04	sim [g]
CKA2021	5.84	3.45	3.84	2.04	0.59	0.53	1.12	sim
WG2020	2.80	2.13	2.22	0.71	0.76	0.32	1.08	sim

[a] monoculture;
[b] intercrop;
[c] partial land equivalent ratio of spring wheat;
[d] partial land equivalent ratio of faba bean;
[e] land equivalent ratio;
[f] observed and
[g] simulated

(the average of the two monocultures, (Fig. 3A). However, a clear difference was observed between monocultures and intercropping after flowering for soil water uptake from the deeper soil layers (60–120 cm). About 27 % of total intercrop water uptake was from deeper soil layers (60–120 cm); however, the share of water from same soil layers was 24 % in monocultures.

With regard to species, intercropped spring wheat took up 35 %, which was more water uptake compared to spring wheat in monoculture at an equivalent density. However, faba bean showed a 36 % reduction in soil water uptake compared to faba bean in monocultures at an equivalent sowing density.

The soil N uptake in intercropping surpassed the average of monocultures. The intercrop soil N uptake was about 20 kg N ha^{-1} higher than the mean of both monocultures (Fig. 3B). When considering individual species, intercropped spring wheat demonstrated a higher N uptake compared to monoculture spring wheat (at equivalent sowing density). Conversely, intercropped faba bean resulted in lower soil N accumulation compared to monoculture faba bean. Biological N fixation in intercropping was about half compared to faba bean in density-equivalent monocultures (Fig. 3B). With regards to radiation interception, the simulated results revealed no substantial differences (-1 %) between intercropping and monocultures. However, as for radiation interception of species, spring wheat in intercropping intercepted 26 % more than observed in spring wheat in monocultures. In contrast, faba bean in intercropping showed a 27 % reduction in radiation interception compared to faba bean in monocultures.

At CKA2020 the simulated daily drought stress per species in monocultures and intercropping revealed that spring wheat exhibited less drought stress when grown with faba bean as compared to spring wheat monoculture. However, drought stress in faba bean was stronger in intercropping at mostly around emergence and after flowering (around DAS ~70). As for N dynamics, spring wheat in the monoculture experienced a stronger limitation of N compared to spring wheat in intercropping. However, there was no N stress for faba bean in both cropping systems during the vegetative growth period. The simulated daily plant growth and radiation interception also followed the same trends as the transpiration reduction factors. Spring wheat in intercrops produced more biomass and intercepted more radiation compared to spring wheat in monocultures, as result, the faba bean growth and radiation interception in intercrops were dramatically reduced (Fig. 4).

Table 5
Comparison of simulated total resource acquisition and resource use efficiency of intercrops and monocultures in high N and high precipitation (CKA2021) conditions. Refer to Tables 2 and 3 for the indices calculation. A ratio > 1 indicates that intercrops had higher resource acquisition, resource use, and land use efficiency than the monocultures. A partial ratio greater than 0.5 for acquisition and 1 for use efficiency indicates that each species had higher resource acquisition and use efficiency, respectively, compared to its monoculture. Grain yield (t ha^{-1}), water uptake (mm), N uptake (kg ha^{-1}), radiation interception (MJ m^{-2}).

Traits	Faba bean			Spring wheat			Both species			
	Mono culture	Inter crop	Partial ratio[a]	Mono culture	Inter crop	Partial ratio[a]	Mono culture	Inter crop	Ratio[b]	Indices
Grain yield	3.84	2.04	0.53	5.80	3.44	0.59	9.68	5.48	1.12	LER[c]
Water uptake	320.80	155.55	0.49	327.70	184.15	0.56	648.50	339.70	1.04	WAR[d]
Water use efficiency	1.20	1.31	1.10	1.77	1.87	1.06	1.49	1.61	1.08	WUER[e]
N uptake	60.70	29.9	0.49	130.2	88.2	0.68	190.9	118.1	1.17	NAR[f]
N use efficiency	6.34	6.83	1.08	4.46	3.90	0.88	5.08	4.64	0.92	NUER[g]
Soil N + BNF uptake	243.00	115.50	0.48	130.20	88.20	0.68	373.14	203.70	1.15	NAR_{BNF}[h]
Soil N + BNF use efficiency	1.58	1.8	1.12	4.46	3.90	0.88	2.60	2.69	1.00	$NUER_{BNF}$[i]
Radiation interception	628.20	313.20	0.50	635.8	355.20	0.56	1264.0	668.3	1.06	RAR[j]
Radiation use efficiency	0.62	0.65	1.07	0.92	0.97	1.06	0.78	0.82	1.06	RUER[k]

[a] the ratio of the given species in the mixture to its respective monoculture
[b] the ratio of intercrops to monocultures;
[c] land equivalent ratio;
[d] water acquisition ratio;
[e] water use efficiency ratio;
[f] N acquisition ratio;
[g] N use efficiency ratio;
[h] N acquisition ratio including biologically fixed N;
[i] N use efficiency ratio including biologically fixed N;
[j] radiation acquisition ratio;
[k] radiation use efficiency ratio.

3.2.4. *Simulated resource acquisition and use efficiency under low N and low precipitation (WG2020)*

Under low N and low precipitation, simulated faba bean resource acquisition ratios (WAR, NAR and RAR) were < 0.5 and the resource use efficiencies (WUER, NUER and RUER) were < 1. In contrast, for spring wheat, the partial ratio of resource acquisition (WAR, NAR and RAR) were > 0.5 and the use efficiency ratios (WUER, NUER and RUER) were also > 1 (Table 7). Spring wheat revealed higher water uptake in intercropping, while faba bean took up less water, although total water uptake was the same in intercropping compared to the average of the monocultures (Fig. 5). On the other hand, there was an increase in total soil N uptake in intercropping compared to monocultures (Fig. 5). The radiation interception and water uptake in intercrops were similar to that of the average of the monocultures (the ratio is nearly 1) (Table 7). However, the N uptake (NAR=1.22), radiation use efficiency (1.15), and water use efficiency (WUER=1.12) of the intercrops were higher than that of the average of the monocultures.

3.2.4.1. Simulated resource uptake by soil depth and over time (WG2020). The differences between the simulated seasonal total water uptake between intercropping and monocultures were generally small. However, post-flowering water uptake from the deeper soil layer (60–120 cm) was considerably different between monocultures and intercropping. About 68 % of the total intercrop water uptake was from the deeper soil layer (60–120 cm layers). In contrast, in monocultures, the share of water from deeper soil layers was only 49 %.

With regard to species, the intercropped spring wheat took up 28 % more water compared to spring wheat in monoculture at an equivalent sowing density. However, faba bean showed a 31 % reduction in total water uptake compared to faba bean in monocultures (Fig. 5A). The soil N uptake in intercropping surpassed the average of monocultures by 26 %. When considering individual species, the soil N availability was higher in intercropped spring wheat, resulting in 28 % increased N uptake over spring wheat in monocultures (Fig. 5B). Intercropped faba bean showed 22 % higher soil N uptake compared to faba bean in monocultures. The biological N fixation in the intercropping was almost half compared to faba bean in the density-equivalent monocultures. Simulated radiation interception showed no substantial differences between intercropping and monocultures, but spring wheat in intercropping intercepted about 10 % more solar radiation than spring wheat in monocultures. Conversely, faba bean in monocultures showed a 11 % reduction in radiation interception (Fig. 5C).

