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Effects of mixing multiple spring wheat and faba bean cultivars in variable densities and environments

Dissertation

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To my late father,

For his endless love, support, and encouragement

CONTENTS

Summary

Intercropping, the practice of cultivating two or more crop species together, is widely recognized as a sustainable crop production system. This approach is valued for its ability to enhance production, stabilize crop performance, and mitigate the effects of extreme climate conditions compared to monoculture. Despite these benefits, there is limited quantitative evidence on the effects of mixtures on compensation and early developmental stages. Additionally, the impact of different cultivars on intercropping under various environmental and management conditions remains largely unexplored.

To address these gaps, we evaluated the mixing abilities of twelve spring wheat entries (ten cultivars and two cultivar mixtures) and two faba bean cultivars under two sowing densities in three environments. Variability among cultivars was created in terms of plant height. We collected data on crop emergence (plants m^{-2}), crop biomass (dry matter), and total grain yield to quantify compensation and measure the effects of the mixture in early and final crop development stages.

Our findings revealed greater biomass compensation in mixtures compared to monocultures, predominantly stemming from the weaker competitor, faba bean. Positive mixture effects on crop emergence were also observed. However, spring wheat emerged as the dominant partner in all three environments. Its dominance, without suppressing faba bean, was evident from the time of emergence and had a legacy effect on plant biomass throughout the later growth stages. Moreover, a highly significant effect of environments and sowing densities was observed, with significant two-way interactions of spring wheat cultivars with multiple factors on total grain yield in the mixture. Additionally, in one environment, spring wheat height was weakly correlated with total grain yield in the mixture.

Our findings underscore the importance of selecting tailored combinations of cereals and legumes, along with appropriate management strategies, to enhance functional complementarity and overall productivity in intercropping. However, the complex nature of these interactions presents a significant challenge. We recommend managing spring wheat dominance early in the growth phase to regulate competition in mixed crops and improve complementarity. Future studies should focus on crop traits that enable a high mixture effect through complementarity and compensation.

Zusammenfassung

Der Anbau von Mischkulturen, d. h. der gemeinsame Anbau mehrerer Pflanzenarten, ist weithin als nachhaltiges Anbausystem anerkannt. Dieser Ansatz wird wegen seiner Fähigkeit geschätzt, die Erträge zu steigern, die Ertragsstabilität zu erhöhen und die Auswirkungen extremer Klimabedingungen im Vergleich zu Monokulturen abzumildern. Trotz dieser Vorteile gibt es nur wenige quantitative Daten über die Auswirkungen von Mischungen auf die Kompensation und die frühen Entwicklungsstadien. Darüber hinaus sind die Auswirkungen verschiedener Kultursorten auf Mischkulturen unter verschiedenen Umwelt- und Bewirtschaftungsbedingungen noch unerforscht.

Um diese Lücken zu schließen, haben wir die Mischungsfähigkeit von zehn Sommerweizensorten, zwei Sortenmischungen aus diesen Sorten und zwei Ackerbohnensorten unter zwei Aussaatdichten in drei Umwelten untersucht. Die Variabilität zwischen den Sorten wurde in Bezug auf die Pflanzenhöhe ermittelt. Es wurden Daten zum Pflanzenaufgang (Pflanzen m^{-2}), zur Biomasse (Trockenmasse) und zum Gesamtertrag der Körner erhoben, um die Kompensation zu quantifizieren und die Auswirkungen der Mischung in den frühen und letzten Entwicklungsstadien der Pflanzen zu messen.

Unsere Ergebnisse zeigen, dass die Biomasse in Mischungen im Vergleich zu Monokulturen stärker kompensiert wird, was vor allem auf den schwächeren Konkurrenten, die Ackerbohne, zurückzuführen ist. Es wurden auch positive Auswirkungen der Mischung auf den Pflanzenaufgang beobachtet. Sommerweizen erwies sich jedoch in allen drei Umwelten als der dominante Partner. Seine Dominanz, ohne die Ackerbohne zu verdrängen, zeigte sich bereits zum Zeitpunkt des Auflaufens und wirkte sich in den späteren Wachstumsstadien auf die Pflanzenbiomasse aus. Darüber hinaus wurde ein hochsignifikanter Einfluss von Umweltbedingungen und Aussaatdichten beobachtet, mit signifikanten Zwei-Wege-Wechselwirkungen von Sommerweizensorten mit mehreren Faktoren auf den Gesamtkornertrag in der Mischung. Darüber hinaus war in einer Umwelt die Höhe des Sommerweizens nur schwach mit dem Gesamtkornertrag in der Mischung korreliert.

