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Investigating the role of genotype, field design and environment in cereal/legume intercropping systems

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To my beloved parents, who,

despite not having had the opportunity for formal education, instilled in me the value of education and tirelessly supported my journey

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Summary

Cropping system diversification through annual intercropping provides a pathway for agricultural production with reduced inputs of fertilizer and pesticides. Cereal/legume intercropping systems are widely used worldwide, particularly by smallholders, producing efficient, high-quality cereal and legume grains in an economically sustainable and environmentally friendly way. However, a significant research gap still demands further investigation regarding understanding species/genotypes to combine, field management, and environmental interactions. However, testing all these combinations is impossible and necessitates using agroecosystem models to understand and support intercropping design for improved resource use efficiency and gain an intended advantage. Nevertheless, testing all possible combinations (genotype x genotype x environment x management) of intercropping in field trials is impossible. The complex interactions in intercropping can be disentangled by the application of a process-based agroecological model, which can help identify the factors that influence intercrop performance. Previous studies on intercrop models have been limited by relatively small datasets, predominantly assessing aboveground plant growth and performance to evaluate the model. These studies often ignored different management strategies, such as cultivar choice and sowing densities.

To contribute to the understanding of genotype × cropping system interactions, a systematic map was conducted to explore the effects of genotype selection in cereal/legume intercropping systems, affect mixture performance, and identify the mechanisms underlying the interactions between genotype and cropping system. Furthermore, we calibrated and evaluated a new process-based intercrop model using an extensive experimental dataset to test whether the model is suitable for comparing intercrop management strategies. The dataset includes all combinations of 12 different spring wheat entries (*Triticum aestivum* L.) with two faba bean (*Vicia faba* L.) cultivars at two sowing densities in three different environments. Additionally, we applied the model with field experiments to explore how the dynamics of crop resource including radiation, water and soil nitrogen (N) acquisition and use drive productivity in intercropping systems across diverse environmental conditions.

To address these gaps, a systematic literature review was conducted to investigate the genotype cropping system interaction. The result highlights that genotype x cropping system (monocultures/intercrop) interactions were tested in 71% of the 69 publications and reported significance in 75% of the studies. These results highlight the importance of genotype selection for better cereal/legume intercropping productivity. The calibrated intercrop model was capable of simulating the absolute mixture (intercrop) effects (AME) for grain yield, above-ground biomass, and topsoil root biomass for both crops. Additionally, the intercrop model reasonably predicted the differences between species and between spring wheat cultivars for grain yield and aboveground plant biomass. The calibrated and robustly tested process-based model can be helpful in designing and pre-evaluating multiple combinations of partner species, genotypes, and management options suitable for intercropping in diverse environment conditions. This should be of particular interest as such models can also help to interpret experimental results in terms of crop growth dynamics and resource acquisition. The assessment of resource acquisition and use efficiency by applying a calibrated and tested intercrop model showed that increased productivity of intercropping systems compared to monocultures was primarily driven by improved resource acquisition, particularly N uptake, and, to some extent, enhanced water use efficiency. However, the degree of these benefits was influenced by environmental conditions.

Overall, these findings emphasize that a careful choice of genotype combination in cereal/legumes is indispensable for enhancing land use efficiency. However, the lack of data on traits and genotypes' effects on intercropping performance demands further efforts in breeding and better field arrangements for intercropping systems, including more genotype evaluation. To improve our understanding of how genotype combination and breeding may help to optimize intercropping systems, future research on genotype effects in intercropping should consider phenology, root growth, soil nutrients, water acquisition timing, and the impact of weeds and diseases. Process-based models are valuable tools for exploring options for the intercropping system by identifying essential resources and interactions among environmental resources as field experiment capacity is limited. However, they also need to be further improved to better represent relevant plant features and mechanisms driving interspecific plant-plant interactions. These measures will support the identification of system traits and plant traits that work together to maximize resource use efficiencies and obtain stable yields at lower resource input levels.

Zusammenfassung

Die Diversifizierung von Anbausystemen durch einjährigen Mischkulturanbau bietet einen Weg zur landwirtschaftlichen Produktion mit geringerem Einsatz von Düngemitteln und Pestiziden. Getreide-Leguminosen-Mischkulturen sind weltweit weit verbreitet, insbesondere bei Kleinbauern, die auf wirtschaftlich nachhaltige und umweltfreundliche Weise effizientes, hochwertiges Getreide und Leguminosen produzieren. Es gibt jedoch noch erhebliche Forschungslücken, die weitere Untersuchungen zum Verständnis dazu wie Arten/Genotypen, Wechselwirkungen zwischen Feldbewirtschaftung und Umwelt beeinflussen. Allerdings machen die Heterogenität in den verschiedenen Umwelten und das Vorhandensein unzähliger Managementstrategien und Genotypen (Genotyp x Genotyp x Umwelt x Management) die Prüfung all dieser Kombinationen in experimentellen Versuchen unmöglich und erfordern die Verwendung von Agrarökosystemmodellen. Agrarökosystemmodelle können dabei helfen, die Gestaltung von Mischkulturanbausystemen zu verstehen und zu unterstützen, um die Effizienz der Ressourcennutzung zu verbessern, indem sie die Faktoren identifizieren, die die Leistung von Mischkulturanbausystemen beeinflussen. Frühere Studien zu Mischkulturmodellen waren durch kleine Datensätze eingeschränkt, bei denen zur Bewertung des Modells überwiegend das Wachstum und die Leistung oberirdischer Pflanzen bewertet wurden. In diesen Studien werden häufig unterschiedliche Bewirtschaftungsstrategien wie Sortenwahl und Aussaatdichte außer Acht gelassen.

Um zum Verständnis der Wechselwirkungen zwischen Genotyp und Anbausystem beizutragen, wurde eine systematische Kartierung durchgeführt, um die Auswirkungen der Genotypauswahl in Getreide/Leguminosen-Mischkultursystemen zu untersuchen, die Leistung der Mischung zu beeinflussen und die Mechanismen zu ermitteln, die den Wechselwirkungen zwischen Genotyp und Anbausystem zugrunde liegen. Darüber hinaus haben wir ein neues prozessbasiertes Mischkulturmodell anhand eines umfangreichen Versuchsdatensatzes kalibriert und bewertet, um zu prüfen, ob das Modell für den Vergleich von Mischkultur-Managementstrategien geeignet ist. Der Datensatz umfasst alle Kombinationen von 12 verschiedenen Sommerweizenarten (*Triticum aestivum* L.) mit zwei Ackerbohnensorten (*Vicia faba* L.) bei zwei Aussaatdichten in drei verschiedenen Umgebungen. Darüber hinaus haben wir das Modell in Feldexperimenten getestet, um zu untersuchen, wie die Dynamik des Bedarfs an pflanzlichen Ressourcen inklusive Strahlung, Wasser, Bodenstickstoff (N) und deren Nutzung die Produktivität von Mischkultursystemen unter verschiedenen Umweltbedingungen beeinflusst.

Um diese Lücken zu schließen, wurde eine systematische Literaturanalyse durchgeführt, um die Wechselwirkung zwischen Genotyp und Anbausystem zu untersuchen. Das Ergebnis zeigt, dass

Wechselwirkungen zwischen Genotyp und Anbausystem (Monokulturen/Zwischenfrüchte) in 71 % der 69 Veröffentlichungen getestet wurden und in 75 % der Studien als signifikant eingestuft wurden. Diese Ergebnisse unterstreichen die Bedeutung der Genotypenselektion für eine bessere Produktivität von Getreide/Leguminosen im Mischkulturanbau. Das kalibrierte Mischkulturmodell war in der Lage, die absoluten Mischungseffekte (AME) für den Kornertrag, die oberirdische Biomasse und die oberirdische Wurzelbiomasse für beide Kulturen zu simulieren. Darüber hinaus konnte das Mischkulturmodell die Unterschiede zwischen den Arten und zwischen den Sommerweizensorten für den Kornertrag und die oberirdische Pflanzenbiomasse angemessen vorhersagen. Das kalibrierte und robust getestete prozessbasierte Modell kann bei der Entwicklung und Vorabbewertung mehrerer Kombinationen von Partnerarten, Genotypen und Bewirtschaftungsoptionen für den Mischkulturanbau unter verschiedenen Bedingungen hilfreich sein. Dies dürfte von besonderem Interesse sein, da solche Modelle auch bei der Interpretation von Versuchsergebnissen in Bezug auf die Wachstumsdynamik von Pflanzen und den Ressourcenerwerb helfen können. Die Bewertung des Ressourcenerwerbs und der Effizienz der Ressourcennutzung durch Anwendung eines kalibrierten und getesteten Mischkulturmodells zeigte, dass die höhere Produktivität von Mischkultursystemen im Vergleich zu Monokulturen in erster Linie auf den verbesserten Ressourcenerwerb, insbesondere die N-Aufnahme, und bis zu einem gewissen Grad auf die verbesserte Wassernutzungseffizienz zurückzuführen ist. Das Ausmaß dieser Vorteile wurde jedoch von den Umweltbedingungen beeinflusst.

Insgesamt unterstreichen diese Ergebnisse, dass eine sorgfältige Auswahl von Genotypkombinationen bei Getreide/Leguminosen zur Verbesserung der Landnutzungseffizienz unerlässlich ist. Der Mangel an Daten über die Auswirkungen von Merkmalen und Genotypen auf die Leistung des Mischkulturanbaus erfordert jedoch weitere Anstrengungen in der Züchtung und bessere Feldanordnungen für Mischkultursysteme, einschließlich einer umfassenderen Bewertung von Genotypen. Um besser zu verstehen, wie die Kombination von Genotypen und die Züchtung zur Optimierung von Mischkultursystemen beitragen können, sollte die künftige Forschung zu den Auswirkungen von Genotypen im Mischkulturanbau die Phänologie, das Wurzelwachstum, die Bodennährstoffe, den Zeitpunkt der Wasseraufnahme und die Auswirkungen von Unkräutern und Krankheiten berücksichtigen. Prozessbasierte Modelle sind wertvolle Instrumente zur Untersuchung von Optionen für das Mischkultursystem, indem sie wesentliche Ressourcen und Wechselwirkungen zwischen Umweltressourcen identifizieren, da die Kapazität von Feldversuchen begrenzt ist. Sie müssen jedoch noch weiter verbessert werden, um relevante Pflanzenmerkmale und Mechanismen, die die Wechselwirkungen zwischen den einzelnen Pflanzen beeinflussen, besser darstellen zu können. Diese Maßnahmen werden die Identifizierung von

Systemmerkmalen und Pflanzenmerkmalen unterstützen, die zusammenwirken, um die Ressourceneffizienz zu maximieren und stabile Erträge bei geringerem Ressourceneinsatz zu erzielen.

Abbreviations, acronyms, and units

°C	degree celsius
AME	absolute mixture effect
ANOVA	analysis of variance
BNF	biological nitrogen fixation
CKA	Campus Klein-Altendorf
CKA2020	Campus Klein-Altendorf in year 2020
cm	centimetre
CS	cropping system
cv.	cultivar
DAS	day after sowing
DM	dry mass
e.g.	exempli gratia
et al.	et alia
FB	faba bean
ha	hectare
HD	high density
kg	kilogram
LAI	leaf area index
LD	low density
LER	land equivalent ratio
LSD	least significant different
MSE	mean squared error
N	nitrogen
NAR	nitrogen acquisition ratio
N_2O	nitrous oxide
NUER	nitrogen use efficiency ratio
Nmin	mineral nitrogen
PLER	partial land equivalent ratio
P	phosphorous
R^2	coefficient of determination
RAR	resources acquisition ratio

RMSE	root mean squared error
RUER	radiation use efficiency ratio
t	ton
SW	spring wheat
s.d.	standard deviation
vs.	versus
WAR	water acquisition ratio
WUER	water use efficiency ratio
WG	Campus Wiesengut
WG2020	Campus Wiesengut in year 2020

Chapter 1

1 General Introduction

1.1 Introduction

In the past decades, agricultural intensification has increased monoculture crop yields (Blomqvist et al., 2020). As a consequence, production systems have been simplified and homogenized, followed by human diets relying on a few staple crops (Gossner et al., 2016; Kaur et al., 2024). Yet, Tian et al. (2021) reported that global crop production should be increased to meet the future world food demand. Agriculture, as the current production system dominated by monoculture, poses a significant threat to the environment (Fusco et al., 2023), with food production and the whole process of the value chain accounting for more than a quarter of total greenhouse gas (GHG) emissions to the atmosphere (Smith et al., 1997; Tilman and Clark, 2015). The application of inorganic fertilizers, including nitrogen (N) and phosphorous, that are less efficiently utilized, leach into water bodies and have a significant share of water pollution (Carpenter et al., 1998; Smith et al., 1997). Likewise, the intensive application of pesticides is also a major characteristic of monoculture agriculture (Maggi et al., 2023). It is estimated that by 2050, N and phosphorous leaching to rivers and marine ecosystems will increase by 2.5 fold, accompanied by comparable pesticide usage, leading to unprecedented ecosystem simplification, loss of ecosystem services, and species extinctions (Tilman et al., 2001). Intensive pesticide usage is detrimental to animals' health and the environment and a significant threat to insect biodiversity, soil fauna, and flora (Beaumelle et al., 2023).

Landscape simplification and intensive agricultural production systems have led to a decline of more than 75 % in flying insects and pollinators observed for some decades (Hallmann et al., 2017; Kunin, 2019). Therefore, there is a critical requirement for sustainable agricultural production systems, which includes a major reduction in the use of chemical pesticides (Kaur et al., 2024). Looking at the European level, despite many amendments to agricultural policy, the majority of the European Union member states are ecological-inefficient, for instance, with regards to the excessive use of fertilizer, which produces considerable amounts of airborne emissions about the current level of GDP per hectare, calling for the adoption of improved management practices and a more effective agricultural policy (Rybaczewska-Błazejowska and Gierulski, 2018). Thus, sustainable agriculture through low-input chemical fertilizers and pesticides to mitigate the negative impact of agriculture on the environment while boosting crop production is the core of attention for researchers, policymakers, and farmers (Altieri, 1999; Füsun Tatlidil et al., 2009; Timpanaro et al., 2023).

Moreover, agriculture diversification in the different forms of production systems can provide the benefits of sustainable intensification within a reasonable footprint (Tilman et al., 2020). One practice is the use of intercropping (i.e., the mixed cultivation of crop species on the same piece of land for at least a certain co-growth period), an old crop production practice that provides the potential to increase yield, improve the delivery of ecosystem services and reduce agricultural inputs (Li et al., 2020). Cereal/legume intercropping systems are widely practiced across the world, particularly by smallholders, producing high quality cereal and legume grains in an economically sustainable, environmentally friendly, and efficient way (Tang et al., 2024). Using legume crops in a mixture with cereals may significantly mitigate N_2O fluxes derived from fertilizer (Senbayram et al., 2015). Furthermore, crop diversification provides farmers with insurance against crop failure (Gaba et al., 2015; Lithourgidis et al., 2011). Nevertheless, despite the potential of intercropping, this form of cultivation is under-represented in modern agriculture (Machado, 2009). Many farmers are reluctant to adopt intercropping as technical demands for weed, fertility, and crop management can increase hand labor requirements considerably when multiple crops grow in the same field (Bedoussac et al., 2015; Himanen et al., 2016), and lack of awareness about the system (Ha et al., 2023).

Table 1. 1. Multi-benefits of cereal/legume intercropping on crop productivity, biodiversity, and crop protection

Indicators	**Direction**	**References (examples)**
Grain yield	+	Lithourgidis et al. (2011; Li et al. (2022); Yu et al. (2016)
Yield stability	+	(Raseduzzaman and Jensen, (2017)
Cereal protein concentration	+	Timaeus et al., (2021); Bedoussac and Justes, (2010)
Production risk	-	Vandermeer, (1989)
	Soil and biodiversity	
Nitrate leaching	-	Tribouillois et al., (2016)
N_2O fluxes	-	Senbayram et al. (2015)
Soil organic matter	+	Lithourgidis et al., 2011; Shili-Touzi et al. (2010)
Biodiversity	+	Kremen and Miles, (2012; Brandmeier et al. (2023)
	Crop protection	
Weed suppression	+	Lithourgidis et al. (2011)
Fungal plant diseases	-	Zhang et al. (2023)
Nematode disease incidence	-	Chadfield et al. (2022)
	Resource availability and use efficiency	
Water use efficiency	+	Yin et al. (2020)
N use efficiency	+	Bahia et al. (2024)
Phosphorus use efficiency	+	An et al. (2023); Tang et al. (2021)
Nutrient availability	+	Ma et al. (2022)

$^{+}$ increment and $^{-}$ reduction

The ecological niche separation concept suggests that species can coexist by having different resource requirements at different times, as well as for different sources of nutrition, resulting in improved intercropping performance compared to monocultures (Malézieux et al., 2009). These ecological mechanisms are a combination of four joint effects, which are called the 4C namely: competition, complementarity, cooperation, and compensation, which are processes or effects occurring simultaneously and dynamically between species over the whole cropping cycle (Justes et al., 2021). The Competition occurs when plants have fairly similar requirements for abiotic resources in space and time, as a result of all one species having a greater ability to use limited resources (e.g., nutrients, water, space, light) than other species (Trenbath, 2015). Complementarity is when plants grow together and have different requirements for abiotic resources in space, time, or form (Jensen, 1996). Complementarity is a paramount feature in cereal/legume intercrops grown under low-N conditions, in which biological N fixation by the legume and intense competition for soil-N by the cereal may synergize to enhance yield and grain quality (Bedoussac and Justes, 2010; Timaeus et al., 2021). Cooperation is when the modification of the environment by one species is beneficial to the partner species (Hinsinger et al., 2011). Compensation is when the failure of one species is compensated by the other due to their different sensitivity to abiotic stress (Döring and Elsalahy, 2022). The degree of whether one process is more dominant depends on different factors, including species in mixtures, environmental conditions, and crop management.

In general, the over-yielding of intercropping compared to monoculture is achieved when the degree of complementarity and cooperation is greater than the degree of competition (Justes et al., 2021). This over-yielding is often quantified by the land equivalent ratio (LER), an index measuring the relative land area required to produce the same yields (or any other services, such as biomass) in monocultures as obtained from a unit area of intercrop. An LER greater than one indicates that intercropping uses the land more efficiently than pure stands to produce the desired outputs (Mead and Willey, 1980). Alternatively, it can also be quantified by absolute (AME), which is the absolute difference between the observed yield in the mixture and the expected yield calculated from the monoculture crop yield and the relative density of the mixture partners (Bedoussac and Justes, 2011). Despite its numerous benefits, intercropping also has some limitations (Huss et al., 2022). Multiple crop cultivation often increases the complexity of planting and crop management and is less compatible with existing machinery, hence increasing labor costs (Himanen et al., 2016). When intercrops differ in their maturity timing, multiple harvests may be necessary. If the crops reach maturity at similar times, they can be harvested together and then sorted. Still, this approach requires specialized equipment, which may not be accessible for resource-limited farmers. (Paul et al., 2024). Some of these challenges can be mitigated through a strip intercropping system, where crops are grown in wider bands. However, the benefits of complementary intercropping decrease as the width of the strips between the two crops increases (van Oort et al., 2020).

Different types of intercropping systems exist, depending on the spatio-temporal arrangement of species (Gaudio et al., 2019). A strip intercropping system (Fig. 1.1 C) is the simultaneous cultivation of two or more crops in adjacent strips (Brooker et al., 2015). The interaction between the two crops as they grow creates a strong border-row effect between the two strips (Gou et al., 2017a). Still, this form of intercropping limits the species interactions and hence relatively reduces complementary resource use but is easier in crop management i.e. harvesting. A relay intercropping system (Fig. 1.1B) is, when two species are grown one after another but do have a certain co-growth period. Such intercropping provides a temporal complementary resource use among species (Yu et al., 2016). Relay intercropping can be practiced predominantly as a strip intercropping system and as alternative row intercropping in limited cases. The advantage of strip intercropping is that it can be managed by current machinery (Thompson et al., 2025). Within the row mixture, also typical in cover crops (Fig. 1.1 A), is another form of intercropping in which two species are sown together in a given plot without a distinct row arrangement. This type of intercropping is predominantly practiced when the two species have the same crop development stage in particular maturity but contrasting morphology. Unlike a relay intercropping system, this arrangement of intercropping provides a higher crop-to-crop interaction and enhances complementary resource use (Gaudio et al., 2019; Paul et al., 2024).

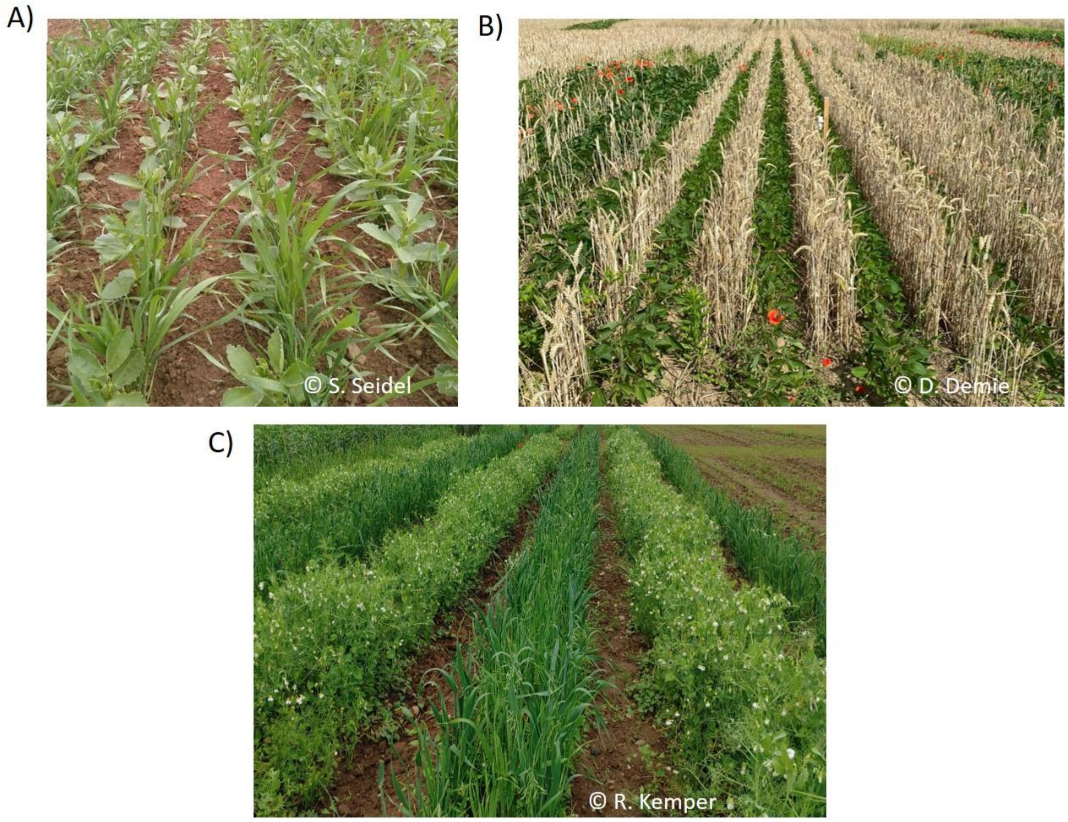


Figure 1.1. Different forms of cereal legume intercropping. A) Within a row mixture of spring wheat and faba bean without distinct row arrangement. The two crops have relatively similar phenology but different morphology. B) Relay intercropping system of wheat/soya bean intercropping with distinct row intercropping. The two crops have relatively different phenology and morphology. C) Strip intercropping system of wheat/pea intercropping in the strip. The two crops have relatively similar phenology and different morphology.

A different set of factors affects the performance of intercropping including species and cultivars to be combined, environmental conditions, and proportion of the species intercropping. Further investigation is needed to determine the multiple advantages of intercropping (Gaudio et al., 2019; Malézieux et al., 2009). It is impossible to test all possible combinations (genotype x genotype x environment x management) of intercropping in field trials. The complex interactions in intercropping (Paul et al., 2024) can be disentangled by process-based agroecological models which can help to identify the relevant influencing factors of intercrop performance. However, the prerequisite is understanding the fundamental mechanisms that occur when mixing crop species.

1.1.1 The potential of genotype choice for cereal/legume intercropping

Numerous studies have shown that the general performance of intercropping systems depends on the genotypes used in the mixture (Hauggaard-Nielsen and Jensen, 2001, Demie et.al., 2022). This is particularly due to the traits required for intercropping, which can boost complementarity and cooperation but reduce competition among species (Davis and Woolley, 1993). Aboveground and belowground morphological and phenological traits include plant height (Nelson et al., 2021; Paul et al., 2024), root architecture and maximum rooting depth (Homulle et al., 2022; Hadir et al., 2024), growth habit (Clark and Francis, 1985; Davis and Garcia, 1983), phenotypic plasticity (Zhu et al., 2015) and light use efficiency (Berghuijs et al., 2020). These traits have to be considered in the breeding process for intercropping.

However, the genotype performance in intercropping is poorly correlated to performance in a monocultures stand (Annicchiarico et al., 2019) because the final performance of intercropping depends on the interaction effects of the species in a given environment (Justes et al., 2021). Additionally, the performance of the selected species genotype in the intercropping cannot be predicted from their performance in monoculture (Paul et al., 2024) because the best genotype in monocultures is not necessarily the best in the intercropping (Demie et al., 2022). Different genotypes of legumes may have different responses in terms of phenology and morphology (Annicchiarico and Filippi, 2007) when compared to monoculture crops versus intercropping. Hence, the specific selection of genotypes for intercropping is important (Giles et al., 2017) and intercrop yield advantage could be achieved by selecting specific traits of both species (Berghuijs et al., 2020). Therefore, it has been suggested that specific breeding of genotypes for intercropping is needed to improve the complementarity of the intercropping partners (Haug et al., 2021, Annicchiarico et al., 2019).

Choosing plant genotypes for specific intercropping systems is, however, laborious and costly because assessing intercropping performance also requires the inclusion of the monocultures in field experiments for comparison and estimation of the benefits of intercropping (Bourke et al., 2021). Testing genotypes in mixtures easily results in a curse of dimensionality. For instance, five genotypes of cereal and five genotypes of legumes result in 25 intercrop combinations that should be tested along with 10 pure stands. Optimal species traits likely depend on the companion species, such that all possible combinations are preferably tested. Incomplete field experimental designs have been proposed to deal with this dimensionality challenge (Hinsinger et al., 2011), and have been shown to be efficient in estimating mixing abilities (Haug et al., 2021). Testers and reciprocal breeding schemes have been proposed to co-breed species (Sampoux et al., 2020). Recent technologies, like genomic selection strategies, can enhance the precision of trait selection in breeding programs focused on intercropping (Bančič et al., 2021). However, better knowledge of genotypes and their associated trait effects in intercropping is needed to make selection more targeted.

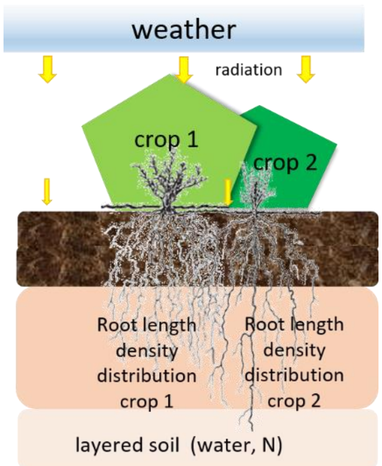
The general and specific mixing ability of genotypes of single species has been studied to determine contrasting traits in sole cropping and mixtures, and the theoretical background of species mixtures has been discussed (Wright, 1985). Historically, multiple studies have evaluated different crop genotypes for complementarity in intercropping (Davis and Woolley, 1993; Francis et al., 1976; Smith, 1985; Smith and Zobel, 1991). Ample research has been conducted but the knowledge on genotype effects in intercropping is fragmented and has not been compiled to deliver the necessary knowledge for designing optimized intercropping systems. The current work (**Chapter 2)** aims to provide an updated overview of the current state of research by linking recent advances on the mechanisms involved in genotype × cropping system interactions.

1.1.2 Process-based modeling of intercropping

Agroecosystem modeling is a systematic way to understand the processes and mechanisms associated with the multi-benefits of the agroecosystem (Ewert et al., 2015). Crop models are widely used to study the influence of climate variability, soil, or management options (Seidel et al., 2019; Asseng et al., 2019; Chenu et al., 2017), and for real-time simulation-based crop management (Seidel et al., 2016). Modeling monoculture crops is vastly studied, with 1D field-scale crop growth models applied in many crop production decisions (Chenu et al., 2017;). For example, the Azodyn crop model is used frequently in cultivar selection (Amalero et al., 2003). Nevertheless, modeling crop mixtures is still in its infancy, and even the existing models ignore the spatial heterogeneity of crop mixtures and simplify the system into a single dimension (Gaudio et al., 2019).

The numerous processes and mechanisms involved in intercrops highlight the need to deal with their complexity by combining concepts from diverse disciplines such as agronomy, physiology, and ecology. Additionally, there is a lack of information regarding intercropping management such as crop genotype selection and combination (Demie et al., 2022), spatial arrangement, and sowing proportion (Chimonyo et al., 2016). However, evaluating a high number of genotypes and their traits under different environments and management under field conditions is costly and laborious. To address these challenges, process-based crop simulation models are widely recognized tools to examine cause-and-effect relationships in crop production. Virtual experiments using crop models can contribute to process understanding and cropping system design (Malézieux et al., 2009).

Currently, a handful of models are available to simulate mixed cropping systems for yield and water use (Chimonyo et al., 2016; Miao et al., 2016; Pinto et al., 2019), light distribution (Munz et al., 2014a; Tsubo et al., 2005), N transport and uptake (Shili-Touzi et al., 2010; Whitmore and Schröder, 2007), and weed suppression (Baumann et al., 2002). One approach to simulate intercrops is the light sharing in strip intercrop systems. Pierre et al., (2023) developed an approach to allow the model Decision Support System for Agro technology Transfer (DSSAT) to run two crop species in intercropping. Berghuijs et al. (2021) calibrated and tested The Agricultural Production Systems sIMulator (APSIM) for wheat-faba bean intercrops and Vezy et al. (2023) proposed a set of generic formalisms for the simulation of intercrops, with an implementation in Simulateur mulTIdiscplinaire pour les Cultures Standard (STICS). However, these modeling studies were mainly dedicated to intercrop model performance in terms of simulation accuracy. Its application included studies with models used to study water use in strip intercropping (Tan et al., 2020; Launay et al. (2009) employed a model to explore light and N use in pea-barley intercropping.
However, process-based agroecosystem modelling offers the possibility of deepening our understanding of the complex resource dynamics and species interactions in intercropping systems. Two important processes should be considered in modeling binary crop mixtures: the aboveground resources competition (radiation) and the belowground resources competition (water and nutrients). Several modeling studies have been published regarding the aboveground resources, including radiation interception (Gou et al., 2017b; Vezy et al., 2023; Yu et al., 2024). However, the simulation of a below-ground competition is in the infancy stage (Gaudio et al., 2019) due to the additional challenge of studying below-ground dynamics in field experimentation.



In intercropping, the two species share the incoming radiation depending on each species proportion (coverage), plant height, and crop-specific parameters such as the light extinction coefficient. The ratio of root length density, rooting depth, and soil layer determines the splitting of soil water and N uptake. In this context, the taller-growing crop captures more radiation, leading to increased shoot and root biomass, which enhances its ability to capture soil resources, ultimately creating dominance over the second crop (Demie et al.,2025).

Figure 1. 2. Schematic representation of competition for resources in intercropping

The complex interactions in the intercrop can be disentangled by process-based agroecological models (Malézieux et al., 2009), which can help to identify the relevant influencing factors of intercrop performance. Louarn et al. (2020) demonstrated that a systematic combination of species traits in intercropping improved over yielding under a virtual experiment using the grassland model. Moreover, the previously published modeling studies focused on above-ground plant performances and intercrop interactions (Gou et al., 2017b; Vezy et al., 2023). The below-ground processes were often ignored, and most attention was given to simulating and testing the above-ground process. So far, only a limited number of studies have been published describing above-ground and below-ground components (Gaudio et al., 2022), specifically testing the model for capturing below-ground plant growth, such as root biomass and root length density.

Given these gaps, intercrop modeling can assist in two critical aspects of intercrop research. Despite its simplifications, the calibrated and evaluated model is a promising tool to simulate the effects of intercropping systems and, thus, support their design (Louarn et al., 2020). This is particularly valuable given that the experimental capacities are limited to exploring various factors and treatments to optimize intercropping systems. Intercrop models can also contribute to interpreting experimental results in terms of crop growth dynamics and resource acquisition. This is particularly important, for those variables that are difficult to measure in field experiments due to their inherent complexity, such as below-ground dynamics of total water acquisition, and nutrient acquisition (Malagoli et al., 2020; Miao et al., 2016).

The intercrop model applied in the current work was implemented within the modeling framework SIMPLACE (Scientific Impact Assessment and Modeling Platform for Advanced Crop and

Ecosystem Management) by combining existing biomass, soil water, and nutrients components for monocultures with intercropping components for radiation and below-ground competition and distribution. The model framework has been developed during the last decade and has been primarily applied to conduct climate change impact assessments, model uncertainty, and crop management studies (Enders et al., 2023). In this thesis, **Chapter 3** describes a new intercrop model calibrated and tested for capturing the mixture effect using an extensive dataset from spring wheat/faba bean intercropping, and **Chapter 4** applies the intercrop model to analyze and better understand resource acquisition and interaction and thus performance in spring wheat/faba bean intercropping.

1.1.3 Resource acquisition in cereal/legume intercropping

Cereal/legume intercropping offers numerous advantages over monocultures, often attributed to complementary resource use of soil water (Yin et al., 2020), soil (N) (Jensen, 1996), and radiation (Gou et al., 2017). To obtain the multiple advantages of the intercropping system, understanding the ecological mechanism linked with planned tempo-spatial diversity and its impact on multiple agroecosystem benefits needs to be improved (Hauggaard-Nielsen et al., 2008). Complementary resource use is often reported as the mechanism behind the performance of intercropping. It is a paramount feature in cereal/legume intercrops grown under low-N conditions, in which biological N fixation by the legume and strong competition for soil-N by the cereal may synergize to enhance yield and grain quality (Jensen,1996; Raza et al., 2023; Rodriguez et al., 2020; Yu et al., 2016). Mixing cultivation increases productivity per unit of incident radiation by increasing solar radiation interception and/or maintaining higher radiation-use efficiency (Wang et al., 2015). Light sharing in the strip intercropping system was explained in different model concepts (Fan et al., 2020; Gou et al., 2017b; Liu et al., 2017; Munz et al., 2014b; Wang et al., 2015). Cereal/legumes within row mixing are one of the prevalent intercropping systems, where mainly wheat, barley, or maize, are cultured with common bean, pea, or faba beans (Fischer et al., 2020; Malagoli et al., 2020). However, interaction, compatibility, and complementarity are very complex and not well studied. Moreover, the competition for radiation which is one of the most important resources for plant growth and development is not well understood in wheat-faba bean mixtures.

In general, the yield advantage obtained compared to constitute monocultures might come from either the improved use of resources, such as light, water, and nutrients, which can be more efficiently acquired and/or converted into biomass by the intercrop compared to the corresponding monocultures (Stomph et al., 2020). Hence, when assessing resource use efficiency, distinguishing resource acquisition efficiency (a fraction of acquired resources from total available resources) and resource conversion efficiency (the ratio between biomass or yield and the amount of acquired resource) are crucial for optimizing intercrops for higher yield and stability. Cereal/legume intercrops have demonstrated both higher resource acquisition efficiency Jensen et al., (2020) and resource use efficiency (Bahia et al., 2024). For instance, a meta-analysis conducted by Tang et al. (2021) reported that cereal/legume intercropping resulted in higher phosphorous use efficiency than its corresponding monocultures. Nevertheless, it remains unclear which resource is either efficiently captured or converted to biomass and yield and under which environment and intercropping design approach this advantage can be realized.

Different intercropping systems have shown that different resource acquisition and use efficiency due to temporal and spatially niche complementarity. In a relay intercropping system, intercropping has demonstrated enhanced total radiation interception compared to what is expected from monocultures; this is primarily due to the extended time the crop stays on the field (temporal arrangement) (Gou et al., 2017a; Zhu et al., 2015; Wang et al., 2015). However, in a cropping system, in which both species have relatively similar phenology, the light interception of intercropping is similar to that of the average of the monocultures as the interception by one species in a closed stand goes inevitably at the expense of light interception by another species (Demie et al., 2025). Hence, in such a system, the contribution of light to the productivity of intercropping compared to the average of the monocultures is negligible, while it is an essential factor for intercropping productivity in relay intercropping systems (Yu et al., 2016).

To my knowledge, there are very limited studies regarding the water consumption of intercropping compared to monocultures, particularly in within-row mixtures, either by modeling approach or field experimentation. A review by Yin et al. (2020) stated that intercropping increases water consumption compared to monocultures. Spatial niche complementarity of water uptake due to spatial root distribution of intercropping might related to the over-yielding of intercropping compared to monocultures (Schmutz and Schöb, 2023). Yet, the total water consumption in intercrops compared to monocultures depends on the intercropping system. In a relay intercropping system, where crops partially share the land, it was reported that intercropping increased total water uptake and use efficiency (Chen et al., 2018; Tan et al., 2020). Mao et al. (2012) revealed that in relay intercropping, maize/pea strip intercropping improved total water uptake and water use efficiency compared to their respective monocultures. But in row mixtures, in which the species in mixtures have relatively the similar phenology, the water consumption of intercropping and monocultures is nearly the same (Demie et al., 2025). Besides the water acquisition efficiency, intercrops have shown higher water use efficiency under water-limited conditions (Bahia et al., 2024).

Numerous studies have been dedicated to understanding and improving the productivity of different cereal/legume intercrop systems by individually assessing various resources. Complementary (N) use is a prominent feature of cereal legume intercropping, reducing inorganic N demand for cereals (Jensen, 1996). Raza et al. (2023) reported that significantly more N was taken up by the intercrops compared to their respective monoculture systems in the case of a wheat/soybean combination. Hauggaard-Nielsen et al. (2001) reported that pea/barley intercrop took up slightly more soil N compared to barley monocultures but significantly more than the pea monoculture, resulting in 25-38% higher land use efficiency. Meta-analyses of different studies also stated that cereals take up more than their proportional share of soil N sources due to competitive interactions (Jensen et al., 2020; Pelzer et al., 2014; Rodriguez et al., 2020; Pelzer et al., 2014; Rodriguez et al., 2020b). Taking advantage of the fact that intercropped legumes derive more of their N from the atmosphere compared to monocultures could reduce N chemical fertilizer input by about 26% globally (Jensen et al., 2020). However, N dynamics are affected by the availability of other resources, such as soil water. Therefore, it is important to consider resource use interactions (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 (Bahia et al., 2024). N 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).

With regards to the 4C in niche partitioning, when plants use the same pool of abiotic resources in space and time, competition results from all processes that occur when one species has a greater ability to use limited resources. Past research has shown that cereals are very competitive for belowground resources such as water and nutrients (Yu et al., 2016). In the case of limited resources (e.g., nutrients, water, space, light), the complementary use of resources plays an important role. Because the species compete for the same pool of resources, the complementary resources use is essential to relax the competition. This results in higher complementarity and cooperation compared to competition. There are two examples of such cases in cereal/legumes within row intercropping of species with relatively identical phenology. Firstly, under limited N conditions, the legumes in intercropping fix more atmospheric N per unit of biomass due to strong competition from cereals (Jensen et al., 2020). Secondly, a spatial water uptake and niche partitioning of intercropped species occurs under limited soil water, driven most likely by a complementary spatial root distribution, which might explain why mixtures outperform monocultures (Schmutz and Schöb, 2023). Facilitation is also one ecological process in which the modification of the environment by one species is beneficial to the other. An example of this is the improved bioavailability of phosphorous in intercropping compared to corresponding monocultures. A study by Li et al. (2007) found that faba bean can mobilize soluble phosphorus in soils through rhizosphere acidification and carboxylate exudates, enhancing soil phosphorus availability to the benefit of both faba bean and maize. Overall, the assumption is that the morphological, physiological, and niche requirement differences among the species may lead to the joint effect of competition, complementarity, and facilitation in the acquisition efficiency of resources, contributing to improved yield in intercrops compared to monocultures (Justes et al., 2021).

Despite the undeniable advantage of field experiments, studying the resource acquisition and use efficiency in crop mixtures via field experiments poses a challenge due to their inherent complexity, particularly in measuring belowground dynamics. For instance, in many field experimental studies, the calculation 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 (Chen et al., 2018; Souza et al., 2023; Te et al., 2023; Bahia et al., 2024) That is, not all input is converted to biomass or grain yield. Using calibrated and tested process-based agroecosystem model simulation offers a promising complementary approach to field experimentation to separate the actual daily crop-specific consumption of different resource uses and explore possible interactions for resource use and acquisition under various environments (Stomph et al., 2020). Furthermore, it remains unclear whether the productivity in intercropping is mainly attributed to enhanced resource acquisition or improved resource use efficiency, particularly for within-row mixtures. The current work explores how the dynamics of crop resource (radiation, water, soil N) demand and use drive crop productivity in faba bean/wheat intercropping systems under different environmental conditions in within-row mixtures (**Chapter 4**).

1.2 Thesis objectives and highlights

Cereal/legume intercropping is a promising approach for sustainable crop production. However, there is still a significant research gap that demands for further investigation regarding, species/genotypes to combine, proportions, and other management factors under diverse environments. However, testing all these combinations is logistically challenging and resource demanding. Therefore, the use of agroecosystem models is required to understand and support intercropping design for improved resource use efficiency and to gain the intended advantage. Yet, understanding major ecological processes in intercropping is a prerequisite. Therefore, the general objective of this thesis was 1) to better understand genotype cropping system interactions for cereal/legume intercropping by synthesizing available evidence and identifying the knowledge gap concerning the mechanisms involved in genotype × cropping system interactions, 2) to calibrate and test a new intercrop model that enables rapid screening for possible management strategies of intercropping. 3) To investigate resource acquisition and use efficiency of intercrops by applying a process-based intercropping model.