At WG2020, spring wheat showed less drought stress when grown with faba bean as compared to its monoculture (Fig. 6C). The drought stress in faba bean was enhanced in intercropping, particularly after emergence and after flowering which was (around DAS ~68, Fig. 6C). The simulated daily plant growth and radiation interception also followed the same trends as the transpiration reduction factors. intercropped spring wheat produced more biomass and intercepted more radiation compared to spring wheat in monocultures. In contrast, faba bean growth and radiation interception in intercrops was lower than in monocultures (Fig. 6B).

4. Discussion

4.1. *General overview*

In this study, we examined which resource (water, N, or radiation) drives intercropping performance. We applied a calibrated and tested process-based intercrop simulation model (Demie et al., 2025) and used data from intercropping field experiments with spring wheat/faba bean collected in three contrasting environments (Paul et al., 2023, 2024; Demie et al., 2025). The study identified specific resource allocations associated with each crop species, which significantly impacted both the productivity of individual species and the overall productivity of the intercropping systems. We specifically used simulated data to assess intercrop and monoculture water and N uptake and radiation acquisition, and biological N fixation and the respective resource use efficiencies. The current modeling approach allowed us to separate the actual crop resource consumption from unproductive resource losses, such as soil evaporation and N leaching, thereby enabling plausible computation of resource acquisition and use efficiencies (Stomph et al., 2020). Additionally, the modeling approach provided daily crop-specific resource acquisition data per crop and for various, which helped in understanding species interactions in intercropping under diverse conditions. Our findings strengthen the hypothesis that the higher

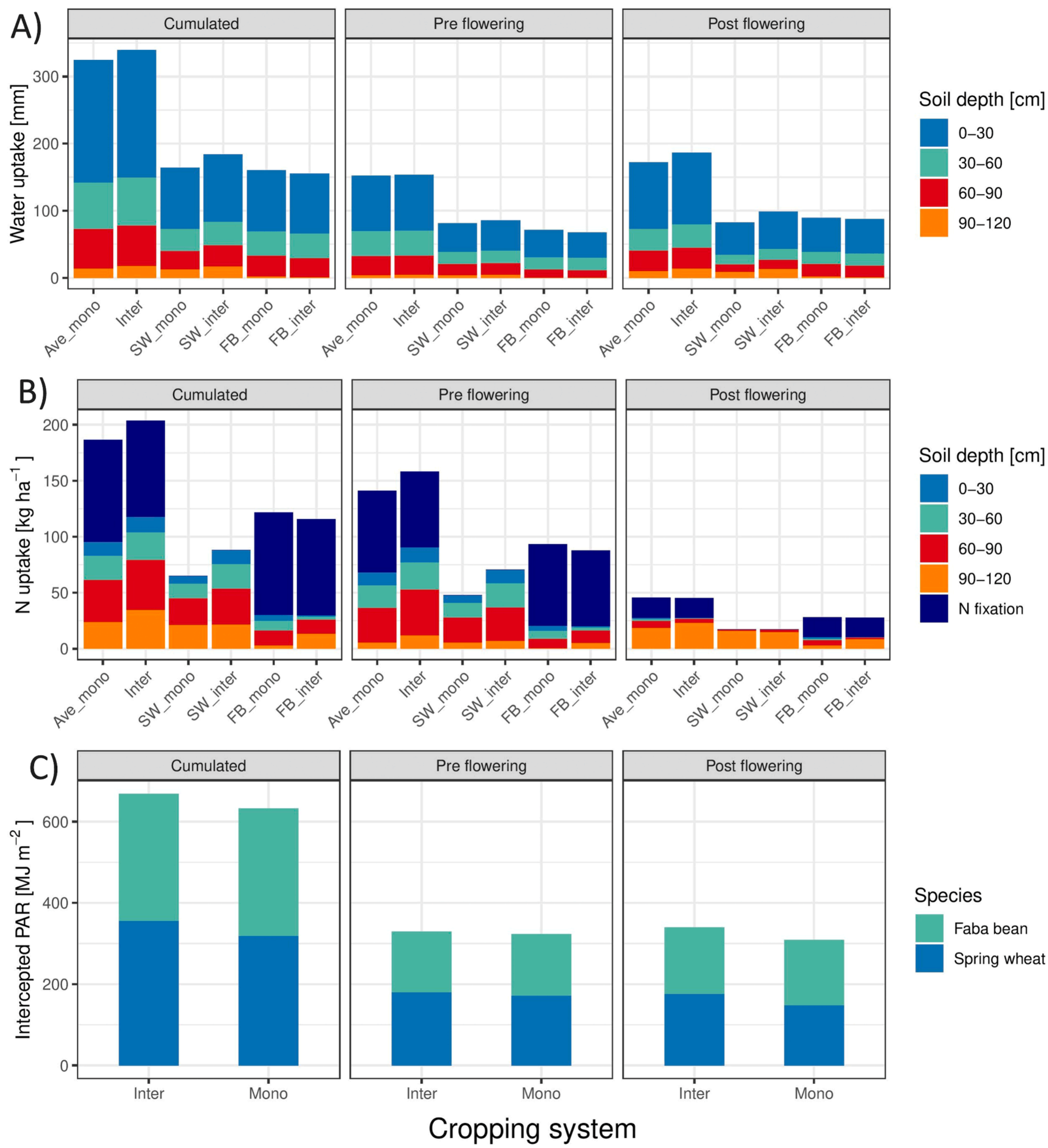

Fig. 1. Simulated crop resource acquisition for A) water uptake B) N uptake and biological fixation and C) radiation, cumulated over the season, from sowing to spring wheat flowering and from spring wheat flowering to harvest at CKA2021. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono is the average of monocultures of SW and FB; inter- intercropping of SW and FB; FB_inter- FB in intercropping; SW_inter- SW in intercropping; SW_mono-SW in monoculture and FB_mono-FB in monoculture. Here, the values of SW_mono and FB_mono represent half of the total uptake in their respective monocultures, because, when intercropped, each species was grown at 50 % of the sowing density used in their monocultures.

productivity of cereal/legume intercropping systems compared to the respective monocultures may be mainly driven by resource acquisition, primarily N uptake as already revealed by several studies (Bahia et al., 2024; Bedoussac and Justes, 2010a, 2010b; Hauggaard-Nielsen et al., 2009, 2001), and enhanced water use efficiency, depending on the environment. However, our approach allowed us to quantify the trends of resource acquisition and use efficiency of the species in intercropping systems by simultaneously assessing the main abiotic resources i.e water, N and radiation. In all environments, intercropping systems exhibited higher soil N acquisition compared to the average monocultures. The model results suggested an early impact of the intercropping with a legacy effect on faba bean growth due to the early dominance of spring wheat resulting in higher water stress for beans and less water stress for spring wheat in the intercropping system (Figs. 4C and 6C). Similar result was reported by Paul et al. (2023), who investigated the effects of spring wheat/faba bean mixtures on early crop development in CKA2020 and WG2020. The authors reported that a small advantage of spring wheat at emergence favored spring wheat dominance at later growth stages and led to superiority over faba bean in terms of biomass growth. Applying the 4 C approach of plant-plant interaction for abiotic resource capture as already described by Justes et al. (2021) and Williams and McCarthy, (2001), spring wheat dominated the legume regarding water uptake, especially in the dry season of 2020 (Fig. S5). At WG2020, complementarity and cooperation were stronger than competition for N use (Fig. S6). Our finding are similar to the results from Bahia et al. (2024), who indicated that the advantages of cereal/legume intercropping can be attributed to the improved use of N and water, the latter being less important in our study. Similar results were also reported by Xu et al. (2019), suggesting that the increased grain yield of intercropping was related to improved N availability.