Unsere Ergebnisse unterstreichen, wie wichtig es ist, maßgeschneiderte Kombinationen von Getreide und Leguminosen zusammen mit geeigneten Bewirtschaftungsstrategien auszuwählen, um die funktionale Komplementarität und die Gesamtproduktivität im Anbau von Mischkulturen zu verbessern. Die komplexe Natur dieser Wechselwirkungen stellt jedoch eine große Herausforderung dar. Wir empfehlen, die Dominanz des Sommerweizens früh in der Wachstumsphase zu steuern, um die Konkurrenz in Mischkulturen zu regulieren und die Komplementarität zu verbessern. Künftige Studien sollten sich auf Pflanzeneigenschaften konzentrieren, die durch Komplementarität und Kompensation einen hohen Mischeffekt ermöglichen.

Abbreviations, acronyms, and units

AIC	Akaike's Information Criterion
AME	absolute mixture effect
ANOVA	Analysis of variance
CKA	Campus Klein-Altendorf
CKA2020	Campus Klein-Altendorf in year 2020
cm	centimetre
CR	competitive ratio
cv.	cultivar
D	Density
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
LD	Low density
LER	land equivalent ratio
N	nitrogen
NER	Net effect ratio
Nmin	mineral nitrogen
P	phosphorus
PEER	partial emergence equivalent ratio
PLER	partial land equivalent ratio
R^2	coefficient of determination
t	ton
SW	Spring wheat
s.d.	standard deviation
vs.	versus
WG	Campus Wiesengut
WG2020	Campus Wiesengut in year 2020
WG2021	Campus Wiesengut in year 2021

1 General Introduction

1.1 Cereal-legume intercropping

Intercropping, an ancient farming practice, is recognized as the new green revolution (Martin-Guay et al., 2018) due to its pivotal role in shaping the trajectory of sustainable agriculture for the future. This diversification of cropping system involves cultivating two or more species as a mixed crop simultaneously on the same field. The most commonly used intercropping system worldwide is the combination of cereals with legumes (see **Fig.1.1**), which has been reported to provide high and stable yields in terms of quantity and quality (Barillot et al., 2012; Lithourgidis et al., 2011; Nelson et al., 2021; Peoples et al., 2009).

Fig. 1.1. Mixed intercropping 82 days after sowing: spring wheat and faba bean fully intermixed in each row.

Cereal-legume intercropping is known for bringing numerous agroecosystem advantages (**Table 1.1**) over monocultures, particularly in low-input organic systems (Bedoussac et al., 2015). Intercropping enhances total agricultural productivity per area by increasing resource use efficiency and enriching soil fertility through complementary and nutrient acquisition (Agegnehu et al., 2008). Various meta-analyses, encompassing numerous studies, have consistently demonstrated that intercropping achieves higher land use efficiency (Li et al., 2023; Martin-Guay et al., 2018; Yu et al., 2016). On average, intercropping utilizes land 17 to 30% more effectively than equivalent areas dedicated to sole crops (Yu et al., 2015). This increased efficiency is attributed to the positive interactions between multiple species in intercropping systems, which have a more pronounced impact on marginal lands compared to monocultures (Martin-Guay et al., 2018). In addition, species diversity can improve the stability and resilience of ecosystems (Raseduzzaman & Jensen, 2017; Tilman et al., 2006) by enhancing overall compensation (Döring & Elsalahy, 2022) and serving as a form of insurance against climatic variability (Yachi & Loreau, 1999). Furthermore, due to its contribution to multiple ecological services and its ability to mitigate adverse climatic effects, intercropping offers a compelling opportunity for the sustainable intensification of agriculture (**Table 1.1**).