Chapter 2 is intended to answer three research questions: (1) How do different genotypes and/or traits of a species in cereal/legume intercropping systems affect the performance of the mixture? (2) What are the mechanisms underlying the interaction of the genotypes in the intercropping system? And (3) What are the current knowledge gaps in genotype evaluation for intercropping systems? To answer these questions a systematic review was conducted to understand the interaction between genotype and cropping system to identify the knowledge gap concerning the mechanisms involved in genotype × cropping system interaction.

Based on the knowledge from **Chapter 2** a new intercrop model was calibrated and tested **(Chapter 3).** This study has two innovations: 1) The evaluation is based on a comparatively extensive experimental dataset compared to past studies. The experimental data are from spring wheat/faba bean (SW/FB) intercrops for three environments. This data set allowed us to evaluate the intercropping model more thoroughly in terms of above- and below-ground dynamics, including roots, which are major aspects of the interaction in intercropping systems. The field experimental data presented in **Chapter 3** is part of already published research (Paul et al. 2023, 2024). A second innovation is the evaluation approach. The evaluation of the intercrop model specifically addressed the difference between the intercrop and the average of the monocultures. Note also that no intercrop data are used here for calibration of the model. Thus, the evaluation is a measure of how well the model, integrating various mechanisms of interaction between the partner crops, simulates the intercrop effect, given information about the performance of the monocultures i.e the model is calibrated using only monoculture data.

In **Chapter 4,** the tested intercrop model was applied along with field experiment data to understand and explore resource acquisition and use efficiency in the intercropping system compared to the corresponding monocultures. The study aimed to answer the following research questions: 1) Which resource (water, radiation, or N) drives the intercropping performance of faba bean and spring wheat under varying conditions? 2) Is intercropping productivity primarily associated with resource acquisition or enhanced resource use efficiency? 3) Which specific resource allocation patterns are associated with each species and impact the productivity of individual species as well as the overall productivity of intercropped systems? The field experimental data presented in this study was also part of already published research (Paul et al. 2023, 2024; Demie et al., 2025). These studies tested multiple SW and FB under diverse intercropping systems. Here, the chapter 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 cultivar, Lennox (spring wheat) and Mallory (faba bean), growing under monocultures and intercropping systems.

In **Chapter 5**, the results of the previous chapters were synthesized and discussed, focusing on understanding the complex factors influencing intercropping, the modeling approaches and limitations of the current intercrop model, and the model application to understand the resource dynamics in spring wheat/ faba bean intercropping under diverse environments.

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Chapter 2

2 Mixture × Genotype Effects in Cereal/Legume Intercropping

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Abstract

Cropping system diversification through annual intercropping provides a pathway for agricultural production with reduced inputs of fertilizer and pesticides. While several studies have shown that intercrop performance depends on the genotypes used, the available evidence has not been synthesized in an overarching analysis. Here, we review the effects of genotypes in cereal/legume intercropping systems, showing how genotype choice affects mixture performance. Furthermore, we discuss the mechanisms underlying the interactions between genotype and cropping system (i.e., sole cropping vs. intercropping). Data from 69 articles fulfilling inclusion criteria were analyzed, out of which 35 articles reported land equivalent ratio (LER), yielding 262 LER data points to be extracted. The mean and median LER were 1.26 and 1.24, respectively. The extracted genotype × cropping system interaction effects on yield were reported in 71% out of 69 publications. Out of this, genotype × cropping system interaction effects were significant in 75% of the studies, whereas 25% reported non-significant interactions. The remaining studies did not report the effects of the genotype × cropping system. Phenological and morphological traits, such as differences in days to maturity, plant height, or growth habit, explained variations in the performance of mixtures with different genotypes. However, the relevant genotype traits were not described sufficiently in most of the studies to allow for a detailed analysis. A tendency toward higher intercropping performance with short cereal genotypes was observed. The results show the importance of genotype selection for better productivity of cereal/legume intercropping. This study highlights the hitherto unrevealed aspects of genotype evaluation for intercropping systems that need to be tackled. Future research on genotype effects in intercropping should consider phenology, root growth, and soil nutrient and water acquisition timing, as well as the effects of weeds and diseases, to improve our understanding of how genotype combination and breeding may help to optimize intercropping systems.

Keywords: cultivar combination, intercropping performance, mixture, mixing ability, trait combination

2.1 Introduction

In the past few decades, agricultural intensification has resulted in increased yields of pure line crops (Blomqvist et al., 2020), this has been accompanied by the simplification and homogenization of production systems and concentration on very few species as human diet staples (Khoury et al., 2014). Genetic uniformity and loss of diversity in the agricultural landscape (Hazell and Wood, 2008; Gregory and George, 2011) are characteristics of intensive agriculture, increasing vulnerability to climate change (Lin et al., 2008) and pathogen invasions (Anderson et al., 2004; Savary et al., 2019). Diversifying crop production systems is a promising pathway to tackle such vulnerabilities (Renard and Tilman, 2019; Tscharntke et al., 2021; Hufnagel et al., 2020). Diversification approaches can be classified into two complementary categories: (1) integration of underutilized crops into the system; and (2) diversification of the production system through crop rotation, mixed cropping, and/or catch crops (Mustafa et al., 2019). More efficient utilization of resources with beneficial effects on the environment could also be gained by the integration of livestock with temporal and spatial crop diversification such as forage legume intercropping with grain cereals (Danso-Abbeam et al., 2021). Crop diversification includes practices that significantly improve crop productivity, especially benefiting rural smallholders (Makate et al., 2016) and enhance overall ecosystem services without compromising crop yield (Beillouin et al., 2021; Ditzler et al., 2021; Tamburini et al., 2020). Annual intercropping is one form of cropping system diversification which allows high productivity and reduction of fertilizer and pesticide input (Bedoussac et al., 2015; Li et al., 2020b). There by substantially minimizing the negative environmental impacts of agriculture. Further, crop diversification provides insurance against crop failure for farmers (Gaba et al., 2015; Lithourgidis et al., 2011).

Mixing crop species may be done with annual crops or perennial crops on a gradient of complexity from two to several species (Finckh and Wolfe, 2015, Malézieux et al., 2009). Cereal/legume intercropping systems are widely used across the world, particularly by smallholders, producing high quality cereal and legume grains in an economically sustainable, environmentally friendly, and efficient way. Using legume crops in a mixture with cereals may significantly mitigate N_2O fluxes derived from fertilizer, hence providing an effective way to reduce greenhouse gas emissions from cropping systems (Senbayram et al., 2015). Further, intercropping was found to produce higher cereal protein concentration (Timaeus et al., 2021b; Bedoussac and Justes, 2010), higher grain yields (Yu et al., 2016), higher yield stability (Raseduzzaman and Jensen, 2017), and better abiotic and biotic stress resistance (Timaeus et al., 2021a; Bedoussac et al., 2015) than sole crops.

Intercropping performance is often measured by the land equivalent ratio (LER), an index measuring the relative land area required to produce the same yields (or any other service such as biomass) in sole crops as obtained from a unit area of intercrop. An LER greater than one indicates that intercropping uses the land more efficiently than pure stands to produce the desired outputs (Mead and Willey, 1980).

Several studies have shown that the general performance of intercropping systems depends on the genotypes used in the mixture (e.g. Hauggaard-Nielsen and Jensen, 2001) and that the performance in mixed stand can be poorly correlated to performance in a pure stand (Annicchiarico et al., 2019). Different genotypes of legumes may have different responses in terms of phenology and morphology (Annicchiarico and Filippi, 2007) when compared in sole crops versus mixtures. Hence, specific selection of genotypes for intercropping is important (Giles et al., 2017) and intercrop yield advantage could be achieved by selecting specific traits of both species (Berghuijs et al., 2020). Therefore, it has been suggested that specific breeding of genotypes for intercropping is needed to improve complementarity of the intercropping partners (Haug et al., 2021; Annicchiarico et al., 2019; Berghuijs et al., 2020).

Cereal/legume mixtures could include systems where both species have similar phenology but contrasting morphology, or, alternatively, contrasting phenology and morphology, resulting in temporal and/or spatial niche complementarity (Gaudio, et al. 2019). The ecological niche separation concept posits that the different species involved may have different resource requirements at different times, as well as for different sources of nutrition (Malézieux et al., 2009). In addition to niche complementarity, intercrop performance can also be due to additional ecological mechanisms (Loreau and Hector, 2001). Facilitation effects may exist between mixed species such as synergy in the use of phosphorus (Hinsinger et al., 2011; Tang et al., 2020).(C. Li et al., 2020b) The species complementarity effect, which measures the overall shift of relative yields in mixtures vs. sole crop, has a higher effect on yield gain than the selection effect, which defines how these shifts in relative yields are correlated to sole crop yields (Li et al., 2020a). Complementarity is a paramount feature in cereal/legume intercrops grown under low-N conditions, in which biological N fixation by the legume and strong competition for soil-N by the cereal may synergize to enhance yield and grain quality.

Choosing plant genotypes for specific intercropping systems is, however, laborious and costly, if only because assessing intercropping performance also requires the inclusion of sole crops in field experiments for comparison and estimation of the benefits of mixing. Testing genotypes in mixtures easily results in a curse of dimensionality. For instance, with five genotypes of a cereal and five genotypes of a mixture, 25 mixtures should be tested along with 10 pure stands. Optimal species traits likely depend on the companion species, such that all possible combinations are preferably tested. Note that incomplete designs have been proposed to deal with this challenge of dimensionality (Hinsinger et al., 2011), and shown to be efficient to estimate mixing abilities (Haug et al., 2021). Testers and reciprocal breeding schemes have been proposed to co-breed species (Sampoux et al., 2020). Recent technologies such as genomic selection strategies could help select traits for breeding for intercropping accurately (Bančič et al., 2021). However, better knowledge on genotypes and their associated trait effects in intercropping is needed to make selection more targeted.

General and specific mixing ability of genotypes of single species have been studied to determine contrasting traits in sole cropping and in mixtures and the theoretical background has been discussed with respect to species mixtures (Wright, 1985). Historically, multiple studies have evaluated different crop genotypes for complementarity in intercropping (Davis and Woolley, 1993; Francis et al., 1976; Smith, 1985; Smith and Zobel, 1991). Abundant research has been conducted but the knowledge on genotype effects in intercropping is fragmented and has not been compiled to deliver necessary knowledge for designing optimized intercropping systems. Here, we aim to provide a current update by linking recent advances through a review. In particular, we address the knowledge gap concerning the mechanisms involved in genotype × cropping system interaction. This review is intended to answer the following questions: (i) How do different genotypes and/or traits of a species in cereal/legume intercropping systems affect the performance of the mixture? (ii) What are the mechanisms underlying the interaction of the genotypes in the intercropping system? And (iii) what are the current knowledge gaps in genotype evaluation for intercropping systems?

2.2 Material and methods

2.2.1 Literature search and publication screening

We conducted a systematic map, using the science databases Web of Science, Scopus, Science Direct, and Google Scholar. Keywords used for searching suitable publications were ‘genotype interaction in inter/mixed cropping system’ OR ‘cultivars interaction in inter/mixed cropping system’ OR ‘varieties interaction in inter/mixed cropping system, OR ‘cereals in inter/mixed cropping system’ and scientific names (genus and species name) and common names of cereals species with intercropping and mixed cropping. The slash (/) was not used in a search, here it is used for simplified expression of search terms (i.e. intercropping OR mixed cropping). A full list of the search terms is given in the Appendix Table A. S1. In addition, secondary literature cited in selected papers were also looked up and included if relevant. The latest search was conducted on 12 April 2021.

To select the relevant papers, we used the following inclusion criteria: (i) studies from cereal/legume intercropping with both grain and forage legumes; (ii) studies evaluated at least two genotypes of at least one of the mixed species; (iii) peer-reviewed full-length papers published in English; (iv) studies reporting original research data; and (v) only field experiments, excluding greenhouse or pot experiments. No restriction was made against type of mixture design e.g. with respect to plant density such as additive, replacement (substitution) or intermediate design. The information extracted from the original research articles was categorized in a digital database and analyzed following PRISM guidelines (Moher et al., 2009).

2.2.2 Variables and data extraction

Data on genotype performance originated from different management and different agro-ecological zones, resulting in large differences in yield. Hence, an index was necessary to characterize the performance of genotypes in intercropping in relation to their respective pure stands (Mead and Willey, 1980). We used the LER (Eq. 1) as a key metric to measure intercrop yield advantage (mixture effect) intercrop yield advantage (or disadvantage) by reference to the pure crop yields of mixed genotypes. We also retrieved the results of any analysis of variance analyzing genotype and cropping system main effects and their interaction. Furthermore, individual studies were scrutinized by assessing conclusions and interpretations about the effects of different traits (phenology, and morphology) of species in mixtures to identify the general mechanisms responsible for cereal/legume intercropping yield advantage.

Different variables were extracted from each study (Table 1) in the core set of publications. Information like intercropping design (design of the mixing system i.e. substitutive or additive or intermediate), country of the experiment, number of genotypes, and other related variables were extracted from each publication. Significance (or non-significance) of "genotype" effect, "cropping system" effect (pure vs. mixed stand) and, "genotype" x "cropping system" interaction effect on yield data were extracted from ANOVA tables of the articles. This was done by extracting results from the ANOVA of each paper; any differences among papers regarding the structure of statistical analysis (e.g. fixed vs. random effects) were disregarded. The mechanisms of intercropping performance were extracted from the description of results and the full paper was consulted if needed. Some studies reported various types of mixtures, from different species of either cereals or legumes. Also, in these cases, data were extracted from all combinations in which at least two genotypes of at least one of the partners were evaluated.

Table 2.1: Variables extracted from different studies.

Variables	Definition	Data type/Units
Title	Title of the publication	text
Authors	Authors in publication	text
Year	Publication year	text
Journal	The journal in which the paper was published	text
Country	The country where the experiment was conducted	text
Precipitation	The total rainfall during the growing period	numerical
Soil texture	The texture of the soil in the experimental area	categorical
Species and genotypes	The names of species and genotypes used in the experiment	text
Number of genotypes	The number of genotypes of each species studied in the experiment	numerical
Design	Plant density (additive /replacement /intermediate)	categorical
Response variable	The response variable investigated	text
Replication	How many times the treatment was replicated	numerical
Number of locations	Number of the site where the experiment was conducted	numerical
Number of seasons	Number of seasons during which the experiments were conducted	numerical
Genotype, cropping system, and interaction effects	The statistical significance of interaction, cropping system, and genotype effect	categorical
Interaction traits	List of traits/mechanisms highlighted as causal in crop interactions and intercropping performance	categorical
LER	Land equivalent ratio	numerical

The LER (Eq.1) of each genotype combination was extracted from the subset of papers reporting them, either directly when represented numerically, or in figures. Data from figures were digitalized using a web-based plot digitizer (Rohatgi, 2020), an online system used to extract data from images efficiently and accurately (Burda et al., 2017; Cramond et al., 2019). LER was reported in figures only in five papers (Odo, 1991; Watiki et al., 1993; Barillot et al., 2014; Kontturi et al., 2011; Pappa et al., 2012; Rao and Willey, 1983). The majority of the studies reported mean LER per genotype combination across multiple environments. However, in some cases, the studies reported data individually from each environment. If the mean LER across different environments was not reported, this mean was computed for each genotype combination of the species in the intercrop from the individual environments. When a study reported only the partial land equivalent ratio (PLER), the total land equivalent ratio (LER) was calculated for each genotype combination of the species in intercropping by summing the PLERs:

$$LER_{c+l} = PLER_{c/l} + PLER_{l/c} \quad (1)$$

Where LER_{c+l} is the LER of the cereal genotype c with the legume genotype l; and $PLER_{c/l}$ is the partial LER of genotype c in mixture with legume genotype l (and reciprocally for $PLER_{l/c}$). This genotype combination-specific LER was used in further analysis. If neither LER or partial LER were reported, LER for each genotype in a given cereal-legume combination was calculated from yields in mono-cropping and intercropping.

When other treatments were applied (such as different row spacing, and sowing density or proportion), LERs were extracted or calculated from only one treatment. If different levels of nitrogen were used, data for each level of fertilizer were considered and averages computed for each genotype combination. In one study, results from two species of cereal or legume were reported. Thus, data were recorded from each genotype combination from each species and analyzed. Therefore, at least 2 data points from each paper (depends on number of genotypes of cereals and legumes) were extracted. In this way, we obtained 262 LER data points.

Since only few (10%) LER data points were reported from forage legume species combinations with cereals (2 papers with oats, 1 paper with finger millet and 2 papers with maize) all data from forage and grain legumes were combined and analyzed together.

2.2.2 Data analysis

Main effects of genotype and intercropping and their interaction effects were assessed by counting and calculating the proportion of papers that reported significant or non-significant effects on yields. In addition to the analysis of LER, a fixed effect ANOVA model was used to test the effect of cereal species, design and interaction effect on LER across cereal species by categorizing the data set by cereal species.

Because the number of data points of wheat was low (n=5), and data records from barley and rice was only from replacement design, we excluded these three from analysis. The number of data records per cereal species varied from 25 (finger millet) to 131 (maize) (Fig. 3. Similarly, a fixed effect ANOVA model was used to test the effect of legume species, design and interaction on LER across legume species by categorizing the data set by legume species. However, faba bean, grass pea, guar and hairy vetch, berseem clover and bitter vetch were excluded because the number of data points (two to four) were low. The mean comparison was done by Tukeys's honest significant difference (HSD) test.

To assess the potential of genotype choice for optimizing LER we calculated three indices using the extracted data from the articles (averages across the site years); to obtain these indices we first calculated the maximum, median and minimum LER across different genotype combinations for each paper. Then (i) the difference between maximum and median LER was used as a measure for the potential of combined genotype choice to improve LER in comparison to a random choice; similarly, (ii) the difference between minimum and median LER was taken as a measure for the risk to choose an inappropriate genotype combination in comparison to a random choice; and (iii) the range, i.e. the difference between maximum and minimum LER from a paper was used to characterize the maximum genotype combination effect within a study. The median used to calculate the all three statistics were calculated from each individual paper. The three statistics are equivalent when only two genotypes were evaluated. Because of sampling effects, it is expected that all three differences would tend to increase (in absolute terms) with increasing number of genotype combinations tested within a study (Schwarz, 2011); we therefore plotted the indices against the number of genotype combinations. The extracted LER data were subjected to descriptive statistics; all analyses were conducted with R (R CoreTeam, 2020) and figures were produced using the R package ggplot2 (Wickham, 2016).

2.3 Results

2.3.1 Geographical distribution and characteristics of studies

From about 4000 search hits using all search terms, only 69 papers fulfilled the inclusion criteria (Table 2.2). The reported research studies were conducted in 28 different countries (Table A. S2). The majority of data came from Africa (37%) followed by Europe (24%) and Asia (18%). The included studies considered different contrasting characteristics of genotypes of cereals and legumes evaluated.

Table 2.2: List of cereal and legume species in the 69 selected studies investigating genotype effects in intercropping; because some studies tested more than two species, the sum of studies across all crop species (152) is greater than 2 x 69 = 138.

Common name	Scientific name	No. of studies
Cereals		
Maize	*Zea mays*	30
Oat	*Avena sativa*	8
Wheat	*Triticum aestivum*	8
Finger millet	*Eleusine coracana*	6
Sorghum	*Sorghum bicolor*	6
Barley	*Hordeum vulgare*	5
Rice	*Oryza sativa*	5
Naked oat	*Avena nuda*	1
Durum wheat	*Triticum durum*	1
Legumes		
Common bean	*Phaseolus vulgaris*	17
Cowpea	*Vigna unguiculata*	13
Soybean	*Glycine max*	8
Pigeon pea	*Cajanus cajan*	7
Pea	*Pisum sativum*	7
Faba bean	*Vicia faba*	7
Berseem clover	*Trifolium alexandrinum*	5
Groundnut	*Arachis hypogaea*	3
White clover	*Trifolium repens*	2
Bitter vetch	*Vicia ervilia*	2
Common vetch	*Vicia sativa*	2
Hairy vetch	*Vicia villosa*	2
Guar	*Cyamopsis tetragonoloba*	1
Grass pea	*Lathyrus sativus*	1
Snail clover	*Medicago truncatula*	1
Serradella	*Ornithopus sativus*	1
Runner bean	*Phaseolus coccineus*	1
Caribbean stylo	*Stylosanthes hamata*	1
Subterranean clover	*Trifolium subterraneum*	1

Overall, 9 cereal crop species and 19 legume species were evaluated in 69 publications with maize as the most frequently evaluated cereal species followed by oat and wheat. Common bean was the most frequently evaluated legume followed by cowpea and soybean. In the considered studies, common bean was only intercropped with maize. A single genotype was used in 62 % of the studies for one of the partner species, i.e. in these studies, genotypic variation was only investigated in the other partner. On average, 4 cereal genotypes or 3 legume genotypes were compared per study, when excluding the single genotype studies (Fig. 1). The most diverse comparison included 8 genotypes of cereal (*Avena sativa*) and 7 genotypes of legume species (*Trifolium alexandrinum)*, in a total of 56 cereal-clover combinations.

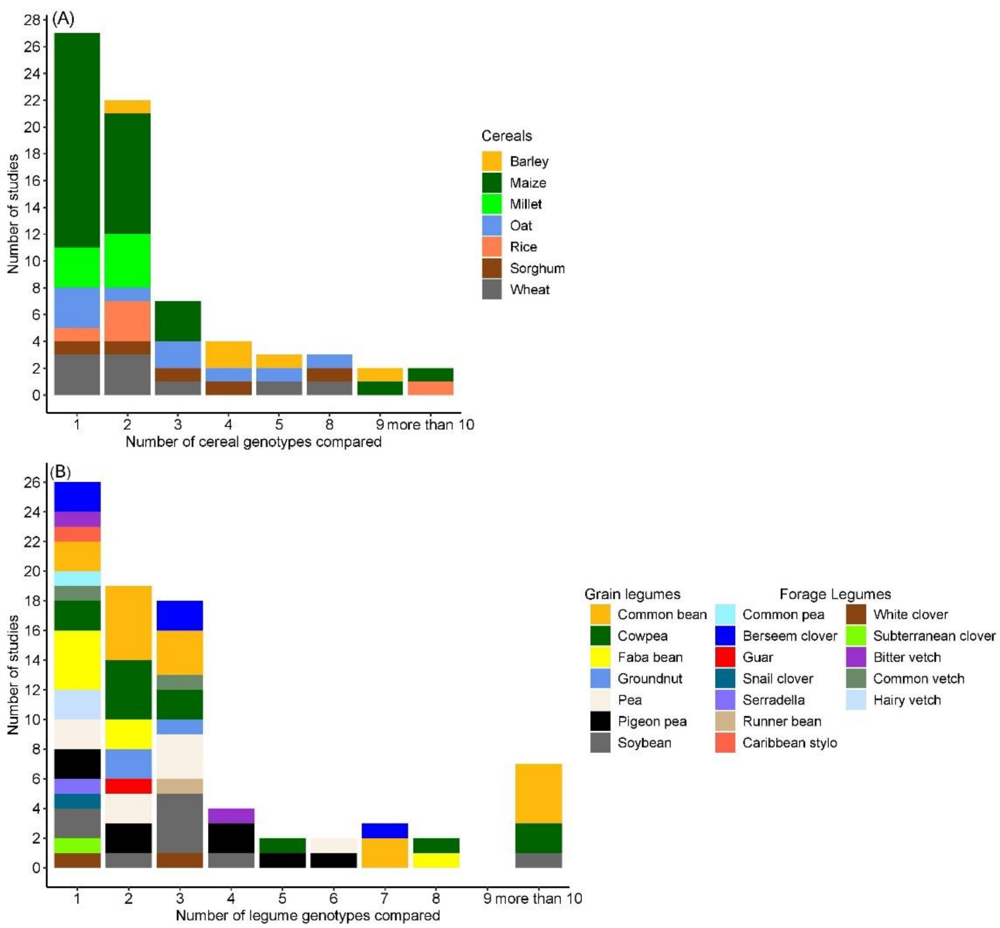

Figure 2.1: (A) Number of cereal genotypes evaluated in combination with legume species (each combination was categorized based on the cereal species). (B) Number of legume genotypes evaluated in combination with cereal species (each combination was categorized based on the legumes species). In both cases if one genotype of one partner is evaluated, the other partner had at least 2 genotypes.

The majority of studies (55) evaluated grain legumes while eight studies evaluated forage legumes and a small proportion (6) of studies evaluated both forage and grain legumes together. The number of genotypes used in the studies varied, with similar numbers of studies reporting on (i) combinations of two or more cereal genotypes with two or more legume genotypes, (ii) one cereal genotype combined with two or more legume genotypes; or (iii) one legume genotype combined with two or more cereal genotypes (Table 2.3).

Table 2.3. Number of studies with one or more than one genotype of cereal and/or legume (*not included in this review) from 69 studies. One paper evaluated two cereal species resulting in a total of 70 data sets (out of one publication, two data sets were extracted).

	1 cereal genotype	>1 cereal genotype
1 legume genotype	*	16
> 1 legume genotype	27	27

2.3.2 Effect of cropping system and genotypes of cereal/legume on intercropping performance

Genotype × cropping system interaction

The extracted genotype × cropping system interaction effects on yield were reported in 49 (71%) studies out of 69 publications. Out of this, genotype × cropping system interaction effects were significant in 37 (75%), of the studies; while 12 (25%) of the studies reported non-significant interactions. The remaining studies did not report the effects of genotype × cropping system. In addition, intercropping main effects were reported in 38 (55%) studies. Out of this, the effect was significant in 27 (71%) and non-significant in 11 (29%) of the publications. Genotype main effects were reported in 37 (53%) studies, out of this, the genotype effect was significant in 25 (67%) and non-significant in 12 (33%) of the publications. The remaining studies did not mention the effects of cropping system and genotype effects.

Table 2.4: Number of studies reporting significant and non-significant genotype, cropping system and interaction effects, categorized by cereals; sig.: significant; n.s.: not significant; n.r.: not reported

Cereal	Cropping system effect			Genotype effect			Interaction effect		
	sig.	n.s.	n.r.	sig.	n.s.	n.r.	sig.	n.s.	n.r.
Barley	2	1	2	2	1	2	2	1	2
Maize	12	8	9	12	9	9	19	7	4
Millet	2	0	5	1	0	5	5	0	1
Oat	5	0	4	3	0	6	6	0	3
Rice	1	0	4	2	0	3	2	0	3
Sorghum	1	0	4	2	0	3	1	0	4
Wheat	4	2	3	3	2	4	2	4	3
Total	27	11	31	25	12	32	37	12	20

LER as metric to gauge yield advantage of genotypes in intercropping

From the 69 studies used for data extraction, 35 studies yielded 36 data sets (one study used two cereal species) and either reported the LERs directly or allowed calculation from the reported yield data. From these 36 data sets, 262 data points (cereal/legume genotype combinations) were extracted, based on a total of 85 cereal and 126 legume genotypes, with a number of cereal/legume combinations (LER) ranging from 2 to 22 per study.

The calculated mean and the median LER were 1.26 and 1.24, respectively (Fig. 2.2) and LER was greater than 1.0 in 85% of the single cases. Although the number of data points for some cereals, especially wheat, may not be sufficient to compare the median LER with other cereals, the overall outcome was robustly > 1 with a highest median LER of 1.38 (n = 25) found in finger millet. The strikingly high variation in maize is in part due to the number of studies. In barley-based cropping systems, all of the LER data were greater than 1 (n=22, range 1.05 to 1.48) (Fig. 2.3).

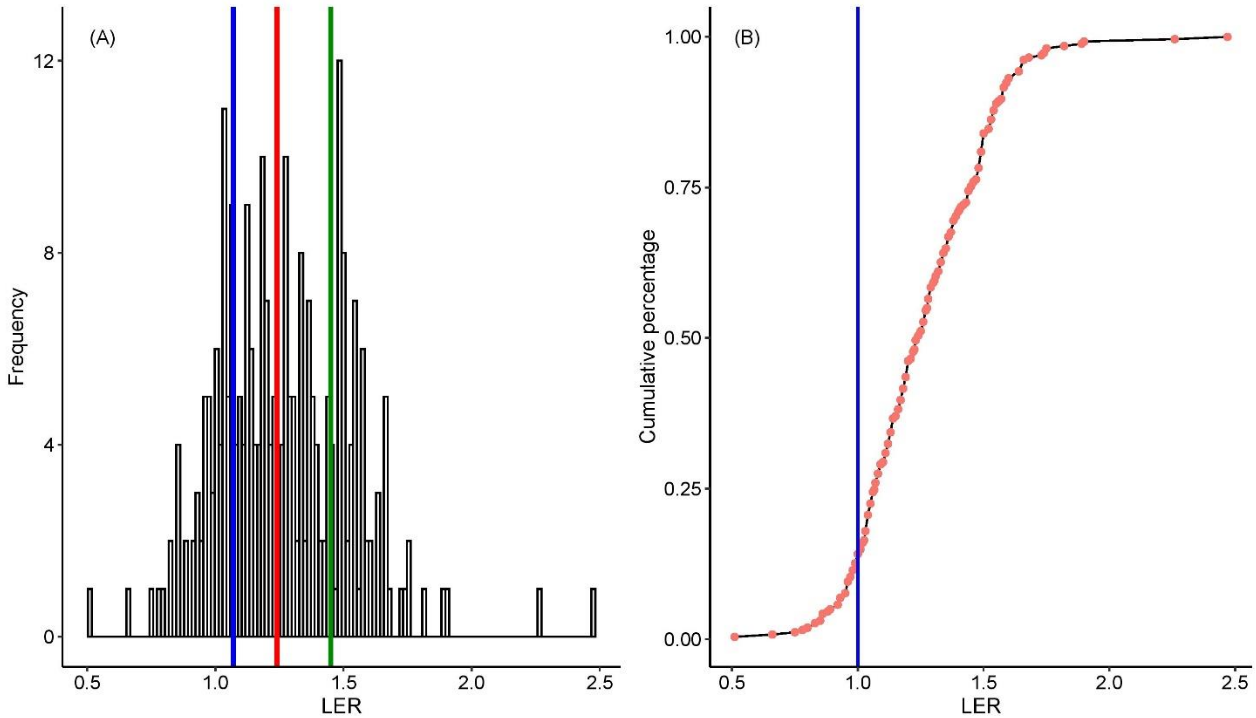

Figure 2.2: (A) Frequency distribution of LER from 35 studies, quartiles marked by blue and green; median marked by red-colored vertical lines; (B) cumulative percentage distribution of LER from 35 studies, 36 (data sets), The vertical blue line in (B) shows LER = 1.

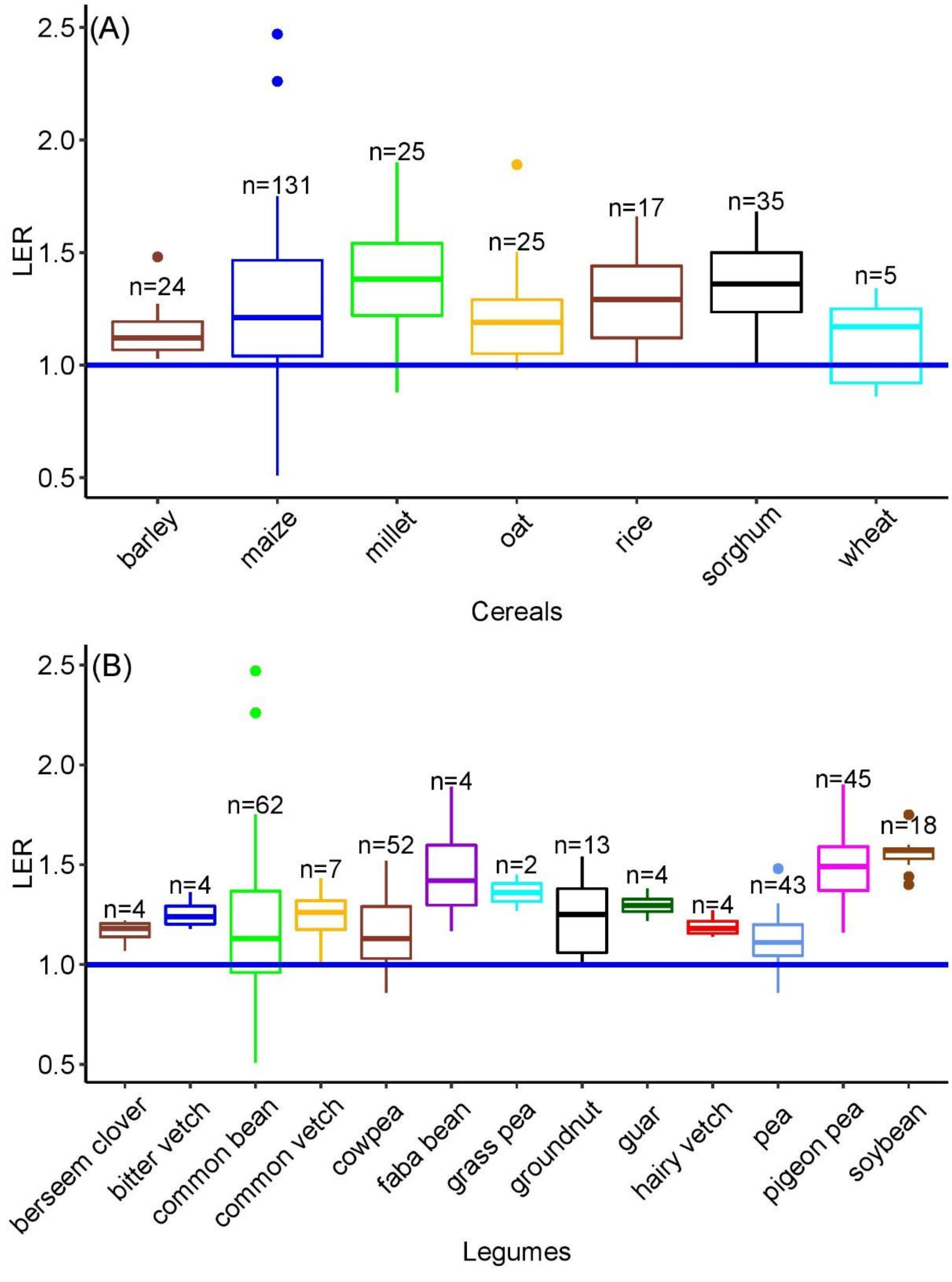

Figure 2.3: A) LER of intercropping systems with different cereal components. B) LER of intercropping systems with different legume components. Extracted from 35 studies with median (horizontal line), upper and lower quartile (boxes) and 1.5 interquartile range (IQR) (whiskers). The horizontal blue line was drawn at LER =1; n: number of data point. Although wheat, faba bean, berseem clover, bitter vetch, hairy vetch and guar data was excluded from the ANOVA (n<5), the data is shown in this graph for comparison.

The analysis of variance resulted in highly significant differences across cereal species and design ($p < 0.01$). In addition, the interaction effect was significant ($p < 0.05$). The pairwise means comparison revealed that finger millet reached higher LERs in additive designs as compared to replacement designs while no effect of design was found in maize and sorghum. (see Table S3 for ANOVA and Figure 4A). The analysis of variance, across legume species and design, resulted in highly significant differences across legume species with pigeon pea and soybean exceeding other species but non-significant effects of design and interaction effect ($p > 0.05$) (see Table S4 for ANOVA).

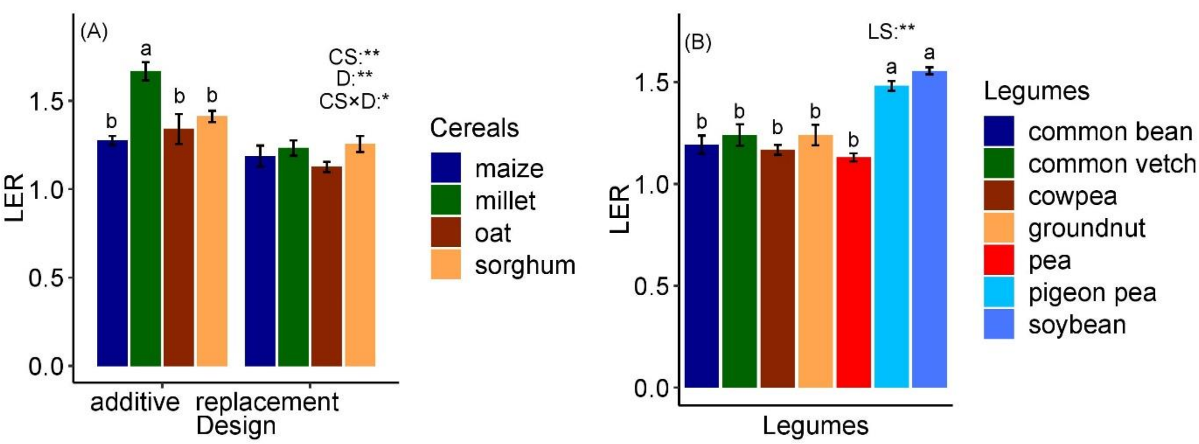

Figure 4: A) Effect of cereal species and design on LER. B) Effect of legume species on LER. The letters show the statistical differences between species. CS: cereals species; D: design and CS×D: species interaction with design; LS: legumes species *: significant ($p<0.05$), **: highly significant ($p<0.01$) and the error bar is the standard error of the mean. The two designs (additive and replacement) is not represented for legumes because, the effect of design is not significant.

The potential of genotype choice for intercropping

The distribution of the LERs within the studies around the median (Fig. 2.5) indicates that genotype specific effects play a role in the performance of mixtures in comparison to sole crops. Overall, the range (i.e. difference between maximum LER and minimum LER within a study) varied between 0 and 1.98, showing the potential of large genotype effects in intercropping. Conversely, there was a risk to obtain low LERs by non-appropriate genotype choice (i.e. as indicated by the difference of minimum LER and median LER, red points in Fig.2.5); the difference between minimum to median ranged from -0.55 to 0. The largest LER range (1.96) was found in a study with 20 different genotypes (Santalla et al., 2001b); in the only other study with 20 genotypes (Hauggaard Nielsen and Jensen, 2001) the range was 0.27, i.e. quite moderate (Table 2.4).

To elaborate the effect of genotypes on intercropping performance in terms of LER, the studies from maize-based were analyzed in detail. A total of 16 studies reported LER in maize intercropping system and yielded 138 LER data records(Santalla et al., 2001). The analysis shows that with increasing number of maize genotypes included in the study, the LER range (maximum - minimum) increased significantly with an R^2 of 0.58 (P=0.00063) and 0.47 (P=0.0046) in the regression of LER against number of genotype combinations, when the study of Santalla et al. (2001) that represents an outlier in terms of the number of genotypes tested (20 compared to 2-15) was included or excluded, respectively.

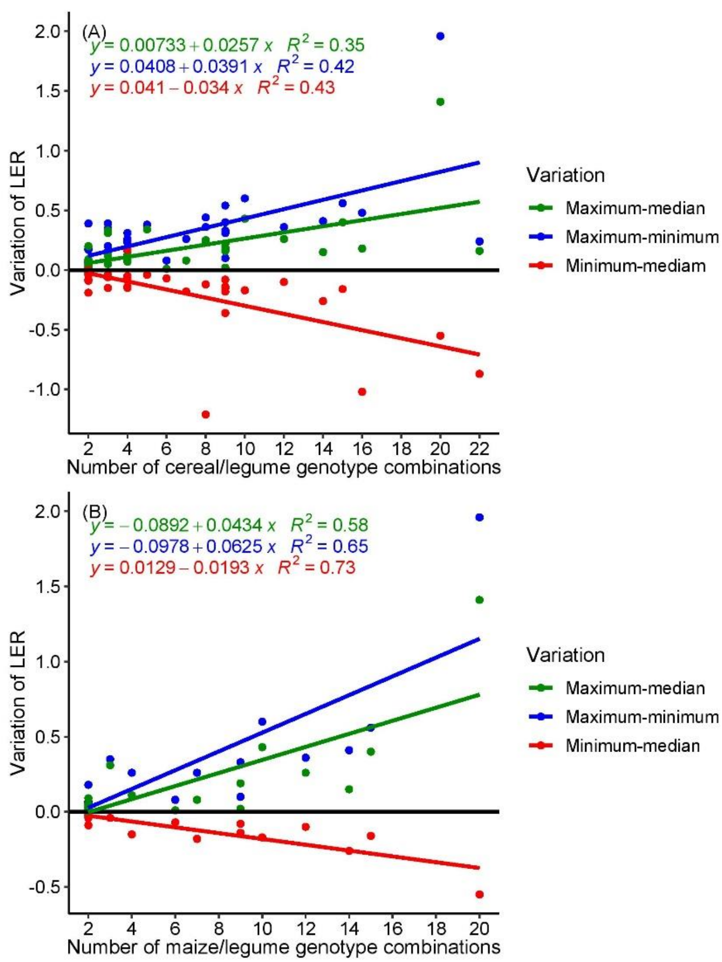

Figure. 2.5 Variation of extracted LER: (A) all data points from cereal/legume intercropping extracted from 35 studies and (B) LER variation from maize-based intercropping extracted from 16 studies.

Table 2.5: Deviations of LER from the Median in cereal/legume intercropping extracted from 35 studies including between 2 and 20 mixtures, i.e. different genotype combinations (N). Note: in some studies, more than one legume species was evaluated; add – additive, repl – replacement design, inter- intermediate.