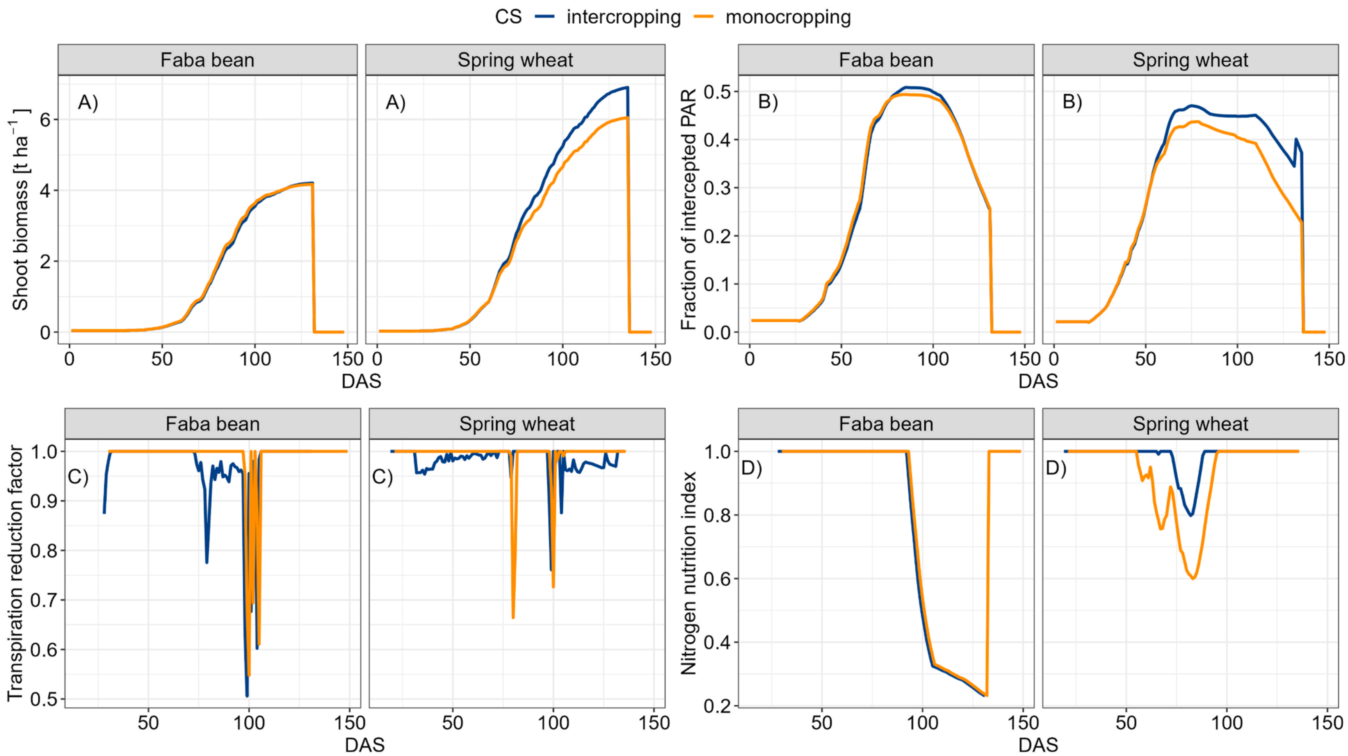

Fig. 2. Simulated daily dynamics for the CKA2021 environment (high soil N and high rainfall) for both cropping system (CS). A) daily shoot biomass; B) fraction of intercepted photosynthetically active radiation (PAR), C) transpiration reduction factor (TRANRF, 0: full stress, 1 no stress) and D) nitrogen nutrition index (NNI, 0: full stress, 1 no stress); spring wheat (SW cv. Lennox) and faba bean (FB cv. Mallory). The flowering of SW occurred at DAS 84 (CKA2021), and the flowering of FB occurred at DAS 78.

Table 6
Comparison of intercrops and monocultures in total resource acquisition and use efficiency in high N and low precipitation (CKA2020) conditions. Refer to Tables 2 and 3 for calculation of indices. A ratio > 1 indicates that intercrops had higher in resource acquisition, resource use, and land use efficiency than the monocultures. A partial ratio greater than 0.5 for acquisition and 1 for use efficiency indicates that each species had higher resource acquisition and use efficiency, respectively, compared to its monoculture. Grain yield (t ha^{-1}), water uptake (mm), N uptake (kg ha^{-1}), radiation interception (MJ m^{-2}).

Traits	Faba bean			Spring wheat			Both species			
	Mono culture	Inter crop	Partial ratio[a]	Mono culture	Inter crop	Partial ratio	Mono culture	Inter crop	Ratio[b]	Indices
Grain yield	3.02	1.02	0.33	3.75	2.65	0.71	6.76	3.65	1.04	LER[c]
Water uptake	209.00	66.50	0.32	214.95	144.59	0.67	423.95	211.09	0.99	WAR[d]
Water use efficiency	1.44	1.53	1.06	1.74	1.83	1.05	1.59	1.73	1.05	WUER[e]
N uptake	54.8	13.4	0.24	93.14	79.52	0.85	147.9	92.9	1.10	NAR[f]
N use efficiency	5.51	7.5	1.36	4.03	3.33	0.83	4.58	3.93	0.91	NUER[g]
Soil N uptake +BNF	173.5	46.1	0.27	93.14	79.52	0.85	266.68	125.7	1.12	NAR_{BNF}[h]
Soil N + BNF use efficiency	1.74	2.2	1.25	4.03	3.33	0.83	2.54	2.90	0.99	$NUER_{BNF}$[i]
Radiation interception	678.5	246	0.36	642.4	405.9	0.63	1320.9	652.1	0.99	RAR[j]
Radiation use efficiency	0.45	0.41	0.91	0.58	0.65	1.12	0.51	0.56	1.04	RUER[k]

[a] the ratio of the given species in the mixture to its respective monoculture
[b] the ratio of intercrops to monocultures;
[c] land equivalent ratio;
[d] water acquisition ratio;
[e] water use efficiency ratio;
[f] N acquisition ratio;
[g] N use efficiency ratio;
[h] N acquisition ratio including biologically fixed N;
[i] N use efficiency ratio including biologically fixed N;
[j] radiation acquisition ratio;
[k] radiation use efficiency ratio.