Table 1.1 Overall benefits of cereal- legume intercropping in agroecosystems

Benefits of cereal-legume intercropping

Increase resource use efficiency and enhance soil fertility

- fix nitrogen by legumes (Peoples et al., 2009)
- improve total P acquisition (Li et al., 2016)
- increase the use of available soil water (Chen et al., 2018)
- maximize total light interception (Barillot et al., 2012)
- improve soil structure & maintain soil organic carbon (Nyawade et al., 2019)

Enhance agricultural productivity

- improve land use efficiency (Agegnehu et al., 2008)
- increase total biomass and grain production (Paul et al., 2023, 2024)
- increase cereal grain protein quality & protein content (Gooding et al., 2007)

Improve resilience and insurance against climate adaptation

- Increase crop diversity and genetic variability (Hughes et al., 2008)
- reduce the incidence of pests and diseases (Hauggaard-Nielsen et al., 2008)
- increase crop emergence (Paul et al., 2023)
- stabilize agricultural production due to seasonal variability (Njeru, 2013)
- enhance overall compensation (Döring & Elsalahy, 2022)

Minimize environmental impact to promote sustainable agriculture

- enhance soil water conservation and reduce run-off (Chen et al., 2018)
- lower use of fertilizers and pesticides (Jensen et al., 2020)
- mitigate greenhouse gas emissions (Naudin et al., 2014)
- promote biodiversity conservation (Afrin et al., 2017)
- enhance carbon sequestration (Cong et al., 2015)

Despite the numerous advantages of intercropping, since the 1950s, this diversifying practice has declined in Europe and some other parts of the world (France et al., 2018). Especially notable is the period following the "Green Revolution" of the 1960s, during which high-yielding crop varieties emerged to feed rapidly growing populations. During this period, monoculture became an economically efficient way to maximize yield with the optimization of mechanical management and the availability of relatively cheap synthetic petrochemical fertilizers and pesticides. Meanwhile, environmental problems became a big concern, stemming from heavy fertilizer and pesticide usage, including greenhouse gas emissions from their manufacture. In addition, the development of pesticide resistance, the loss of diversity, the emergence of secondary pest outbreaks, and increased vulnerability raise significant questions about the sustainability of current monoculture practices (Machado, 2009; Pretty et al., 2018; West et al., 2014). Given the challenges of current agricultural practices, it is crucial to consider diversified intercropping systems as a viable solution for promoting sustainable agriculture in the future.

1.2 Ecological processes involved in intercropping

The intercropping system is a complex system due to multiple interactions and linked processes during the entire growing period between intercrops and their environment. For example, intercropping systems have different resource dynamics compared with monocropping systems, particularly when one species modifies the environment of another, thus introducing complexity in evaluating intercropping systems (Bybee-Finley & Ryan, 2018). Different plant-plant interaction processes like complementarity, compensation, facilitation, and competition (**Fig.1.2**) are determine the final performance of intercropping (Creissen et al., 2013; Justes et al., 2021). Therefore, to fully realize and analyze the potential benefits of intercropping, it is important to understand the underlying ecological processes. In the following sections, we will discuss all the ecological processes (**Fig.1.2**) to understand the interconnectedness between intercrops within this diverse cropping system.

Complementarity is the result of increased resource use efficiency in space, time, or form in a mixed cropping system (Justes et al., 2021). This efficiency arises from the diverse root system architectures and aboveground structures of different plant species or varieties, enabling access to distinct nutrient "pools" and the occupancy of varied niches. When two different plant species are intercropped together, it is unlikely that they will compete for exactly the same resource (Hauggaard-Nielsen & Jensen, 2001) compared to single plant species-based monoculture. Particularly in cereal-legume intercropping systems, cereals rely more on soil inorganic N (NO_3^-, NH_4^+) and legumes on symbiotic atmospheric N_2 fixation, particularly in low-input and organic cropping systems (Berghuijs et al., 2020; Creissen et al., 2013). For instance, in conditions of low nitrogen input, the intercropping of oats and mung bean led to intense competition for nitrogen in the soil by oats, ultimately causing the mung bean to depend on atmospheric nitrogen (Luo et al., 2021). This resulted in increased yield and nitrogen accumulation per unit area. Among other contested resources, the absorption of photosynthetically active radiation (PAR) was notably improved in the wheat-pea crop mixture due to the diverse canopy structure (Barillot et al., 2012, 2014). Enhanced utilization of diverse growth resources can effectively inhibit weed growth to a greater extent in intercrops compared to sole crops, addressing a major issue in organic farming systems (Hauggaard-Nielsen et al., 2006).