Author	Cereal species	Legume species	No. cereal genotypes	No. legume genotypes	Range (max-min)	Max-median	Min - median	Design	(N)
Klimek-Kopyra et al., 2015	*Avena nuda*	*Vicia faba*	1	2	0.39	0.2	-0.19	add	2
Li et al., 2020	*Avena sativa*	*vetch genotype*	1	3	0.2	0.05	-0.15	add	3
Baxevanos et al., 2017	*Avena sativa*	*Pisum sativum*	3	3	0.31	0.16	-0.15	repl	9
Ross et al., 2004	*Avena sativa*	*Pisum sativum*	2	2	0.25	0.11	-0.14	repl	4
Kontturi et al., 2011	*Avena sativa*	*Pisum sativum*	1	3	0.16	0.12	-0.04	add	3
Baxevanos et al., 2021	*Avena sativa*	*Vicia sativa*	4	1	0.17	0.11	-0.06	repl	4
Pappa et al., 2012	*Hordeum vulgare*	*Pisum sativum*	2	1	0	0	0	repl	2
Hauggaard-Nielsen and Jensen, 2001	*Hordeum vulgare*	*Pisum sativum*	4	6	0.24	0.16	-0.87	repl	22
Sanou et al., 2016	*Eleusine coracana*	*Vigna unguiculata*	2	2	0.13	0.08	-0.05	repl	4
Reddy et al., 1990	*Eleusine coracana*	*Vigna unguiculata*	3	3	0.4	0.22	-0.18	repl	9
Yadav and Yadav, 2001	*Eleusine coracana*	*Cyamopsis etragonoloba*	2	2	0.16	0.085	-0.075	repl	4
Rao and Willey, 1983	*Eleusine coracana*	*Cajanus cajan*	2	4	0.44	0.25	-1.21	add	8
Ramakrishna and Ong, 1994	*Oryza sativa*	*Vigna unguiculata*	2	2	0.23	0.13	-0.09	repl	4
		Arachis hypogaea		2	0.13	0.07	-0.06	repl	4
		Cajanus cajan		2	0.31	0.13	0.17	repl	4
Rahlakrishna et al., 1992	*Oryza sativa*	*Cajanus cajan*	1	5	0.38	0.34	-0.04	repl	5
Tefera and Tana, 2002	*Sorghum bicolor*	*Arachis hypogaea*	3	3	0.54	0.18	-0.36	add	9
Odo, 1991	*Sorghum bicolor*	*Vigna unguiculata*	2	1	0.17	0.08	-0.09	repl	2
Queiroz et al., 1988	*Sorghum bicolor*	*Vigna unguiculata*	8	1	0.36	0.24	-0.12	repl	8

Author	Cereal species	Legume species	No. cereal genotypes	No. legume genotypes	Range (max-min)	Max-median	Min - median	Design	(N)
Rao and Willey, 1983	*Sorghum bicolor*	*Cajanus cajan*	4	4	0.48	0.18	-1.02	add	16
Barillot et al., 2014	*Triticum aestivum*	*Pisum sativum*	1	3	0.39	0.33	-0.06	repl	3
Haymes and Lee, 1999	*Triticum aestivum*	*Vicia faba*	2	1	0.17	0.09	-0.08	add	2
Egbe et al., 2010	*Zea mays*	*Vigna unguiculata*	1	10	0.6	0.43	-0.17	repl	10
Watiki et al., 1993	*Zea mays*	*Vigna unguiculata*	1	15	0.56	0.4	-0.16	add	15
Goshime et al., 2020	*Zea mays*	*Phaseolus vulgaris*	9	1	0.33	0.19	-0.14	add	9
Gebeyehu et al., 2006	*Zea mays*	*Phaseolus vulgaris*	2	7	0.41	0.15	-0.26	add	14
Javanmard et al., 2020	*Zea mays*	*Lathyrus sativus.,*	2	1	0.06	0.03	-0.03	add	2
		Vicia villosa		1	0.09	0.04	-0.04	add	2
		Vicia ervilia.,		1	0.04	0.02	-0.02	add	2
		Trifolium alexandrinum		1	0.05	0.02	-0.02	add	2
R.L Molatudi, 2012	*Zea mays*	*Phaseolus vulgaris*	1	2	0.18	0.09	-0.09	add	2
Pierre et al., 2017	*Zea mays*	*Glycine max*	1	3	0.35	0.31	-0.04	add	3
Zaeem et al., 2019	*Zea mays*	*Glycine max*	2	3	0.08	0.01	-0.07	add	6
Yang et al., 2018	*Zea mays*	*Glycine max*	3	3	0.1	0.02	-0.08	add	9
Javanmard et al., 2009	*Zea mays*	*Vicia ervilia,*	2	1	0.07	0.03	-0.03	add	2
		Trifolium alexandrinum		1	0.04	0.02	-0.02	add	2
		Vicia villosa		1	0	0	0	add	2
		Phaseolus vulgaris		1	0.07	0.03	-0.03	add	2
Tamado, 2007	*Zea mays*	*Phaseolus vulgaris*	1	7	0.26	0.08	-0.18	add	7
Nassary et al., 2020	*Zea mays*	*Phaseolus vulgaris*	2	1	0.09	0.05	-0.04	add	2
Muraya et al., 2006	*Zea mays*	*Phaseolus vulgaris*	2	2	0.26	0.11	-0.15	add	4
Dasbak and Asiegbu, 2009	*Zea mays*	*Cajanus cajan*	2	6	0.36	0.26	-0.1	add	12
Santalla et al., 2001b	*Zea mays*	*Phaseolus vulgaris*	2	10	1.96	1.41	-0.55	repl	20
Nassary et al., 2020b	*Zea mays*	*Phaseolus vulgaris*	1	2	0.07	0.03	0.03	repl	2

2.3.3 Mechanisms underlying the interactions between genotypes and cropping system

In 20 out of the 69 studies, contrasting phenological or architectural characteristics of cereal and/or legume genotypes were highlighted, suggesting that the temporal and spatial differences among genotypes contributed to intercrop performance. These traits were broadly categorized into phenological and morphological traits (Table 2.6).

The phenological traits include growth duration (days to maturity, days required from emergence to flowering, and harvesting time), whereas morphological traits include shoot architecture (plant height) and growth habit (determinate/ indeterminate growth) of the genotypes of each species. The reported phenological legume traits that affect intercropping, growth habit and growth duration, were reported more often than the morphological traits (long/short straw and climbing/bushy beans). However, no trend can be extracted from the provided information. In case of the cereals, only the phenological traits growth duration and the morphological trait plant height were reported. Three studies reported a better intercropping performance for early maturing cereals (maize, barley, sorghum) whereas three others for late maturing cereals (sorghum, oat maize). In case of plant height, five out of six studies reported improved intercropping performance for shorter cereal genotypes. Thus, besides a tendency for higher intercropping performance in case of short cereal genotypes, no conclusion can be drawn.

Table 2.6: Mechanisms of genotypes (G) complementarity in cereal/legume intercropping as mentioned in the consulted literature. The empty cells are in the case no traits were mentioned. The first and second number in the second column ("No. of G") refers to the number of genotypes on the first and of the second species mentioned in the first column ("Cereal/legume").

Cereal/legume	N. of G	Phenological and morphological traits that improve intercropping performance		Reference
		Cereals	Legumes	
Barley/pea	1x2		long straw > short straw pea	Pappa et al., 2012
Barley/pea	5x6		determinate > indeterminate pea	Hauggaard-Nielsen and Jensen. 2001
Barley/berseem clover	4x3	early > late mature barley shorter > tall stature barley		Ross et al. 2004
Sorghum/groundnut	3x3	late > early maturing sorghum when intercropped with early maturing groundnut	late > early maturing groundnut when intercropped with early maturing sorghum	Tefera and Tana, 2002
Sorghum/cowpea	2X1	short > tall stature sorghum		Odo, 1991
Sorghum/cowpea	4x4	early > late mature sorghum		Rao and Willey, 1983
Rice/pigeon pea	2x2		determinate > indeterminate pigeon pea	Ramakrishna and Ong, 1994
Millet/cowpea	2x2		early > late mature cowpea	Ntare, 1990
Millet/cowpea	2x8		early > early mature cowpea when intercropped with late mature millet	Ntare, 1989
Oat/faba bean	1x2		indeterminate > determinate faba bean	Klimek-Kopyra et al., 2015
Oat/common vetch	3x3		medium > late mature common vetch	R. Li et al., 202)
Oat/ common vetch	4x1	late > early mature oat and short > tall oat		Baxevanos et al., 2021
Wheat/faba bean	2x1	tall > short straw of the oat		Haymes and Lee, 1999
Maize/cowpea	1x10		early > late mature cowpea	Egbe et al., 2010
Maize/bean	2x7	late > early mature of maize		Gebeyehu et al., 2006
Maize/bean	2x10	short > tall maize		Davis and Garcia, 1983
Maize/common bean	1x2		climbing > bushy bean	Clark and Francis, 1985
Maize/cowpea	3x2	early > late mature maize		Ewansiha et al., 2014
Maize/bean	2x1	short >tall maize		Munz et al., 2014
Maize/faba bean	1x3		late > early mature faba bean	Fischer et al., 2020

2.4 Discussion

2.4.1 Evaluation of the performance of different cereal/legume species and genotypes

The systematic assessment of LER from 35 independent studies showed the mean and median values of 1.26 and 1.24 (Fig. 2.2A). This result is not far from the previously published meta-analysis result median values of 1.17 (Yu et al., 2015) and 1.16 (Yu et al., 2016) and 1.3 (Martin-Guay et al., 2018). These studies focus on yield performance of crop species mixtures regardless of genotype. The median LER of 1.24 across 16 maize-based studies in our study is in line with a meta-analysis from 43 studies of maize/soybean of intercropping that reported an LER of 1.32 (Xu et al., 2020). Although the mean and median varied among different cereals, median LER was above one in all cereals.

The species and design effects were highly significant ($p< 0.01$) (Fig. 2.4A), with a significant interaction ($p< 0.05$), mainly due to the higher LER of finger millet (1.66) compared to other species in additive designs. However, in replacement designs, no differences were observed among species. The overall LER was higher in additive designs compared to replacement designs.(Cousens, 1996) In an additive design, the planting density of both species in mixture may be equivalent or somewhat reduced compared to their sole stand resulting in planting densities leading to density equivalent ratios > 1 and up to 2. For example, pea-oat mixtures may be composed of 100% peas and 20% oats compared to the pure stand densities (Gronle et al., 2015) or wheat-winter pea mixtures of 70% wheat with 50% pea Timaeus et al.,2022 (this volume). In replacement designs, the density of one sole crop species is proportionally (based on sole crop densities) replaced by the other species resulting in a density equivalent ratio of 1. For example, they may be composed of 50% barley and 50% pea compared to pure stand densities (Pappa et al., 2012). Although, the planting proportion has an effect on LER the range of effects depends on the species in the mixture because tillering in the case of cereals can compensate variable sowing densities (e.g. (Finckh et al., 1999; Finckh and Mundt, 1992).

Compared to other cereal crops, millet intercropped with short legumes such as cowpea, and pigeon pea. Intercropping the tall millet and sorghum cereals with shorter legumes permits better radiation use efficiency (Marshall and Willey, 1983; Matthews et al., 1991). Due to less resource competition by spatial segregation, yield in mixture and mono-cropping is comparable for both species which increased LER in additive compared to replacement designs. Nevertheless, a meta-analysis by Raseduzzaman and Jensen, (2017) reported that in intercropping, replacement designs lead to higher yield stability compared to additive designs. The analysis of variance across legume species (excluding faba bean, grass pea, guar and hairy vetch, berseem clover and bitter vetch with n<4 data points) resulted in significant differences. However, the effects of design and interaction were not significant (P>0.05) (see Table A. S5**)** with greater LER for pigeon pea and soybean compared to other legume species (see Table S6**).** These two legume species are frequently intercropped with C4 cereals such us maize, millet and sorghum which may increase the LER due to temporal niche differentiation (Yu et al., 2015; Xu et al., 2020).

The interaction between different cereal and legume genotypes and different cropping systems was significant in 75% of the studies that reported interaction effects of genotype × cropping system. This implies that in many studies, genotypes behave differently in sole vs. intercropping, often resulting in changes in performance ranking of varieties between the sole crop and mixture (Baxevanos et al., 2017; Woolley and Rodriguez, 1987). The analyses of variation of different genotypes of cereal/legume intercrops within each selected study (Fig. 2.5) revealed that the choice of the specific genotype combination could result in positive or negative yield effects compared to the median of all genotype combinations within each study. The largest LER range was found in a study with 20 different genotypes (Santalla et al., 2001b). This indicates the potential for high LER in case of appropriate genotype choice and highlights the potential for genotype or trait combination to optimize intercropping systems. However, this finding also emphasizes the need to develop a more general understanding of the mechanisms underlying these differences.

2.4.2. Concept of cereal/legume intercropping niche complementarity

Out of 20 studies assessing the mechanisms underlying the intercropping performance 10 studies reported that intercropping performance was improved by cereal genotype while 10 studies reported the improvement was by legumes genotype. In some studies, however, a relatively high number of genotypes did not affect the intercropping performance. For instance in the study of Hauggaard-Nielsen and Jensen (2001), none of the five barley genotypes affected LER while pea genotype affected intercropping performance in terms of LER (Table 2.6).

In an intercropping system with annual species, the niche differentiation is a general mechanism underlying the yield advantage and better resource use efficiencies (Lithourgidis et al., 2011). Niche differentiation improves the use of resources according to species complementarity for light interception and the use of both soil mineral nitrogen and atmospheric nitrogen (Bedoussac et al., 2015). The selection of cereal and legume genotypes for better complementarity is important because the traits required for intercropping are those which enhance the complementary effects between the partners (Davis and

Woolley, 1993). Niche differentiation among plant species occurs for the various environmental resources such as light, water, and nutrient availability. It is driven by plant phenology and morphology that allows for partitioning of resources over time and space that facilitates coexistence (Silvertown, 2004). The trait differences in genotypes of cereals and legumes result in differences in phenology and morphology of the plants. Therefore, in cereal/legume mixtures both species could have similar phenology but contrasting morphology or contrasting phenology and morphology, resulting in temporal and/or spatial niche complementarity (Gaudio et al., 2019). The contrasting characteristics of the genotypes play an important role in the complementarity of the species in intercropping (Gebeyehu et al., 2006; Hauggaard-Nielsen and Jensen, 2001).

The ecological niche separation concept describes the fact that different species involved may have different resource requirements at different times, as well as different sources of nutrition, e.g. root exploitation of top subsoil layers by one component versus deeper exploitation by the other component, different growth patterns, or different affinities for the same nutrient (Malézieux et al., 2009). The temporal and spatial segregation of species in intercropping is useful in two ways: better resource capture, hence utilization of more resources, and enhanced resource use efficiency in a given unit of resource (Willey, 1990). The maturity rate and the growth habit of cereal and legumes define either the domination or suppression of one of the species in the mixture (Baxevanos et al., 2021). However, besides niche-separation additional mechanisms such as mutual beneficial interactions via the soil microbiome including biological nitrogen fixation have to be considered (Hauggaard-Nielsen et al., 2009). Thus, in cereal legume mixtures the contribution of biological nitrogen fixation through the leguminous partner is affected by the mineral N-supply level with strong effects on the competitive interactions and overall biological nitrogen fixation by the legume (Li et al., 2021; Wang et al., 2015).

Temporal niche complementarity of cereal/legume intercropping

A trend for enhanced intercrop performance due to a specific trait related to phenology or temporal combination cannot be identified from the evaluated studies. Days required for maturity is one of the important factors for complementarity of species in intercropping. In this review, out of 20 studies reported that phenological and morphological traits affected intercropping performance with 12 studies indicated that the difference of days of maturity of different genotypes of cereals and/and or legumes had an effect on the intercropping performance. However, it also varies in some cases, with a late maturing genotype of either of the species meeting better the aim of cultivation compared to an early maturing genotype. In contrast, early genotypes could also be better compared to late maturing genotypes of one of the species (Table 2.6**)**. In the study of Ntare (1989), intercropping an early maturing cowpea genotype with a relatively late maturing millet genotype performed better by reducing the co-growth period to escape moisture scarcity and minimizing all components not affected equally in drought prone areas. Another example of temporal complementarity is the combination of determinate field peas with a cereal where peas started maturing and releasing nitrogen from the roots around the time when the cereal flowers and requires increased N to fill its grains (Timaeus et al., 2021b; Jensen et al., 2020). The rate of development and time between sowing and harvesting of the components in intercropping provide the opportunity of temporally complementary use of incident radiation, thereby improving intercropping performance (Keating and Carberry, 1993). Tefera and Tana (2002) reported that the temporal niche complementarity of different genotypes in sorghum/groundnut intercropping influences the general performance of intercropping: partners that have a lower co-growth period produced higher yields compared to genotypes that have equal or higher co-growth period. Similar temporal niche complementarity was reported for millet/cowpea (Ntare 1990), maize/cowpea systems (Egbe et al., 2010) and bean/maize systems (Gebeyehu et al., 2006). Depending on the aim of cultivation, the selection of cereal and legume genotypes with contrasting maturity periods will increase the intercropping yield advantage (Ross et al., 2004).

Spatial niche complementarity of cereal/legume genotypes

Spatial niche complementarity can be exploited by the spatial arrangement of one component to maintain its full population while allowing more space (and thus more resources) for another component (Willey, 1990). The spatial arrangement for better resource use efficiency could be classified as above-ground (canopy structure of both components) and below ground (root system) (Gaudio et al., 2019). Canopy structure has considerable implications for intercropping systems. The erect open canopy of one component allows more transmission of radiation to shorter crops and enables more radiation use efficiency (Willey, 1990). The use of abiotic resources is improved according to species complementarity for light interception and the use of both soil mineral and atmospheric nitrogen.

In this review, 11 studies reported morphological differences of the genotype of either cereal or legumes to be involved in intercropping complementarity (Table 2.6). In most of these papers (7) plant height was observed. Whether the taller or the shorter genotype performed better varied. However, a tendency towards higher intercropping performance was observed with short cereal genotypes. Plant height and branching of long cycle pea genotypes varied between the sole and mixed cropping systems. This reveals the importance of the pea genotype choice in terms of morphology for intercropping systems (Barillot et al., 2014). The study by Hauggaard-Nielsen and Jensen (2001) revealed that pea genotypes with determinate growth absorbed more radiation under the barley canopy, which enhanced the intercropping performance compared to intercropping systems with indeterminate pea genotypes.

The growth habit of different genotypes of one species significantly affects the performance of other species, and thereby of intercropping performance mainly by affecting radiation interception. Ramakrishna and Ong (1994) reported that the indeterminate pigeon pea genotype with indeterminate growth habit reduces the yield of rice by half due to the competitive advantage for radiation. In the barley/pea intercropping system, spatial complementarity due to pea genotypes has resulted in better nitrogen use efficiency of barley. An indeterminate pea genotype resulted in a greater proportion of peas in the intercrop yield due to high competitiveness, whereas a determinate pea genotype with normal leaves caused the highest degree of complimentary use of nitrogen sources by allowing barley to exploit the soil N sources efficiently, while they contribute with fixed nitrogen. However, indeterminate pea genotypes caused a reduced nitrogen uptake and yield of barley (Hauggaard-Nielsen and Jensen, 2001; Pappa et al., 2012). Based on the analyzed studies, we cannot draw a conclusion. In two articles, the intercropping performance was higher in case the growth of the legume partner was determinate, whereas in one study, it was higher for the indeterminate genotype.

2.4.3 Gaps of genotype and trait evaluation in cereal/legume intercropping

Even though ample research reported on cereal legume intercropping, the number of publications that evaluated cereal/legume genotypes for complementarity in intercropping systems was very limited. Among the studies analyzed (69), only 20 (29%) articles indicate the contrasting traits of genotypes that contribute to intercropping performance. From those, the general mechanisms underlying the genotype cropping system were broadly classified as phenological and morphological heterogeneity of cereal and/or legume genotypes. However, in most of the studies, the contrasting characteristics of genotypes of either cereal and legumes and/or both of the species were not described well. The phenology of the crops has an impact on resource use over time (Gaudio et al., 2019). Consequently, cultivating genotypes with different phenological characteristics results in different temporal niche complementarity. The latter can increase the land use efficiencies, especially if nitrogen is released after grain filling of the legumes benefiting the cereals. Nevertheless, in most of the studies, sufficient information on phenology was not provided and none of the studies reported the differences in the phenological stages of the genotypes.

Root growth and thus water and nutrient uptake are some of the most important factors in temporal and spatial heterogeneity (Hauggaard-Nielsen and Jen Yin et al., 2020). Root system distribution in time and space can partly explain competition. For instance, barley roots grow faster than pea roots (Hauggaard-Nielsen et al., 2001) and start nutrient acquisition earlier. Different genotypes of either the cereals or the legumes could have different root characteristics which influence the competitive ability of the species. Streit et al. (2019) reported that mixtures of winter faba bean and winter wheat over yielded more below- than above-ground. The authors concluded that genotype differences in root biomass and over yielding indicate the breeding potential of winter faba bean cultivars for mixed cropping. Legumes provide nitrogen to the agroecosystem through their exclusive capability to fix atmospheric nitrogen in a symbiotic relationship with soil rhizobia, but different genotypes of a legume species might have different capabilities in nodulation (Rodiño et al., 2011). Only a very limited number of studies considered the nutrient acquisition of different genotypes of cereals and legumes in intercropping. Different species have temporal niche differentiation in nutrient acquisition (Zhang et al., 2017). The symbiotic association of different legume genotypes and their rhizobia could also differ. The spatial complementarity of the genotypes in nutrient acquisition is therefore important to increase performances of intercropping. Hence, future research needs to address how different genotypes respond to nutrient competition, with a particular focus on below-ground traits.

Pest and disease resistance is one of the most important advantages of intercropping (Finckh et.al., 2021). However, there are only a limited number of studies which have considered genotype differences concerning pest and disease resistance in cereal/legume intercropping. Recent work has highlighted the importance of plant-plant interactions, either direct by mechanical, physical or chemical cues, or mediated through soil/air microbiota, and the way they can affect plant immune system or other functions (Subrahmaniam et al. 2018; Rahman et al., 2019; Pélissier et al., 2021; Zhu and Morel, 2019). Life cycle assessment (LCA) is a convenient, effective, and rarely used (but see (Naudin et al., 2014) approach for analyzing the environmental impact of cereal/legume intercropping, especially on nitrogen cycle.

There are only a few studies considering the socio-economic importance of genotypes of both cereals and legumes species. Goshime et al. (2020) involved the farmers in the evaluation of genotypes. Different quality parameters of the genotypes not included in most of the papers hence could affect the acceptance of intercropping by farmers. The forage quality differences of legume genotypes were mostly ignored and the number of studies on this topic is very limited. The consumer and market preference of different genotypes of cereals and or legumes is also important in the selection of genotypes for intercropping.

Therefore, in addition to morphological and phenological traits, other traits (roots, water and nutrient acquisition, quality) and advantages in pest and weed suppression deserve attention to understand the mixing ability of different genotypes. Future research should consider pedigree analysis, functional genes or key traits when selecting varieties tested in intercropping.

2.5 Summary and conclusions

We evaluated the observations of studies that included at least two genotypes of one species in cereal/legume intercropping. While the number of studies is inadequate for obtaining a comprehensive and reliable insight, our results point to the potential of genotype selection in intercropping, and future research should therefore emphasize genotype × cropping system interaction in cereal/legume intercropping. In total, the majority of the studies reported that there was a significant genotype-cropping system interaction revealing the importance of genotype selection for intercropping for more land productivity. Among the 69 analyzed studies, only 35 studies reported LER values. We determined a median LER of 1.24 which indicated that a combination of specific genotypes cereals and legumes improves the land productivity by 24% on average. In addition, 85% of the LER data points of cereal/legume intercropping were greater than 1. On the other hand, 15% of the specific cereal/legume genotype combinations resulted in LER<1 revealing that judicious choice of genotype combination in cereal/legume is indispensable.

Furthermore, the analysis of variance across cereal species and design indicated that different species have different land use efficiency in the different design types with finger millet having higher land use efficiency than other crops in additive designs while no difference was observed between the species in replacement designs. The number of studies which report LER from different wheat genotypes was very limited (but see Timaeus et al, 2022, this volume); because of the high importance of wheat for global food security, we suggest that more research is needed to investigate the performance of different wheat genotypes in intercropping. Conversely the effect of design on land use efficiency in legumes is not significant while species effect is significant. Temporal and spatial heterogeneity between the genotypes of the cereals and those of the legumes was mentioned in the selected studies as the main mechanism enhancing overall performance of cereal-legume intercropping. However, the spatio-temporal heterogeneity of genotypes was not described sufficiently in most of the studies to allow a detailed analysis. Hence, future research studies should consider and report the genotypes' traits more comprehensively, including root growth, soil nutrient and water acquisition, and diseases, among others. In most studies, only some agronomic traits of genotypes were emphasized ignoring other genotypic functional traits. Further, we recommend that future research needs to evaluate a higher number of genotypes and their traits on various sites and under different climate and management conditions. It is impossible to test all possible combinations (genotype x genotype x environment x management) of intercropping in field trials. The complex interactions in intercropping can be disentangled by process-based agro-ecological models which can help to identify the relevant influencing factors of intercrop performance. However, the prerequisite is an understanding of the basic mechanisms.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

All authors listed have made a substantial, direct and intellectual contribution to the work and approved it for publication.

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Chapter 3

3 Evaluating a new intercrop model for capturing mixture effects with an extensive intercrop dataset

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Abstract

Cereal-legume intercrops have numerous advantages over monocultures. However, the intercrop's performance depends on the plant genotypes, management, and environment. Process-based agro-ecosystem models are important tools to evaluate the performance of intercrop systems as field experiments are limited in the number of treatments. The objective of this study was to calibrate and evaluate a new process-based intercrop model using an extensive experimental dataset and to test whether the model is suitable for comparing intercrop management strategies. The data set includes all combinations of 12 different spring wheat entries (SW, Triticum aestivum L.) with two faba bean (FB, Vicia faba L.) cultivars, at two sowing densities, in three different environments. The results show that the intercrop model was capable of simulating the absolute mixture (intercrop) effects (AME) for grain yield, above-ground biomass, and topsoil root biomass, for both crops. However, the intercrop model does not perform better than a benchmark that ignores the intercrop effects when simulating plant height, fraction of intercepted radiation, volumetric soil water content, and subsoil root biomass. The intercrop model predicted reasonably well the differences between species and between SW cultivars for grain yield and aboveground plant biomass. Overall, the tested process-based model can be a useful tool for designing and pre-evaluation multiple combinations of crop management, species, and cultivars suitable for intercropping in diverse conditions.

Keywords: Cropping system, Cultivar choice, Diversification, Crop modeling, Crop mixtures

3.1 Introduction

Intercropping is a cropping system where more than one species or cultivar is grown at the same time on the same field. Also referred to as 'crop mixtures', intercropping provides multiple advantages over monocultures, including on average higher yield on a given piece of land (Lithourgidis et al., 2011; Li et al., 2023), reduced production risk (Vandermeer, 1989), improved weed suppression (Lithourgidis et al., 2011), increased (sub) soil nitrogen (N) availability (Seidel et al., 2019), decreased nitrate leaching (Tribouillois et al., 2016), improved soil organic matter content, carbon sequestration (Lithourgidis et al., 2011; Shili-Touzi et al., 2010), and increased biodiversity (Kremen and Miles, 2012; Brandmeier et al., 2023). One of the prevalent intercrop systems is mixing cereals (such as wheat, barley, and maize) with grain legumes (such as bean, pea, and faba bean), which are often mixed within the row (Fischer et al., 2020; Malagoli et al., 2020). Research has shown that in comparison to their respective monoculture systems, wheat-faba bean intercrop significantly increases productivity and reduces nitrate leaching and runoff (Xu et al., 2019).

The numerous processes and mechanisms involved in intercrops highlight the need to deal with their complexity by combining concepts from diverse disciplines such as agronomy, physiology, and ecology. Additionally, there is a lack of information regarding intercropping management such as crop species; genotypes selection and combination (Demie et al., 2022), spatial arrangement, and sowing proportion (Chimonyo et al., 2016). Several studies have shown that intercrop performance depends on the genotype combination (Annicchiarico et al., 2019; Demie et al., 2022). However, evaluating a high number of genotypes and their traits under different environments and management under field conditions is costly and laborious. To address these challenges, process-based crop simulation models are widely recognized tools to examine cause-and-effect relationships in crop production. Virtual experiments using crop models can contribute to process understanding and cropping system design (Malézieux et al., 2009). They can be used to study the influence of climate variability, soil, or management options (Seidel et al., 2019; Asseng et al., 2019; Chenu et al., 2017), and for real-time simulation-based crop management (Seidel et al., 2016). Currently, a handful of models simulate mixed cropping systems for yield and water use (Chimonyo et al., 2016; Miao et al., 2016; Pinto et al., 2019), light distribution (Munz et al., 2014; Tsubo et al., 2005), nitrogen transport and uptake (Shili-Touzi et al., 2010; Whitmore and Schröder, 2007), and weed suppression (Baumann et al., 2002). One approach to simulate intercrops is the light sharing in strip intercrop systems. Pierre et al. (2023) developed an approach to allow the model Decision Support System for Agro technology Transfer (DSSAT) to run two crop species in intercropping. Berghuijs et al. (2021) calibrated and tested The Agricultural Production Systems sIMulator (APSIM) for wheat-faba bean intercrops, and

Vezy et al. (2023) proposed a set of generic formalisms for the simulation of intercrops, with an implementation in Simulateur mulTIdiscplinaire pour les Cultures Standard (STICS).

Nevertheless, the previously published studies on intercrop models have been limited by relatively small data sets, predominantly assessing aboveground plant growth and performance to evaluate the model. These studies often ignored different management strategies such as species and cultivar choice, or sowing densities. Therefore, the objectives of this study were 1) to evaluate a new intercrop model, based on the LINTUL5 model (Wolf, 2012) and (2) to assess the suitability of the model to compare intercrop management strategies concerning the interaction between the intercrop effect and the environment. The intercrop model is implemented within the modeling framework SIMPLACE (Scientific Impact Assessment and Modeling Platform for Advanced Crop and Ecosystem Management) by combining existing biomass, soil water, and nutrients components for monocultures with intercropping components for radiation and below-ground competition and distribution. The model framework has been developed during the last decade and allows the integration of climate change impact assessments, model uncertainty, and crop management (Enders et al., 2023).

An innovation in this study, compared to previous studies, is that the evaluation is based on a comparatively extensive experimental dataset. The experimental data are from spring wheat/faba bean (SW/FB) intercrops, for three environments, each with twelve SW entries two FB cultivars, and two sowing densities (Paul et al., 2023). Measured variables are plant height, radiation interception, plant above-ground biomass, root biomass, soil moisture, and grain yield. The same measurements were also carried out on the monocultures in all cases. This data set allows us to evaluate the intercropping model more thoroughly in terms of above and below-ground dynamics, including roots, which is a major aspect of the interaction in the intercropping systems. A second innovation is the way the evaluation is performed. Evaluation concerns specifically the difference between the intercrop and the average of the monocultures. This is more pertinent than evaluating the error in simulating directly the results of the intercrop since it is specifically the effect of intercropping compared to the monoculture that is of major interest. Note also that no intercrop data are used here for calibration of the model. Thus, the evaluation is a measure of how well the model, integrating various mechanisms of interaction between the partner crops, simulates the intercrop effect, given information about the performance of the monocultures. We also introduce a new model skill measure (Wallach et al., 2019), which compares the error of the intercrop model with a benchmark. The benchmark is the error if one assumes that there is no intercrop effect so that the results of the intercrop are exactly equal to the average of the monocultures. The intercrop model has positive skill if the error is smaller than that of the benchmark.

3.2 Material and methods

3.2.1 Field experiments

Experimental site

The field experiments were conducted at two research facilities in one and two years, respectively. Experiments were conducted in 2020 and 2021 at the research facility Campus Klein-Altendorf (CKA) of the University of Bonn located in Rheinbach near Bonn, Germany (50° 37' N, 6° 59' E) at an altitude of 186 m a.s.l. The soil at the experimental station is classified as Haplic Luvisol (hypereutric, siltic) from loess (IUSS Working Group WRB, 2006) and characterized by a silty-loamy texture with clay accumulation in the subsoil between about 45 and 95 cm soil depth (Barej et al., 2014). The mean annual air temperature and precipitation (2008–2021) were 10.5 °C and 652 mm, respectively. In 2020, an experiment was also conducted at the organically managed research facility Wiesengut (WG) of the University of Bonn, which is located at 50° 47' N, 7°15' E at an altitude of 65 m a.s.l. The WG soil is characterized as a silt loam texture with Haplic Fluvisol (IUSS Working Group WRB, 2006) soil type. The average yearly temperature and annual rainfall at WG were 10.7°C and 733 mm (1991-2020), respectively. The mean monthly temperature and precipitation of the growth period are given in Fig. B. S1: (A) CKA2020, (B) CKA2021, and (C) WG2020. A detailed description of these experiments is available in Paul et al. (2024, 2023).

Experimental setup and cultivars

The field experiments were performed as a randomized complete block design with four replicates except in CKA 2021 where a sowing error occurred, leading to less than four replications in most of the treatments. Some treatments were replicated three times, some two times, and some treatments were not replicated. Despite this, we proceeded to analyze the data from the treatments that adhered to the originally intended sowing ratio of spring wheat (SW) to faba bean (FB) (50:50) and respective monocultures. In CKA2021, the considered treatments included all monocultures crops and 50:50 intercrops of the twelve SW entries (ten cultivars and two mixtures of these SW cultivars), and two FB cultivars similar to the treatments in WG2020 and CKA2020 (Table B. S1). The plot size was 1.5 × 10 m with a 21 cm row distance, respectively (Table B. S2). The SW cultivars were selected based on their similarity regarding grain quality and maturity time, but divergence in terms of plant height, i.e. including shorter, medium, and taller genotypes. All combinations were each sown using two sowing densities, 80 % (low density, LD) and 120 % (high density, HD) of the crop density typically used by farmers in the region for monocultures (100 %, 400 seeds m^{-2} for SW and 45 seeds m^{-2} for FB). At both densities, SW and FB were mixed in a 1:1 ratio, i.e. in substitutive mixtures, which means 5 0% of seeds of each species from the respective monocultures crops (high/low density) were mixed to obtain the respective density (high/low) in the intercrop (Paul et al., 2023). No fertilizer, pesticide, or irrigation was applied during the growth period. FB was sown at 6 cm soil depth by a seeding machine type Hege 95 B. Subsequently, SW was sown directly over FB with a Hege 80 seeder at 3 cm soil depth. Mechanical weeding was performed twice, about three and five weeks after sowing. For more details see Paul et al., (2023). However, due to the research site WG being organically managed, there was a higher weed infestation.

Measurements

Crop phenology and above-ground biomass growth

Crop development was observed based on the BBCH-scale (Biologische Bundesanstalt, Bundessortenamt and CHemical industry), Meier, (2001) which is a common system to monitor crop phenological development of mono- and dicotyledonous plant species. Agronomic data including plant above-ground biomass at three different plant growth stages, plant height at two distinct growth stages, root biomass, and grain yield, were collected. Results on grain yield (Paul et al., 2024) and partially on biomass have been already published (Paul et al., 2023). Table 1 shows a summary of the plant and soil-related data and measurement frequency for the data used in the current study. Treatments composed of two SW cultivars with both FB cultivars were selected as key treatments where the data collection was intensified.

Table 3.1. Measured plant and soil variables used in the current study. Group 1 comprises the key treatments, namely the monocultures of two SW cultivars Lennox and SU Ahab, two FB monocultures, and intercrops of both wheat cultivars with the Mallory FB cultivar. Group 2 comprises the remaining 10 SW cultivars grown as monocultures and intercropping with two FB cultivars. Data was collected during field experiments (CKA, 2020 and 2021 ad (WG, 2020).

Measured variables	Group1[1] measurement frequency	Growth stage	Group2 measurement frequency	Growth stage	Measurements from
developmental stage	3	emergence, flowering, and maturity	3	emergence, flowering, and maturity	each species
grain yield	1	maturity	1	maturity	each species
above-ground biomass	3	vegetative, flowering, and maturity	1	flowering	each species
plant height	2	flowering and maturity	1	flowering	each species
leaf area index	2	vegetative and flowering	0	-	each species
root biomass	2	vegetative and flowering	0	-	each species
volumetric soil water content	3-4	vegetative and flowering, maturity	0	-	monocultures and intercrops
PAR	2-3		0	-	monocultures and intercrops

[1] key treatment. Volumetric soil water content and intercepted photosynthetically active radiation (PAR) were measured three times in 2021. Leaf area index and root biomass were measured only in 2021.

Photosynthetically active radiation (PAR) interception and leaf area index

The PAR was measured two times in 2020 and three times in 2021 with an SS1 Sunscan canopy analysis system (Delta 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. The LAI (leaf area index) was determined destructively by cutting plants 1 m long sections from the 3rd and 4th rows of the plots, scanned using the LI-3100C Area Meter (Li-Cor, Biosciences GmbH, Bad Homburg, Germany), and calculated for one square meter.

Soil water content

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 (30cm, 45cm, 60cm, and 90cm). The soil moisture content was measured four times on different days after sowing (DAS) during the growth period in 2020 (CKA2020: DAS ~55, ~ 73, ~ 97, ~ 114) and (WG2020: DAS ~ 57, ~ 77, ~ 104, ~ 119) and three times in 2021 (CKA2021: DAS ~ 67, ~98 and ~ 129).

Root biomass

Root samples were taken with a soil auger with an inner diameter of 9 cm down to 100 cm (divided every 10cm) soil depth in the selected plots planted with two spring wheat cultivars, Anabel and SU Ahab, and one faba bean cultivar, Fanfare, on June 9^{th} and on July 5^{th}/6^{th} 2021 at CKA. The root sampling in intercrops covered always one FB and one SW plant For a detailed description see Hadir et al. (2024). Soil cores were washed, sorted, oven-dried at 40 $^{\circ}$C for 48 h, and weighed. An FTIR spectroscopy (Kemper et al., 2023) was used to quantify the root mass proportion per species and layer.

3.2.2 Model description

All crop models are simplifications of the complex dynamics of crop growth, and necessarily make a large number of assumptions. However, process-based dynamic models are still the best quantitative source of our knowledge of plant growth (Stöckle and Kemanian, 2020). Model complexity depends on the type of research question, data available, and efficiency in terms of demand for parametrization. This is particularly difficult for intercropping since multiple and complex interactions are known to occur between the intercrop components with their environment, but are difficult to quantify in the field. Our model makes several simplifying assumptions that help to make it more manageable. In particular, we assume that (a) there are no interactions with pests and diseases; (b) facilitation such as in-season N transfer from the legume crop to the cereals (as studied by Jensen, (1996) was not considered, and (c) the radiation interception model we used was developed for strip intercropping system (Gou et al., 2017b). However, the intercrop model considers various processes on a daily time step such as crop growth, soil water and N dynamics and water and N uptake by the roots, atmospheric N fixation of legumes, temporal and spatial niche competition for radiation, soil water and soil N, and grain yield production. The major processes will be explained in the following.

The simulations were conducted in the modeling platform SIMPLACE (Scientific Impact Assessment and Modelling Platform for Advanced Crop Ecosystem Management, Enders et al., 2023). The framework comprises a series of SimComponents, which are a set of functions that represent important crop and soil-related processes.

Selected SimComponents for the current study were LINTULPhenology, LINTUL5NPKDemand, SlimNitrogen, LINTUL5Biomass, SlimRoots, and SlimWater. An overview of key SimComponents is given by (Wolf, 2012) and Seidel et al. (2019).

The LINTULPhenology component calculates the crop developmental stages (DVS) based on the ratio between accumulated degree days and species-specific temperature sum requirement. Temperature sum starts to be accumulated at emergence, the crop reaches flowering at DVS 1, and physiological maturity at DVS 2. The DVS for each species in the intercrop is modeled separately. However, each species in the intercrop was simulated with the same crop parameters as the monocultures without re-parameterization. The radiation use efficiency (RUE) approach was implemented in the RadiationInterception SimComponent based on the approach of Monteith and Moss, (1977), with a linear relationship between the accumulated crop biomass and intercepted radiation (IPAR). To calculate potential biomass, a linear regression between accumulated biomass and radiation interception is used. The LINTUL 5 default canopy extinction coefficient (k) value was used to calculate daily radiation interception.

The SimComponent LINTUL5NPKDemand calculates the daily uptake rates of NPK (nitrogen, phosphorous, and potassium) depending on plant-available NPK in the rooted soil layers, root properties, and crop NPK demand (Wolf, 2012). In the case of FB, it is assumed that 80 % of the daily demand for nitrogen is fulfilled through biological fixation, while the remaining 20 % is sourced from soil N (Klippenstein et al., 2022). Faba bean in both monocultures and intercrops was simulated with the same assumption of biological nitrogen fixation (g m $^{-2}$) and soil nitrogen source.

The SimComponent LINTUL5Biomass calculates the biomass part from LINTUL5 taking the NPK stress factor NPKI into account. The daily increase in biomass may be reduced by reduction factors for transpiration (TRANRF, in case of drought stress) and nitrogen nutrition index (NNI), in case of N limitation. TRANRF is based on the ratio between actual and potential crop transpiration which are both calculated by the SimComponent SlimWater. The factors NNI and TRANRF range from 0 (full N or drought stress, no biomass increase) to 1 (no N or drought limitation).

The component SlimNitrogen calculates the plant N uptake, N turnover, and leaching of soil mineral N in layered soil (Addiscott and Whitmore, 1991). For each layer, the calculation considers the application of nitrate or ammonium fertilizer (if there is an application), leaching of nitrate and ammonium, supply from organic matter mineralization, nitrification, and crop N uptake to calculate the daily changes. The

SlimWater SimComponent simulates soil water dynamics using a tipping bucket approach (Addiscott et al., 1986; Addiscott and Whitmore, 1991). Soil water movement is simulated by layer by considering plant water uptake, soil evaporation, surface runoff, and percolation.