4.2. *Water use of monocultures and intercropping systems*

The water use of intercrops is influenced by interspecific competition and species complementarity (Yin et al., 2020). Our results show that the competition for water plays an important role, particularly in faba bean, which is drought-sensitive (Amede et al., 1999; Balko et al., 2023). Since cereals are strong competitors in cereal/legume intercropping (Yu et al., 2016; Paul et al., 2023), under limited water conditions, faba bean in intercropping takes up less water, resulting in reduced plant growth compared to monocultures. Similar to our results, Launay et al. (2009)

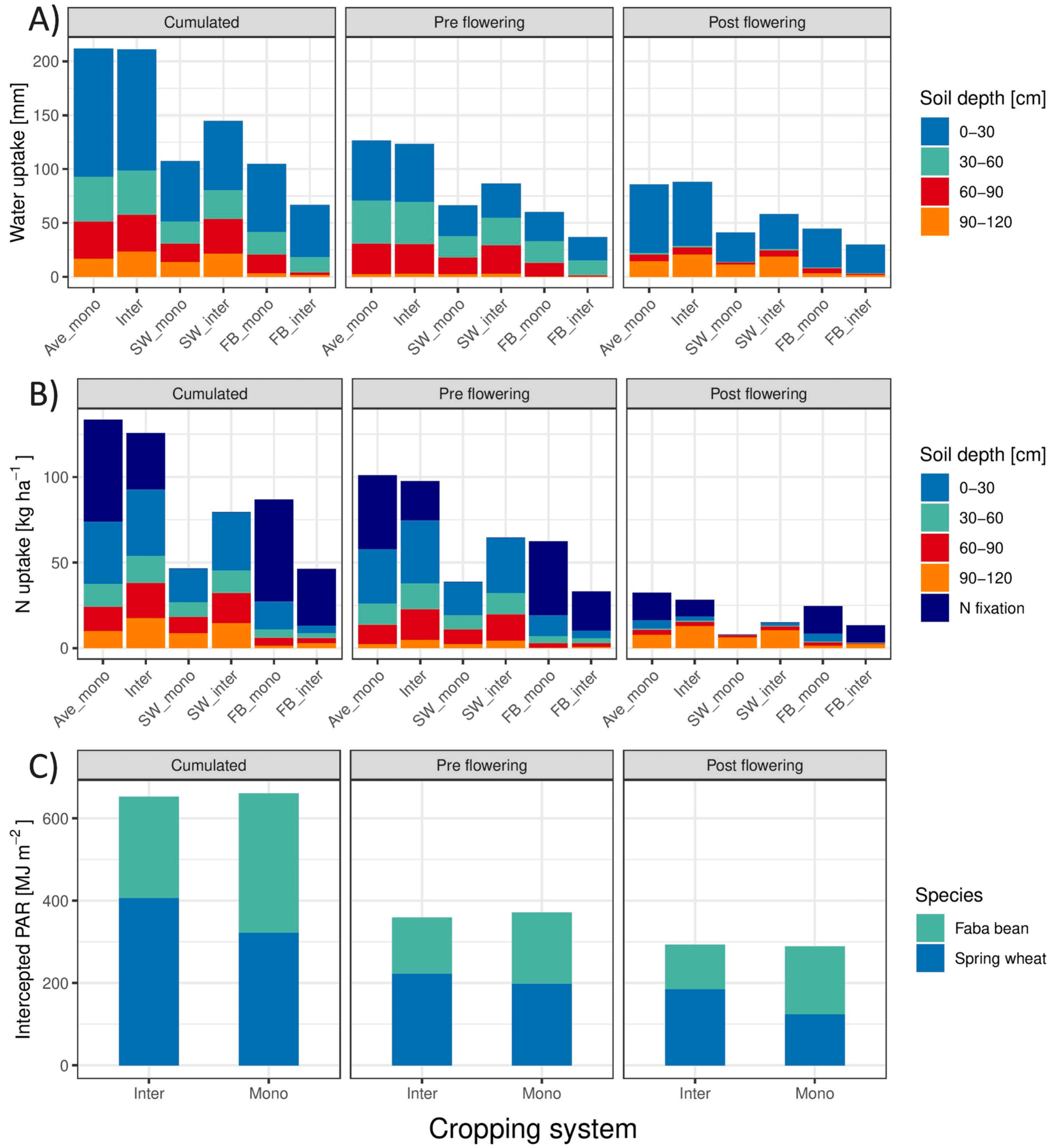

Fig. 3. Simulated cumulative crop resource acquisition for A) water uptake B) N uptake and biological fixation C) radiation, cumulated over the season, from sowing to spring wheat flowering and from spring wheat flowering to harvest at CKA2020. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono corresponds to the average of monocultures of SW and FB; inter- intercropping of SW and FB; FB; FB_inter- FB in intercropping; SW_inter- SW in intercropping; SW_mono-SW in monoculture and FB_mono- FB in monoculture. Here, the values of SW_mono and FB_mono represent half of the total uptake in their respective monocultures, because, when intercropped, each species was grown at 50 % of the plant density used in their monocultures.

reported in a simulation study that pea growth was associated with soil moisture availability in pea/barley intercropping.

These results highlighted that water consumption of monocultures and intercropping systems varied greatly due to environmental conditions and crop species (Fig. S9). However, the total water uptake between monocultures and intercrops (for the two species together) was comparable, as already reveled in other studies (Bahia et al., 2024; Morris and Garrity, 1993). This tendency was reflected in both observed and simulated volumetric soil water content (Figs. S2–3), in which both intercrops and monocultures showed similar soil water content across different measurement data and soil depths. It is important to note that the observed soil moisture data exhibit high temporal variability, introducing some uncertainties into the analysis. Nevertheless, our results contradicts the review findings of Yin et al. (2020) who stated intercropping increases (total) water consumption compared to monocultures.