Compensation is a process when the failure of one species is restored by the companion species in the crop mixture and the normal functionality of the system recovers after disturbance or stress (Döring & Elsalahy, 2022). The reason behind this is that two different species in intercropping are less likely to be affected in the same manner and simultaneously lost by biotic and abiotic stresses, such as diseases, pests, or extreme weather conditions. (Raseduzzaman & Jensen, 2017). Hence, if a particular species is unable to thrive under certain stress conditions, other species can potentially compensate by utilizing the available resources and benefiting from reduced competition (Creissen et al., 2013).

Through this process of higher compensation, species mixtures have demonstrated remarkable yield stability (Döring & Elsalahy, 2022) across environments compared to the system where they grow as monocrops, particularly under varying levels of stress (Creissen et al., 2013). Therefore, to secure stable yields under adverse climate change with unpredictable weather conditions as well as biotic stresses, intercropping has been suggested to be more resilient compared to the current monoculture system (France et al., 2018).

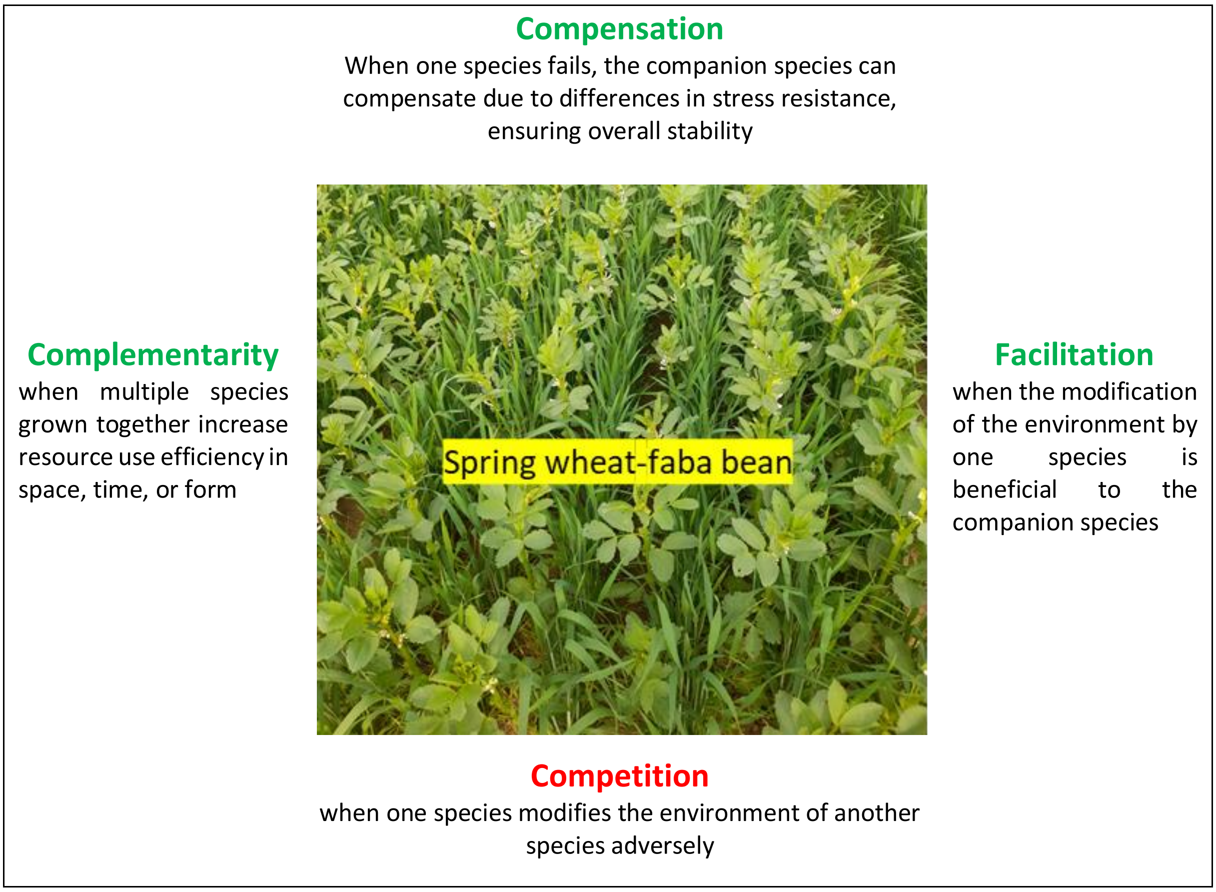

Fig. 1.2 Multiple ecological processes involved in intercropping system (Justes et al., 2021, adapted).