The SlimRoot SimComponent (Addiscott and Whitmore, 1991) calculates the daily increase of seminal and lateral root biomass in different soil layers and converts it to root length per layer. Maximum rooting depth and maximum growth per day are crop-specific. At sowing, the initial biomass is provided via the seed parameters and used for the daily growth of the seminal roots which determine the vertical root penetration. Lateral roots are produced if the assimilates provided by the shoot are more than the assimilates needed by the seminal root. Root decay starts to occur at a user-defined DVS, in this case, at DVS1.

Intercrop model description

The new intercrop model implemented in SIMPLACE[1] was assembled by using all crop-related SimComponents twice (one for each crop) and by using soil-related SimComponents once (one common soil) adding components to split radiation and water/nutrient uptake. The crop water demand per species was aggregated, potential transpiration of both crops was summed up and weighted by their area fraction to get field-scale data, and handed over to the root water uptake routine. The uptaken water was then disaggregated. For example, the actual transpiration was split up to calculate it per crop by using the below-ground allocation SimComponent (see below) while considering water uptake per layer and root length densities of both crops. The details of the equation were documented in (Krauss, 2018).

Radiation interception in intercrop model

The radiation interception for intercrops is based on the proportion of each species and further species-specific plant characteristics. The radiation interception model is based on Gou et al. (2017b) in which two intercropped species share the incoming radiation based on their actual plant height, actual LAI, predefined proportion of each species in intercropping and a canopy extinction coefficient. The radiation interception model in intercropping was originally developed to simulate radiation interception in a strip intercropping system. Here we tested the model for in-row mixing of two species. The daily plant height increment was simulated by using the temperature-based approach of Gou et al. (2017b), but a stress effect was used in case of drought and/or nitrogen limitation. The equation is given as follows:

$$H_{d+1} = Fstress_{\,d} * r * (T_d - T_b) * H_d * \left(1 - \frac{H_d}{H_{max}}\right) + H_d \qquad (1)$$

Where H_{d+1} is plant height increment, r is a relative plant growth rate, d is day, T_d is the temperature (°C) at day d, T_b is the base temperature, H_d is the height at day d, Hmax is the maximal crop height, and $Fstress_d$ is a factor between 0 and 1 that reduces the daily potential growth due to drought (TRANRF) or N (NNI) stress at the day d. The model considers the minimum stress as a decision rule i.e. Fstress_d = min(TRANRF, NNI). The height growth stops when the temperature sum is higher than the maximum temperature sum. The relative plant growth rate is adapted from Berghuijs et al. (2020).

Root growth, water, and N uptake in the intercrop model

The below-ground factor calculates the below-ground resource allocation according to the proportion of each species in intercrop and crop-specific root parameters. The below-ground allocation factor considers the root length density (RLD), the Root Restriction Factor (RRF), which is calculated by the SlimRoot SimComponent considering RLD and root age, and the proportion of each species in intercropping. 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 potential transpiration for each crop is then scaled to the proportion of each species in intercropping, the demands of each crop in intercrops, and its root distribution. The below-ground allocation component calculates the water uptake and N as well as the root growth of each species from their root distribution and species-specific parameters. Further details can be found in Krauss, (2021). The RLD and RRF are scaled according to the proportion of each crop and the common RLD and RRF are the sum of the scaled RLDs and RRFs.

Model setup and inputs

The intercrop model was set up for the three environments. The required daily weather data minimum, mean, and maximum air temperature, wind speed, precipitation, and global solar radiation were available from the research facilities. Soil properties such as soil texture, bulk density, soil carbon, and hydraulic properties were collected as reported elsewhere (Seidel et. al. 2019). The crop proportion in intercropping (equiproportional substitutive mixture) and sowing dates were set according to the field experimental design and management (Table B. S2). The initial soil mineral nitrogen was set according to measurements conducted around sowing. The initial soil volumetric water content values were set to field capacity (Table B. S3). The maximum plant height (as observed in CKA2021, where it was assumed potential growth due to the good growth conditions) was set for each species and cultivar.

3.2.3 Model calibration

The model was calibrated with the data of the two SW cultivars Lennox and SU Ahab as we have the most measurements for them and for both FB cultivars (key treatments). The other SW cultivars were simulated with the same parameters calibrated for the selected two cultivars and kept the maximum measured plant height and initial biomasses respective for each cultivar. We compared the data from monocultures of all three experimental environments with the observation, minimized the deviation (calibration) and then applied the calibrated model to the intercrop data (validation). Firstly, the phenology parameters were calibrated to fit the observed emergence, anthesis, and maturity dates. For this, the temperature sum from sowing to emergence (parameter TSUMEM), temperature sum from emergence to anthesis (TSUM1), and temperature sum from anthesis to maturity (TSUM2) were adjusted for each species (Table B. S4). Following this, the parameter RUE and developmental stage at which leaf death starts (parameter DVSDLT) were estimated using the leaf area index and fIPAR. Furthermore, the proportion of dry matter translocated to leaf and stem was calibrated for FB comparing observed and simulated leaf area index and shoot biomass values. The daily root elongation rates per species (parameter MSRLD) were adjusted to simulate the maximum rooting depth measured on two dates at field experiment CKA2021. Estimated parameter values are shown in Supplementary (Table B. S4). Parameter estimation was done by trial and error, without optimization software, given that the number of parameters adjusted was few and field experiments were only three (Seidel et al., 2018). Since the aim of this study is to test how well the model can simulate the differences between monocultures and intercropping, the intercrop model was calibrated, using only the monocultures.

3.2.4 Model evaluation

Model evaluation in capturing the intercropping effect

The model evaluation in this study was focused on how well the intercrop model simulates the intercrop effects. The selected metric for this is the Absolute Mixture Effect (AME), defined as

$$AME_{total} = y_{intercrop} - 0.5(y_{SW,mono} + y_{FB,mono}) \qquad (2)$$

where $y_{intercrop}$ is the value of the variable in question (e.g. grain yield) for the intercrop and $y_{SW,\ mono}$ and $y_{FB,\ and\ mono}$ are the values for the SW and FB monocultures respectively. The factor 0.5 is appropriate here because all the intercrops are 50:50 intercrops (substitutive intercropping). If each species in the intercrop behaves simply like the monoculture (no intercrop effect) then $AME_{total} = 0$.

If there are separate measurements for each species in the intercrop (grain yield, biomass, root biomass, etc.), then one can evaluate an AME for SW and for FB separately:

$$AME_{SW} = y_{SW,intercrop} - 0.5(y_{SW,mono}) \quad (3)$$

$$AME_{FB} = y_{SW,intercrop} - 0.5(y_{FB,mono}) \quad (4)$$

Note that AME_{total} can be 0 while both AME_{SW} and AME_{FB} are not 0 if there is compensation of effects between the two species. For the case of plant height, equations 4 and 5 are replaced by

$$AME_{SW} = y_{SW,intercrop} - (y_{SW,mono}) \quad (5)$$

$$AME_{FB} = y_{SW,intercrop} - y_{FB,mono}) \quad (6)$$

For those variables where species-specific values were not available separately (i.e soil water content and fIPAR), the AME was calculated according to the following equations:

$$AME_{SWC} = SWC_{intercrop} - 0.5(SWC_{SW} + SWC_{FB}) \quad (7)$$

$$AME_{fiPAR} = fiPAR_{intercrop} - 0.5(fiPAR_{SW} + fiPAR_{FB}) \quad (8)$$

Where AME_{SWC} is AME of soil water content; $SWC_{intercrop}$ is soil water content in intercropping; SWC_{SW} is soil water content in SW monocultures and SWC_{FB} soil water content in FB monocultures. AME_{PAR} is AME of fIPAR; $fIPAR_{intercrop}$ is fIPAR in intercropping; PAR_{SW} is fIPAR in SW monocultures and PAR_{FB} is fIPAR in FB monocultures.

To improve the statistical robustness when evaluating a model, Yang et al (2014) suggested the use of more than one performance measure; therefore, to evaluate how well the intercrop model simulates AME, we used the metric of mean squared error (MSE, to calculate the model skill) and relative mean squared error (RMSE) defined as:

$$MSE = \left(\frac{1}{n}\right)\sum_{i=1}^{n}(AME_i^{obs} - AME_i^{sim})^2 and\ RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(AME_i^{obs} - AME_i^{sim}\right)^2} \quad (9)$$

where $AME_{i,}^{obs}$ (treatment mean of the replication) and AME_i^{sim} are the observed and simulated values of AME for situation i, respectively. The above equation can be applied to AME_{total} or AME_{SW} and AME_{FB}, for any of the measured variables.

The simplest assumption about AME is that AME is 0 (no intercrop effect). In the case of mixture effects, we assume that the process-based intercrop model agrees better with the measurements than that simple assumption (observed AME=0). Thus, the latter is used as a benchmark. We introduced the skill score (Wallach, 2019) in model evaluation, which is measured in terms of the likelihood ratio of a model concerning some reference (benchmark). Therefore, we define the model skill measure:

$$model\ skill = 1 - \frac{MSE\ of\ intercrop\ model}{MSE\ of\ benchmark} \qquad (10)$$

A positive skill value indicates that the intercrop model has a smaller MSE than if one assumes no intercrop effect. A value of 1 indicates that the intercrop model is perfectly simulating these values (e.g. observed is equal to simulated yield). This skill measure can be thought of as the fraction of the intercrop effect that is explained by the intercrop model.

Model evaluation in capturing management effects

To evaluate how well the model simulates management effects (choice of species, cultivar, sowing density) we look at differences in AME between two different management (mgt) decisions, mgt1 and mgt2 for both simulated and observed values. For example, mgt1 could involve SW cultivar1, while mgt2 could involve SW cultivar2. Given that multiple cultivars of SW were used in the field experiment, we selected two cultivars that showed very low and high observed AME of grain yield from each of the three environments. We then compared the simulated AME differences between selected cultivars with the observed differences (simulated differences vs. observed differences between the two cultivars). Similarly, for sowing density, we considered high sowing density for mgt1 and low sowing density for mgt2. Then we assessed how much these differences can be explained by the intercrop model compared to the benchmark that assumes no intercrop effect. The measure of the management effect is then expressed as:

$$\Delta AME = AME_{mgt2} - AME_{mgt1} \qquad (11)$$

Where ΔAME is the difference between AME of management2 and AME of management 1; AME_{mgt2} is AME of trait in question, for example grain yield for management2; AME_{mgt1} is AME of trait in question for example grain yield for management1.

3.3 Results

3.3.1 Model calibration with monoculture data

The fit of the calibrated model to the observations of the monoculture treatments in all three environments was generally good with RMSE of 0.6 t ha− 1 , 2.1 t ha− 1 , 0.15 m, 0.08 for grain yield, shoot biomass, plant height, and fraction of intercepted radiation respectively (Fig. B. S2 - S6). Exceptions were biomass at flowering and harvest at WG2020, where the simulated values were strongly overestimated compared to the measured values.

3.3.2 Model evaluation with intercrop data

Grain yield and absolute mixture effect

The intercrop model performed well in simulating the absolute grain yield (Fig. 3.1) and AME (Table 3.2 and Fig. 3.2). The experimental data consistently showed positive AME for SW grain yield, though with a substantial range between 0.56 and 0.84 t ha^{-1} (Table 3.2). In contrast, the AME for FB grain yield ranged from − 0.79 ha^{-1} to +0.41 ha^{-1}, depending on the environmental conditions. In both observed and simulated AME of SW grain yield was consistently larger than AME of FB. In most cases, the skill of the intercrop model was substantial, ranging from 0.29 to 0.84 (Table 3.2). The skill was negative, i.e. MSE was larger than for the benchmark, in the two cases with the smallest AME values, which favored the benchmark model since it assumes AME=0. RMSE for the intercrop model was not particularly large for those two cases, but those were the two cases with the smallest values of RMSE for the benchmark.

Table 3.2. Model evaluation of absolute mixture effect (AME) of grain yield (all t ha^{-1}) in both monocultures and intercrops. Results are averages over cultivars of faba bean (FB) and spring wheat (SW) and sowing densities for three environments.

Environment	AME[1]	Observed	Simulated	Model skill[2]	RMSE IM[3]	RMSE[5] B[4]
CKA2020	AME_{total}	-0.13	0.33	-3.00	0.50	0.20
	AME_{FB}	-0.79	-0.46	0.77	0.38	0.82
	AME_{SW}	0.66	0.79	0.84	0.27	0.69
CKA2021	AME_{total}	1.25	0.57	0.60	0.80	1.30
	AME_{FB}	0.41	0.15	0.29	0.48	0.58
	AME_{SW}	0.84	0.42	0.59	0.59	0.93
WG2020	AME_{total}	0.55	0.35	0.74	0.20	0.50
	AME_{FB}	-0.01	-0.37	-18.00	0.38	0.08
	AME_{SW}	0.56	0.72	0.84	0.22	0.58

[1] Absolute mixture effect; [2] Model skill is the skill measure compared to the no-mixture effect (benchmark), [3] Intercrop model; [4]Benchmark model and [5] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

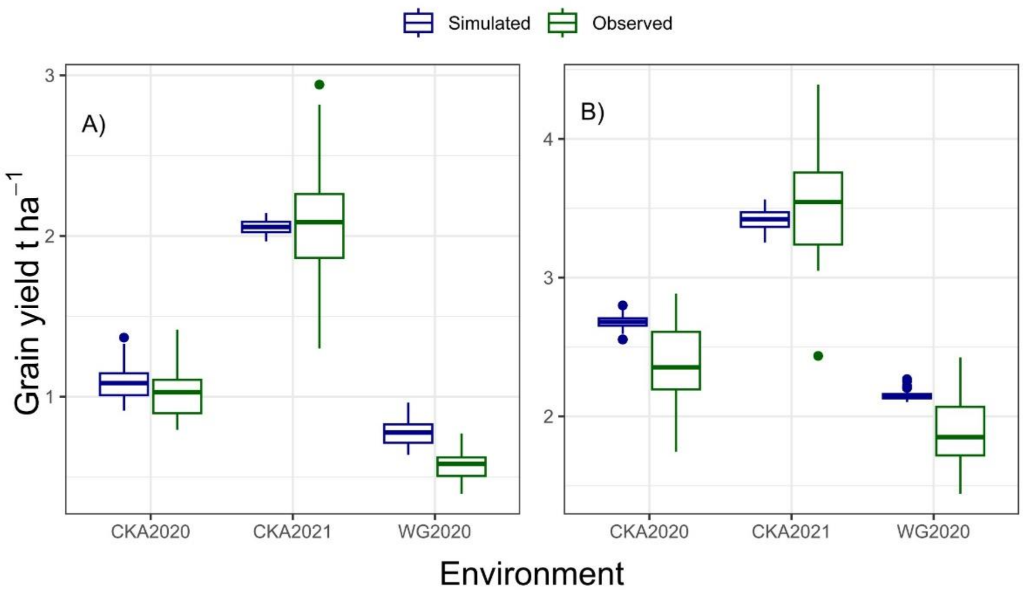

Figure 3.1. Simulated and observed absolute dry matter grain yield (t ha^{-1}) of faba bean (left panel) and spring wheat (right panel) grown across an intercropping system (average for all intercropping treatments), under three environments. Observations per site were 48 per species for CKA2020 and WG2020 and 38 per species for CKA2021.

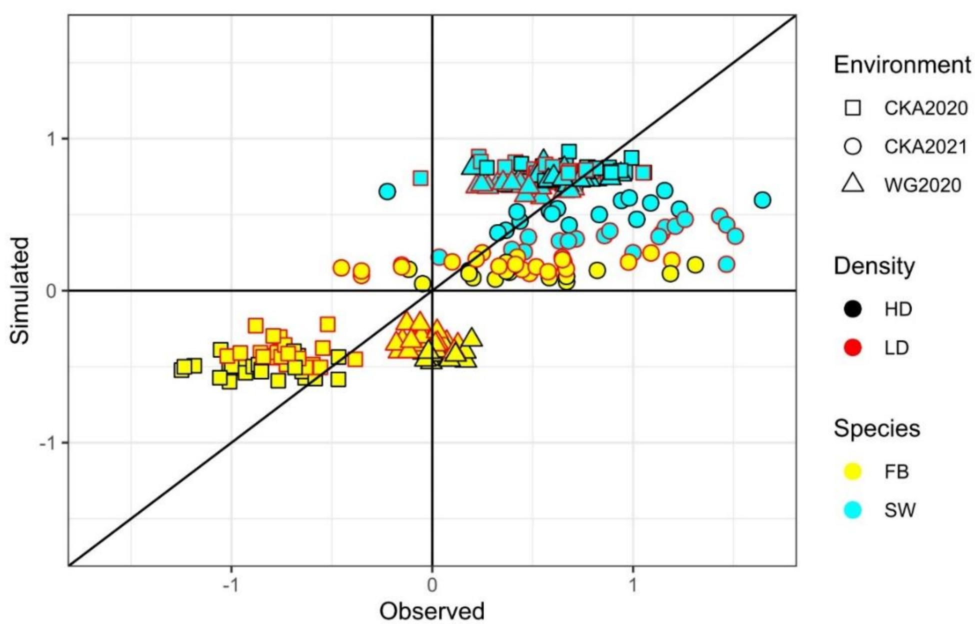

Figure 3.2. Simulated and observed absolute mixture effect (AME) of dry matter grain yield (t ha^{-1}) for faba bean (FB) and spring wheat (SW) grown under three environments (CKA 2020 and 2021, WG2002) and two plant densities (HD- high sowing density, LD- low sowing density). Overall R^2 is 0.59.

Above-ground biomass

The observed and simulated above-ground biomass AME of SW was consistently positive. However, the AME for FB was negative in many cases (Fig. 3.3). The skill was 0.37 for FB, 0.46 for SW, and 0.33 for the total of both species, based on squared error averaged over the environments, growth stages, cultivars, and sowing densities. In CKA2020 and CKA2021, skill varied between 0 and 0.91, while in WG2020 many of the skill measures were negative (Table B. S5).

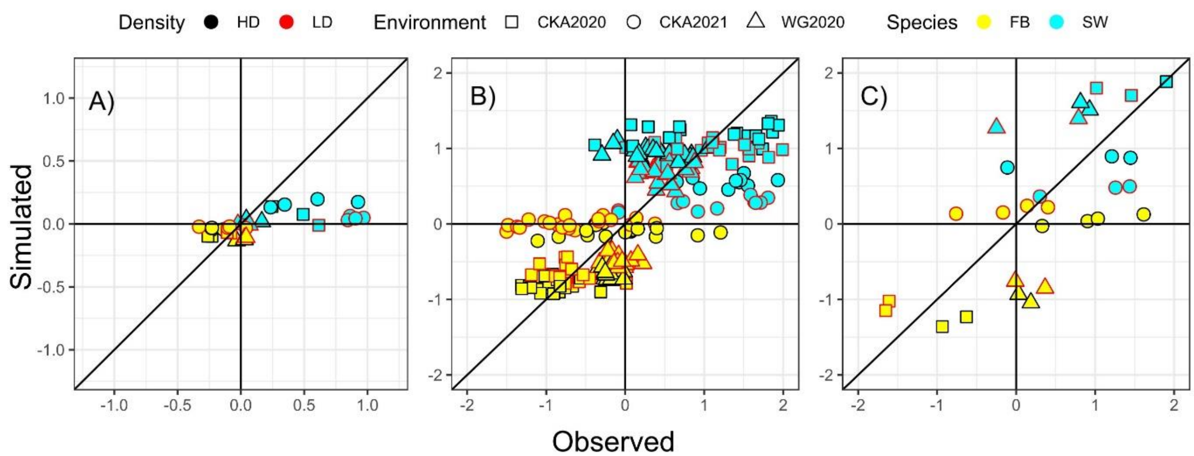

Figure 3.3. Simulated and observed absolute mixture effect (AME) for above-ground biomass during A) the vegetative stage, B) around flowering, and C) at maturity, for faba bean (FB) and spring wheat (SW) grown under three environments (CKA 2020 and 2021, WG2020) and two planting densities (HD- high sowing density, LD- low sowing density). The distance of a point from the vertical line is the error of the benchmark. Overall R^2 for AME is 0.42

Plant height

The observed AME for plant height was low for both species (Fig. 3.4 and Table B. S6). As a result, the skill was negative in most cases, showing the benchmark performed slightly better than the intercrop model (Table S6). However, the RMSE was 0.05m and 0.08m which is quite low for SW and FB, respectively highlighting the low impact of intercropping on plant height.

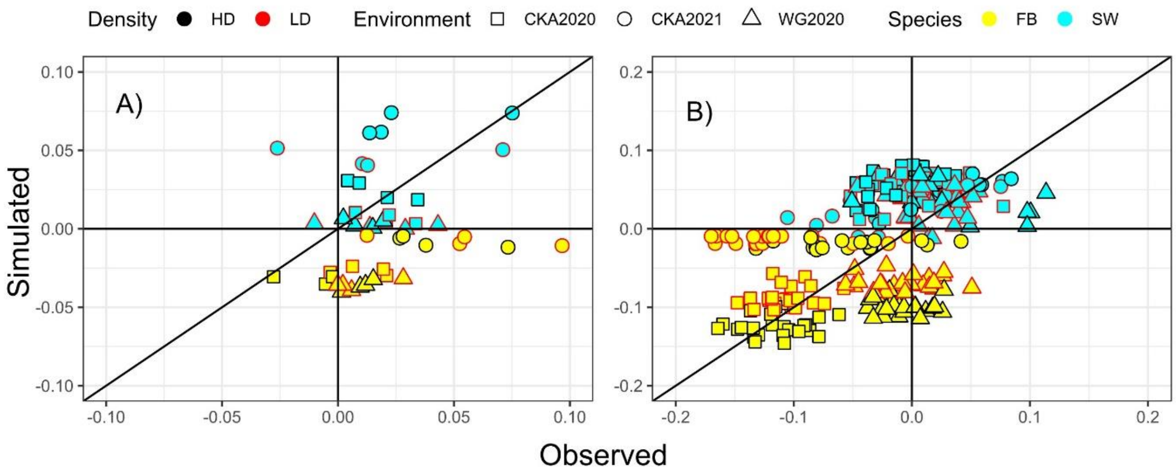

Figure 4. Simulated and observed absolute mixture effect (AME) for plant height at A) vegetative and B) flowering stage for faba bean (FB) and spring wheat (SW) for three environments (CKA 2020 and 2021, WG2020) and two planting densities (HD- high sowing density, LD- low sowing density). Overall R^2 for AME is 0.30.

Fraction of intercepted radiation

Observations showed that intercropping had a minor effect on the fraction of intercepted radiation for both crop species (fIPAR, Fig. 3.5). The measurements are shown only for the two species together since it was not possible to measure radiation interception of SW and FB separately in in-row intercropping. The intercrop model performed reasonably well (RMSE 0.04-0.05), but the benchmark performed slightly better (Table B. S7).

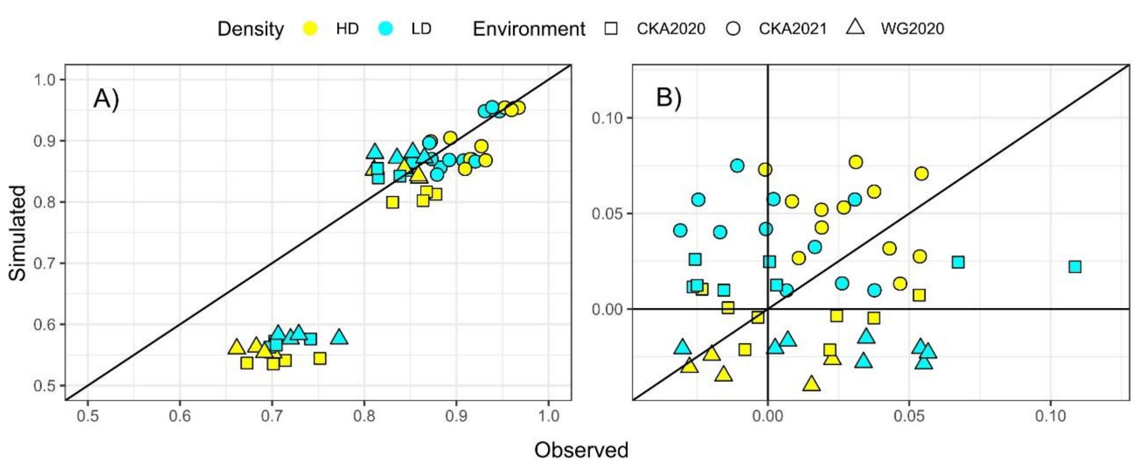

Figure 3.5. Simulated and observed A) fraction of intercepted photosynthetically active radiation (fPAR) and B) absolute mixture effect (AME) of the fraction of intercepted photosynthetically active radiation (fIPAR) at different measurement dates. Overall R2 is 0.88 for fPAR and 0.05 for AME of fPAR. Three environments (CKA 2020 and 2021, WG2020), HD- high sowing density, LD- low sowing density.

Root biomass

Observations showed that there was a root mass advantage in intercropping for SW at both observed dates compared to monocultures, especially in the topsoil layers (0–20 cm) (Fig. B. S8-9). However, the model underestimated the root biomass in the upper 10 cm (Fig. S8, S9). The AME values for both species were much larger in the top layer (0–30 cm) than in the lower layers. For the 0–30 cm layer, the model skill was large, in the range of 0.46–0.86 depending on the development stage and species (Table S8). For the lower soil layers, the AME was small, and skill was often negative.

Volumetric soil water content.

The effect of intercropping on soil moisture was small, with values of RMSE ranging from 0.01 to 0.042 volumetric soil water content (VSWC). The skill scores here are all close to 0, indicating the similar performance of the intercropping model with the benchmark (Table B. S9).

Intercrop model capability to simulate management effects

Effect of species and environment

In general, both observed and simulated AME values were substantially larger for SW than for FB. The skill for simulating ΔAME of grain yield ranged between 0.12 and 0.92. For above-ground biomass, the model effectively represented the differences between species at CKA2020 and CKA2021, with skill values between 0.24 and 0.81. However, model performance at WG2020 showed that the model was not able to capture species differences (Table 3.3).

Table 3.3. Evaluation of the intercrop model simulating species interaction in intercropping (all cultivars and both densities) in grain yield in (t ha^{-1}) and shoot biomass (t ha^{-1}) for both monocultures and intercrops at different growth stages.

Environ-ment	Traits	Develop-ment Stage	Faba bean AME[1]		Spring wheat AME		ΔAME[4]		Mo del skill	RMSE[7]	
			obs[2]	sim[3]	obs	sim	obs	sim		IM[5]	B[6]
CKA2020	Grain yield	Maturity	-0.79	-0.46	0.66	0.79	1.45	1.25	0.92	0.41	1.40
CKA2021			0.41	0.15	0.84	0.42	0.43	0.27	0.27	0.70	0.83
WG2020			-0.01	-0.37	0.56	0.72	0.57	1.09	0.12	0.55	0.59
CKA2020	Biomass	vegetative	-0.17	-0.08	0.35	0.05	0.52	0.13	0.39	0.44	0.56
		flowering	-0.84	-0.75	1.42	1.09	2.26	1.84	0.81	1.02	2.44
		maturity	-1.21	-1.19	1.50	1.86	2.71	3.05	0.95	0.55	2.77
CKA2021		vegetative	-0.16	-0.03	0.71	0.11	0.88	0.14	0.24	0.70	0.90
		flowering	-0.41	-0.04	1.88	0.41	2.29	0.45	0.25	2.27	2.63
		maturity	0.44	0.12	1.36	0.69	0.92	0.57	0.25	1.40	1.70
WG2020		vegetative	0.02	-0.12	0.06	0.01	0.05	0.13	-0.2	0.11	0.10
		flowering	-0.14	-0.58	0.42	0.81	0.56	1.39	-1.0	0.90	0.60
		maturity	0.14	-0.90	0.57	1.45	0.43	2.34	-9.0	1.90	0.50

[1] Absolute mixture effect; [2] observed; [3] simulated; [4] the difference between the AME of two species; [5] Intercrop model; [6]Benchmark and [7] RMSE IM and RMSE B are root mean squared errors of the intercrop model and the benchmark respectively.

Effect of cultivars

We considered here only two SW cultivars in each environment, the cultivars with the smallest and largest observed AME values averaged over sowing densities. The two SW cultivars for each environment were: CKA2020- KWS starlight vs Anabel; CKA2021: Lennox vs Sonett and WG2020: Lennox vs mix_group 1. The two FB cultivars were Mallory and Fanfare. The intercrop model was capable of simulating the cultivar differences between the two SW cultivars AME of grain yield though consistently underestimating the size of the difference, with a skill range of 0.21-0.24. For faba bean, the intercrop model performed similarly to the benchmark that considers no intercrop effects, with a skill that approached zero (Table 3.4)

Table 3.4. Evaluation of the intercrop model in regards to the effect of spring wheat (SW) and faba bean (FB) cultivars on AME of grain yield at three environments. The two SW cultivars for each environment were: CKA2020- KWS starlight vs Anabel; CKA2021: Lennox vs Sonett and WG2020: Lennox vs mix_group 1. The two FB cultivars are Mallory and Fanfare. See Table S1 for the details about the cultivars.

Environment	AME	Cultivar 1		Cultivar 2		ΔAME[4]		Model skill	RMSE[7]	
		AME[1] obs[2]	AME sim[3]	AME obs	AME sim	obs	sim		IM[5]	B[6]
CKA2020	AME_{SW}	0.38	0.72	0.75	0.78	0.37	0.06	0.24	0.34	0.39
CKA2021		0.55	0.39	0.96	0.48	0.41	0.09	0.21	0.45	0.51
WG2020		0.45	0.71	0.66	0.73	0.20	0.02	0.21	0.19	0.21
CKA2020	AME_{FB}	-0.89	-0.46	-0.69	-0.47	0.08	-0.18	-0.02	0.28	0.28
CKA2021		0.1	0.12	0.69	0.16	0.17	-0.05	0.07	0.72	0.75
WG2020		-0.04	-0.37	0.03	-0.37	0.11	-0.01	-0.06	0.12	0.12

[1] Absolute mixture effect; [2] observed; [3] simulated; [4] the difference between the AME of the two cultivars; [5] Intercrop model; [6]Benchmark and [7] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

Effect of sowing density

Observations showed that the sowing density had a significant effect on the AME of grain yield for both crop species. However, this effect i.e. the difference between the AME of two densities was not captured by the intercrop model, except in very few cases (Table 3.5).

Table 3.5. Evaluation of intercrop model in simulating the effect of sowing density of faba bean (FB) and spring wheat (SW) on absolute mixture effect (AME) of grain yield t ha^{-1}.

Environment	AME	Low density		High density		ΔAME[4]		Model skill	RMSE[7]	
		AME[1] Obs[2]	AME Sim[3]	AME obs	AME sim	obs	sim		IM[5]	B[6]
CKA2020	AME_{FB}	-0.73	-0.41	-0.85	-0.51	0.12	0.10	0.25	0.18	0.21
CKA2021		0.34	0.17	0.48	0.12	-0.14	0.05	-0.04	0.58	0.57
WG2020		-0.04	-0.34	0.02	-0.41	-0.06	0.07	-1.30	0.16	0.10
CKA2020	AME_{SW}	0.58	0.79	0.73	0.79	-0.15	0.00	0.04	0.26	0.27
CKA2021		0.89	0.34	0.71	0.52	0.18	-0.18	-0.32	0.65	0.56
WG2020		0.48	0.69	0.65	0.74	-0.17	-0.05	0.14	0.24	0.26
CKA2020	AME_{total}	-0.07	0.38	-0.12	0.28	-0.03	0.10	-30.0	0.27	0.23
CKA2021		0.6	0.51	1.19	0.64	0.04	-0.13	-0.09	0.71	0.68
WG2020		0.22	0.36	0.67	0.33	-0.23	0.02	-0.13	0.33	0.31

[1] Absolute mixture effect; [2] observed; [3] simulated; [4] the difference between the AME of two densities; [5] Intercrop model; [6]Benchmark and [7] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

3.4 Discussion

The current study specifically focused on evaluating the capability of a process-based intercrop model to simulate the intercropping effects of a spring wheat/faba bean intercropping under different management conditions. In this study, the crop parameters were calibrated for monoculture using the data from monoculture treatments without recalibration for intercrops. Therefore, this is not a test of how well the model simulates the effect of the environment on a monoculture. It is however a rigorous test of how well the model can simulate the differences between monocultures and intercropping. This approach differs from previous studies that have evaluated intercrop models. Past studies typically looked at errors in the model, but not at the errors from the difference between monocultures and intercrop, focusing mostly on the model's capability to simulate environmental effects on the monocultures and the effects of intercropping (Berghuijs et al., 2021; Gou et al., 2017a; Munz et al., 2014a; Githui et al., 2023; Pierre et al., 2023). To evaluate the model, we introduce an original measure of intercrop model performance, namely a model skill measure that measures model MSE compared to MSE assuming that there is no intercrop effect.

A major objective of the simulation of intercrops is to improve process understanding and to develop a rapid screening tool for possible management strategies. It is therefore important to evaluate how accurately the model can evaluate differences between different management strategies. This has not been done in previous studies but is done here for three major management decisions, namely choice of species, choice of cultivars, and choice of sowing density.

The calibrated and evaluated model, despite its simplifications, is a promising tool to simulate the effects of intercropping systems and, thus, to support their design. This should be of particular interest as experimental capacities are limited to studying the large range of factors and treatments to optimize intercropping systems. Such models can also help to interpret experimental results in terms of crop growth dynamics and resource acquisition. Though only calibrated based on sole crop treatments, the presented intercrop model was able to simulate in-row mixture effects on grain yield, shoot, and root biomass, while considering species and cultivars differences. The relatively simplistic assumptions in the model to account for above and below-ground competition of considered species for resources may be of use for other intercropping systems including other species combinations, but this awaits further testing.

3.4.1 Capability of the model to simulate intercropping effects

Considering the aboveground plant growth, the intercrop model captured the intercropping effect on most of the variables. The model skill was large for grain yield and above-ground biomass when intercrop effects were large. When intercrop effects were small, which was, in general, the case for plant height and light interception, the benchmark was quite good and the intercrop model often did not perform better. Additionally, we evaluated the model capabilities in terms of simulating the crop species individually, as well as the model performance of the SW and FB under an intercropping system and for different plant densities in terms of above and below-ground biomass production and soil moisture. The field experiment dataset offered substantial opportunities, as data on key variables were collected separately for each species including root biomass, facilitating a comprehensive evaluation of the model. It was assumed that there are no substantial effects of one crop on a given process of another crop, for instance, radiation use efficiency, therefore the model explicitly simulates species interactions and traits plasticity such as grain yield and biomass due to competition. Evaluating the intercrop model based on how well the model simulates the intercrop effect on each species in intercropping enables to ensure that the model could be employed for in silico analysis of different species intercropping and management effects as it was used by Launay et al. (2009) and Githui et al. (2023).

Modeling below-ground resource (water, N) competition is an important element for designing optimal field arrangements for intercropping systems (Gaudio et al., 2019). We have found that the intercrop model has reasonable skill in simulating the effect of intercropping on the topsoil root biomass of each species. As below-ground competition depends strongly on root biomass, the good performance of the intercrop model shows the potential to reasonably capture belowground dynamics in terms of water and nutrient uptake (Table S8). To our knowledge, this is one of the first studies that specifically address below-ground dynamics of root growth and resource uptake of row intercropping systems, which can further help to elucidate competition and complementary effects of intercropping systems.

The intercrop model performance in simulating the AME of soil water content was similar to the benchmark. Both, the measured and the simulated data showed low AME values, meaning that soil water content in intercropping is similar to the average of the two monocultures (SW and FB). There is limited research on water use of intercropping, particularly in row mixed intercropping. Our results suggest that the total water consumption of the intercrop is perhaps similar to the average water consumption of the monocultures. However, the study by Mao. et al. (2012) highlight that actual water use in intercropping from expected use ranged from −13.7 % to +19.8 %. However, since the study is based on a relay intercrop experiment of maize/pea intercrop it is not directly comparable with our design of mixing within the row. Few modeling studies have been published on evaluating competition for soil water in strip intercropping systems (Tan et al., 2020; Miao et al., 2016), but no studies have looked into the competition for soil water in row intercropping.

In the current study, the intercrop model successfully simulated the intercrop effect on key variables such as grain yield, above-ground biomass, and root biomass without re-parametrization for intercropping. This highlights the ability of the intercrop model to simulate interspecific interactions and plant plasticity due to competition (Ajal et al., 2022). In this model, the daily increment in plant growth was regulated by water (TRANRF) and nitrogen availability (nitrogen-limited, NNI). Thus, under limited resources, the competition of one species affects the growth of the other species (Justes et al., 2021). For instance, cereals are highly competitive (Miao et al., 2018) for soil water, resulting in drought stress for intercropped legumes, hence, the plant growth of legumes is limited while that of cereals increases, allowing them to capture more resources. Likewise, under limited nitrogen availability, the growth of cereals can be limited, however, since the legumes fix atmospheric nitrogen and fulfill most of its demand (Klippenstein et al., 2022) they grow faster. Therefore, the ability of the model to capture the traits of plasticity due to intercropping is important because it is relevant for understanding the productivity of species grown in intercrops as compared to sole crops (Ajal et al., 2022).

3.4.2 Intercrop model performance on simulating management strategies

It was often reported that the performance of intercropping depends on the genotypes and their traits, the environment, and the management (Demie et al., 2022; Paul et. al., 2024). Optimizing species and cultivar combinations allows for maximizing the overall performance of intercropping (Berghuijs et al., 2020). However, the complexity of the interactions in intercropping makes it a challenging task to understand the drivers for high productivity in intercropping.

The intercrop model demonstrated a high skill level, indicating the capability to simulate species differences and intercropping regarding the AME of above-ground biomass and grain yield. The SW cultivar differences observed in the field experiment (lowest and highest observed AME of grain yields) were also reasonably predicted by the intercrop model. Consequently, the model can assist in making informed choices in selecting SW cultivars, optimizing their suitability for intercropping scenarios, and potentially enhancing overall grain yields (Brooker et al., 2015).

Understanding species-interspecific interactions is important in the decision of species choice for intercropping (Cheriere et al., 2020). SW in intercropping exhibited a higher degree of competitiveness than FB hence SW in intercropping was more productive than SW in monoculture, resulting in a consistently positive AME of grain yield and above-ground biomass. A similar response was reported in the literature, where cereals are considered strong competitors in cereal/legumes intercropping (Yu et al., 2016; Paul et al., 2023). On the contrary, FB tended to exhibit a negative AME at CKA2020 and WG2020 which are characterized by drought stress environment, and a positive AME, at CKA2021 which is characterized as a relatively moist environment. This trend is particularly observed in key plant traits such as grain yield and above-ground biomass. The crops grown in 2020 (CKA2020 and WG2020) suffered from drought stress. Under these conditions, SW with its deeper root system (Fig. B. S7) accessing subsoil water tends to suppress FB. This phenomenon of vigorous rooting system of cereals suppressing legume intercropping was demonstrated in Corre-Hellou and Crozat. (2005), and early rapid growth hence resulted in early dominance and legacy effect at a later stage of SW (Paul et al., 2023). Consequently, FB in mixtures faces a disadvantage compared to FB in monocultures, while SW in mixtures takes an advantage over SW monocultures. 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 respective monoculture. Site-specific partner combinations of cereals and legumes together with appropriate management practices are a key element in enhancing total productivity in intercropping (Paul et. al.,2024; Nelson et al., 2021, Zhu et al., 2023). Launay et al. (2009) reported that the relative productivity depended on the selected species and cultivars and environment.

Planting density significantly affects the growth dynamics and overall productivity of intercropping. According to Yu et al. (2016) and Paul et al. (2024), higher grain yields in mixed cropping systems are observed at increased sowing densities compared to lower sowing densities. The management strategy sowing density was poorly simulated compared to the benchmark. The model's approach, which relies on considering only initial crop dry weight (seed weight) and the number of plants that emerged per m^2 (model parameter RINPOP) which mainly affects root growth as a proxy for sowing density effects, may be overly simplistic and inadequate in capturing the true complexity of density-dependent processes in plant growth. Consequently, poor simulation results are plausible given these limitations. Therefore, improved equations need to be implemented in the model to simulate the sowing density effect in intercropping. A similar approach is used in the STICS model as mentioned in Brisson et al. (2003) in which plant density introduced as an input parameter corresponds to the density of emerged plants. However, it was not tested if the approach captures the density effect in intercropping.

3.4.3 Specifications and limitations

Compared to the crop model applied in monocultures, the only new mechanism in the intercrop model is the shading of one species by another, which determines the radiation interception by each species. The model was able to simulate the competition for and complementary use of water and N by the two intercropped species. Each species takes up water and N as in the monocultures models depending on the demand, root biomass, root length density, and available soil N and water, but by doing so depletes the amount available for the other species. Biological nitrogen fixation (kg N ha^{-1}) by the legume in the intercrop follows the same equation as for the monoculture but is increased because the cereal reduces available soil N. Thus competition and complementarity are a consequence of modeling the two species together, without any new mechanisms being required other than competition for light.

A limitation of this study was that the model was evaluated only for the spring wheat-faba bean intercropping dataset, even though this allowed a thorough model evaluation. Expanding the scope by including simulations of intercrops with various other cereals/legumes would enhance the model's applicability. In addition, the field experimental data exhibited high variability among different replicates, with only a few treatments showing significant differences. The preselected SW cultivars used for calibration (key treatments with higher intensity of data collection) had similar characteristics and differed only slightly in plant height and initial biomass. This consequently led to minor differences in simulated values. Additionally, the experiment at the organically managed research station (WG), was partly affected by weed infestation. The weed infestation varied between monocultures and intercrops, leading to high data variability. In the simulation, no component accounted for weed competition, resulting in a disparity between the simulated and observed mixture effects in this specific environment. Additionally, at CKA2021 there was no replication in most of the treatments leading to further uncertainties.