Overall, the intercropping system showed slightly higher water use efficiency of 4–12 % compared to monoculture (Tables 5–7) depending on the environment. However, Mao et al. (2012) reported a high variability of water use efficiency in a relay intercropping of maize/pea. Schmutz and Schöb (2023) suggested that the over-yielding of intercropping compared to monoculture might be related to spatial exploitation of available water resources. Our results show that the water acquisition ratio (WAR) is nearly 1, emphasizing the poor (only post-flowering) spatial niche complementarity of spring wheat and faba bean in our intercropping system. However, the water use efficiency ratio (WUER) was slightly higher than 1, indicating a minor water conversion efficiency in the intercropping system compared to monocultures. This can be explained by the small differences in rooting depth of the species (Hadir et al., 2024), with most of the water uptake

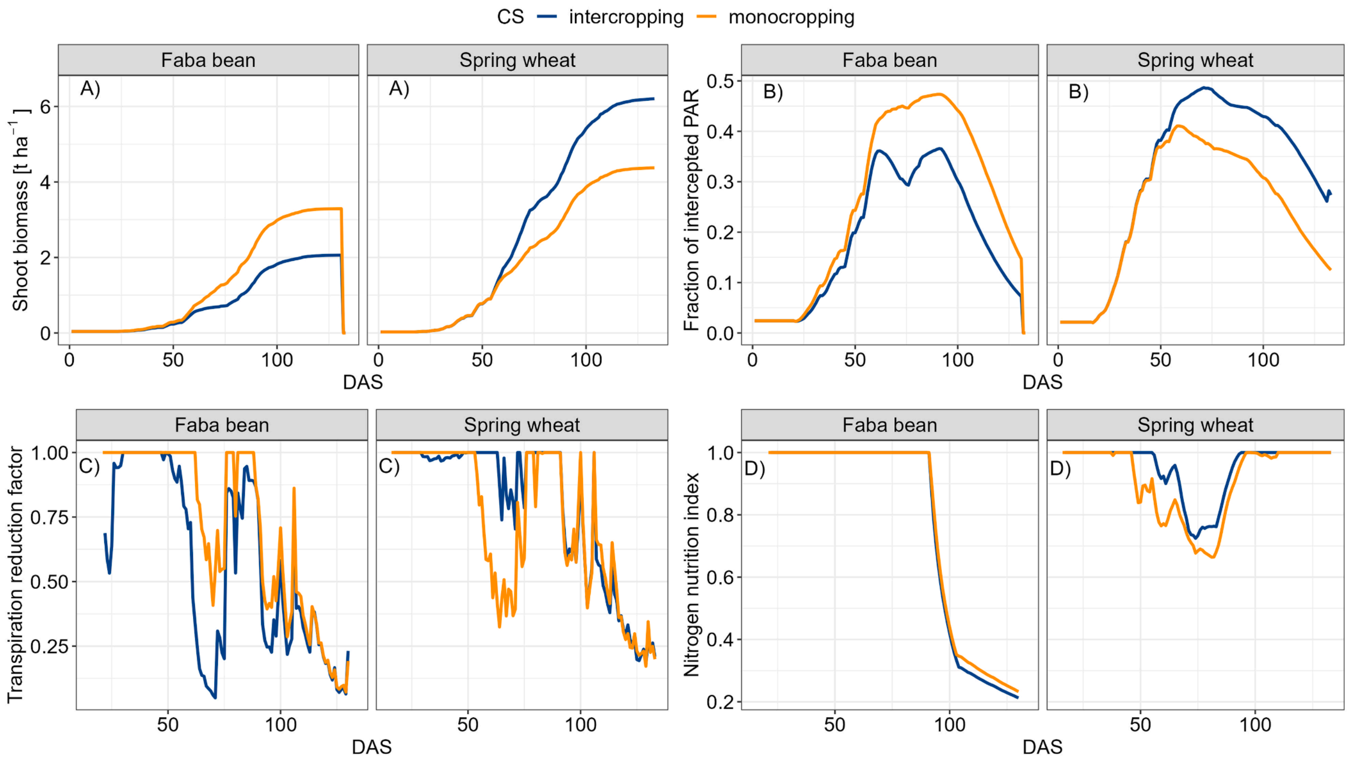

Fig. 4. Simulated daily dynamics for the CKA2020 environment (high soil N and low rainfall) for both cropping systems (CS). A) daily shoot biomass; B) fraction of intercepted photosynthetically active radiation (PAR), C) transpiration reduction factor (TRANRF, 0: full stress, 1 no stress) and D) nitrogen nutrition index (NNI, 0: full stress, 1 no stress) of spring wheat (SW cv. Lennox) and faba bean (FB cv. Mallory). The flowering of SW occurred at DAS 83 (CKA2020), and the flowering of FB occurred at DAS 74.

Table 7

Summary of comparison of intercrops and monocultures in total resource capture and use efficiency in low N and low precipitation (WG2020). Refer to Tables 2 and 3 for the calculation of the indices. A ratio > 1 indicates that intercrops had higher resource acquisition, resource use, and land use efficiency. A partial ratio greater than 0.5 for acquisition and 1 for use efficiency indicates that each species had higher resource acquisition and use efficiency, respectively, compared to its monoculture. Grain yield (t ha^{-1}), water uptake (mm), N uptake (kg ha^{-1}), radiation interception (MJ m^{-2}).

Traits	Faba bean			Spring wheat			Both species			
	Mono culture	Inter crop	Partial ratio[a]	Mono culture	Inter crop	Partial ratio	Mono culture	Inter crop	Ratio[b]	Indices
Grain yield	2.22	0.70	0.32	2.80	2.22	0.79	5.02	2.80	1.11	LER[c]
Water uptake	223.70	77.70	0.35	243.60	156.75	0.64	467.30	234.45	0.99	WAR[d]
Water use efficiency	0.99	0.90	0.91	1.15	1.42	1.23	1.07	1.19	1.12	WUER[e]
N uptake	31.8	18.4	0.58	168.6	108.4	0.64	200.6	126.7	1.22	NAR[f]
Nitrogen use efficiency	6.96	3.81	0.55	1.66	2.05	1.23	2.5	2.21	1.13	NUER[g]
Soil N uptake +BNF	211.2	63.16	0.30	168.6	108.38	0.64	379.8	171.5	0.94	NAR_{BNF}[h]
Soil N + BNF use efficiency	1.05	1.11	1.05	1.66	2.05	1.23	1.32	1.63	1.16	$NUER_{BNF}$[i]
Radiation interception	679	278.3	0.41	742.8	409.0	0.55	1421.8	687.3	0.96	RAR[j]
Radiation use efficiency	0.33	0.25	0.77	0.38	0.54	1.44	0.35	0.41	1.15	RUER[k]

[a] the ratio of the given species in the mixture to its respective monoculture
[b] the ratio of intercrops to monocultures;
[c] land equivalent ratio;
[d] water acquisition ratio;
[e] water use efficiency ratio;
[f] N acquisition ratio;
[g] N use efficiency ratio;
[h] N acquisition ratio including biologically fixed N;
[i] N use efficiency ratio including biologically fixed N;
[j] radiation acquisition ratio;
[k] radiation use efficiency ratio.

occurring from topsoil where both species have high root length densities. Additionally, the temporal niche complementarity was less important as the two species were sown at the same time and have relatively similar phenological development. In contrast, in a relay intercropping system, where crops only partially share the land, it was reported that intercropping increased total water uptake and use efficiency (Chen et al., 2018; Tan et al., 2020).