Facilitation, is when the modification of the environment by the presence of one species is beneficial to the companion species (Bedoussac et al., 2015). For example, in the spring wheat-lentil intercropping system, spring wheat provides physical support to lentil to avoid lodging and increase the photosynthesis of lentil. This cooperation between spring wheat and lentil decreases mechanical harvest losses and thereby increases the overall production (Loïc et al., 2018). In addition, cereal-legume intercropping has been reported to improve phosphorus (P) uptake by mobilizing sparsely soluble soil P (Li et al., 2007). To give an example, in a faba bean and maize intercropping system, a 20% to 38% increase in P uptake was reported depending on the supplied P fertilizer (Li et al., 2003).

This kind of facilitation is also observed for other limiting soil nutrients such as iron, zinc, or manganese that are chemically mobilized by one species and made available for the companion species (Li et al., 2014; Zhang & Li, 2003). Facilitation is further exemplified by instances where one species modifies the quality of another through disruptive mechanisms, rendering it a less appealing host for predators or parasites (Machado, 2009). For example, onions are strategically planted with carrots, serving to mask the scent of carrots from carrot flies, thus reducing the risk of infestation (Sullivan 2003). Moreover, due to the dilution effects of the host density (Boudreau, 2013), insect populations were notably reduced in 52% of cases, while only 15% of cases showed an increase in intercropping compared to monocultures (France et al., 2018). Compared to monocultures, intercropping has been reported to reduce disease in 73% of cases in more than 200 studies, primarily due to foliar fungi (Boudreau, 2013). Additionally, in crop mixtures, spring wheat is known for changing the growing environment positively for other species by releasing allelochemicals into the soil (Aslam et al., 2017). This kind of facilitation provided by intercrops makes this cropping system more productive and stable, particularly in stressful environments.

Competition in intercropping is an interaction between two species where at least one exerts a negative effect on the other (Bedoussac et al., 2015). Particularly when both species occupy the same niche and have similar requirements for abiotic resources (e.g., nutrients, water, space, light) in space and time (Justes et al., 2021). Therefore, exploitation of limiting resources by one species decreases the growth and abundance of others, especially when one species has a greater ability to absorb limiting resources than the companion species (Dybzinski & Tilman, 2009). Competition can occur between two individuals of the same species (intraspecific competition) and between different species (interspecific competition). According to the classical theory of competition, intraspecific competition is greater than interspecific competition because plants of identical species have the same growing habit and similar requirements for resources (Goldberg & Barton, 1992; Mangla et al., 2011). Therefore, competition for limiting resources in intercropping is reduced when multiple species grow together compared to single-species-based monoculture.

In a nutshell, to quantify and conclude the final net effect of the intercropping system, it is important to understand the various ecological processes underpinning plant-plant interactions that occur simultaneously in crop mixtures. By selecting a species mixture with a higher positive interaction effect, we can increase the beneficial effect of intercropping. Therefore, the success of intercropping depends on a good balance between complementarity, compensation, facilitation, and competition. However, this thesis will primarily focus on compensation by comparing and quantifying it in two distinct cropping systems: intercropping versus monoculture in **Chapter 2**.

1.3 Impact of intercropping on crop developmental stages (Crop emergence)

Throughout the plant's life cycle, the balance of various ecological processes (**Fig.1.2**) in intercropping varies. The intensity and direction of those plant-plant interactions are reported to shift considerably among multiple growth stages (Goldberg et al., 2001; Schiffers & Tielborger, 2006). To understand the underlying mechanism of competition and facilitation, it is necessary to study the strength of plant-plant interactions at all stages of the life cycle (Leger & Espeland, 2010), including germination, emergence, and initial root and shoot development (Mangla et al., 2011). However, most studies on intercrops concentrated on the final yield at harvest as an overall effect over the whole growing cycle and thereby neglected the possible interference between species at the very beginning of the growth stage (Benincasa et al., 2012; Mangla et al., 2011; Tielbörger & Prasse, 2009). Yet, the measurement of plant-plant interaction at a single point in the growing stage cannot conclude the lifetime dynamics of intercropping (Goldberg et al., 2001; Schiffers & Tielborger, 2006). This highlighted the importance of studying plant-to-plant interactions at different stages of the growing cycle to understand the potential performance of interspecific interactions in intercropping (Dong et al., 2018).