3.5 Conclusions

The intercropping model based on the soil-crop model LINTUL5 is found to be a promising tool for designing intercropping systems, despite its simplifications. Experiments are limited in the number of treatments but models can help to interpret experimental results in terms of crop growth dynamics and resource acquisition. Calibrated using only data for sole crop treatments, the intercrop model was able to simulate in-row mixture effects on grain yield, shoot, and root biomass, while considering species and cultivar differences. The intercrop model demonstrated a high skill level, underlining the capability to simulate species differences and intercrop performance regarding the AME of above-ground biomass and grain yield. The effect of SW cultivar choice was also reasonably predicted by the intercrop model. The limitations of using a soil-crop model to design intercropping systems must however be kept in mind. It must also be considered that many of the hoped-for benefits of intercropping, such as increased biodiversity or reduced weed populations, are not simulated by crop models. Crop models can be an important aid in intercrop design, but will need to be coupled with other considerations.

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CRediT authorship contribution statement

Dereje T. Demie: Methodology, Visualization, Data curation, Writing- Original draft preparation. **Daniel Wallach:** Methodology, Writing- Reviewing and Editing. **Thomas F. Döring:** Conceptualization, Funding Acquisition, Methodology, Data curation, Writing- Reviewing and Editing. **Frank Ewert:** Conceptualization and Methodology and Funding Acquisition. **Thomas Gaiser:** Methodology, Writing- Reviewing and Editing. **Sofia Hadir:** Data curation, Writing- Reviewing and Editing. **Gunther Krauss:** Methodology and Software and Writing- Reviewing and Editing. **Madhuri Paul:** Data curation, Writing- Reviewing and Editing. **Ixchel M. Hernández-Ochoa:** Writing- Reviewing and Editing. **Rémi Vezy:** Writing- Reviewing and Editing. **Sabine J. Seidel:** Funding Acquisition, Conceptualization, Methodology, Data curation, Writing- Original draft preparation.

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Chapter 4

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

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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 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.

keywords: abiotic resource capture, intercrop model**,** cropping system simulation, crop diversification, crop competition

4.1 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; Li, 2022; Martin-Guay et al., 2018). Intercropping cereals with legumes is considered as a more sustainable form of crop production can be a suitable alternative (Li et al., 2020; Lithourgidis et al., 2011; Kremen and Miles, 2012; Martin-Guay et al., 2018, Bedoussac et al., 2015), with several ecological processes 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 under intercropping system, 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 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 spring/wheat 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.

4.2 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.

4.2.1 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 sea level. The soil at the experimental station is classified as Haplic Luvisol (hypereutric, siltic) from loess (IUSS Working Group WRB, 2006) and characterized by a silty-loamy texture with 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 63m m above sea 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 C. S1). The total precipitation during the growth period (March-August) at CKA2021 (458.5mm) 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. C. S1).

4.2.2 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 C. 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.

4.2.2 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).

4.2.3 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 LINTUL5Phenology, 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.

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.

Crop radiation interception

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.

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).

4.2.4 Data processing and calculations

In this study, we used both simulated and field experimental datasets. Nevertheless, most of the data was derived from the process-based simulation model as it is not feasible to measure certain variables particularly soil-related dynamics directly in field experiments, especially 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.

Table 4.1. Observed and simulated data used in the current study (x stands for data available). Grain yield and biomass were in dray 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

The primary objective was to compare resource acquisition between two cropping systems (monocultures vs. intercrops). 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 intercrops). 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 species, we considered the following terms:

SW_mono = Total resource capture of spring wheat in monocultures *0.5 (1)

FB_mono =Total resource capture of faba bean in monocultures *0.5 (2)

Ave_mono = (SW_mono+ FB_mono) (3)

inter = SW_inter+ FB_inter (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 (expected) is the average of resource capture of monocultures of SW and FB; inter is the sum of resource capture of spring wheat and faba bean in intercropping; SW_inter is resource capture of spring wheat in intercropping; FB_inter is resource capture of 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 SW; Y_{SW_inter} is the grain yield of SW in intercropping, $Y_{SW,mono}$ is the grain yield of SW in monoculture and $pLER_{FB}$ is the partial land equivalent ratio of faba bean; Y_{FB_inter} is the grain yield of FB 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:

Yield=resource acquisition × resource use efficiency (6)

Here, the resource use efficiency implies resource conversion efficiency where by definition, efficiency is the ratio of yield to resource acquired. In the present study, we were interested in three resources: intercepted radiation, actual transpiration 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 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.

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, resource acquisition ratio (Table 2) and 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 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 obtain 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) and for clarity we propose to call this the resource use efficiency ratio.

Table 4.2. 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}: N use of FB in intercropping including fixation BNF NU_{FB_mono}: N use of FB in monoculture including fixation
N acquisition ratio including BNF	NAR_{BNF}	$NAR_{SW} + NAR_{FB_{BNF}}$	Total N use including BNF fixation
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, water uptake in mm, N in kg ha^{-1}, radiation in MJ m^{-2}

Table 3.3. 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}

4.3 Results

4.3.1 Grain yield of monocultures and intercrops under diverse environments

The observed and simulated intercropping grain yield revealed a significant increase in land use efficiency (Table 4.4), 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 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).

Table 4.4. simulated and observed grain yield and land equivalent ratios in three environments (CKA 2020,2021 and WG2020).

	Grain yield (t ha^{-1})				LER			
Environment	Spring wheat mono[1].	Spring wheat inter[2].	Faba bean mono.	Faba bean inter.	$pLER_{SW}$[3]	$pLER_{FB}$[4]	LER[5]	source
CKA2020	3.46	2.69	4.10	1.07	0.78	0.26	1.04	obs[6]
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[7].
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.

[1] monoculture; [2] intercrops; [3] partial land equivalent ratio of spring wheat; [4] partial land equivalent ratio of faba bean; [5] land equivalent ratio; [6] observed and [7] simulated

4.3.2 Resource use in intercropping and monocultures under diverse environments

Observed resource use in intercrops and monocultures

The observed soil water content (Fig. C. S2-S3) and intercepted photosynthetically active radiation (IPAR) (Fig. C. 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.

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 4.5). 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 4.5). 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.

Table 4.5. 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[1]	Mono culture	Inter crop	Partial ratio[1]	Mono culture	Inter crop	Ratio[2]	Indices
Grain yield	3.84	2.04	0.53	5.80	3.44	0.59	9.68	5.48	1.12	LER[3]
Water uptake	320.80	155.55	0.49	327.70	184.15	0.56	648.50	339.70	1.04	WAR[4]
Water use efficiency	1.20	1.31	1.10	1.77	1.87	1.06	1.49	1.61	1.08	WUER[5]
N uptake	60.70	29.9	0.49	130.2	88.2	0.68	190.9	118.1	1.17	NAR[6]
N use efficiency	6.34	6.83	1.08	4.46	3.90	0.88	5.08	4.64	0.92	NUER[7]
Soil N +BNF uptake	243.00	115.50	0.48	130.20	88.20	0.68	373.14	203.70	1.15	NAR_{BNF}[8]
Soil N+BNF use efficiency	1.58	1.8	1.12	4.46	3.90	0.88	2.60	2.69	1.00	$NUER_{BNF}$[9]
Radiation interception	628.20	313.20	0.50	635.8	355.20	0.56	1264.0	668.3	1.06	RAR[10]
Radiation use efficiency	0.62	0.65	1.07	0.92	0.97	1.06	0.78	0.82	1.06	RUER[11]

[1] the ratio of the given species in the mixture to its respective monoculture [2] the ratio of intercrops to monocultures, [3] land equivalent ratio; [4] water acquisition ratio; [5] water use efficiency ratio; [6] N acquisition ratio; [7] N use efficiency ratio; [8] N acquisition ratio including biologically fixed N; [9] N use efficiency ratio including biologically fixed N; [10] radiation acquisition ratio; [11] radiation use efficiency ratio.

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. 4.1). 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 cm-120 cm soil depth). Species-wise, the intercropped spring wheat water uptake was slightly higher (30 mm) than spring wheat in monoculture (Fig. 4.1A). The soil N uptake in intercropping surpassed the average of monocultures by 20%, particularly, before flowering (Fig. 4.1B). The N acquisition in intercropping was greater compared to the monocultures, due to enhanced acquisition from the deeper soil layers (90 cm-120 cm soil depth, Fig. 4.1B).

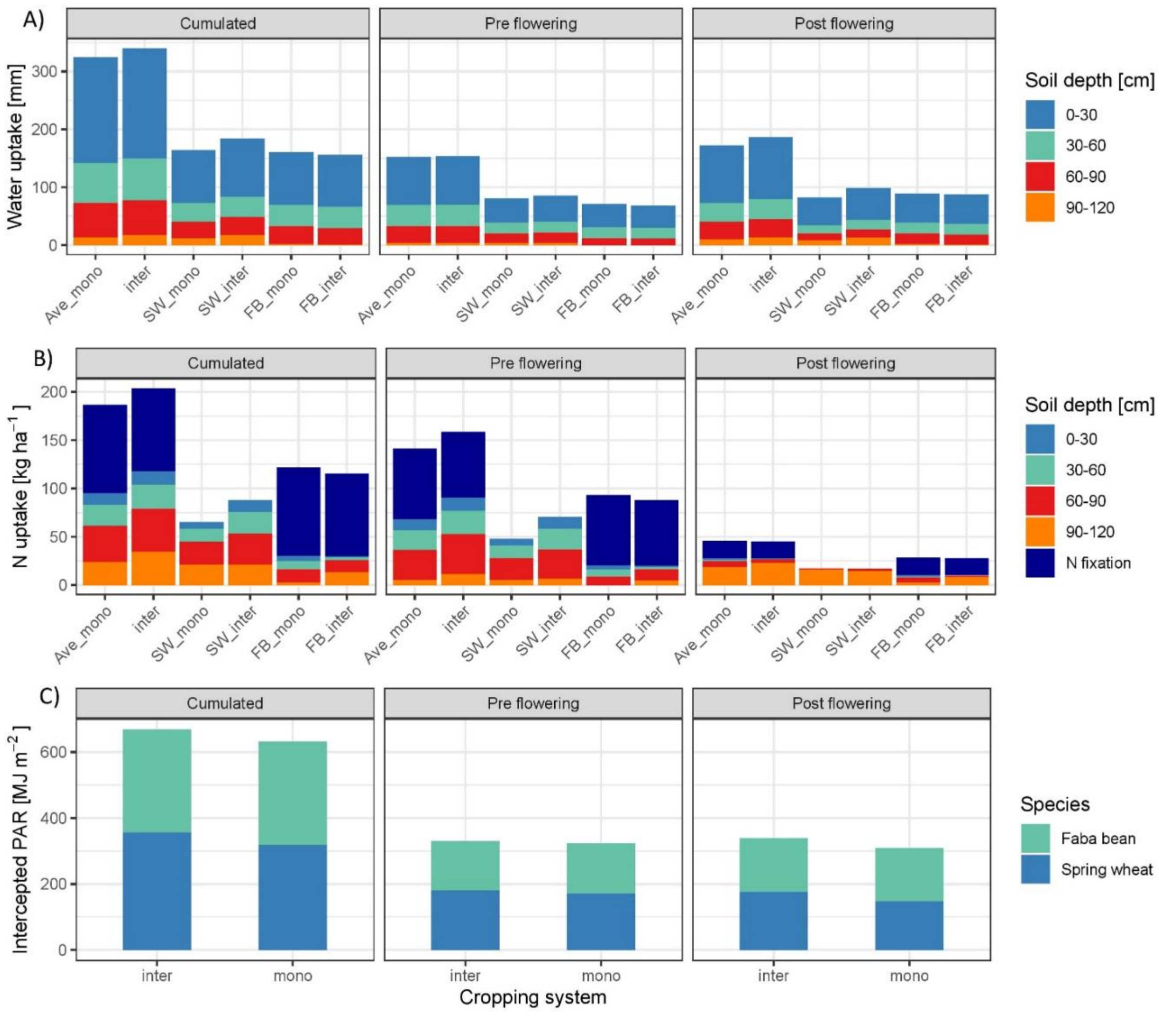

Figure 4.1. Simulated crop resource acquisition for A) water uptake B) N uptake and fixation and C) cumulative radiation, from sowing to spring wheat flowering and from spring wheat flowering to harvest. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono is the average of monocultures 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 plant density used in their monocultures.

Simulated daily plant growth showed that, in this condition (higher N and higher precipitation), the faba bean growth (daily above ground biomass), radiation interception, drought stress and nitrogen nutrition index was comparable in both intercrops and monocultures. However, the spring wheat intercrops were relatively, less water and N stressed, consequently resulting in relatively higher shoot biomass and radiation interception compared to spring wheat in monocultures (Fig. 4.3). The radiation interception of spring wheat in intercropping exceeded that of the spring wheat monocultures after ~DAS 70 which is after flowering (Fig. 4.3B) resulted in post flowering higher biomass (Fig 4.3A).

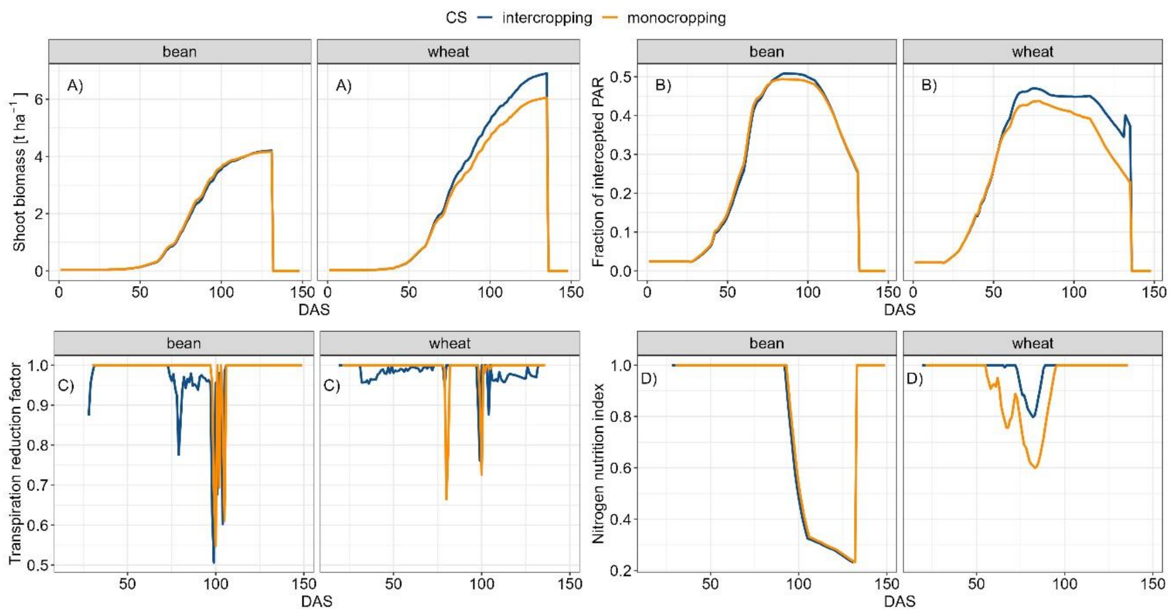

Figure 4.2**.** Simulated daily dynamics for the CKA2021 environment (high soil N and high rainfall) for both cropping system (CS). A) daily shoot biomass; B) fraction of intercepted photosynthetically active radiation (PAR), C) transpiration reduction factor (TRANRF) and D) nitrogen nutrition index (NNI) of Spring wheat (SW cv. Lennox); faba bean (FB cv. Mallory). The flowering of SW occurred at DAS 84 (CKA2021), and the flowering of FB occurred at DAS 78.

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 4.6). 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 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. 4.3). On the other hand, there was an increase in total soil N uptake (Fig. 4.3). 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 4.6). However, the LER for grain yield was only 1.04 %.

Table 4.6. 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[1]	Mono culture	Inter crop	Partial ratio	Mono culture	Inter crop	Ratio[2]	indices
Grain yield	3.02	1.02	0.33	3.75	2.65	0.71	6.76	3.65	1.04	LER[3]
Water uptake	209.00	66.50	0.32	214.95	144.59	0.67	423.95	211.09	0.99	WAR[4]
Water use efficiency	1.44	1.53	1.06	1.74	1.83	1.05	1.59	1.73	1.05	WUER[5]
N uptake	54.8	13.4	0.24	93.14	79.52	0.85	147.9	92.9	1.10	NAR[6]
N use efficiency	5.51	7.5	1.36	4.03	3.33	0.83	4.58	3.93	0.91	NUER[7]
Soil N uptake +BNF	173.5	46.1	0.27	93.14	79.52	0.85	266.68	125.7	1.12	NAR_{BNF}[8]
Soil N+BNF use efficiency	1.74	2.2	1.25	4.03	3.33	0.83	2.54	2.9	0.99	$NUER_{BNF}$[9]
Radiation interception	678.5	246	0.36	642.4	405.9	0.63	1320.9	652.1	0.99	RAR[10]
Radiation use efficiency	0.45	0.41	0.91	0.58	0.65	1.12	0.51	0.56	1.04	RUER[11]

[1] the ratio of the given species in the mixture to its respective monoculture [2] the ratio of intercrops to monocultures, [3] land equivalent ratio; [4] water acquisition ratio; [5] water use efficiency ratio; [6]N acquisition ratio; [7] N use efficiency ratio; [8] N acquisition ratio including biologically fixed N; [9] N use efficiency ratio including biologically fixed N; [10] radiation acquisition ratio; [11] radiation use efficiency ratio.

Simulated resource uptake by soil depth and over time (CKA2020)

No considerable differences between total water uptake over the growth period between intercropping and monocultures (the average of the two monocultures) were observed (Fig. 4.4A). However, a noticeable difference was observed between monocultures and intercropping after flowering with regards to water uptake from the deeper soil layer (60-120cm). About 44% of total intercrop water uptake was from deeper soil (60-120cm) layers, but in monocultures, the share of water from deeper soil layers was 24%. Species-wise, spring wheat in intercrop took up 35%, which was more water compared to spring wheat in monoculture at an equivalent density. However, faba bean showed a 36% reduction in water uptake compared to faba bean in monocultures at an equivalent density.

The soil N uptake in intercropping surpassed the average of monocultures. Intercrops soil N uptake was about 20 kg N ha^{-1} (Fig. 4.4B) more than the mean of both monocultures. When considering individual species, intercropped spring wheat demonstrated higher N uptake compared to spring wheat in monocultures (at equivalent planting density). Conversely, intercropped faba bean showed less soil N accumulation compared to faba bean in monocultures. Biological N fixation in the intercropping was about half compared to faba bean in density-equivalent monocultures (Fig. 4.4B). With regards to radiation interception, the simulated results revealed no substantial (-1%) differences between intercropping and monocultures. However, as for radiation interception of species, spring wheat in intercropping intercepted 26% more than that observed in spring wheat in monocultures. Conversely, faba bean in intercropping a 27% reduction in radiation interception compared to faba bean in monocultures.

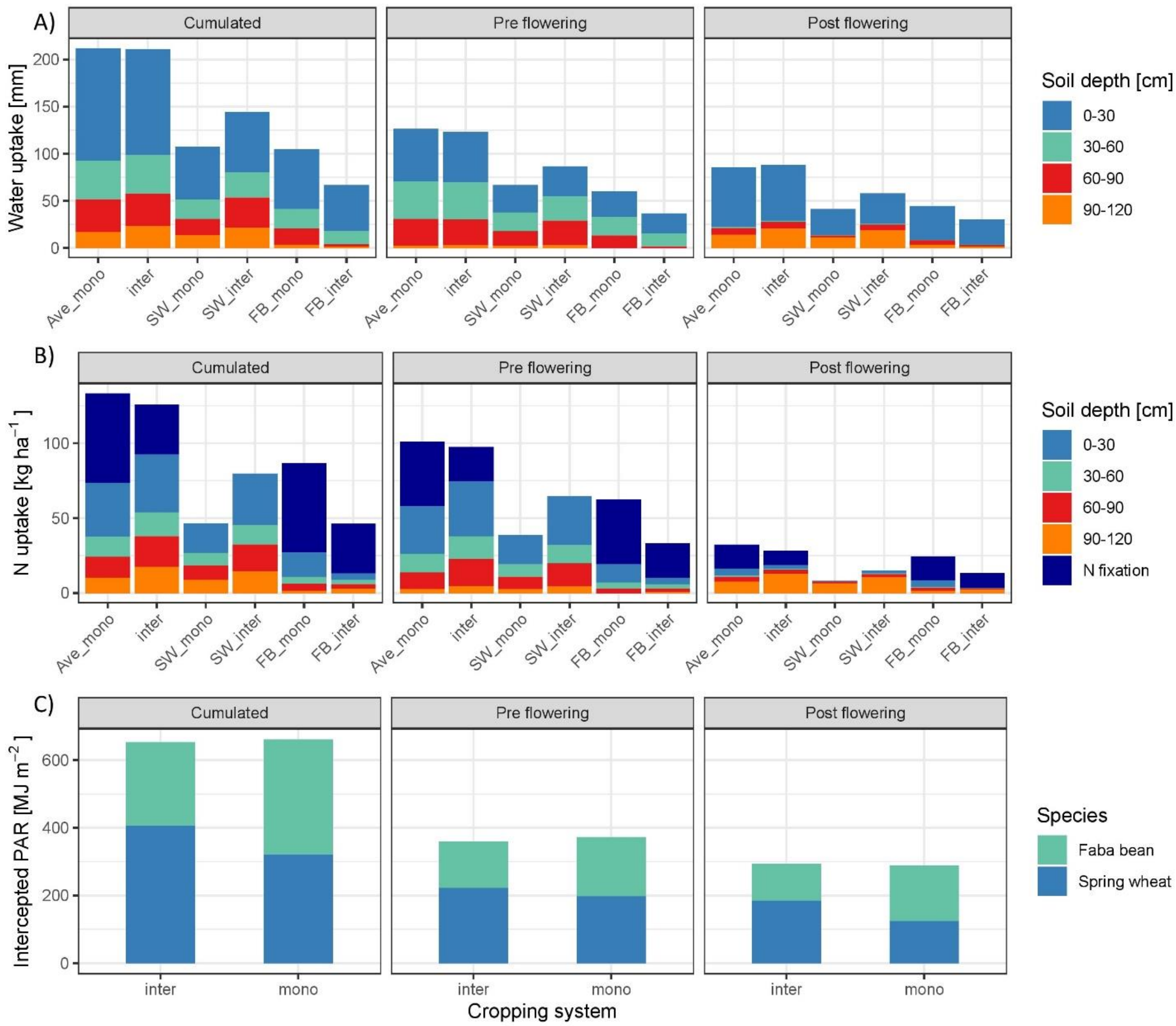

Figure 4.3. Simulated crop resource acquisition for A) water uptake B) N uptake and fixation C) radiation cumulative, from sowing to spring wheat flowering and from spring wheat flowering to harvest. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono corresponds to the average of monocultures 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.

An evaluation of the simulated daily drought stress per species in sole and intercropping revealed that spring wheat exhibited less drought stress when grown with faba bean as compared to monocultures. However, drought stress in faba bean was mostly enhanced by intercropping at faba bean emergence and after 70 DAS, which was around the flowering of faba bean. Likewise, spring wheat in the monoculture also experienced a stronger limitation of N compared to intercropping. The simulated daily plant growth and radiation interception also followed the same trends as transpiration reduction factors. Spring wheat in intercrops produced more biomass and intercepted more radiation compared to spring wheat in monocultures. However, faba bean growth and radiation interception in intercrops were dramatically reduced (Fig. 4.5).

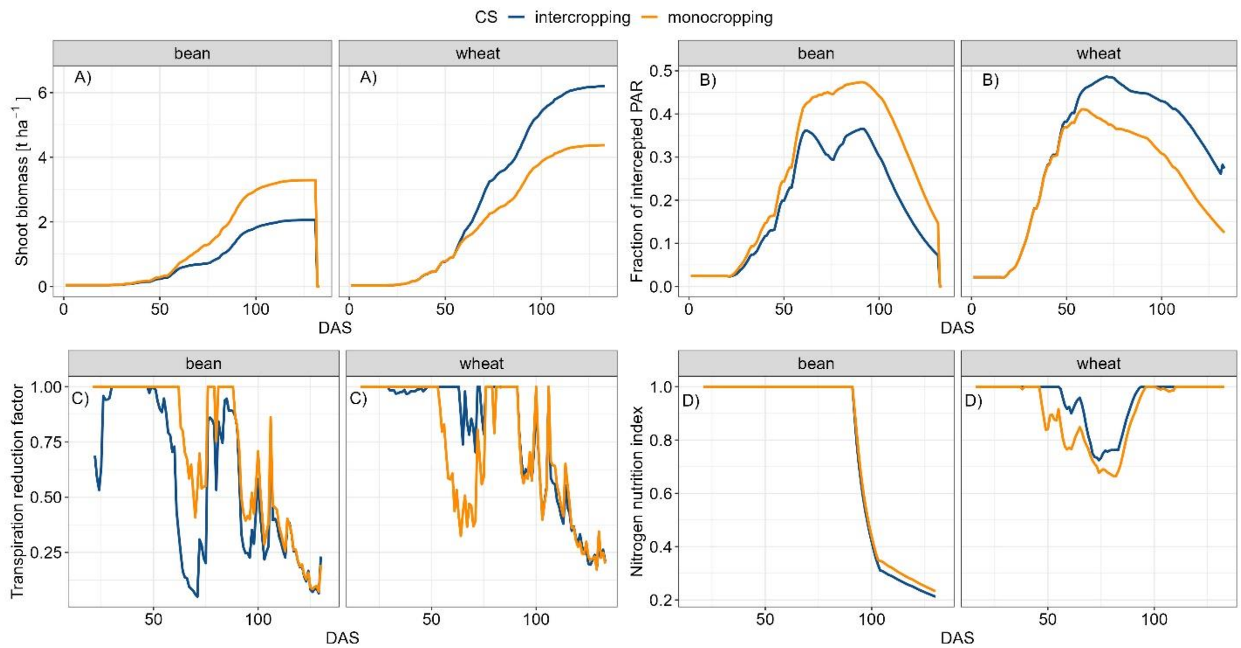

Figure 4.4. Simulated daily dynamics for the CKA2020 environment (high soil N and low rainfall) for both cropping systems (CS). A) daily shoot biomass; B) fraction of intercepted photosynthetically active radiation (PAR), C) transpiration reduction factor (TRANRF) and D) nitrogen nutrition index (NNI) 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.

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

Resource acquisition <0.5 and resource use efficiency < 1 for faba bean were observed under this condition (low N and low precipitation). In contrast, for spring wheat, the partial ratio of resource acquisition > 0.5 and use efficiency was also > 1 (Table 7). spring wheat increased water uptake in intercrop, while faba bean takes up less water. But total water uptake was the same in intercrop as the average of the monocultures. Simply, there was the transfer of water uptake from faba bean to spring wheat. On the other hand, there was an increase in total N uptake from soil (Table 7). The radiation interception and water uptake in intercrops were nearly similar to that of the average of the monocultures (the ratio is nearly 1) (Table 6). However, the N uptake (NAR=1.22), radiation use efficiency (1.15), and water use efficiency (WUER=1.12) of intercrops are larger than that of the average of the monocultures.

Table 4.7. 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 Mono culture	Faba bean Inter crop	Faba bean Partial ratio[1]	Spring wheat Mono culture	Spring wheat Inter crop	Spring wheat Partial ratio	Both species Mono culture	Both species inter crop	Ratio[2]	Indices
Grain yield	2.22	0.70	0.32	2.80	2.22	0.79	5.02	2.80	1.11	LER[3]
Water uptake	223.70	77.70	0.35	243.60	156.75	0.64	467.30	234.45	0.99	WAR[4]
Water use efficiency	0.99	0.90	0.91	1.15	1.42	1.23	1.07	1.19	1.12	WUER[5]
N uptake	31.8	18.4	0.58	168.6	108.4	0.64	200.6	126.7	1.22	NAR[6]
Nitrogen use efficiency	6.96	3.81	0.55	1.66	2.05	1.23	2.5	2.21	1.13	NUER[7]
Soil N uptake +BNF	211.2	63.16	0.30	168.6	108.38	0.64	379.8	171.5	0.94	NAR_{BNF}[8]
Soil N+BNF use efficiency	1.05	1.11	1.05	1.66	2.05	1.23	1.32	1.63	1.16	$NUER_{BNF}$[9]
radiation interception	679	278.3	0.41	742.8	409.0	0.55	1421.8	687.3	0.96	RAR[10]
Radiation use efficiency	0.33	0.25	0.77	0.38	0.54	1.44	0.35	0.41	1.15	RUER[11]

[1] the ratio of the given species in the mixture to its respective monoculture [2] the ratio of intercrops to monocultures, [3] land equivalent ratio; [4] water acquisition ratio; [5] water use efficiency ratio; [6] N acquisition ratio; [7] N use efficiency ratio; [8] N acquisition ratio including biologically fixed N; [9] N use efficiency ratio including biologically fixed N; [10] radiation acquisition ratio; [11] radiation use efficiency ratio.

Simulated resource uptake by soil depth and over time (WG2020)

The differences between total water uptake over the growth period between intercropping and monocultures were minor. However, post-flowering water uptake from the deeper soil layer (60-120cm) was noticeably different between monocultures and intercropping. About 68% of total intercrop water uptake was from deeper soil (60-120cm layers), but in monocultures, the share of water from deeper soil layers was only 49%. Species-wise, spring wheat in intercrop took up 28% more water compared to spring wheat in monoculture at an equivalent density. However, faba bean showed a 31% reduction in total water uptake compared to faba bean in monocultures at equivalent sowing density (Fig. 4.6A).

The soil N uptake in intercropping surpassed the average of monocultures by 26%. When considering individual species, intercropped spring wheat faced increased availability for soil N, resulting in 28% higher N uptake over spring wheat in monocultures (at equivalent sowing density) (Fig. 4.6B). Intercropped faba bean showed a 22% higher in soil N uptake compared to faba bean in monocultures. The biological N fixation in the intercropping had almost halved compared to faba bean in density-equivalent monocultures. The simulation results revealed no substantial differences in radiation interception between intercropping and monocultures. Spring wheat in intercropping intercepted about 10% more solar radiation than that of the spring wheat in monocultures. Conversely, faba bean in monocultures showed an 11% reduction in radiation interception (Fig.4.6C).

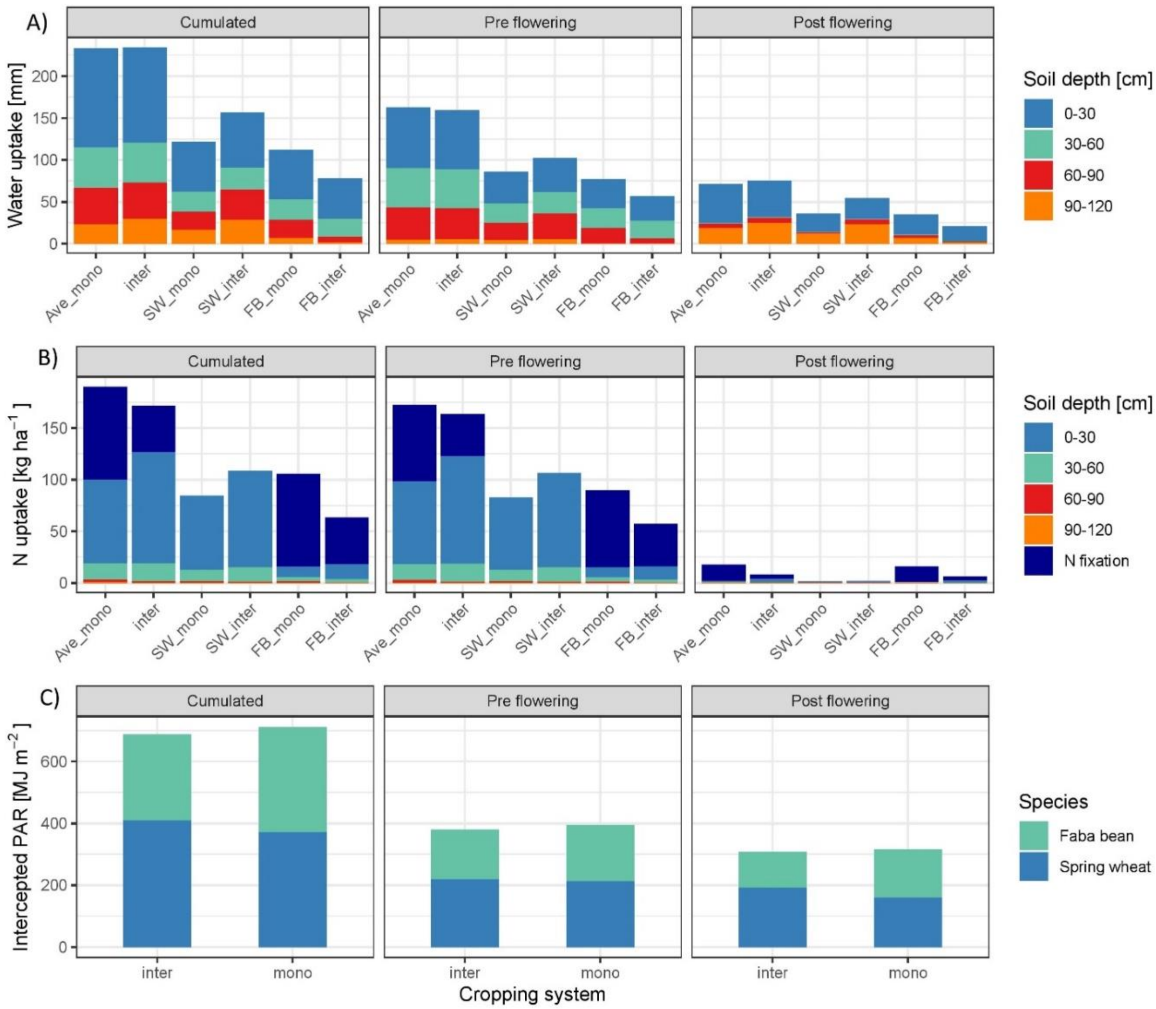

Figure 4.5. Simulated crop resource acquisition: A) water uptake B) N uptake and fixation C) radiation cumulative, from sowing to spring wheat flowering and from spring wheat flowering to harvest. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono is the average of monocultures of SW and FB; inter- intercropping of SW and FB; FB; 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.

The simulation of daily drought stress per species in sole and intercropping revealed that spring wheat showed less drought stress when grown with faba bean as compared to monoculture (Fig.4.6C). The drought stress in faba been was mostly enhanced in intercropping at faba bean emergence and after DAS 68 which was around the flowering of faba bean (Fig. 4.6C). The simulated daily plant growth and radiation interception also followed the same trends as transpiration reduction factors. Spring wheat in intercrops produced more biomass and intercepted more radiation compared to spring wheat in monocultures.

However, faba bean growth and radiation interception in intercrops was lower than in monocultures (Fig. 4.6B).

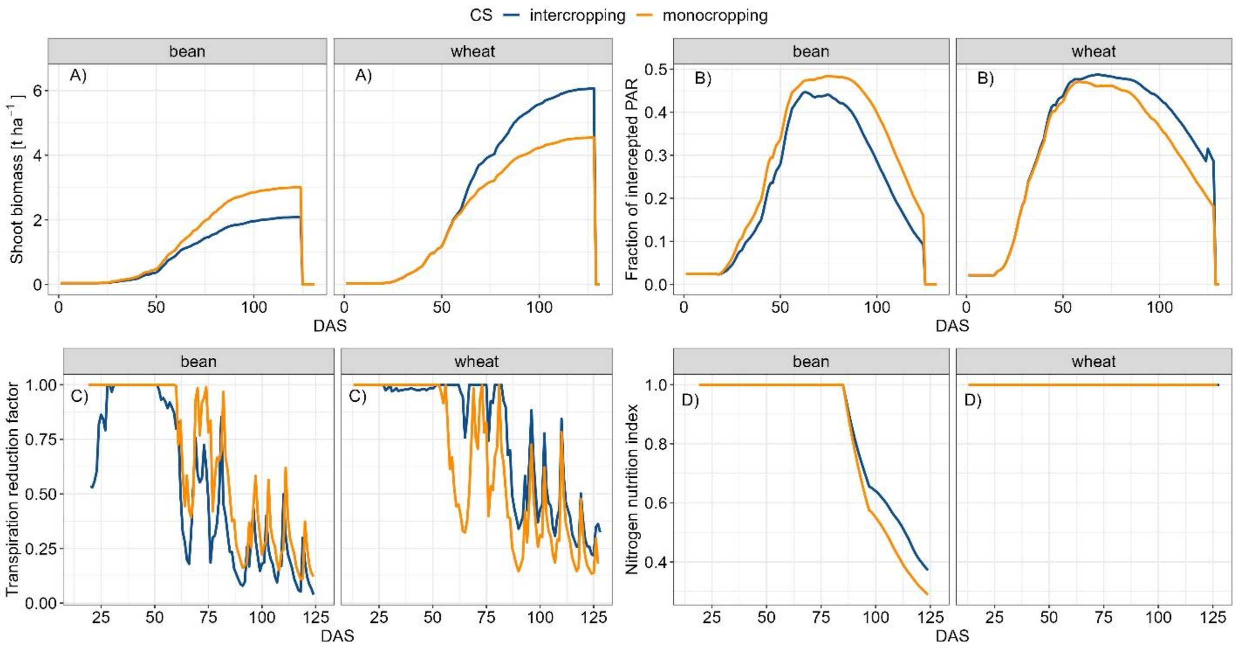

Figure 6. Simulated daily dynamics for the WG2020 environment (low soil N and low rainfall) for both cropping systems (CS). A) daily shoot biomass; B) fraction of intercepted photosynthetically active radiation (PAR), C) transpiration reduction factor (TRANRF) and D) nitrogen nutrition index (NNI) of Spring wheat (SW cv. Lennox); faba bean (FB cv. Mallory). The flowering of SW occurred at DAS 78 (WG2020), and the flowering of FB occurred at DAS 68.

4.4 Discussion

4.4.1 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 field experiments on spring wheat/faba bean intercropping collected in three contrasting environments (Paul et al. 2023, 2024; Demie et al., 2025). The study identified specific resource allocation associated with each crop species, which significantly impacted both the productivity of individual species and the overall productivity of 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 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 provides daily crop-specific resource acquisition data, which helps in understanding species interactions in intercropping under diverse conditions. Our findings indicate that the higher productivity of intercropping systems compared to monocultures is 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. In all environments, intercropping systems exhibited higher soil N acquisition compared to the average monocultures. The model results suggest an early impact of the intercropping with a legacy on faba bean growth effect due to the early dominance of spring wheat (Fig. 4.5C and 4.7C). This 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**.** Applying the 4C approach of Justes et al. (2021), spring wheat dominated the legume regarding water uptake, especially in the dry season of 2020. At WG2020, complementarity and cooperation were stronger than competition for soil N uptake and N fixation. Our finding is 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 an improved N availability.

4.4.2 Water use of monocultures and intercropping systems

Water use of intercrops is influenced by interspecific competition and species complementarity (Yin et al., 2020a). 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) reported in a simulation study that pea growth was associated with soil moisture availability in pea/barley intercropping.

The result highlights that the water consumption of monocultures and intercropping systems varied greatly due to environmental conditions and crop species. However, the total water uptake between monocultures and intercrops (for the two species together), has already been reveled in other studies (Bahia et al., 2024; Morris and Garrity, 1993) . This tendency was reflected in both observed and simulated volumetric soil water (Fig. C. S3-5), 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 result contradicts the review findings of Yin et al. (2020) who stated intercropping increases (total) water consumption compared to monocultures.

Overall, intercropping system showed slightly higher water use efficiency ratios compared to monoculture (WUER of 4-15 %) (Table 4.5-4.7) 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. However, our results show that compared to the water acquisition ratio (WAR), the water use efficiency ratio (WUER) was slightly higher, emphasizing poor (only post-flowering) spatial niche complementarity of spring wheat and faba bean. This can be explained by the small differences in rooting depth of the species Hadir et al. (2024), with most of the water uptake occurring from topsoil where both species have high root length density. 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, tends to suppress faba bean (Fig. 5 and 7). The early rapid growth of spring wheat resulted in early dominance over faba bean and legacy effect at a later stage (Paul et al., 2023). Consequently, the faba bean faces a disadvantage in intercrops compared to the faba bean in monocultures, while the opposite was observed for spring wheat. This phenomenon of rooting system in cereals over 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 respective monocultures (Fig. 4.3A). 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 a 4C approach as described by (Bedoussac and Justes, 2011; Justes et al., 2021) there is competition for water among the partners, but the degree of competition depends on environmental conditions. An evaluation of the simulated daily drought stress per species in monocultures and intercropping (Fig. 3C, 5C, 7C) 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.

4.4.3 N use of monocultures and intercropping

The intercropping of faba bean and spring wheat increased soil N uptake compared to the average of the monocultures in all environments. 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 (Table 4.5-7). On the other hand, the soil N use efficiency ratio (NUER) exceeded 1 only in low-N soils (WG2020, Table 4.5-7). 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 inorganic and atmospheric N sources by intercrop components, resulting in reduced competition for soil N (Jensen, 1996). Applying the 4C 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). 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 result 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) result 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 is controlled by growth rate), however, biological N fixation is 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 were characterized as water-limited environments and drier condition, the faba bean in intercropping showed reduced biomass growth compared to the faba bean in monoculture (Fig. 5A and 7A). Hence the faba bean the proportion of N derived through biological N fixation in intercropping was significantly reduced compared to the faba bean in monoculture. At CKA2020 which was characterized as higher soil N content and limited 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 is almost similar in intercropping and in the monocultures. (Table C.S4). This result highlights the dependency of biological N fixation on both soil N content and moisture availability. A similar finding was reported by Jensen (1996), 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. The study by Naudin et al. (2010) revealed that the N fixation in pea/wheat intercropping was lower than the monoculture due to reduced pea growth in intercropping compared to monocultures. However, in all environments, the proportion of biologically fixed per unit of biomass was higher in intercropping compared to monocultures as also revealed by (Jensen, 1996). This is primarily due to the strong competition in cereals, as already revealed in several studies (Li et al., 2011, 2009; Zhang et al., 2017).