The crops grown in 2020 (CKA2020 and WG2020) suffered from drought stress. Under these conditions, spring wheat, with its vigorous rooting system accessing subsoil water, tended to suppress faba bean

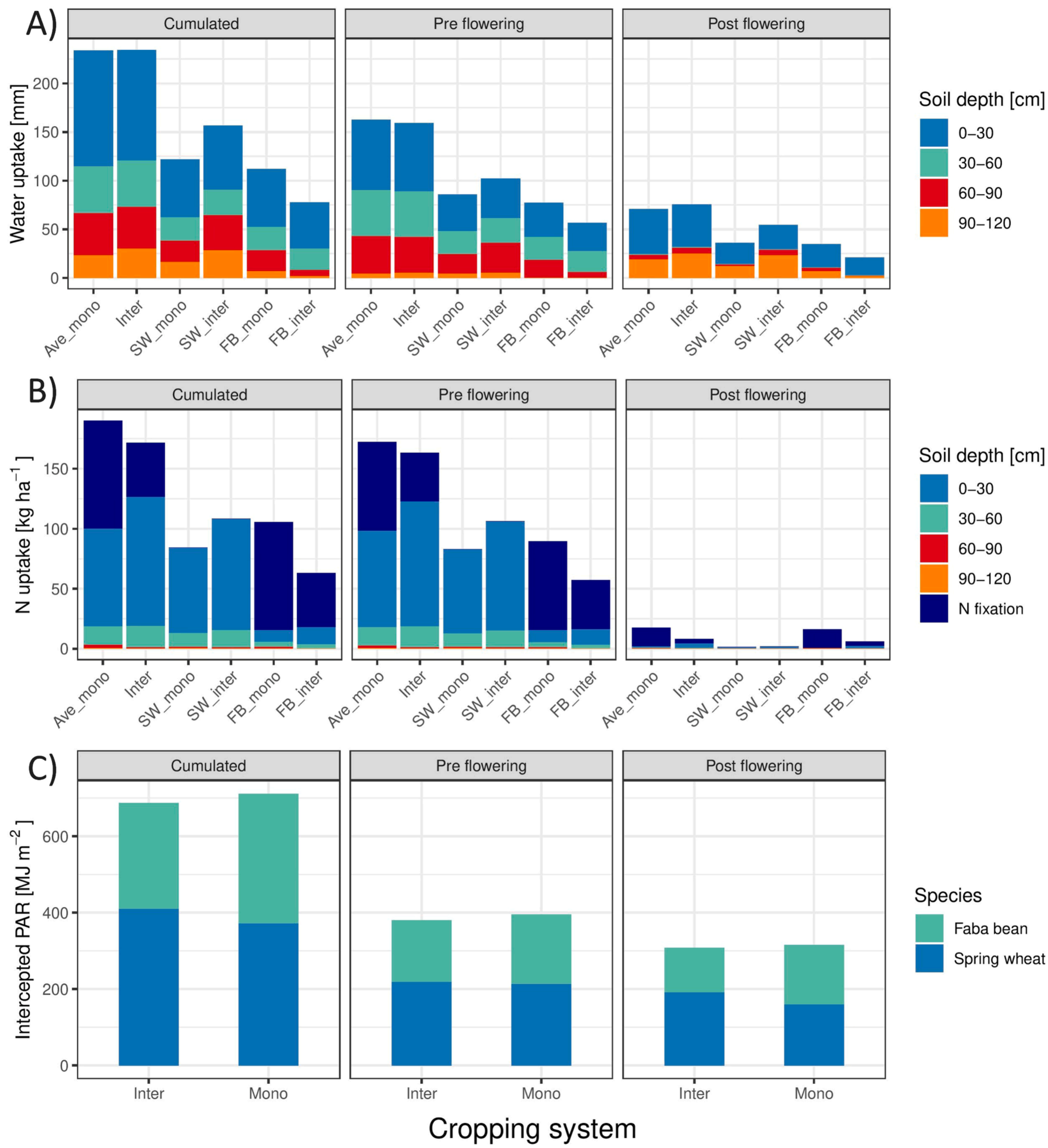

Fig. 5. Simulated cumulative crop resource acquisition for A) water uptake B) N uptake and biological fixation and C) radiation, cumulated over the season, from sowing to spring wheat flowering and from spring wheat flowering to harvest at WG2020. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono is the average of monocultures of SW and FB; inter- intercropping of SW and FB; FB_inter- FB in intercropping; SW_inter- SW in intercropping; SW_mono-SW in monoculture and FB_mono-FB in monoculture. Here, the values of SW_mono and FB_mono represent half of the total uptake in their respective monocultures, because, when intercropped, each species was grown at 50 % of the sowing density used in their monocultures.

(Figs. 4 and 6). The early rapid growth of spring wheat resulted in an early dominance over faba bean and legacy effect at a later stage (Paul et al., 2023). Consequently, intercropped faba bean faced a disadvantage compared to faba bean in monocultures, while the opposite was observed for spring wheat. This phenomenon of contrasting rooting system in cereals and legumes in intercropping was already demonstrated (Corre-Hellou and Crozat. (2005); Hauggaard-Nielsen et al. (2003). However, in 2021 (CKA2021), there was an adequate amount of precipitation and thus plant available water, allowing both species to grow almost as well as they do in the respective monocultures (Fig. 2A). In line with our simulation results, Hadir et al. (2024) observed root growth in the same experiment and reported that the early root growth of one spring wheat cultivar negatively impacted faba bean root growth. Yet, this did not hinder the shoot growth and grain yield of faba bean, which might be due to sufficient available soil moisture. Root competition is generally greater in nutrient-poor environments compared to shoot competition for radiation (Yu et al., 2022). Using the 4 C approach as described by (Bedoussac and Justes, 2011; Justes et al., 2021) there was competition for water among the partners, but the degree of competition depended on environmental conditions. An evaluation of the simulated daily drought stress per species in monocultures and intercropping systems (Figs. 2C, 4C, 6C) revealed that spring wheat exhibited less drought stress when grown with faba bean as compared to sole cropping in all three environments. However, drought stress in faba bean was mostly enhanced in intercropping at faba bean emergence and around flowering (CKA2020 and WG2020). Particularly drought stress during flowering affected the productivity of the species in intercropping.