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 intercrops 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 (Fig. 4.3D, 4.5D, 4.7D) 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. 4.2). The daily simulations of NNI 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. 4.3D). 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. 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)

4.4.4 Radiation capture in intercropping and monocultures

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 density. However, absolute radiation interception of faba bean in intercropping at CKA2021 is almost comparable to respective monocultures at equivalent density. 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, (2010) has revealed that durum wheat and winter pea intercrop 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 also have similar phenology; 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 (Fig. 4.2C, 4.4C, 4.6C). This is because the spring wheat was very competitive and captured more resources and grew vigorously, resulting in higher biomass (Fig. 3A, 5A, and 7A) and intercepted more radiation compared to the faba bean (Fig. 3B, 5B, 7B). Several studies showed that the species-specific and overall yield is depends on the partners combination (Cheriere et al., 2020; Mahmoud et al., 2022). A meta-analysis by Yu et al. (2016). on cereal/legume intercropping has shown that cereals had 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 height differs strongly, the radiation interception in intercropping can be greater than the monocultures (Gou et al., 2017; Zhang et al., 2008). Additionally, in spring wheat/faba bean intercropping, both species have short stature and relatively similar plant height, 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 a 4C approach as described by Justes et al. (2021), there is competition for radiation among the partners, but the degree of competition depends on the environmental conditions, but no complementarity among partners (Fig. S9). Therefore, the higher productivity of intercropping was not associated with an enhanced radiation capture except for CKA2021. However, species have shown differences in radiation capture due to the interception of radiation by one species in a closed stand, which goes inevitably at the expense of radiation interception by another species.

In the intercropping system, both species with a similar spatial and/or temporal niche tend to compete intensively, which in turn results in reduced biomass and grain yield production of the relatively weaker species while potentially enhancing the growth and productivity of the dominant species (Vandermeer, 1992). Despite the reduced yield of the weaker species, the overall productivity of the intercropping system can still surpass that of monoculture's yield, primarily due to the higher yield contribution of the dominant species.

4.4.5 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 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. Resource acquisition, competition, and complementarity can vary greatly depending on the characteristics of the crops involved (Mahmoud et al., 2022; Stomph et al., 2020). To develop a more comprehensive understanding of resource use efficiency and interactions in intercropping, future studies should explore a broader range of species combinations. This would help in forming a general framework for 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 crop systems.

4.5 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

Dereje T. Demie: Methodology, Visualization, Data curation, Writing- Original draft preparation. **Daniel Wallach:** Methodology, Writing- Reviewing and Editing. **Thomas F. Döring:** Data curation, Writing- Reviewing and Editing. **Frank Ewert:** Methodology and Funding Acquisition. **Thomas Gaiser:** Writing- Reviewing and Editing. **Madhuri Paul:** Data curation, Writing- Reviewing and Editing. **Ixchel M. Hernández-Ochoa:** Conceptualization and Writing- Reviewing and Editing. **Sabine J. Seidel:** Funding Acquisition, Conceptualization, Methodology, Data curation, Writing- Original draft preparation.

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Chapter 5

5 General Discussion

5.1 The trait combinations in cereal/legume intercropping

The selection of appropriate partner genotypes of the species in intercropping is crucial for enhancing the system's performance (Davis and Woolley, 1993; Demie et al., 2022a; Holland and Brummer, 1999; Paul et al., 2024). This is primarily because the used intercropping combination should enhance complementarity and cooperation between the partners while minimizing competition, often through niche differentiation (Davis and Woolley, 1993; Francis et al., 1976; Smith and Zobel, 1991). The analysis of published studies on cereal/legume intercropping showed that most cases had significant interactions between cereal and legume genotypes and cropping systems (Chapter 2, Table 2.4**)**. Specifically, 75% of the studies reporting genotype × cropping system interactions found them essential. This indicates that genotype performance depends on the cropping system: a genotype that performs well in monoculture may not necessarily be the best in an intercropping system, and vice versa (Moutier et al., 2022). Contrastingly, the study by Paul et al. (2024), who evaluated twelve entries of spring wheat and two faba bean cultivars, revealed that there was no significant main effect of spring wheat and faba bean cultivars on the total grain yield in the mixture. The possible explanation for this disparity is that the cultivars used in the experiment were similar in phenology and morphology because the cultivars are bred for monocultures, and there is a lack of cultivars to select for intercrops (Bourke et al., 2021; Louarn et al., 2020).

The reason behind these differences in genotype cropping system interaction in a given environment is the contrasting characteristics of genotypes of species in terms of phenology and intercropping, which plays a vital role in the complementarity of the species (Gebeyehu et al., 2006; Hauggaard-Nielsen and Jensen, 2005). For instance, different genotypes of a given species may have varying phenology, with some maturing earlier and others later (days to maturity). Combining two species with different phenology can enhance temporal complementarity in resource use, by reducing competition for resources simultaneously (Ntare, 1989). However, it is essential to note that this type of combination (complete mixture) can complicate harvesting, as one crop may be ready for harvest while the other is not. Looking at the corresponding monocultures, the plants in monocultures compete for the same resources at the same time (no niche differentiation), which enhances competition compared to complementarity. However, the intercrop competition is relatively relaxed, considering that the inter-specific (two species) competition is more minor than the intra-specific competition (Garcia-Cardenas et al., 2024).

However, testing various genotypes by genotype interaction in diverse environments is a complex task, and the field experiment capacity is limited. A process-based crop model can assist in the rapid screening of several genotypes for various environments (Demie et al., 2025; Gou et al., 2017; Vezy et al., 2023). However, a prerequisite is developing and testing an intercrop model that captures the species and genotype effects well, which is a current research gap. In (Chapter 3) we tested the capability of a new process-based intercrop model to capture the genotype effect (Chapter 3, Table 3.4). The model captured intercrop effect differences between two spring wheat cultivars in a given environment. Consequently, the model can assist in making informed choices in selecting spring wheat cultivars, optimizing their suitability for intercropping scenarios, and potentially enhancing overall grain yields (Brooker et al., 2015). This should be of particular interest as a substantial objective of simulation of intercrops is to improve the understanding of major processes and to develop a rapid screening tool for diverse species and cultivars under various environments. Such models can also be used to test different management strategies and to interpret experimental results, especially given the inherent complexity of field experiments.

5.1.1 Current research gaps in genotype trait evaluation

Most studies evaluating genotype-cropping system interactions primarily focus on assessing different cereal and legume genotypes for their combining ability (Annicchiarico et al., 2019; Moutier et al., 2022). However, only a few experiments investigate the general mechanisms underlying genotype-cropping system interactions (Nelson and Robichaux, 1997; Ntare, 1989; Odo, 1991; Santalla et al., 2001). Among the 69 studies analyzed (Chapter 2), only 20 (29%) articles indicated that the contrasting traits of genotypes contribute to intercropping performance. Among the range of niche complementarity mechanisms reported in cereal-legume intercropping, differences in days to maturity and growth habits between species are often highlighted (Chapter 2, Table 2.6). Despite ample evidence of genotype-cropping system interactions, most research has focused on species-level mechanisms, overlooking cultivar-level interactions.

For instance, belowground complementarity is one of the prominent features of cereal/legume intercrops (Hadir et al., 2024). Root growth and, thus, water and nutrient uptake are the most critical factors in temporal and spatial complementarity (Hauggaard-Nielsen and Jensen, 2001). Root system distribution in time and space can partly explain competition. For instance, barley roots grew faster than pea roots (Hauggaard-Nielsen et al., 2001) and started nutrient acquisition earlier. Different genotypes of cereals or legumes could have different root characteristics, which influence the species' competitive ability. Streit et al. (2019) reported that mixtures of winter faba bean and winter wheat over yielded more belowground than aboveground. Yet, root mass overyielding depends on the cereal cultivars, sowing depth, and sowing density (Hadir et al., 2024), emphasizing the potential of cultivar choice. Studying resource acquisition and the use efficiency of different genotypes in intercrops through field experiments can be complex and tedious. A process-based simulation model offers a promising approach to exploring possible resource use and acquisition interactions under diverse environments (Chapter 4). Legumes provide N to the agroecosystem through their exclusive capability to fix atmospheric N in a symbiotic relationship with soil rhizobia. Still, different genotypes of a legume species might have different capabilities in nodulation (Rodiño et al., 2011). The symbiotic association of different legume genotypes and their rhizobia could also differ. Hence, future research needs to address how different genotypes of legumes respond to cropping systems, particularly in biological N fixation. Pest and disease resistance is one of the most essential advantages of intercropping (Finckh et al.,2020). However, only a limited number of studies have considered genotype differences concerning pest and disease resistance in cereal/legume intercropping. Most importantly, it is critically important to consider the social acceptance of genotypes for wider adaptability of intercropping systems. Yet, there are only a few studies that evaluate the socio-economic importance of genotypes of both cereals and legume species. Different nutritional quality parameters of the genotypes are not included in most of the articles and hence could affect the acceptance of intercropping by farmers (Timaeus et al., 2021). The forage quality differences of legume genotypes were mostly ignored, and the number of studies on this topic is very limited (Javanmard et al., 2009). The consumer and market preference of different cereals and/or legume genotypes is also important in selecting genotypes for intercropping. The involvement of farmers in the evaluation of genotypes in intercrops might assist in understanding farmers' preferences for genotypes (Goshime et al., 2020). Overall, morphological and phenological traits, root traits among others, differences in water nutrient acquisition of different genotypes, and advantages in pest and weed suppression deserve attention to understand the mixing ability of different genotypes. Future research should consider pedigree analysis, functional genes, or key traits when selecting varieties tested in intercropping (Rubiales et al., 2023). This highlights a need for re-designing breeding programs to accommodate inter-specific interactions, as genotypes bred for monocultures are not the best adapted to the intercropping system (Bourke et al., 2021). One breeding approach highlighted by Wolfe et al. (2021) suggests shifting the focus from improving the monoculture yield of individual crops to optimizing multiple interacting species and genotypes. This joint selection strategy aims to enhance cropping systems' overall performance across time and space. The results show the importance of genotype selection for better cereal/legume intercropping. Furthermore, the assessment highlights the hitherto unrevealed aspects of genotype evaluation for intercropping systems that must be tackled.

5.2 Niche complementarity in cereal/legume intercropping

In plant ecology, the niche is defined by axes of resource uses and environmental conditions within which the population of plant species can maintain its coexistence (Lu et al., 1989; Silvertown, 2004). According to niche theory formulated by Vandermeer (1972) to explain competition and coexistence of different species, if the niches of two species are similar, the two species cannot coexist in the same community over years because of intense interspecific competition for resource. However, if their niches are different, the species in question can coexist and be productive due to the complementary use of resources (Silvertown, 2004). The niche of the two species in the mixture can be separated in time by a reduced co-growth period (temporal) or space (spatial). In the context of intercropping, the species involved should have a minimal niche overlap; otherwise, if the two species have sufficiently the exact niche requirement, they compete with one another intensively (Vandermeer, 1989). In agronomic terms, the weaker species might not be productive compared to the corresponding monocultures, and/or the productivity of intercropping can be below expected (Döring and Elsalahy, 2022). Selecting cereal and legume genotypes that minimize niche overlap and enhance complementary resource use can be crucial for improving land use efficiency (Demie et al., 2022).

5.3 What determines the yield advantage of cereal/legume intercropping?

The yield advantage in intercropping compared to monocultures arises from two factors: 1) the enhanced acquisition of resources such as water, N, and light compared to monocultures, and/or 2) the more efficient conversion of these captured resources into biomass and yield due to facilitated interactions in intercropping systems (Stomph et al., 2020).

5.3.1 Is yield advantage associated with enhanced resource acquisition?

Enhanced resource acquisition in intercrops predominantly occurs when the two species have a reduced niche overlap either in time or in space and, as a result, reduced competition (Bedoussac et al., 2015). The model-based analysis of intercrops under three contrasting environments showed that, under all environments, intercrops have demonstrated a higher N accumulation compared to monocultures (Chapter 4, Table 4.4-6). The higher N acquisition of intercrops was mainly due to intercrop components' complementary use of inorganic and atmospheric nitrogen sources, resulting in reduced competition for soil N (Jensen, 1996). 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). Contrastingly, the N-use efficiency of intercrops was higher than monocultures only in low-N soils (Chapter 4, Table 4.4-6) at an organically managed research site. This highlights the fundamental connection between intercrop productivity and N availability rather than a change in soil N and biologically fixed N use efficiency. Cereals performed better under low N growing conditions when grown in intercrops with legumes than monocultures because of the reduced competition for nitrogen (Stomph et al., 2020; Yu et al., 2016).

When resources are substantially limited, cereals are very competitive due to their deeper rooting system accessing subsoil resources, hence likely suppressing legumes. This phenomenon of vigorous rooting system of cereals suppressing intercropped legume was reported by Corre-Hellou et al. (2007). Under this conditions the legumes' biomass production and the total atmospheric nitrogen fixation was reduced. Nevertheless, due to the competitive influence of cereals, the nitrogen fixation per produced biomass is higher than the nitrogen fixation of legumes in monocultures (Rodriguez et al., 2020). However, the degree of competition is minimal under sufficient soil water and nutrient availability. Consequently, the biomass of intercropped legumes is equal to or higher than expected from monocultures, which enhances biological nitrogen fixation (Chapter 4, Fig. 4.2). These differences in niche occupancy, based on soil resource availability, lead to complementary nitrogen use, improving acquisition and increasing intercrop performance (Xing et al., 2023; Yu et al., 2016). Our findings have important implications for introducing legumes into managed cropping systems or selecting species combinations with different functional groups when designing cropping systems and were demonstrated as a promising approach for sustainable managed crop production.

Beyond that, we have seen that there is minimal (under high precipitation conditions) or no (under limited water availability) enhanced water and light acquisition (Chapter 4) in intercrops compared to the averages of the two monocultures. In such cases, there is only a simple transfer of water and radiation from faba bean to spring wheat due to higher competitive capacity. This is due to niche overlap (crop resource use over time and space). In the intercropping system in which both species have a similar spatial and/or temporal niche, they tend to compete intensively, which, in turn, would result in reduced biomass and grain yield production of the relatively weaker species while potentially enhancing the growth and productivity of the dominant species (Vandermeer, 1989). Despite the weaker species' reduced yield, the intercropping system's overall productivity can still surpass that of monoculture's yield, primarily due to the higher yield contribution of the dominant species. Overall, the result revealed that there is a small (high precipitation) or no (low precipitation) increase in light and water acquisition in intercrop. Still, there is a significant increase in N uptake in all cases, highlighting the generic importance of N to cereal/legume intercrop productivity.

5.3.2 Is yield advantage associated with enhanced resource conversion efficiency?

Resources conversion efficiency is defined as the amount of biomass or grain yield produced per unit of captured resources (Hodapp et al., 2019; Ullah et al., 2019). It is given for a defined area as:

Conversion efficiency =grain yield or biomass /captured resources

In cereal/legume intercropping, there are varying results regarding resource use efficiency, particularly in radiation and water use efficiencies (Mao et al., 2012; Stomph et al., 2020). It was also highly influenced by the design of the intercropping system (i.e., relay intercropping or fully mixed intercropping). We found that there is slightly higher water and radiation use efficiency in intercrops compared to monoculture and only higher soil and biologically fixed N use efficiency under low soil (organic site) (Chapter 4, Table 4.4-5). Our simulation result highlights that there are only very small differences in resource conversion efficiency between spring wheat/faba bean intercropping systems and monocultures. This result does not fully agree with a recent study: Bahia et al. (2024) reported that water use efficiency positively correlates with nitrogen use efficiency. Pea–barley intercropping yield advantages can be attributed to improved water use efficiency and N. It should be noted that resource conversion efficiency is genetically controlled and environmentally influenced; if the environment (i.e., intercropping system) is insufficient to influence the plant's physiological process, there will be no change in resource conversion efficiency.

5.4 Current state and limitations of process-based intercrop model

Process-based crops models can be used to study the influence of climate variability, soil, or management options (Asseng et al., 2019; Chenu et al., 2017; Seidel et al., 2019) and for real-time simulation-based crop management (Seidel et al., 2016).

Currently, several crop models simulate mixed cropping systems has been published focusing on for yield and water use (Chimonyo et al., 2016; Miao et al., 2016; Pinto et al., 2019) light sharing (Munz et al., 2014; Tsubo et al., 2005), nitrogen transport and uptake (Shili-Touzi et al., 2010; Whitmore and Schröder, 2007), and weed suppression (Baumann et al., 2002) One approach to simulate intercrop effect is the light sharing among the partners in intercrop. Pierre et al. (2023) developed an approach to allow the model Decision Support System for Agro technology Transfer (DSSAT) to run two crop species in intercropping. Berghuijs et al. (2020) calibrated and tested the Agricultural Production Systems sIMulator (APSIM) for wheat-faba bean intercrops, and Vezy et al. (2023) proposed a set of generic formalisms for the simulation of intercrops, with an implementation in Simulateur mulTIdiscplinaire pour les Cultures Standard (STICS). Yu et al. (2024) tested a simple routine capturing light competition in the Model for Nitrogen and Carbon in Agroecosystems (MONICA). Nevertheless, the previously published studies on intercrop models have used relatively small datasets, predominantly on aboveground plant growth and performance, to evaluate the model.

These studies often ignored different management strategies, such as species and cultivar choice or sowing densities. If the intercrop model is not tested for capturing a mixture effect of different genotypes, it might have limited application for testing different genotype trait combinations for informed choice on selecting genotypes for intercropping. Most importantly, none of these studies have tested the intercrop model in capturing root growth and dynamics. In Chapter 3, we tested the model for capturing different intercropping management options, including genotype as well as root growth and dynamics of each species in intercropping. In Chapter 2, it has been revealed that intercrop performance depended on the genotype combination. However, evaluating a higher number of genotypes and their traits under different environments and management under field conditions is costly and laborious. To address these challenges, process-based crop simulation models are widely recognized tools to examine cause-and-effect relationships in crop production. Virtual experiments using crop models can contribute to process understanding and cropping system design (Malézieux et al., 2009).

Nevertheless, the current intercrop models have shortcomings in representing some of the ecological processes involved in cereal/legume intercrops. None of the intercrop models considers facilitation, one of the ecological processes involved in cereal/legume intercropping. For example, a study by Li et al. (2007) showed that faba bean can mobilize soluble phosphorus in soils through rhizosphere acidification and carboxylate exudates, enhancing soil phosphorus availability to the benefit of both faba bean and maize. Despite its complications, it would be worthwhile to consider such an ecological process to mimic what happened in actual crop fields. Intercrops are frequently reported to reduce weed infestation compared to monocultures. However, most intercrop models have overlooked weed competition, except for a recent study by Lebreton et al. (2024). This study used an individual-based 3D model, FLORSYS, which simulates daily crop-weed seed and plant dynamics. Regardless of its substantial importance, below-ground competition, which heavily depends on root biomass, remains underrepresented in many intercrop models. This issue is addressed in Chapter 3 despite its simplifications, where we simulated and tested the intercrop effect on roots. This study is among the first to specifically examine the below-ground dynamics of root growth and resource uptake in in-row intercropping systems, offering further insights into competition and complementarity effects in these systems (Demie et al., 2025). It must also be considered that crop growth models do not simulate many of the hoped-for benefits of intercropping, such as increased biodiversity or reduced weed populations.

It was observed that different intercrop models implement various modeling approaches. For instance, in STICS, plant height simulation is based on the leaf area index and the canopy extinction coefficient (k) (Vezy et al., 2023). This simplified approach neglects some crucial factors, such as temperature and stress, although these factors are considered in simulating the leaf area index. We attempted a similar approach, but unfortunately, it did not yield satisfactory results. Consequently, we developed a new modeling approach for plant height that incorporates temperature, stress factors (drought and nitrogen), and plant growth rate (Demie et al., 2025). This approach produced a very good fit for the observed data, emphasizing the need for continuous improvement of intercropping models to capture major processes effectively. Yet the new intercrop model implemented in SIMPLACE also has some limitations. For instance, the effect of sowing density was poorly simulated compared to the observed data. The model's approach, which relies on considering only initial crop dry weight (seed weight) and the number of plants that emerged per m^2 (model parameter RINPOP), which mainly affects root growth as a proxy for sowing density effects, may be overly simplistic and inadequate in capturing the true complexity of density-dependent processes in plant growth. Therefore, improved equations need to be implemented in the model to simulate the sowing density effect in intercropping. Overall, while crop models crop models are always a simplified representation of reality they should take into account relevant plant and soil processes. Balancing the simplicity of the intercrop model with consideration of essential features is significantly crucial.

5.4.1 How does the process-based crop model support intercropping research?

The numerous processes and mechanisms involved in intercrops highlight the need to deal with their complexity by combining concepts from diverse disciplines such as agronomy, physiology, and ecology. Additionally, there is a lack of information regarding intercropping management, such as crop species genotype selection, combination (Demie et al., 2022), spatial arrangement, and sowing proportion, which is a difficult task in field experiments and often requires a modeling approach (Gaudio et al., 2019). Several studies have shown that intercrop performance depends on the genotype combination (Annicchiarico and Filippi, 2007; Demie et al., 2022). It is recommended that research evaluates a higher number of genotypes and their traits on various sites and under different climate and management conditions. Testing all possible combinations (genotype × genotype × environment × management) of intercropping in field trials is impossible. However, evaluating a high number of genotypes and their traits under different environments and management under field conditions is costly and laborious. The complex interactions in intercropping can be disentangled by process-based agroecological models robustly calibrated using field experiment data, which can help to identify the relevant influencing factors of intercrop performance. Process-based crop simulation models are widely recognized tools for examining cause-and-effect crop production relationships. Virtual experiments using crop models can contribute to process understanding and cropping system design (Malézieux et al., 2009). The intercrop model can assist intercropping research in three broad ways.

Firstly, the intercrop model can assist in breeding and genotype selection for intercropping. One of the objectives of simulating intercropping is to conduct a rapid test of different trait combinations and identify the most important traits for breeding or selection. However, the prerequisite is that the model should incorporate the relevant plant features and mechanisms driving interspecific plant-plant interactions and rely on parameters closely linked to the traits that breeders would be interested in (Weih et al., 2022). In addition, the model should be calibrated and validated with field data that are assessed in intercrops, including species' different genotypes and crop management, such as sowing density and fertilizer (Rubiales et al., 2023). These measures will support the identification of system traits and plant traits that work together to maximize resource use efficiencies, mitigate loss of nutrients and environmental side effects, and obtain stable yields at lower input levels.

Secondly, intercrop models can be scaled up to regional or national levels, allowing for forecasts of intercropping performance compared to monocultures, as well as evaluations of economic and environmental efficiencies. Most importantly, scaling up these models aids in identifying species or genotype combinations that optimize intercropping performance under specific soil and weather conditions. Our preliminary results show that root traits, particularly rooting depth, have a more robust interaction effect with precipitation than other traits, such as plant height, in a given environment in a high rainfall growth period, higher intercropping performance achieved under conditions of low nitrogen input when tall and shallow rooting depth spring wheat are intercropped with relatively short but deeper rooting faba bean cultivars. However, in low rainfall conditions, higher intercropping performance can be achieved as long as the species' rooting depth differences are high enough for spatial complementarity of water use, regardless of which species has a deeper rooting system (Demie et al., 2024). This underscores the importance of selecting appropriate genotypes and management practices for specific environments, a process that intercrop models can effectively support, given the limitations of field experiments. The intercrop model can also be employed to assess the impact of climate change on crop production. This is particularly valuable for comparing intercropping systems with other cropping systems, such as monocultures and crop rotations, subsequently assisting in making informed decisions to adapt resilient systems to specific conditions.

Thirdly, intercrops can assist in interpreting field experiment results and simulate a complex process, consequently assist in optimizing intercrop management. Despite the undeniable advantages of studying different methods, such as resource acquisition and use efficiency in crop mixtures via field experiments, this approach poses a challenge due to the inherent complexity of underlying mechanisms. 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. However, not all input is converted to biomass or grain yield. Despite its simplifications, calibrated and tested process-based agroecosystem model simulations offer a promising approach to separating the actual daily crop-specific consumption of different resource uses (over depth) and exploring possible interactions for resource use and acquisition under different environments (Stomph et al., 2020). Here, the prerequisite is that the model sufficiently captures both below-ground and above-ground competition and complementarity without over-complication. The model has to be capable of explicitly simulating interspecific interactions and plant plasticity due to competition. This can be achieved by rigorously testing the model for capturing the mixture effect without re-calibration for intercropping (Demie et al., 2025.; Vezy et al., 2023). In (Chapter 2) it was revealed that different species exhibited different land-use efficiencies in the different design (additive vs. replacement) types, with finger millet having the highest land-use efficiency among cereals (Fig. 2.4). Evaluating which species, genotype combinations, and crop management are most effective can be a complex task. Still, this process can be disentangled using crop models.

5.5 Concluding remarks

This thesis explores the role of genotype, field design, and environments in cereal/legume intercropping systems. The result highlights that judicious choice of genotype combination in cereal/legume is indispensable for enhancing land use efficiency. However, the lack of data on traits and genotypes' effects on intercropping performance demands further efforts, such as including more genotypes in evaluation, to improve breeding and better field arrangements for intercropping systems. Nevertheless, experimental capacities are limited to exploring the wide range of meaningful factor combinations to optimize intercropping systems. Despite its simplifications, the calibrated and evaluated model is a promising tool to simulate the effects of intercropping systems and, thus, support their design. This should be of particular interest as such models can help interpret experimental results regarding crop growth dynamics and resource acquisition. The assessment of resource acquisition and use efficiency by employing a calibrated and tested intercrop model indicated that increased productivity of intercropping systems compared to monocultures was primarily driven by improved resource acquisition, particularly N uptake, and enhanced water use efficiency. However, the extent of these benefits was influenced by environmental conditions. Hence, designing a site-specific spring wheat/faba bean intercropping system enhances the availability of N and use efficiency, which helps minimize the need for excessive N input. Process-based crop models are valuable tools for exploring management options for the intercropping system by assisting in identifying essential resources and interaction mechanisms among environmental resources as field experiment capacity is limited. Crop models can be an important aid in intercrop design but will need to be coupled with relevant plant features and mechanisms driving interspecific plant-plant interactions in the model. These measures will support the identification of system traits and plant traits that boost complementarity to maximize resource use efficiencies and obtain stable yields at lower input levels. However, the shortcomings of using a soil-crop model to design intercropping systems must be kept in mind. It must also be noted that crop models do not simulate many benefits of intercropping, such as increased biodiversity or reduced weed populations. Future research aims to address the mechanisms underlying performance differences among different genotypes. Additionally, improvements to the intercrop model are needed to capture the key processes within intercropping systems better.

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Appendix A: supplementary material for Chapter 2

Table A. S1. Detailed list of publication search terms

Cereals genotype evaluation intercropping, Cereals genotype evaluation mixed cropping, Cereals genotype evaluation mixture,
Legumes genotype evaluation intercropping, Legumes genotype evaluation mixed cropping, Legumes genotype evaluation mixture,
Barley genotype evaluation intercropping, barley genotype evaluation mixed cropping, barley genotype evaluation mixture,
Hordeum vulgare genotype evaluation intercropping, *Hordeum vulgare* genotype evaluation mixed cropping, *Hordeum vulgare* genotype evaluation mixture,
Maize genotype evaluation intercropping, Maize genotype evaluation mixed cropping, Maize genotype evaluation mixture,
zea mays genotype evaluation intercropping, *zea mays* genotype evaluation mixed cropping, *zea mays* genotype evaluation mixture,
Wheat genotype evaluation intercropping, wheat genotype evaluation mixed cropping, wheat genotype evaluation mixture,
Triticum aestivum genotype evaluation intercropping, *Triticum aestivum* genotype evaluation mixed cropping, *Triticum aestivum* genotype evaluation mixture,
Oat genotype evaluation intercropping, Oat genotype evaluation mixed cropping, Oat genotype evaluation mixture,
Avena sativa genotype evaluation intercropping, *Avena sativa* genotype evaluation mixed cropping, *Avena sativa* genotype evaluation mixture,
Sorghum genotype evaluation intercropping, sorghum genotype evaluation mixed cropping, sorghum genotype evaluation mixture,
Sorghum bicolor genotype evaluation intercropping, *Sorghum bicolor* genotype evaluation mixed cropping, *Sorghum bicolor* genotype evaluation mixture,
Millet genotype evaluation intercropping, millet genotype evaluation mixed cropping, millet genotype evaluation mixture,
(*Eleusine coracana*) genotype evaluation intercropping, (*Eleusine coracana*) genotype evaluation mixed cropping, (*Eleusine coracana*) genotype evaluation mixture

Table A. S2. Countries of cereal/legume experiment conducted

Country	No. of studies	Country	No. of studies
Australia	1	Ghana	1
Burkina Faso	1	Greece	1
Canada	4	India	4
China	6	Iran	2
Colombia	2	Italy	1
Costa Rica	1	Ivory Coast	1
Côte d'Ivoire	1	Kenya	2
Denmark	2	Niger	3
Egypt	2	Nigeria	6
UK	4	Poland	1
Ethiopia	5	South Africa	1
Finland	1	Spain	4
France	2	Tanzania	2
Germany	3	USA	5

Table A.S3. Analysis of variance of LER across cereal species and design

Source	DF	Sum of Square	Mean Square	F Value	Pr(> F)
Cereal	3	0.7459	0.2486	3.97	0.0089
Design	1	1.1171	1.1171	17.82	0.0000
Cereal:Design	3	0.5668	0.1889	3.01	0.0311
Error	208	13.0425	0.0627		
Total	215	15.4724			

Table A. S4. Pairwise Mean Comparison of cereal species within each two designs. Tukeys's Honest Significant Difference (HSD) Test, Alpha = 0.05

Cereals	design = additive means:	group	design = replacement means:	group
maize	1.2759	b	1.1872	a
millet	1.6675	a	1.2326	a
oat	1.3411	b	1.1266	a
sorghum	1.4124	b	1.2560	a

Table A. S5. Analysis of variance of LER across legume species and design

Source	DF	Sum of Square	Mean Square	F Value	Pr(> F)
Legumes	6	5.2348	0.8725	18.09	0.0000
Design	1	0.0000	0.0000	0.00	0.9867
Legumes:Design	5	0.3626	0.0725	1.50	0.1894
Error	227	10.9450	0.0482		
Total	239	16.5425			

Table A. S6. Pairwise Mean Comparison of legumes species Tukeys's Honest Significant Difference (HSD) Test, Alpha = 0.05

Legumes	means	group
common bean	1.19	b
common vetch	1.24	b
cowpea	1.17	b
groundnut	1.24	b
pea	1.13	b
pigeon pea	1.48	a
soybean	1.55	a

Appendix B: supplementary material for Chapter 3

Supplementary material

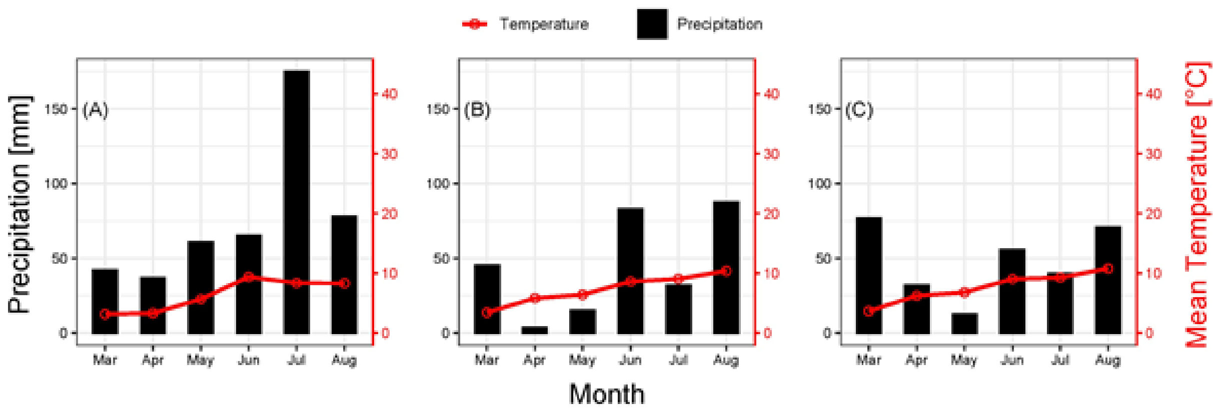

Figure B. S1. The mean monthly temperature °C and precipitation (mm) during growth period A) CKA2021; B) CKA2020 and C) WG2020.

Table B. S1. Ten SW cultivars and two mixed groups of SW cultivars with their characteristics scores based on a 1-9 scale according to the German Federal Plant Variety Office A high figure (score 9) indicates that the cultivar shows the character to a high degree and low figure (score 1) indicates that a cultivar shows the character to a low degree. Group 1 consists of cultivars lists 1- 5 and Group to includes a list from 6-10, adapted from Paul et. al. (2024).

Nr	Cultivar		Height	Ear emergence	Protein	Maturity	Brown Rust	Fusarium
1	Anabel		3	4	6	5	5	-
2	Jasmund		3	5	7	5	5	5
3	Lennox		2	5	9	5	2	6
4	Saludo		7	6	9	5	3	5
5	Sorbas		7	5	8	5	5	3
1:5	Group 1	Median	3	5	8	5	5	5
6	Chamsin		4	4	8	5	6	4
7	KWS Starlight		6	6	6	6	4	4
8	Quintus		5	6	7	5	3	3
9	Sonett		5	4	9	5	5	6
10	SU Ahab		4	5	7	5	4	5
6:10	Group 2	Median	5	5	7	5	4	4

Table B. S2. Experimental design. HD: high sowing density; LD: Low sowing density; SW: Spring wheat; FB: Faba bean

Cropping system	Row distance	No. of rows per plot	No. of seed per m^2		No. of seed per m^2	
			HD		LD	
			FB	SW	FB	SW
Sole FB	21cm	6	54	-	36	-
Sole SW	21cm	6	-	480	-	320
Intercrop	21cm	6	27	240	18	160

Table B. S3. Soil properties of Wiesengut (WG) and Campus Klien Altendorf (CKA)

location	Depth (cm)	wilting point	field capacity	saturation	bulk density	carbon	sand	silt	clay
CKA	0.15	0.13	0.31	0.48	1.30	0.78	8.32	74.91	16.77
CKA	0.30	0.13	0.30	0.42	1.50	0.88	8.32	74.91	16.77
CKA	0.45	0.16	0.31	0.40	1.56	0.59	6.49	73.12	20.40
CKA	0.50	0.18	0.32	0.42	1.50	0.43	7.29	67.83	24.88
CKA	0.60	0.19	0.32	0.41	1.53	0.40	6.67	66.44	26.90
CKA	0.70	0.20	0.32	0.40	1.57	0.37	6.21	65.70	28.09
CKA	0.78	0.20	0.32	0.40	1.59	0.31	6.70	64.06	29.23
CKA	1.00	0.19	0.32	0.39	1.61	0.26	7.95	64.75	27.30
CKA	1.25	0.18	0.32	0.39	1.61	0.26	7.95	64.75	27.30
CKA	1.75	0.17	0.32	0.39	1.61	0.26	7.95	64.75	27.30
CKA	2.00	0.16	0.32	0.39	1.61	0.26	7.95	64.75	27.30
CKA	2.10	0.15	0.32	0.39	1.61	0.26	7.95	64.75	27.30
WG	0.15	0.17	0.33	0.45	1.30	7.50	11.00	74.00	15.00
WG	0.30	0.14	0.29	0.42	1.30	5.00	11.00	74.00	15.00
WG	0.45	0.14	0.29	0.42	1.50	2.50	20.00	58.00	22.00
WG	0.50	0.14	0.29	0.42	1.70	2.00	25.00	53.00	22.00
WG	0.60	0.14	0.29	0.42	1.20	2.00	25.00	54.00	21.00
WG	0.70	0.14	0.29	0.42	1.20	1.00	25.00	54.00	21.00
WG	0.78	0.14	0.29	0.42	1.20	1.00	25.00	54.00	21.00
WG	1.00	0.14	0.29	0.42	1.20	0.30	25.00	54.00	21.00
WG	1.25	0.14	0.29	0.42	1.20	0.30	39.54	39.46	21.00
WG	1.75	0.12	0.29	0.42	1.20	0.30	39.54	39.46	21.00
WG	2.00	0.12	0.29	0.42	1.20	0.30	39.54	39.46	21.00
WG	2.10	0.12	0.29	0.42	1.20	0.30	39.54	39.46	21.00

Table B. S4. Crop parameters are set according to calibrated, observed and literature data for each species based on sole cropping and key treatments only. Ranges refer to cultivar differences.

Parameters	Unit	Description	model value	parameter	Data used for calibration
			SW	**FB**	
TDWI	g m^{-2}	initial biomass (seed weight)	15-25	25-28	measured
TSUMEM	^{0}c	temperature sum from sowing to emergence	100	160	observed date of emergence
Tsum1	^{0}c	temperature sum from emergence to anthesis	900	660	observed date of anthesis
Tsum2	^{0}c	temperature sum from anthesis to maturity	950	1000	observed date of maturity
r	-	the relative growth rate of plant	0.00567	0.00705	Berghuijs et al., (2020)
Hmax	m	maximum plant height	0.73-0.99	0.91-1.06	observed at CKA2021
MSRLD	mm	maximal seminal root elongation per day	0.0155	0.145	observed at CKA2021
DVSDLT	-	development stage above which death of leaves starts in dependence on mean daily temperature	1.3	1.3	observed data
FSTB	g m^{-2}	fraction of above-gr. DM to steams as a function of DVS DVS=0-0.54; 0.54-1	-	0.25 and 0.4	observed Leaf area index and shoot biomass
FLTB	g m^{-2}	fraction of above-gr. DM to leaves as a function of DVS" DVS=0-0.54; 0.54-1	-	0.75 and 0.6	observed Leaf area index and shoot biomass

DM- Dry matter; DVS- Development stage; Development stage 0 is emergence, 1 is flowering and 2 is maturity

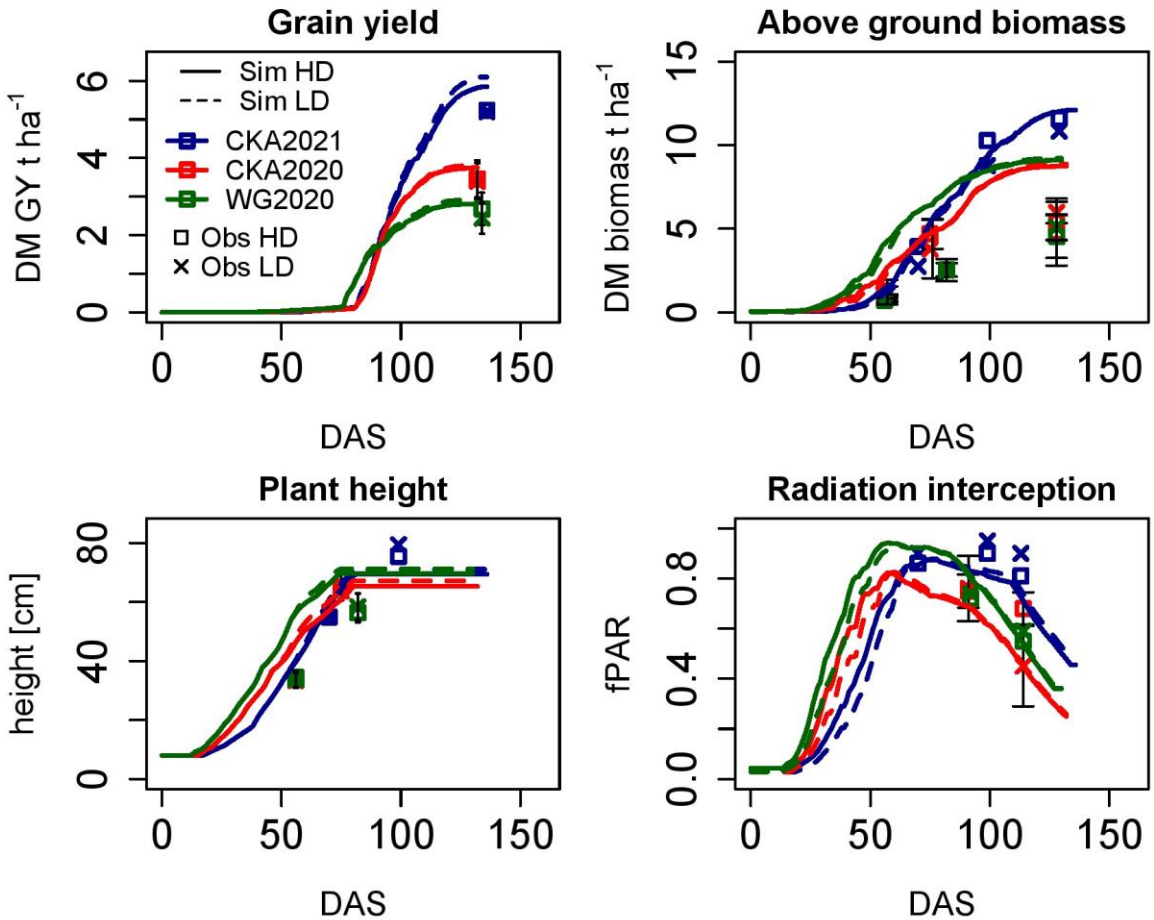

Figure B. S2. Model calibration results of SW- spring wheat cv. Lennox for three environments. The legend given in the grain yield panel is similar for all panels. The vertical line represents the standard deviation of 3 or 4 replicates for CKA2020 and WG2020. However, for CKA2021, as the treatment was not replicated, no standard error is shown. Sim-simulated; Obs-observed; HD- high density and LW- low density.