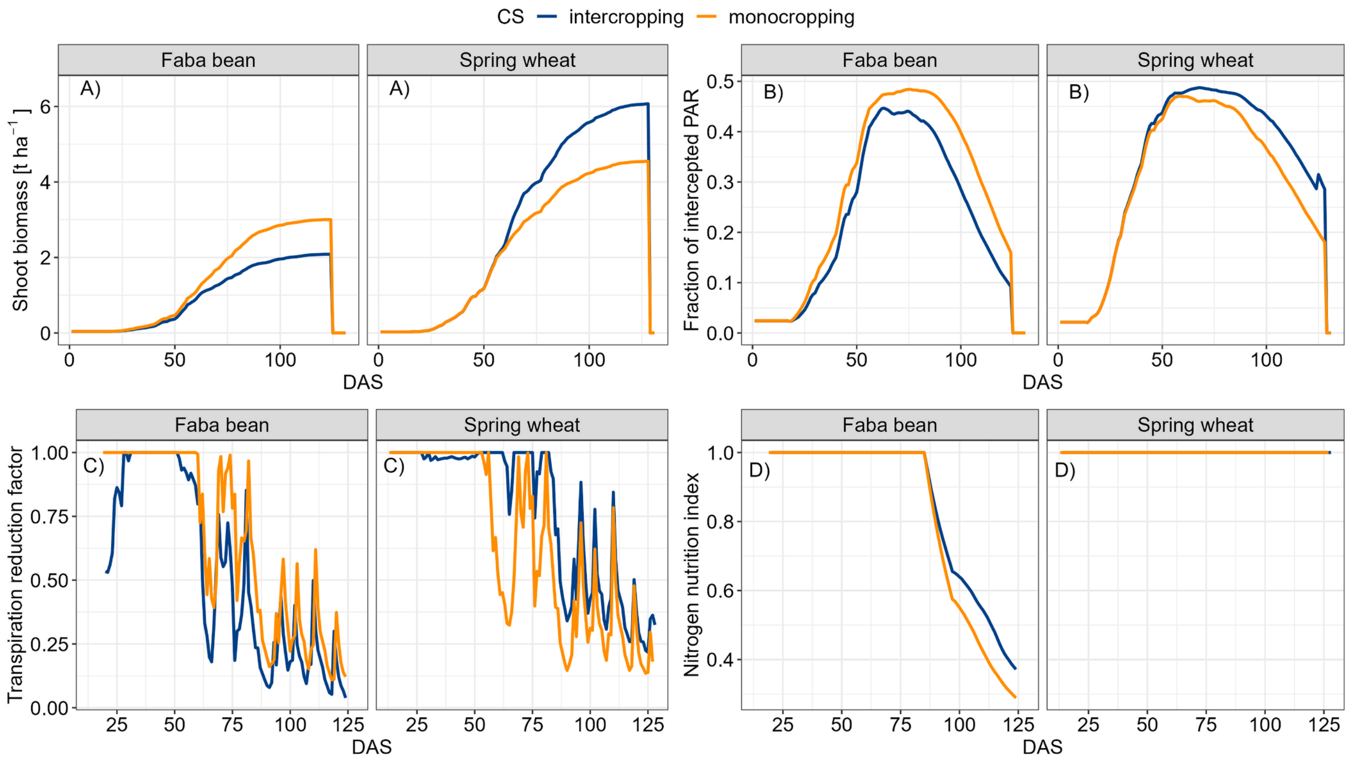

Fig. 6. Simulated daily dynamics for the WG2020 environment (low soil N and low rainfall) for both cropping systems (CS). A) daily shoot biomass; B) fraction of intercepted photosynthetically active radiation (PAR), C) transpiration reduction factor (TRANRF, 0: full stress, 1 no stress) and D) nitrogen nutrition index (NNI, 0: full stress, 1 no stress) of spring wheat (SW cv. Lennox) and faba bean (FB cv. Mallory). The flowering of SW occurred at DAS 78 (WG2020), and the flowering of FB occurred at DAS 68.

4.3. N use of monocultures and intercropping systems

The intercropping of faba bean and spring wheat increased soil N uptake compared to the average of the monocultures in all environments (Fig. S10). This highlights the well-known fact that in cereal/legume intercropping, an enhanced N use is a prominent feature as the two intercropped species use soil N and atmospheric N in complementary ways (Bedoussac et al., 2015; Jensen et al., 2020; Naudin et al., 2010). The model results show that in all environments, the N acquisition ratio (NAR) ranged from 1.10 to 1.22, indicating that intercrops captured 10 – 22 % more N than monocultures (Tables 5–7). On the other hand, the soil N use efficiency ratio (NUER) exceeded 1 only in low-N soils (WG2020, Tables 5–7). This highlights the fundamental connection between intercrop productivity and N availability rather than a change in N use efficiency. The higher N acquisition of intercrops was mainly due to the complementary use of mineralizing soil nitrogen and atmospheric N sources by intercrop components, resulting in reduced competition for soil N (Jensen, 1996). Applying the 4 C approach Justes et al. (2021) to the N acquisition ratio, a high degree of complementarity was observed under low N conditions (WG2020) compared to the higher N soil conditions (CKA2020 and CKA2021) (Fig. S6). In this simulation study, it was revealed that spring wheat in intercropping took up the majority (81 %) of soil N while the rest was taken up by faba bean and complemented by atmospheric N fixation. This findings aligns with the study from Bedoussac et al. (2015) who analyzed different experiments conducted under different conditions and concluded that almost all of the available mineral N was consumed by intercropped cereals, which have only this source to fulfill its demand. This condition made the spring wheat in intercropping grow faster and intercept more radiation, and the legacy effect of early growth (Paul et al., 2023) resulted in over-yielding compared to spring wheat in monocultures. Additionally, the high accessibility of soil water for spring wheat in intercropping compared to monoculture helped to uptake more soil N as drought stress negatively affects crop N uptake (He and Dijkstra, 2014).

The N acquisition of faba bean was demand-based (crop water and nutrient uptake are controlled by growth rates and availabilities). However, biological N fixation was found to be highly dependent on water availability. Under water-limited conditions, plant growth and development are limited, resulting in decreased plant N demand (Sprent, 1971). At WG2020, which was characterized as a water-limited environments, the faba bean in intercropping showed reduced biomass growth compared to the faba bean in monoculture (Figs. 4A and 6A). Hence the proportion of N derived through biological N fixation the faba bean in intercropping was considerably reduced compared to the faba bean in monoculture. At CKA2020 which was characterized as higher soil N content but limited soil moisture, the proportion of N derived through atmosphere N fixation is relatively higher in intercrop compared to monocultures. Nevertheless, at CKA2021, which a wet season with higher soil nitrogen content, the biological N fixation in intercropping was almost similar to the N fixation in intercropping and in the monocultures (Table S3). The total amount of fixed N decreases in intercropping compared to monocultures. However, the proportion of fixed N increased as soil N was reduced by the cereal N uptake stimulating N fixation under sufficient soil water availability. This result highlighted the dependency of biological N fixation on both soil N content and moisture availability. A similar finding was reported by Jensen (1996) and Naudin et al. (2010), who stated that the pea plant growth was negatively affected by competition by barley, hence reducing N fixation in pea/barley intercropping compared to legume monocultures.

Another substantial advantage of growing spring wheat in an intercrop with a legume is the reduced competition for soil N compared to spring wheat monocultures. In an intercropping scenario with 50:50 of spring wheat and faba bean, only 50 % of the area is dedicated to spring wheat. Faba bean, which can fix atmospheric N, does not (or only to some extent) rely on soil N (Klippenstein et al., 2022). As a result, only half of the spring wheat planting density of the monocultures compete for the same amounts of soil N in the intercrop, and thus, access more N compared to a spring wheat monoculture (Figs. 2D, 4D, 6D) as the inter-specific competition is weaker than the intra-specific competition (Vandermeer, 1989). This increased access to soil N can lead to higher N uptake by spring wheat in the intercrop which results in less N stress (Fig. 2). The daily NNI simulations (for N stress) revealed that spring wheat profited from more plant-available N in the soil when intercropped with faba bean mainly after 50 days after sowing to flowering (Fig. 2D). Although the initial mineral N concentrations in the topsoil at the organically managed site WG were low, the enhanced mineralization from the carbon-rich topsoil (Paul et al., 2023) provided substantial soil N for spring wheat during the season. Our results revealed that the average NUE of intercrops and monocultures were similar though there was a disparity among environments. This provides support for the site-specific partner combination selection of cereal and legumes with appropriate management practice to enhance the complementarity needed (Mahmoud et al., 2022; Paul et al., 2023).

4.4. Radiation use of monocultures and intercropping systems

The simulated cumulative radiation interception in monoculture and intercropping showed a minimal gain in radiation interception in spring wheat/faba bean intercropping. Spring wheat intercepted more radiation in intercropping compared to the spring wheat in monocultures at CKA2020 and WG2020, while it was a reverse for faba bean at equivalent sowing densities. However, the absolute radiation interception of faba bean in intercropping at CKA2021 was almost comparable to the radiation interception in respective monocultures at equivalent density (Fig. S11). Cereals are considered strong competitors in cereal/legume intercropping (Yu et al., 2016; Paul et al., 2023), which enables them to capture more radiation, hence increasing biomass production. The reason for the similarity of monoculture and intercrops in radiation interception may be due to temporal niche similarity. Bedoussac and Justes, (2010a) have revealed that durum wheat and winter pea intercropping showed improved light use due to species complementarity for leaf area index and height. However, in our case, spring wheat and faba bean intercropping, both species were sown at the same time and both have also similar phenological development and plant heights, the accumulated intercepted radiation in intercropping could be similar to the average of the two monocultures. Therefore, in such an intercropping system, the complementarity for radiation use may be negligible. However, species showed differences compared to their respective monoculture in total radiation interception during the growth period (Figs. 1C, 3C, 5C). This is because the spring wheat was very competitive and captured more resources and grew vigorously, resulting in higher biomass (Figs. 2A, 4A, and 6A) and intercepted more radiation compared to faba bean (Figs. 2B, 4B, 6B). Several studies showed that the species-specific and overall yield depends on the partner's combination (Cheriere et al., 2020; Mahmoud et al., 2022). A meta-analysis by Yu et al. (2016) on cereal/legume intercropping showed that cereals have a greater relative yield than legumes. However, in an intercropping system where the species are sown at different times (relay intercropping) or where the maximum plant heights differs strongly, the radiation interception in intercropping can be greater than the average of the monocultures (Gou et al., 2017; Zhang et al., 2008). Additionally, in spring wheat/faba bean intercropping, in most years both species have been bred for short stature and relatively similar plant height, in which may lead to less complementarity in radiation capture as compared to intercropping of long-stature cereals like maize with short-stature legumes like soybean (Yu et al., 2015). Depending on the functional plant traits considered, the complementarity and competition between the partners can be positive or negative (Mahaut et al., 2023). Applying the 4 C approach as described by Justes et al. (2021), there was competition for radiation among the partners, but the degree of competition depended on the environmental conditions, but no complementarity among partners was observed (Fig. S8). Therefore, the higher productivity of intercropping was not associated to an enhanced radiation capture except for CKA2021. Though, species have shown differences in radiation capture due to the interception of radiation by one species in a closed canopy stand goes inevitably at the expense of the radiation interception of the other species.

4.5. Limitations of the study

One of the limitations of this study is the limited availability of data regarding observed N dynamics throughout the growing season. We only used initial soil N content at the time of sowing. However, the model has been rigorously tested and validated for its ability to capture the interaction effects in intercropping systems (Demie et al., 2025). Despite the constraints imposed by limited experimental data, the process-based model remains a valuable tool for exploring resource acquisition patterns and interactions between species in intercropping systems. Future research should aim to collect more comprehensive N data throughout the growing season to test and improve model accuracy and enhance our understanding of N dynamics in intercropping contexts.

Another limitation of this study is that the data presented was derived solely from the spring wheat/faba bean intercropping system. This makes it difficult to generalize the findings to other species combinations or intercropping configurations (field arrangement). However, spring wheat/faba bean intercropping systems enhance land use efficiency under low soil N content due to complementary N use, but under higher soil N content, higher land use efficiency can be obtained under sufficient water availabilities. Resource acquisition, competition, and complementarity can vary greatly depending on the characteristics of the crops involved (Mahmoud et al., 2022; Stomph et al., 2020). Future studies should explore a different cultivars spring wheat and faba bean particularly contrasting root traits to facilitate complementary water acquisition predominantly under limited soil water availabilities in order to maximize intercropping system productivity. This would assist in creating a general framework on how different species interact and utilize resources in diverse intercropping systems. Expanding the research scope would also improve the applicability of the results to different agricultural environments and other cereals and legumes species intercropping.

5. Conclusions

Optimizing resource availability is crucial for maximizing the productivity of intercropping, with N acquisition playing a pivotal role in overall intercrop yield. Spring wheat/faba bean intercropping demonstrated enhanced productivity when faced with high water and limited N availability, allowing for a reduction in inorganic N fertilizer input. In all the studied environments, intercropping showed an enhanced N acquisition compared to monocultures. Soil water availability was determinant for the productivity of faba bean within the intercropping system. In environments with low precipitation, faba bean suffered considerably from drought stress, especially during flowering when intercropped with spring wheat as compared to sole faba bean. N availability significantly influenced the productivity of spring wheat in intercropping. The type of plant species and their access to soil water and N reserves shape the dynamics of crop radiation interception, ultimately influencing the overall productivity of intercropping systems. Overall, our findings suggest that the increased productivity of intercropping systems compared to monocultures was primarily driven by improved resource acquisition, particularly N uptake, and enhanced water use efficiency under low precipitation. However, the extent of these benefits was influenced by environmental conditions. Therefore, a comprehensive understanding of these interactions is essential for optimizing the management of intercropping and for reducing N inputs. The choices of species/cultivar combinations should be site-specific. For instance, under limited soil water, choose species with contrasting root lengths (shallow versus deep rooting) to enhance spatial complementary water uptake. Similarly, under limited soil N availability, choose legume species/genotypes with higher nitrogen fixation efficiencies. Process-based models are useful tools to explore options for the intercropping system by assisting in identifying crop ideotypes for specific environmental conditions as a field experiment capacity is limited.

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CRediT authorship contribution statement

Hernandez-Ochoa Ixchel M: Writing – review & editing, Validation, Conceptualization. **Paul Madhuri:** Writing – review & editing, Data curation. **Gaiser Thomas:** Writing – review & editing, Resources. **Ewert Frank:** Writing – review & editing, Resources, Funding acquisition. **Döring Thomas F:** Writing – review & editing, Funding acquisition, Data curation. **Wallach Daniel:** Writing – review & editing, Conceptualization. **Seidel Sabine J:** Writing – review & editing, Resources, Methodology, Data curation, Conceptualization. **Demie Dereje Tamiru:** Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2025.109817.

Data availability

Data will be made available on request.

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