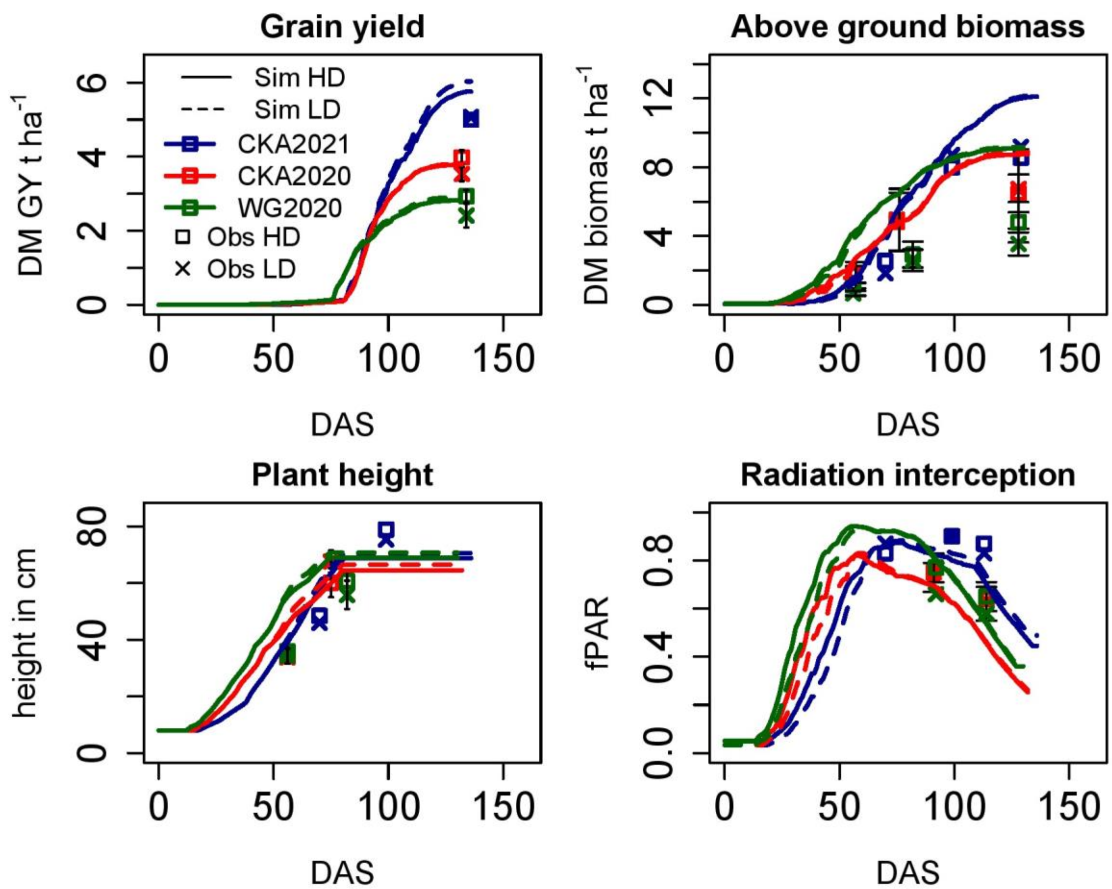

Figure B. S3. Model calibration results of SW–spring wheat cv. SU Ahab. The legends given in the grain yield panel are similar for all panels. The vertical line represents the standard deviation of 3 or 4 replicates for CKA2020 and WG2020. However, for CKA2021, as the treatment was not replicated, no standard error is shown. Sim-simulated; Obs-observed; HD- high density and LW-low density.

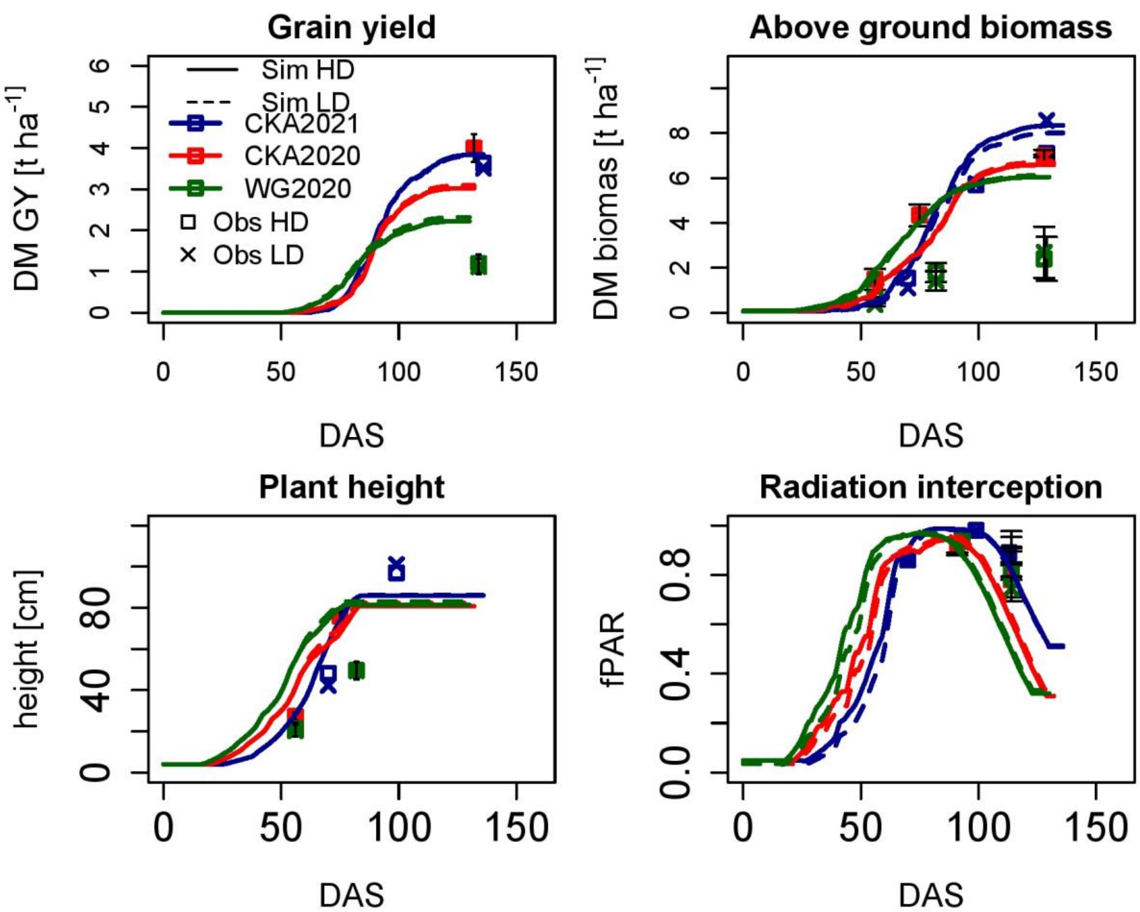

Figure B. S4. Model calibration result of FB-faba bean cv. Mallory. The vertical line represents the standard deviation of 3 or 4 replicates for CKA2020 and WG2020. However, for CKA2021, as the treatment was not replicated, no standard error is shown. Sim-simulated; Obs-observed; HD- high density and LW-low density.

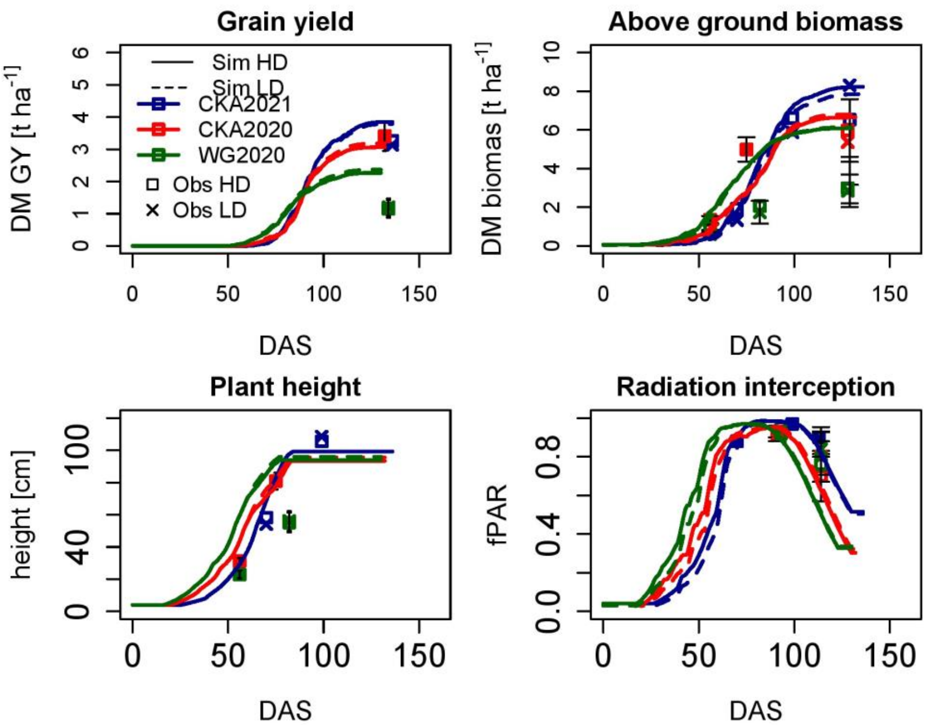

Figure B. S5. Model calibration result of FB-faba bean cv. Fanfare. The vertical line represents the standard deviation of 3 or 4 replicates for CKA2020 and WG2020. However, for CKA2021, as the treatment was not replicated, no standard error is shown. Sim-simulated; Obs-observed; HD- high density and LW-low density.

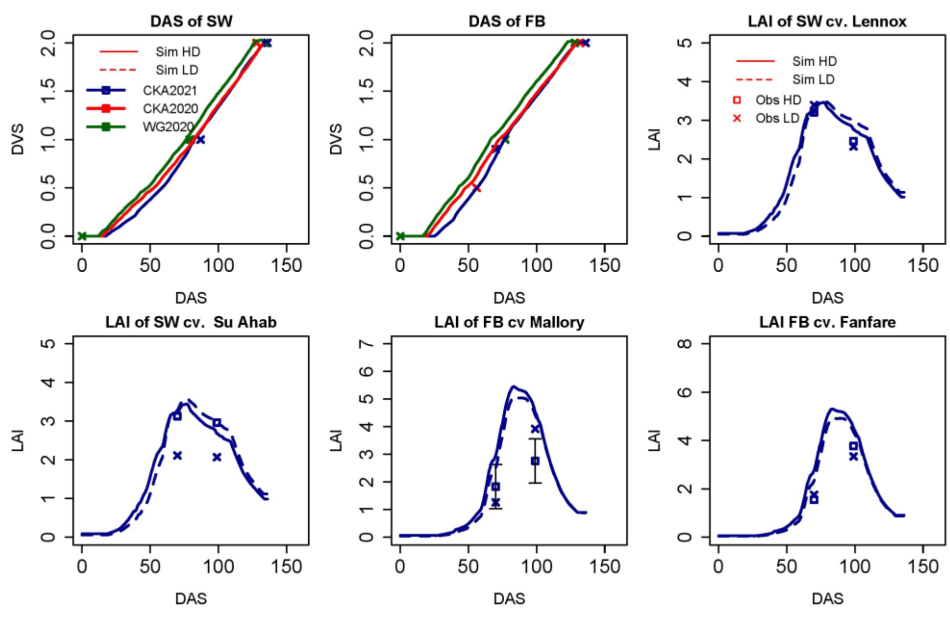

Figure B. S6 Model calibration: observed (obs) and simulated (sim) development stages (DVS, three environments) and leaf area index (LAI, only CKA2021) of SW-Spring wheat and FB- faba bean (monocultures). The vertical line represents the standard deviation of 3 or 4 replicates for CKA2020 and WG2020. However, for CKA2021, as the treatment was not replicated, no standard error is shown Sim-simulated; Obs-observed; HD- high density and LW-low density.

Table B. S5. Model evaluation of (absolute mixture effect) AME of shoot biomass (t ha^{-1}). Results are averages over cultivars of Faba bean (FB) and Spring wheat (SW) and sowing densities.

Environment	Development stage	AME	Simulated AME[1]	Observed AME	Model skill	RMSE[4] IM[2]	RMSE B[3]
CKA2020	vegetative	AME_{total}	-0.03	0.09	-0.29	0.34	0.3
		AME_{FB}	-0.08	-0.17	0.67	0.1	0.18
		AME_{SW}	0.05	0.35	0.15	0.38	0.41
	flowering	AME_{total}	0.34	0.25	0.33	0.73	0.9
		AME_{FB}	-0.75	-0.84	0.89	0.27	0.87
		AME_{SW}	1.09	1.42	0.71	0.86	1.62
	maturity	AME_{total}	0.67	0.15	-0.07	0.82	0.79
		AME_{FB}	-1.19	-1.21	0.81	0.53	1.28
		AME_{SW}	1.86	1.50	0.91	0.45	1.53
CKA2021	vegetative	AME_{total}	0.07	0.25	0.13	0.59	0.63
		AME_{FB}	-0.03	-0.16	0.24	0.17	0.19
		AME_{SW}	0.11	0.71	0.20	0.67	0.75
	flowering	AME_{total}	0.36	0.7	0.03	1.4	1.7
		AME_{FB}	-0.04	-0.41	0.02	0.73	0.74
		AME_{SW}	0.41	1.88	0.30	1.76	2.11
	maturity	AME_{total}	0.81	0.9	0.62	1.2	1.96
		AME_{FB}	0.12	0.44	0.07	0.78	0.82
		AME_{SW}	0.69	1.36	0.51	1.06	1.64
WG2020	vegetative	AME_{total}	-0.11	0.04	-3.40	0.19	0.09
		AME_{FB}	-0.12	0.02	-15	0.13	0.03
		AME_{SW}	0.01	0.06	0.19	0.08	0.09
	flowering	AME_{total}	0.23	0.14	0.32	0.34	0.42
		AME_{FB}	-0.58	-0.14	-5.00	0.45	0.18
		AME_{SW}	0.81	0.42	-0.07	0.52	0.5
	maturity	AME_{total}	0.55	0.35	0.6	0.57	0.91
		AME_{FB}	-0.90	0.14	-25.00	1.05	0.2
		AME_{SW}	1.45	0.57	-0.64	0.95	0.74

[1] Absolute mixture effect; [2] Model skill is the skill measure compared to the no-mixture effect (benchmark), [3] Intercrop model; [4]Benchmark model and [5] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark;

Table B. S6. Model evaluation of (absolute mixture effect) AME of plant height (m) at different development stages. Results are averages over cultivars of Faba bean (FB) and Spring wheat (SW) and sowing densities.

Environment	Development stages	AME	Observed AME	Simulated AME	Model Skill	RMSE IM	RMSE B
CKA2020	vegetative	AME_{total}	0.01	-0.01	-1.2	0.04	0.02
		AME_{FB}	0	-0.02	-4.3	0.03	0.01
		AME_{SW}	0.02	0.01	0.28	0.01	0.02
	flowering	AME_{total}	-0.11	-0.05	0.61	0.07	0.12
		AME_{FB}	-0.11	-0.11	0.93	0.02	0.11
		AME_{SW}	-0.005	0.05	-5	0.06	0.02
CKA2021	vegetative.	AME_{total}	0.07	0.04	0.75	0.03	0.07
		AME_{FB}	0.04	-0.007	-0.3	0.06	0.05
		AME_{SW}	0.02	0.05	-0.17	0.04	0.03
	flowering	AME_{total}	-0.07	0.02	-0.33	0.11	0.1
		AME_{FB}	-0.08	-0.01	0.22	0.09	0.1
		AME_{SW}	0.008	0.03	-0.01	0.04	0.04
WG2020	vegetative	AME_{total}	0.009	-0.04	-1.6	0.08	0.05
		AME_{FB}	0.009	-0.03	-11	0.045	0.01
		AME_{SW}	0.01	0.002	0.09	0.02	0.02
	flowering	AME_{total}	0.004	-0.02	-3.29	0.06	0.03
		AME_{FB}	-0.008	-0.08	-9.2	0.08	0.02
		AME_{SW}	0.01	0.03	-0.62	0.05	0.03

[1] Absolute mixture effect; [2] Model skill is the skill measure compared to the no-mixture effect (benchmark); [3] Intercrop model; [4]Benchmark model and [5] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark;

Table B. S7. Model evaluation of intercrop model in simulating (absolute mixture effect) AME of a fraction of intercepted photosynthetically active radiation (fIPAR).

Environment	Observed AME [1]	Simulated AME	Model skill[2]	RMSE[5] IM[3]	RMSE B[4]
CKA2020	0.01	0.01	0.02	0.04	0.04
CKA2021	0.01	0.05	-1.50	0.05	0.03
WG2020	0.01	-0.03	-1.50	0.04	0.03

[1] Absolute mixture effect; [2] Model skill is the skill measure compared to the no-mixture effect (benchmark); [3] Intercrop model; [4]Benchmark model and [5] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

Table B. S8. Evaluation of intercrop model in simulating absolute mixture effect (AME) of root biomass at different soil depths. The observed data was from the field experiment CKA2021. Root biomass is given in t ha^{-1}.

AME	Soil depth (cm)	Development stage	Observed AME[1]	Simulated AME	Model Skill[2]	RMSE[5] IM[3]	RMSE B[4]
AME_{total}	0-30	vegetative	0.91	0.80	0.86	0.35	0.95
	0-30	flowering	1.34	0.71	0.69	0.79	1.42
	30-60	vegetative	0.02	0.31	-47.0	0.30	0.04
	30-60	flowering	0.07	0.28	-4.7	0.22	0.09
	60-100	vegetative	0.04	0.04	-1.0	0.06	0.04
	60-100	flowering	0.05	0.20	-7.50	0.15	0.50
AME_{SW}	0-30	vegetative	0.08	-0.03	0.70	0.14	0.26
	0-30	flowering	0.22	-0.07	0.46	0.34	0.46
	30-60	vegetative	-0.02	-0.02	0.77	0.03	0.06
	30-60	flowering	0.04	0.01	0.23	0.08	0.09
	60-100	vegetative	0.01	-0.09	-7.9	0.10	0.03
	60-100	flowering	0.03	-0.05	-1.3	0.09	0.06
AME_{FB}	0-30	vegetative	0.45	0.37	0.78	0.33	0.71
	0-30	flowering	0.52	0.37	0.65	0.51	0.87
	30-60	vegetative	-0.03	0.20	-25.0	0.20	0.04
	30-60	flowering	-0.07	0.12	-5.0	0.19	0.07
	60-100	vegetative	0.01	0.09	-59.6	0.08	0.01
	60-100	flowering	-0.02	0.11	-16.5	0.13	0.03

[1] Absolute mixture effect; [2] Model skill is the skill measure compared to the no-mixture effect (benchmark); [3] Intercrop model; [4]Benchmark model and [5] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

Table B. S9. Evaluation of intercrop model in simulating absolute mixture effect (AME) of VSWC (average all-over treatments and sampling date.

Environment	Soil depth (cm)	Observed AME[1]	Simulated AME	Model Skill[2]	RMSE[5] IM[3]	RMSE B[4]
CKA2020	30	0.0021	0.0038	-0.05	0.018	0.017
	45	0.0002	0.0014	-0.08	0.32	0.32
	60	-0.0049	0.0003	0.05	0.022	0.022
	90	-0.0194	-0.0008	0.05	0.048	0.049
CKA2021	30	-0.0019	0.0013	0.06	0.035	0.036
	45	0.0009	0.0025	-0.01	0.040	0.040
	60	-0.0021	0.0021	-0.00	0.03	0.030
	90	0.0072	0.0033	0.03	0.035	0.036
WG2020	30	-0.0125	0.0020	-0.15	0.024	0.022
	45	-0.0151	0.0024	-0.34	0.031	0.027
	60	-0.0034	0.0017	0.07	0.039	0.040
	90	0.0219	0.0010	0.03	0.043	0.044

[1] Absolute mixture effect; [2] Model skill is the skill measure compared to the no-mixture effect (benchmark); [3] Intercrop model; [4]Benchmark model and [5] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

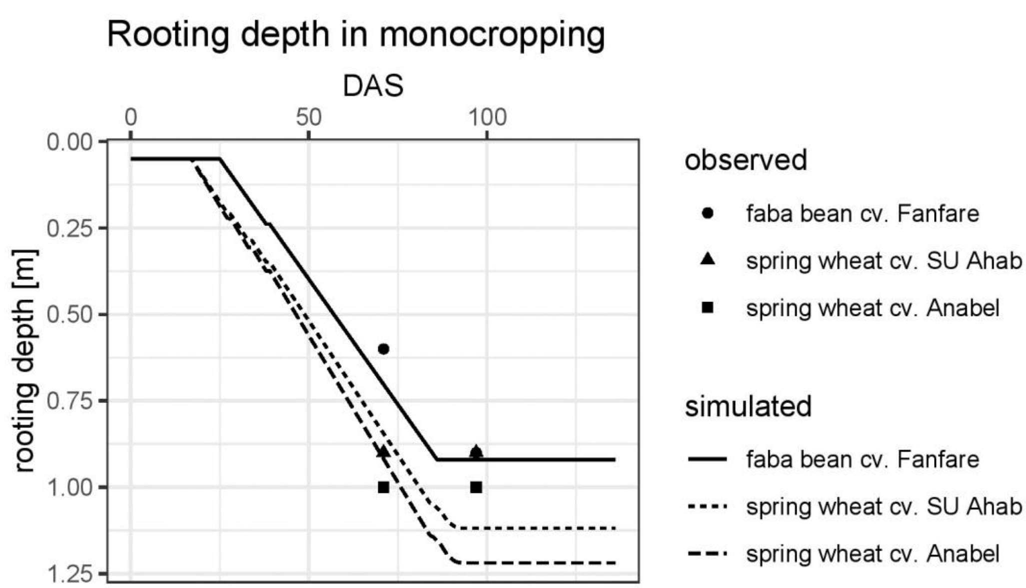

Fig. B. S7. Maximum rooting depth over the growth period in sole cropping (three treatments, CKA2021); (FB flowering) and the second (SW flowering) sampling date.

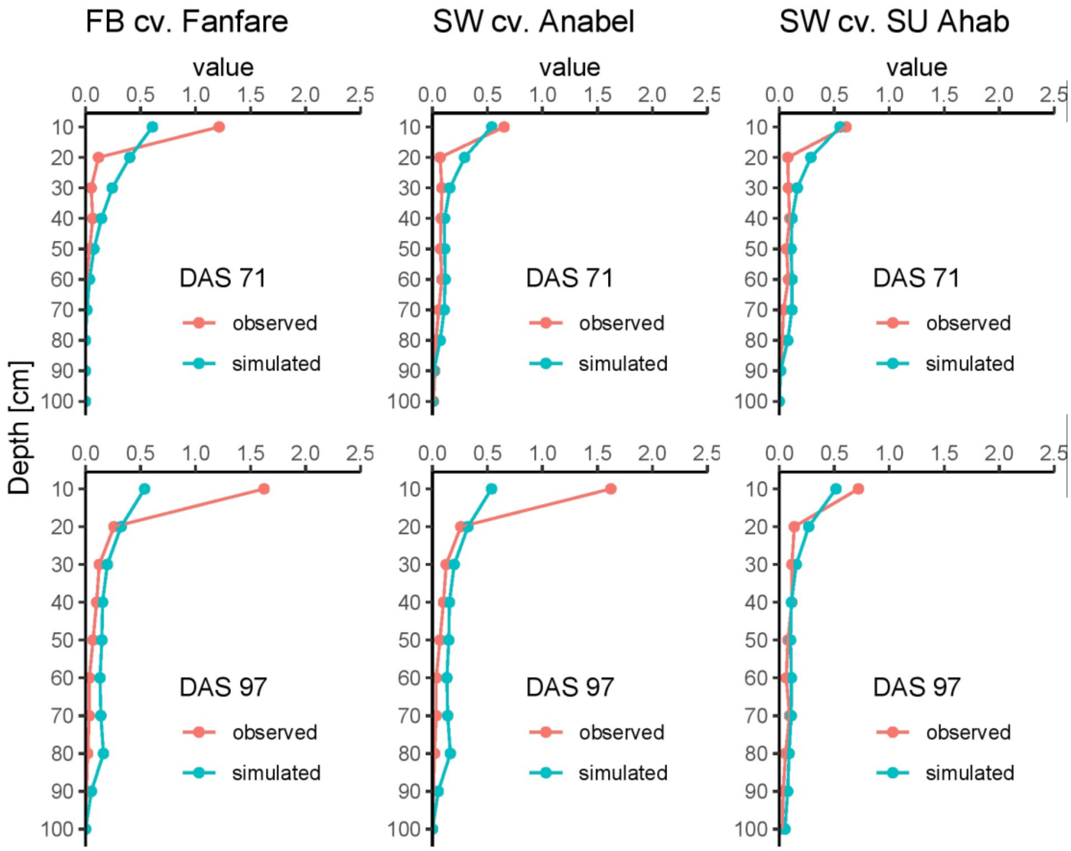

Fig. B. S8. Observed and simulated root biomass in monocultures. The observed data was from the field experiment CKA 2021. Root mass is given in t ha^{-1}.

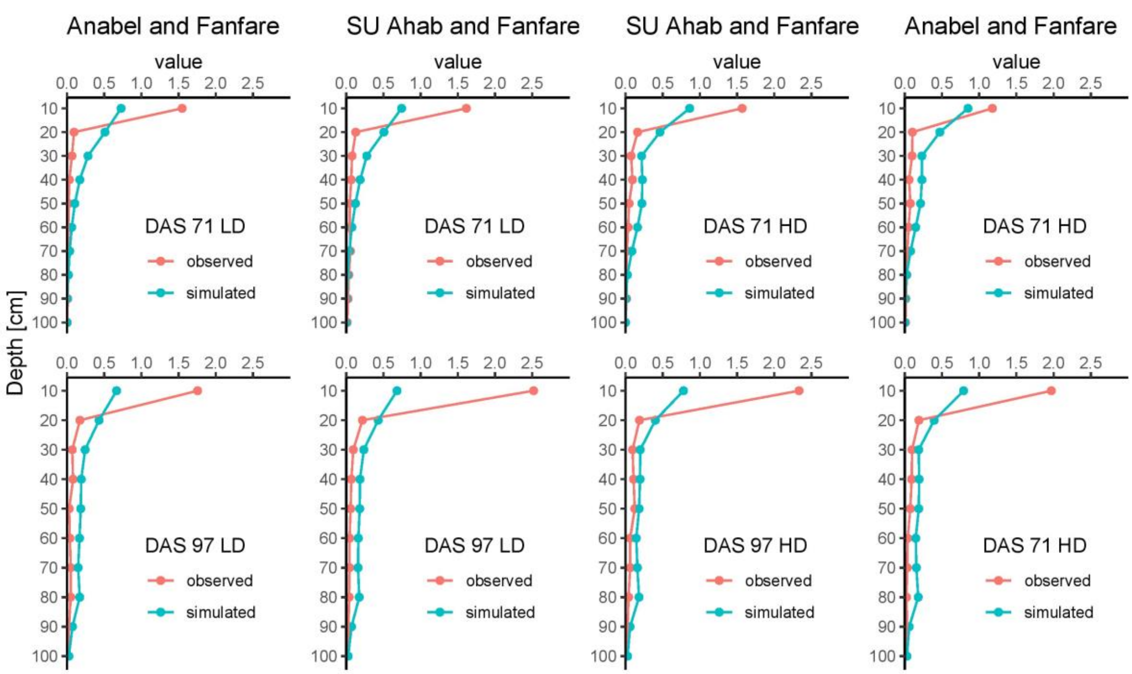

Figure B. S9. Observed and simulated root biomass in t ha^{-1} in the intercrop. The observed data was from the field experiment CKA 2021; HD – high sowing density; LD – low sowing density.

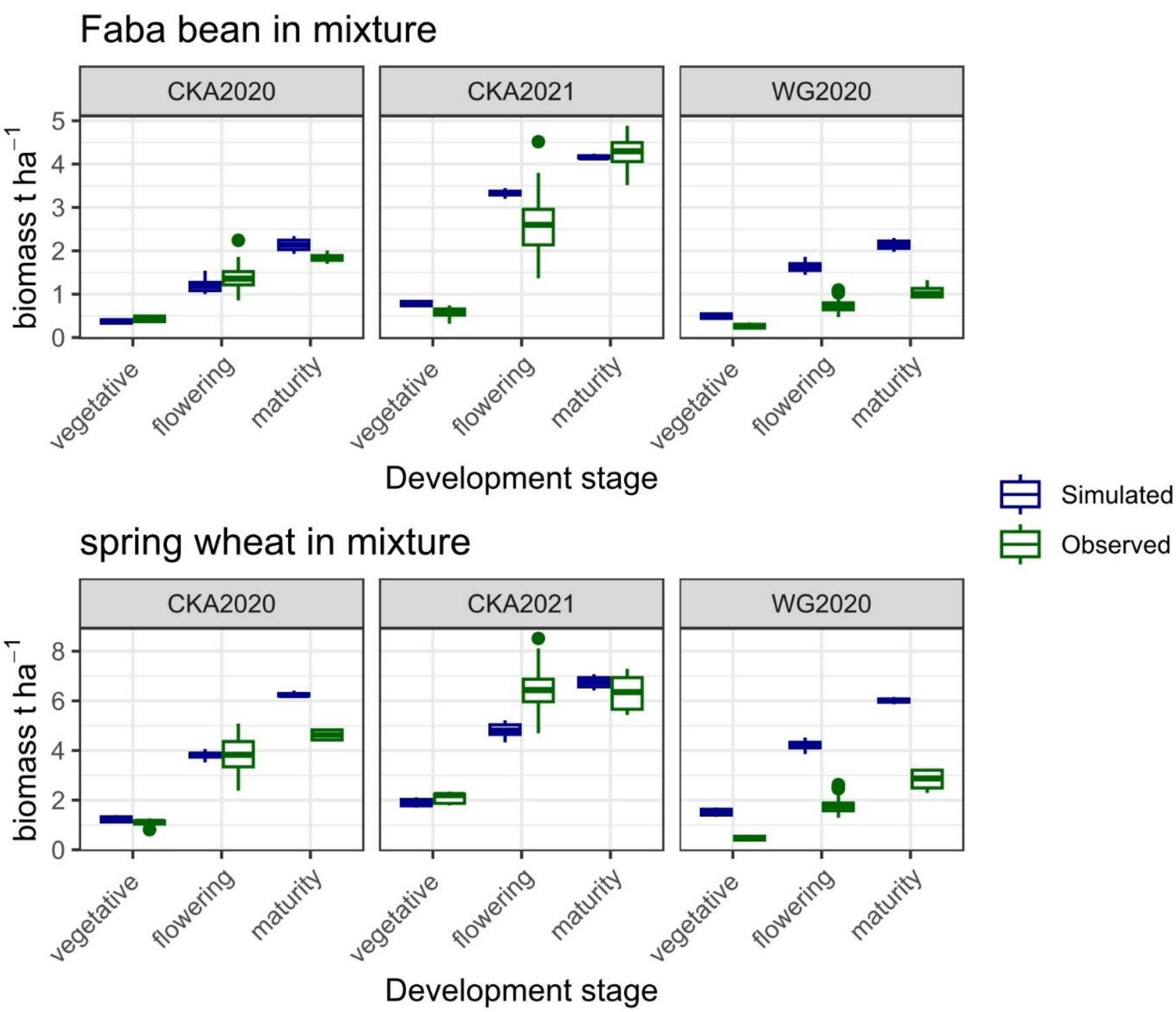

Figure B. S10. Simulated and observed absolute dry matter shoot biomass yield (t ha^{-1}) of faba bean (top panel) and spring wheat (bottom panel) grown under an intercropping system (average for all intercropping treatments), under three environments.

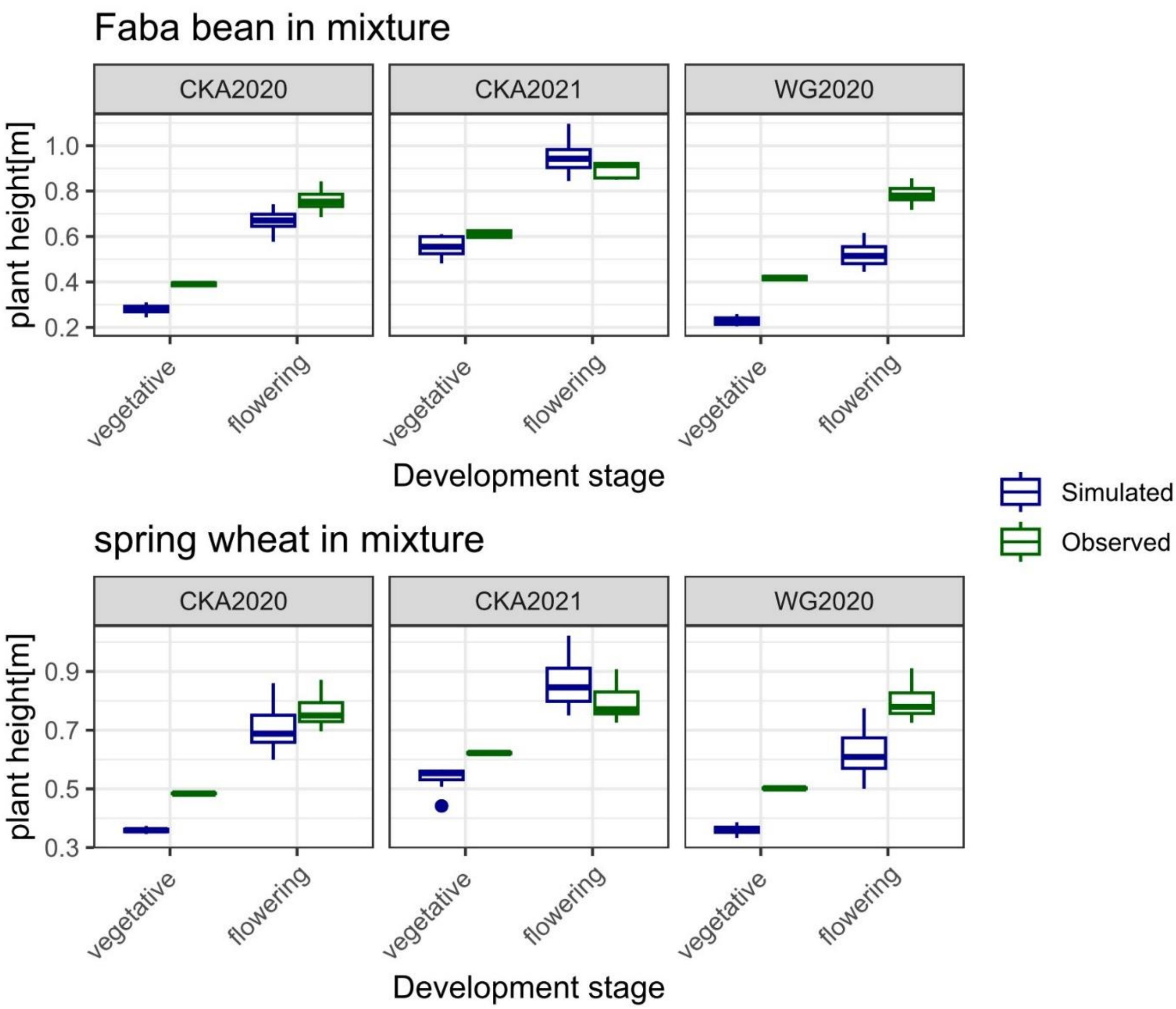

Figure B. S11. Simulated and observed absolute dry matter shoot biomass yield (t ha^{-1}) of faba bean (top panel) and spring wheat (bottom panel) grown under an intercropping system (average for all intercropping treatments), under three environments.

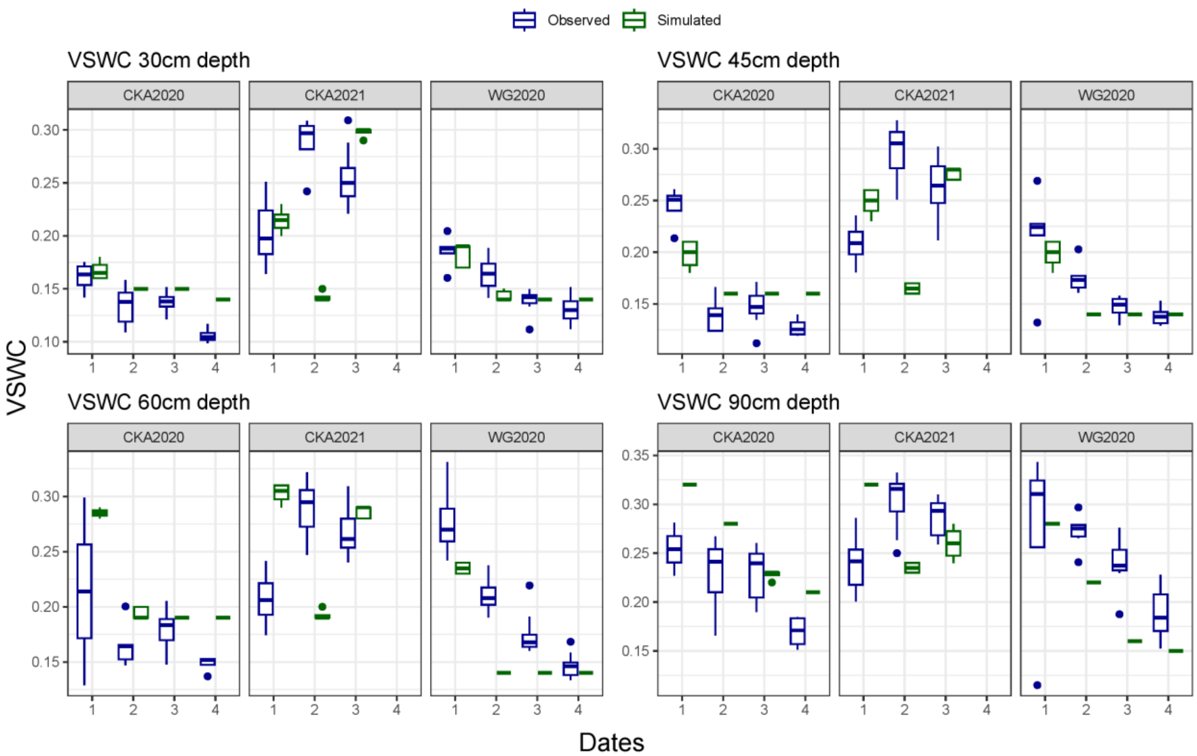

Figure B. S12. simulated and observed volumetric soil water content (VSWC) of faba bean spring wheat grown under an intercropping system (average for all intercropping treatments), under three environments during the growth period in 2020 (CKA2020: ~55, ~ 73, ~ 97, ~ 114 DAS) and (WG2020: ~ 57, ~ 77, ~ 104, ~ 119 DAS) for date 1,2,3 and 4 respectively and three times in 2021 (CKA2021: ~ 67, ~98 and ~ 129 DAS) for date 1,2 and 3 respectively.

Appendix C: supplementary material for Chapter 4

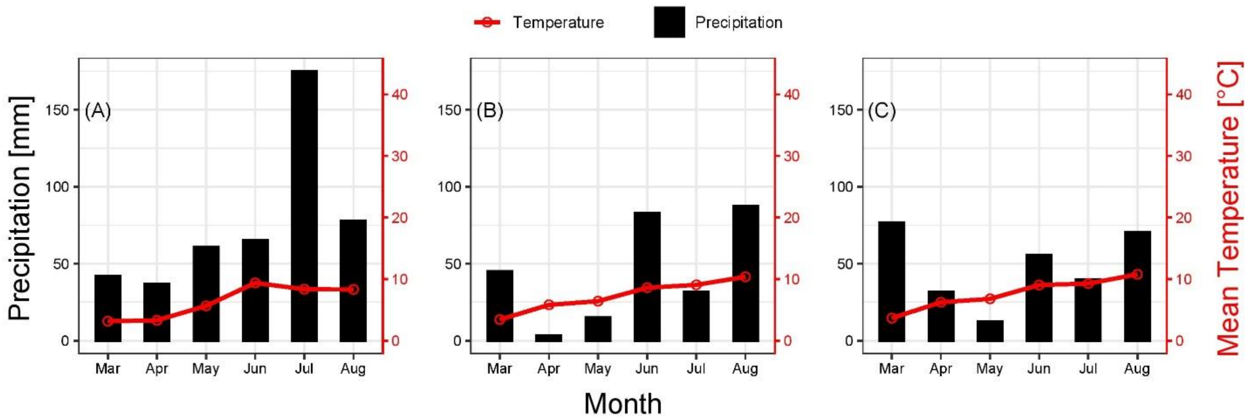

Figure C. S1. The mean monthly temperature °c and precipitation (mm) during growth period A) CKA2021; B) CKA2020 and C) WG2020

Table S1. Total N (N_{min}), and mineral N concentrations in three soil layers (0-30 cm, 30-60 cm, 60-90 cm) at sowing at Campus Klein-Altendorf (CKA) and Wiesengut WG).

Environment	NO_3			NH_4 kg/ha			Nmin kg/ha		
	Soil depth (cm)			Soil depth (cm)			Soil depth (cm)		
	0-30	30-60	60-90	0-30	30-60	60-90	0-30	30-60	60-90
CKA2021	16.00	27.00	55.00	0.00	0.00	0.00	16.00	27.00	55.00
CKA2020	33.99	16.25	21.50	6.61	2.89	1.83	40.60	19.15	23.33
WG2020	10.82	2.09	0.91	9.21	3.67	1.77	20.03	5.76	2.68

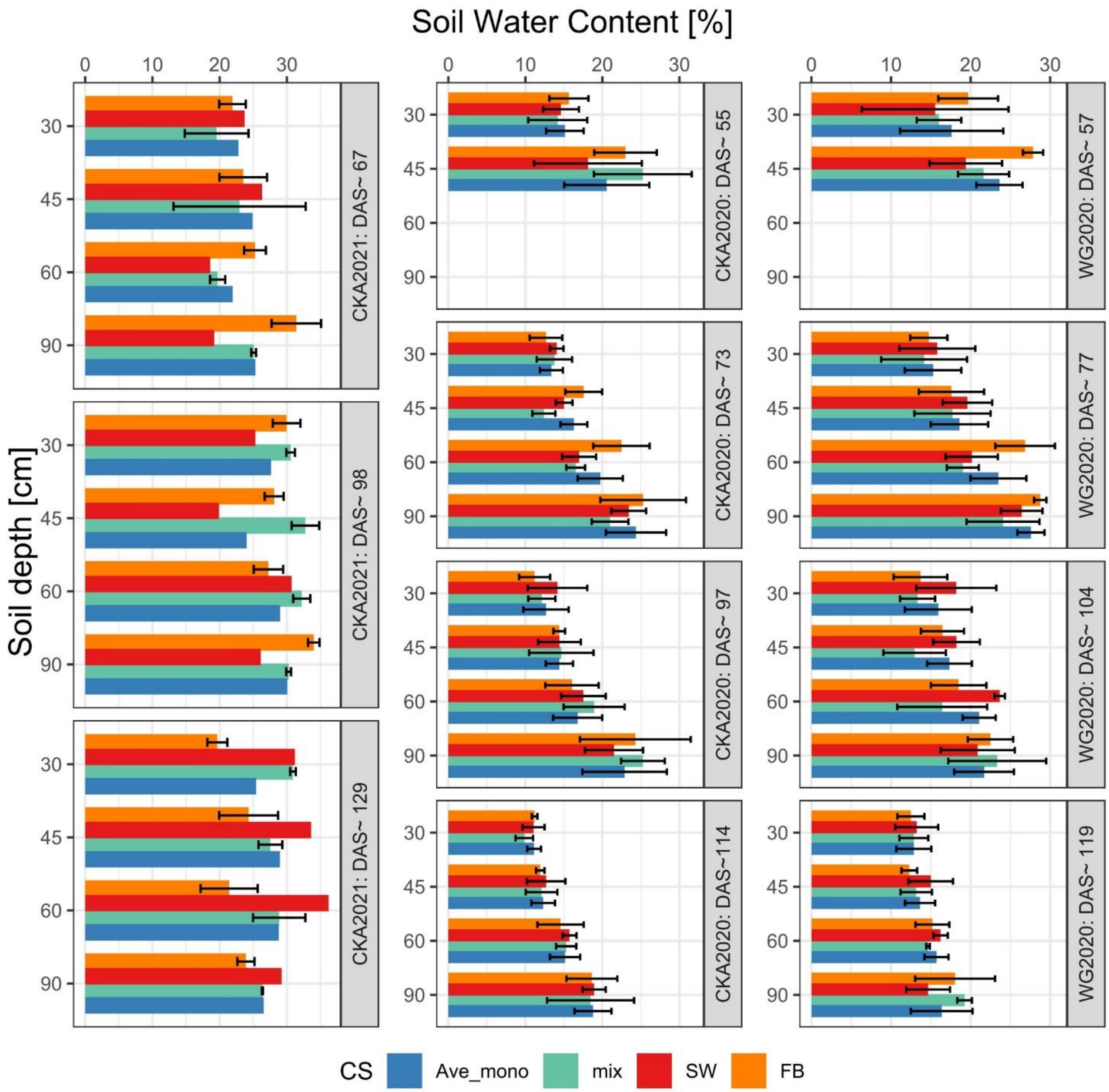

Figure C. S2. Measured soil water content at different depths and days after sowing (DAS). FB- faba bean cv. Mallory, SW- spring wheat cv. Lennox; Ave_mono- the average of the two mono-crops and mix- intercropping of faba bean and spring wheat at high density. The vertical line is the standard deviation of the mean of replicates (2, 3, or 4).

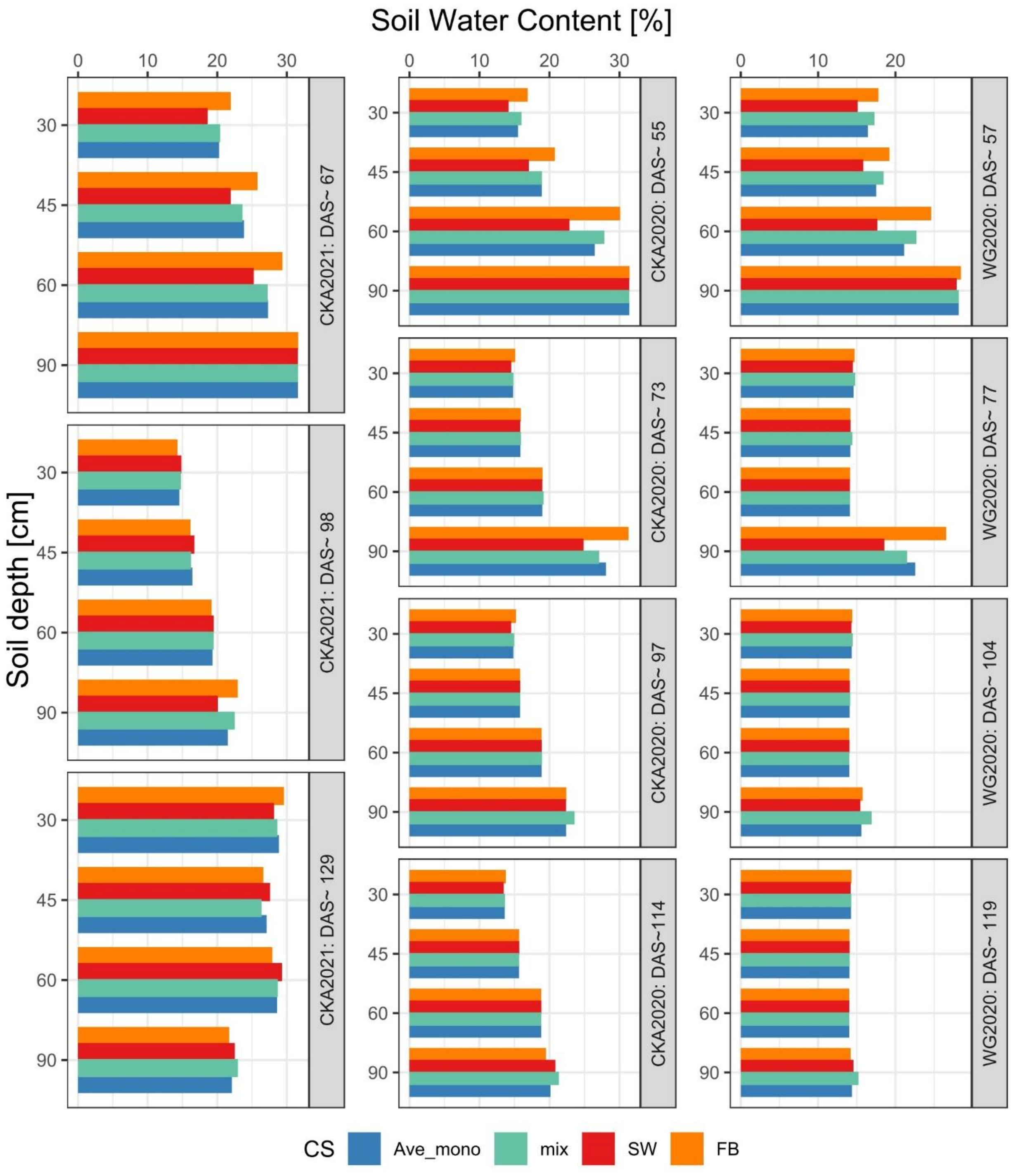

Figure C. S3. Simulated soil water content at different depths and days after sowing (DAS). FB- faba bean cv. Mallory, SW- spring wheat cv. Lennox; Ave_mono- the average of the two mono-crops and mix-intercropping of faba bean and spring wheat at high density.

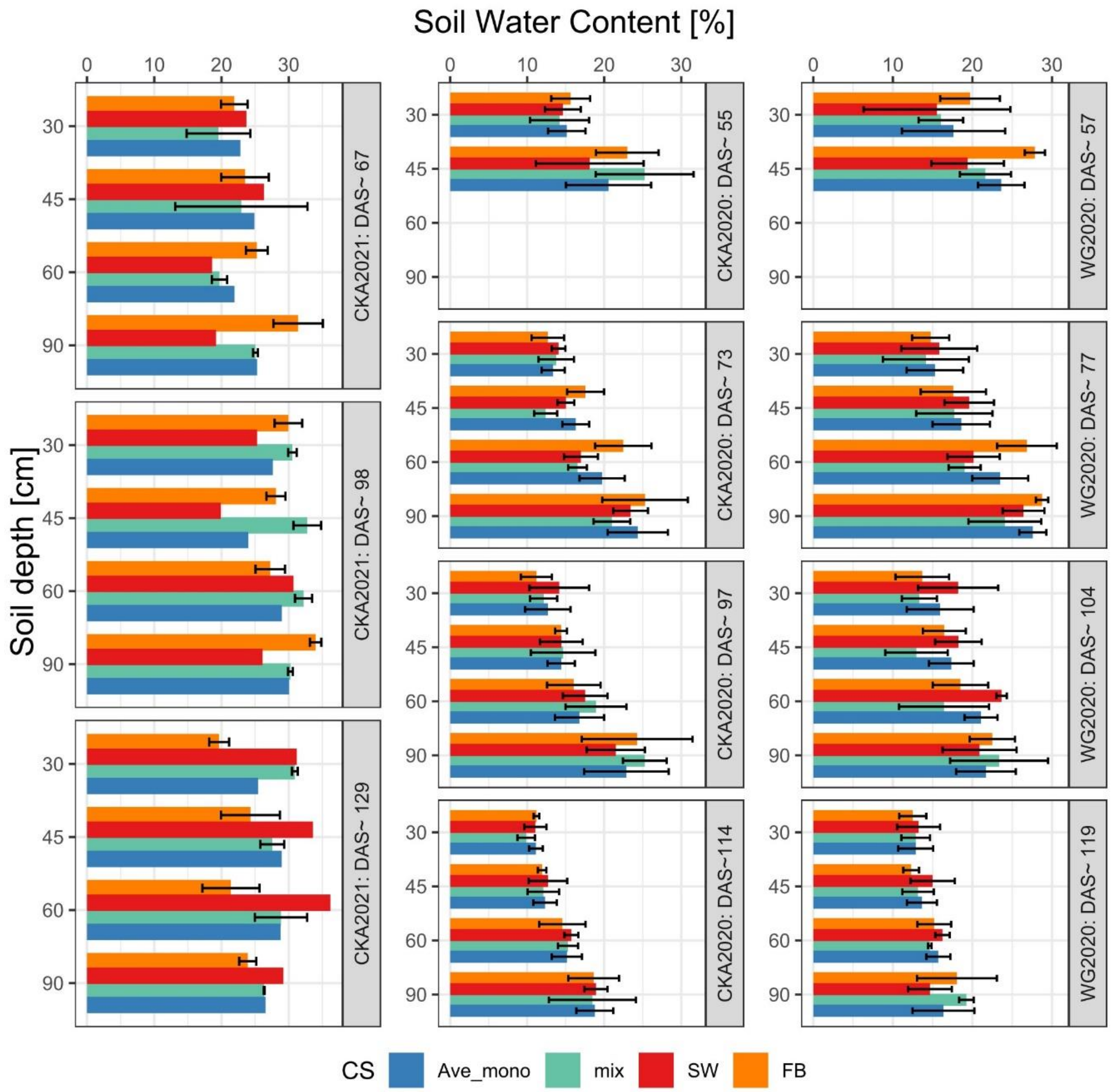

Figure C. S4. Measured soil water content at different soil depths on different days after sowing (DAS). FB- faba bean cv. Mallory, SW- spring wheat cv.SU Ahab; Ave_mono- the average of the two mono-crops and mix-intercropping of faba bean and spring wheat at high density. The vertical line is the standard deviation of the mean of replicates (2, 3, or 4).

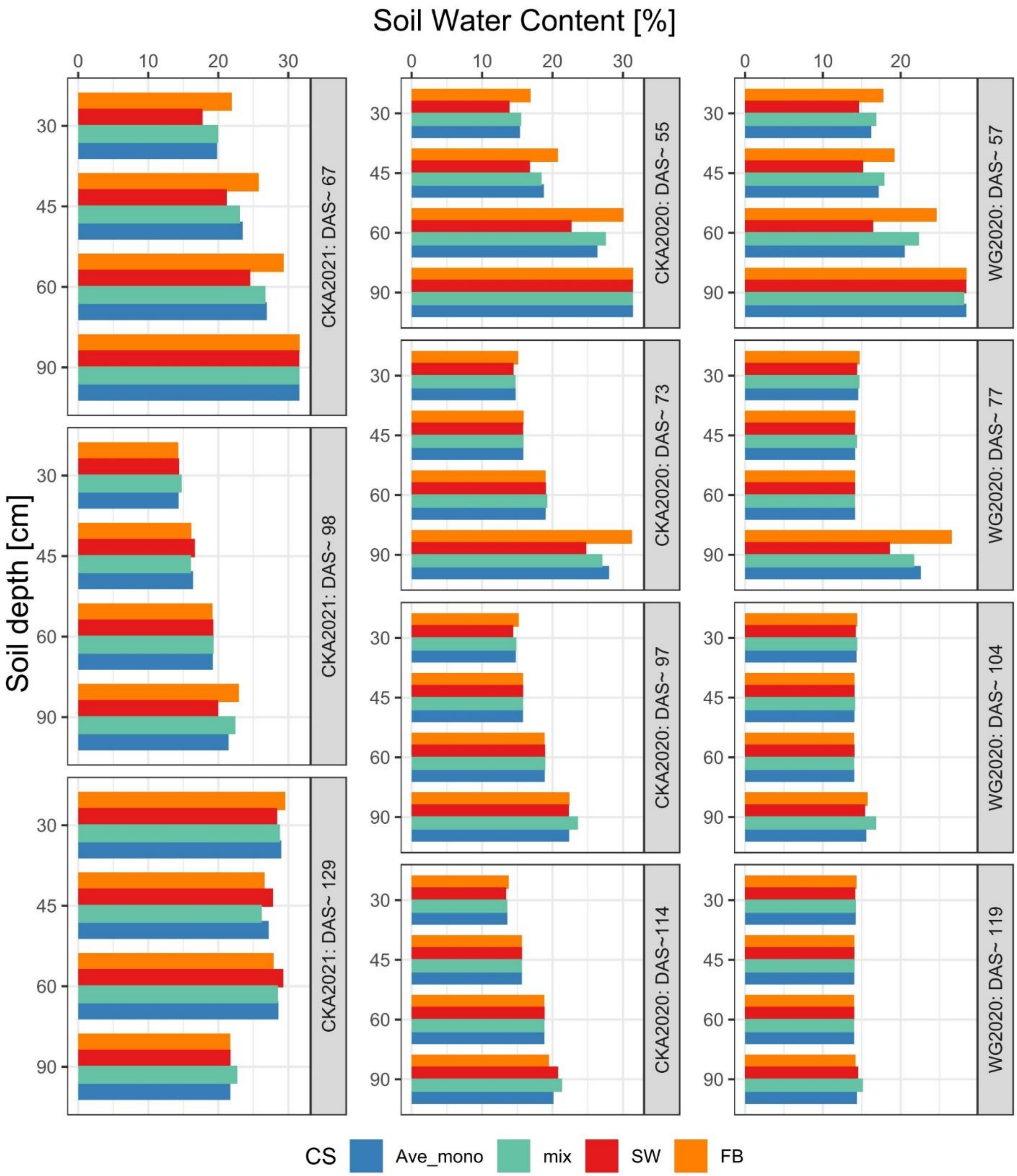

Figure C. S5. Simulated soil water content at different soil depths on different days after sowing (DAS). FB- faba bean cv. Mallory, SW- spring wheat cv.SU Ahab; Ave_mono- the average of the two mono-crops and mix-intercropping of faba bean and spring wheat at high density.

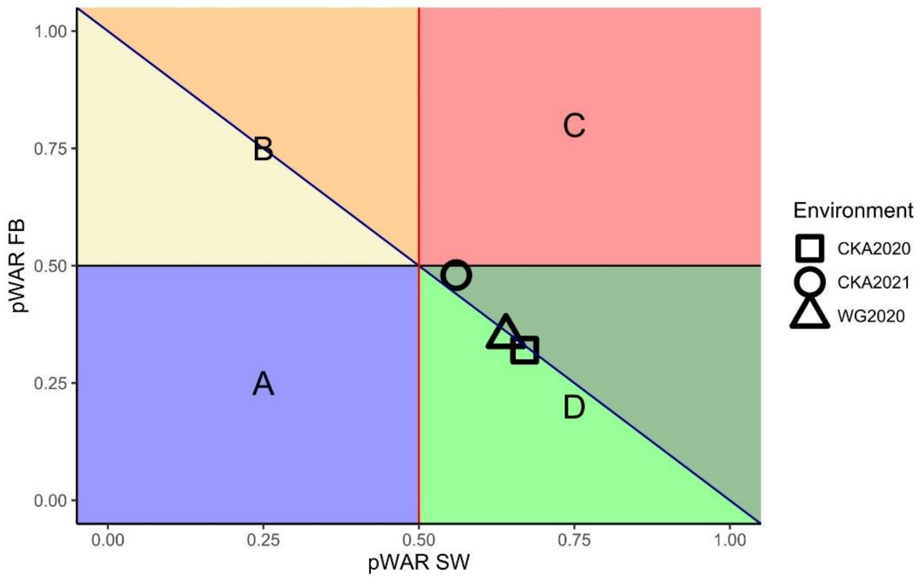

Figure. C. S6 simulated 4 C approaches for partial water acquisition ratio (WAR) of SW and FB intercrops for three environments. In area A) both species are suppressed in the mixture due to competition; Area B) corresponds to situations in which faba bean suppresses spring wheat; In area (C) both species grow better in the mixture (per plant or row) than they did as monocultures; In area D) The spring wheat suppresses faba bean.

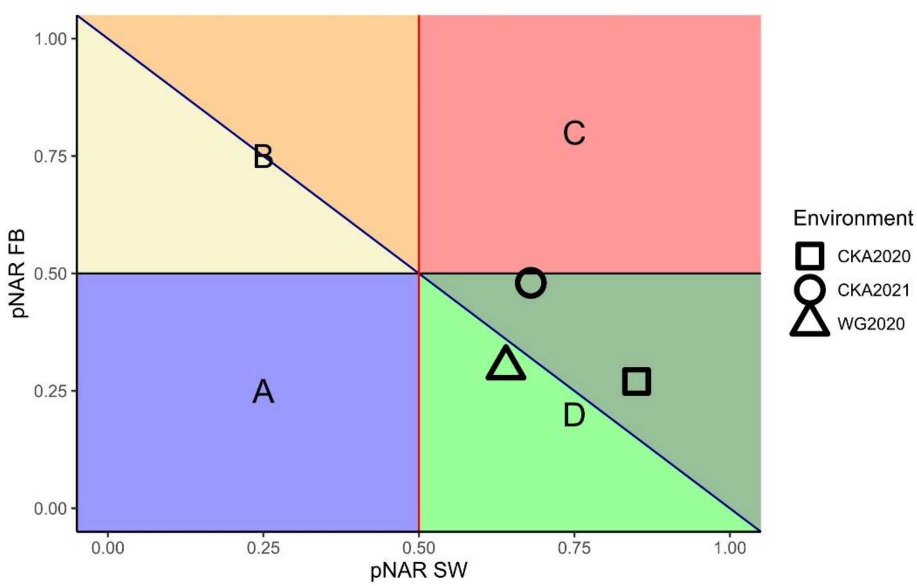

Figure. C. S7 simulated 4 C approaches for partial N acquisition ratio (NAR) of SW and FB intercrops for three environments. In area A) both species are suppressed in the mixture due to competition; Area B) corresponds to situations in which faba bean suppresses spring wheat; In area (C) both species grow better in the mixture (per plant or row) than they did as monocultures; In area D) The spring wheat suppresses faba bean.

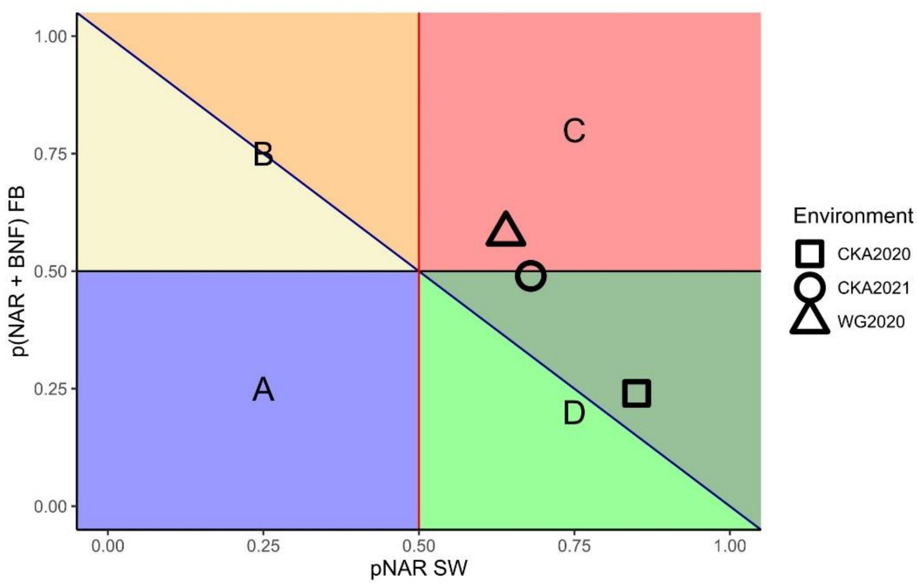

Figure. C. S8 simulated 4 C approaches for partial N acquisition ratio including biological nitrogen fixation (NAR+BNF) of SW and FB intercrops for three environments. In area A) both species are suppressed in the mixture due to competition; Area B) corresponds to situations in which faba bean suppresses spring wheat; In area (C) both species grow better in the mixture (per plant or row) than they did as monocultures; In area D) The spring wheat suppresses faba bean.

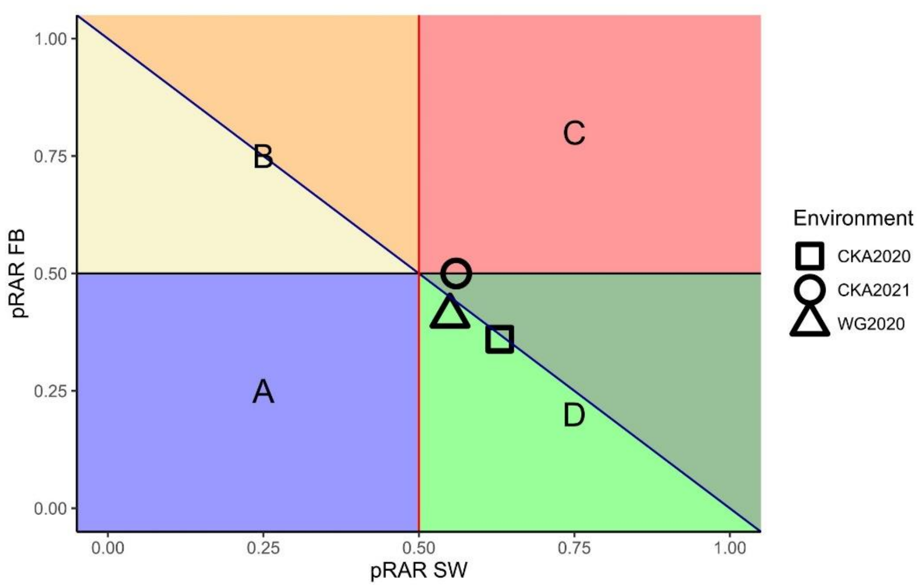

Figure. C. S9 simulated 4 C approaches for partial radiation acquisition ratio (RAR) of SW and FB intercrops for three environments. In area A) both species are suppressed in the mixture due to competition; Area B) corresponds to situations in which faba bean suppresses spring wheat; In area (C) both species grow better in the mixture (per plant or row) than they did as monocultures; In area D) The spring wheat suppresses faba bean.

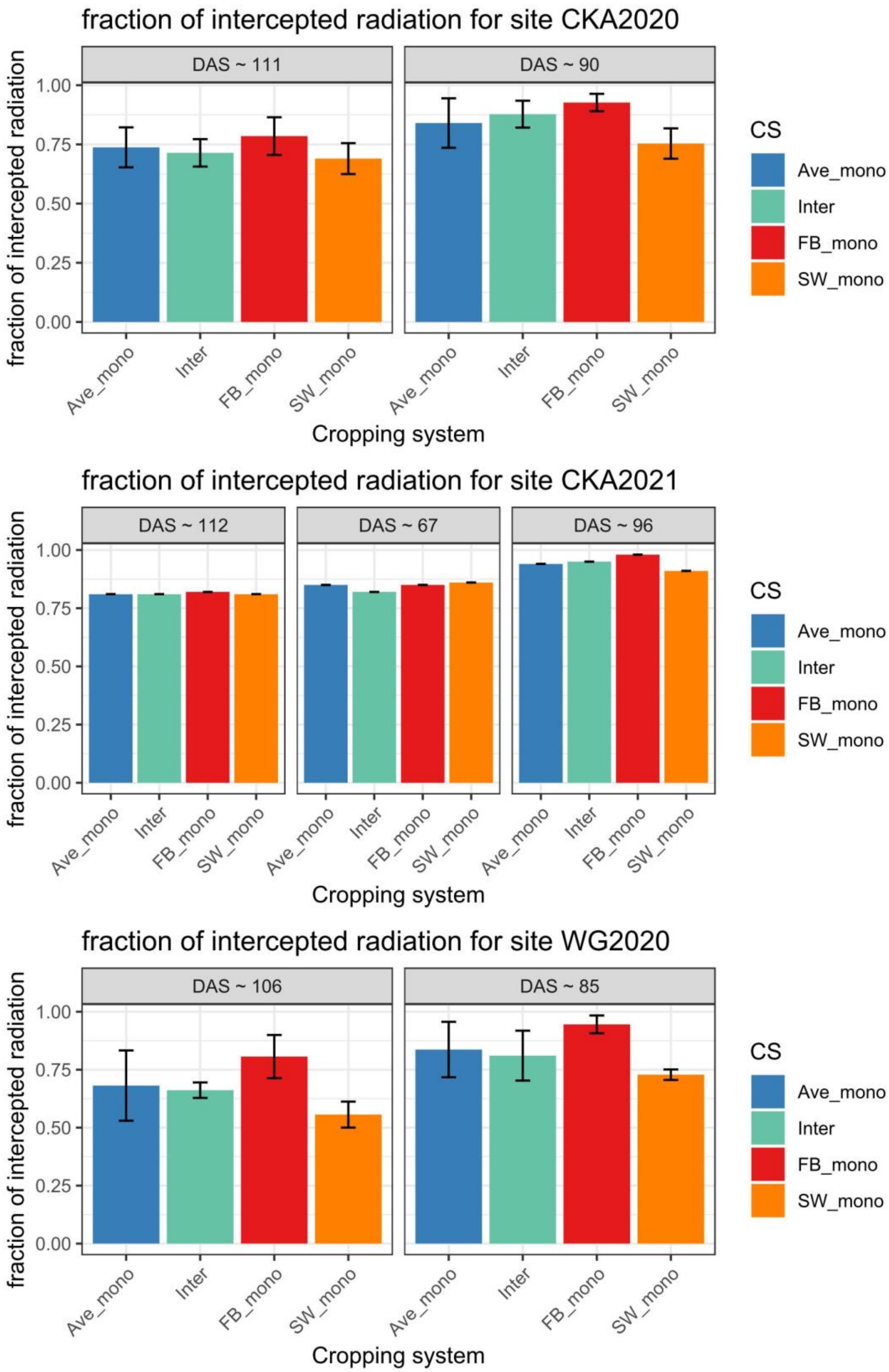

Figure. C. S10. Observed fraction of intercepted radiation on different days after sowing (DAS). FB- faba bean cv. Mallory, SW- spring wheat cv.SU Ahab; Ave_mono- the average of the two mono-crops and inter-intercropping of faba bean and spring wheat at high density.

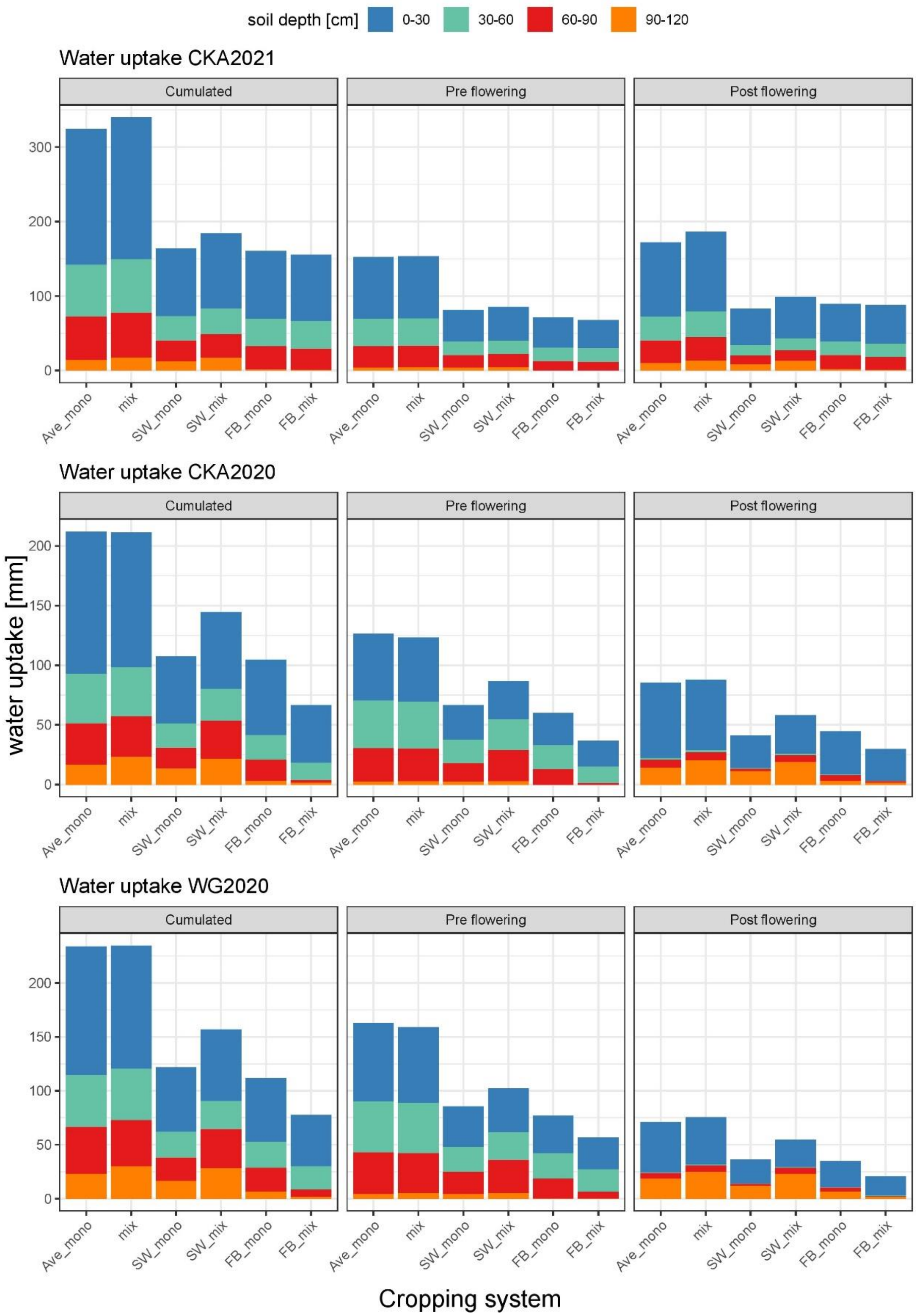

Figure. C. S11 Simulated crop water uptake cumulative, from sowing to spring wheat flowering and from spring wheat flowering to harvest across the three environments. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono- is the average of monocultures of SW and FB; mix- intercropping of SW and FB; SW_mix- SW in intercropping; SW_mono-SW in monoculture and FB_mono- FB in monoculture.

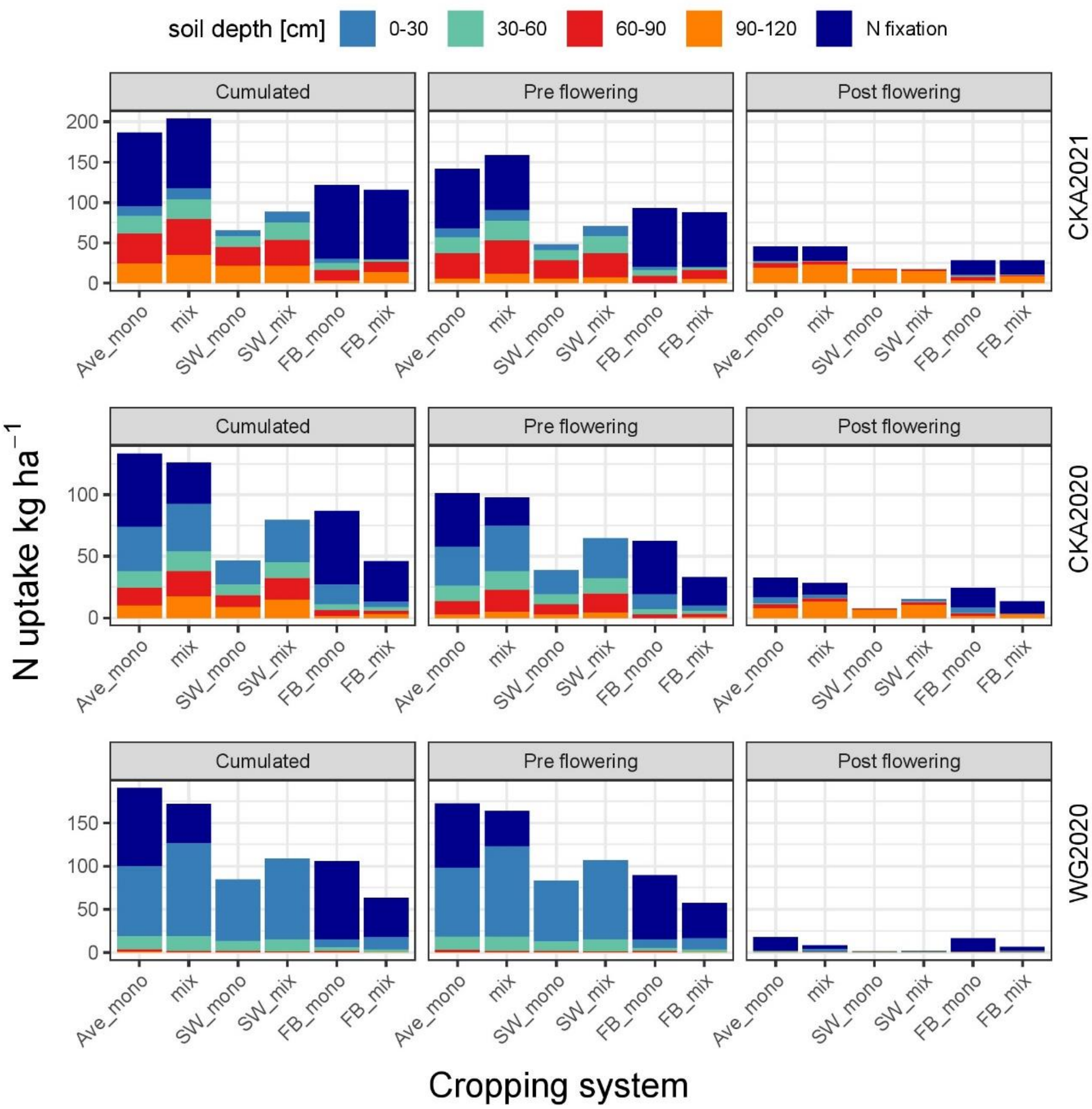

Figure. C. S12 Simulated crop nitrogen uptake from soil and biological fixation of atmospheric N. by faba bean. Cumulated over the whole season, from sowing to spring wheat flowering, and from spring wheat flowering to harvest across the three environments. Spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono- is the average of monocultures of SW and FB; mix- intercropping of SW and FB; SW_mix- SW in intercropping; SW_mono-SW in monoculture and FB_mono- FB in monoculture.

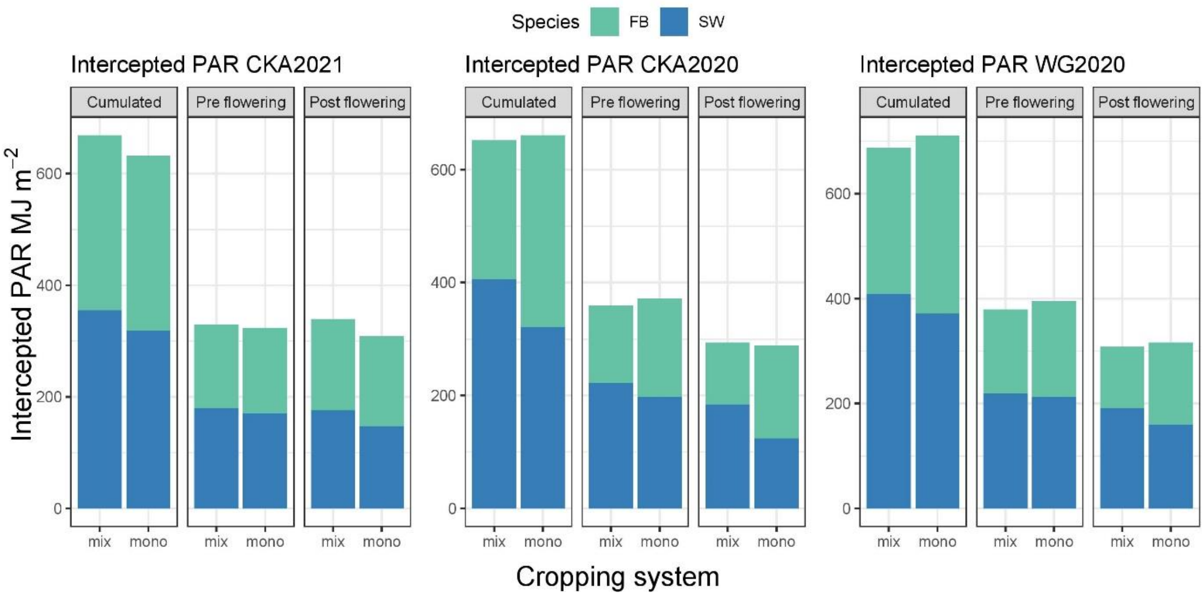

Figure. C. S13 Simulated intercepted PAR, cumulative, pre and post-flowering of spring wheat (SW) for three environment spring wheat (SW) cv. Lennox and faba bean (FB) cv. Mallory. Ave_mono- is the average of monocultures of SW and FB; mix- intercropping of SW and FB.

Appendix D: List of further publications

Co- author contributions

Drees, L., **Demie, D.T.,** Paul, M.R., Leonhardt, J., Seidel, S.J., Döring, T.F., Roscher, R., 2024. Data-driven crop growth simulation on time-varying generated images using multi-conditional generative adversarial networks. Plant Methods 20, 93.

Paul, M.R., **Demie, D.T.**, Seidel, S.J., Döring, T.F., 2024. Evaluation of multiple spring wheat cultivars in diverse intercropping systems. Eur. J. Agron. 152. https://doi.org/10.1016/j.eja.2023.127024

Paul, M.R., **Demie, D.T**., Seidel, S.J., Döring, T.F., 2023. Effects of spring wheat / faba bean mixtures on early crop development. Plant Soil. https://doi.org/10.1007/s11104-023-06111-6

Hadir, S., Doring, ¨ T.F., Justes, E., **Demie, D.T.,** Paul, M., Legner, N., Kemper, R., Gaiser, T., Weedon, O., Ewert, F., Seidel, S.J., 2024. Root growth and belowground interactions in spring wheat - faba bean intercrops. Plant Soil https://doi.org/ 10.1007/s11104-024-06742-3.

Conference contributions

Demie, D. T., Madhuri P., Hadir, S., Gaiser,T., Döring ,T. F., Wallach,D., and Seidel S.J. 2023. Modeling crop growth and performance in cereal/legume mixture. Poster präsentation Mitt. Ges. Pflanzenbauwiss. 33: 215–216 (2023)

Demie, D.T., Kumar, A., Wallach, D., Gaiser, T., Thomas, F.D., Seidel, S.J. 2024. Understanding and designing spring wheat/faba bean intercropping systems by virtually testing cultivar traits and management options. oral presentation at European society of agronomy (ESA), Renne, France https://events.institut-agro.fr/event/1/attachments/9/421/ESA2024-Book_of_Abstracts.pdf

Demie, D.T., Ewert, F., Gaiser, T., Wallach, D., Thomas, F.D., Seidel, S.J. 2024. Resource acquisition and interspecific interactions in spring wheat /faba bean intercropping. poster presentation at Landscape conference 2024, Berlin https://landscape2024.org/custom/media/landscape24/Landscape_2024_Book_of_Abstracts.pdf

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Delighted
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