Fig. 1.3 Early crop development of spring wheat and faba bean intercropping at crop emergence stage (around 23 days after sowing) in the field experiment.

Crop emergence, i.e. the emergence of the shoot from a germinated seed through soil (**Fig.1.3**), is the most sensitive growth stage to competition (Mangla et al., 2011) and often determines subsequent plant performance and success for the future (Verdú & Traveset, 2005). While negative effects are relatively rare during the early stages after germination, they play a significant role in determining the final biomass of the plants (Goldberg et al., 2001). The interactions that are initially facilitative or neutral may transition to intense competition towards the end of the growing season when resource demand is higher (Schiffers & Tielborger, 2006). Particularly in the cereal-legume crop mixture, cereals achieve an advantageous position in the early stages due to faster root growth and an early uptake of nutrients, especially N (Bedoussac et al., 2015). These traits enable cereals to grow quickly during initial developmental stages, providing them with a strategic advantage in subsequent competition by securing early access to environmental resources (Bellostas et al., 2003). For instance, in a pea-barley crop mixture, it has been observed that the yield reduction of peas is likely induced during the early growth stages (Tofinga et al., 1993). Furthermore, the early interference of partner crops in an intercrop can also mitigate weed infestation and thereby influence the final intercrop composition, both of which are crucial for achieving the goals of organic food production (Bellostas et al., 2003). In this thesis, our focus lies on exploring the effects of the spring wheat and faba bean crop mixture, particularly during the crop emergence stage. Detailed elaboration and discussion of this aspect will be provided in **Chapter 3**.

1.4 The complex interactions in intercropping systems

Similar to the life cycle of the plant, the balance between different ecological processes in intercropping also varies across different environmental conditions and management practices. The dynamic environmental factors, the managemental strategies, and the interactions among these factors, collectively determine the final yield in intercropping. For example, the performance of cereal/legume intercropping is reported to vary depending on the availability of nitrogen and soil water in the system (Bedoussac et al., 2015; Chen et al., 2018; Corre-Hellou et al., 2006; Hauggaard-Nielsen & Jensen, 2001; Mao et al., 2012; Naudin et al., 2014). Particularly in low-input cropping systems, cereals are often noted as superior competitors for soil organic nitrogen, whereas legumes rely more on atmospheric nitrogen (Bedoussac et al., 2015; C. Li et al., 2020). Furthermore, in maize-pea intercropping, water use efficiency is observed to fluctuate depending on the growing conditions (Mao et al., 2012).

Just like environmental conditions, various management decisions such as species and cultivar selection, sowing time, sowing density, and fertilizer application rates significantly influence the relative competitiveness and performance of intercropped species (Yu et al., 2015). For example, the diverse aboveground and belowground traits of selected cultivars, including differences in canopy structure and height (Paul et al., 2024; Pronk et al., 2003), root system architecture (Corre-Hellou et al., 2007), and nutrient uptake capacity (Corre-Hellou et al., 2006), play a crucial role in determining the degree of interspecific competition for growth resources. In addition to selecting suitable cultivars, it is also crucial to choose the optimal sowing density to maximize the ecological benefits between component species. The optimal plant density in intercropping is anticipated to be higher than the density of each sole crop (Hauggaard-Nielsen et al., 2006). For example, in sorghum-pigeonpea intercropping, optimum density for intercrop pigeonpea was considerably higher than the sole crop optimum (Natarajan & Willey, 1980). Additionally, it is essential to strike the right balance in sowing density between dominant and dominated species to ensure balanced competition among component species. Therefore, to manage competitive effects in cereal-legume intercropping, it is suggested to maintain a higher density of dominated species and a lower density of the dominant species (Benincasa et al., 2012) to reduce the asymmetrical competition between intercrops .

The final performance of the mixture was significantly influenced not only by the main factor, but also by the interaction between all the environmental and managemental factors (Bedoussac et al., 2015). These interactions are essentially complex, exhibiting dynamic changes over time, space, and management practices (Paul et al., 2023, 2024). For that reason, the generalization of cultivar selection for optimal intercropping systems is rather difficult. In contrast to monoculture, the successful implementation of intercropping requires a higher level of skill and knowledge. This underscores the importance of conducting more intercropping studies aimed at identifying compatible cultivars finely tuned to specific growing conditions and production systems, thereby facilitating the reorientation of agriculture towards more sustainable practices.

1.5 Cultivar selection: optimizing intercropping research design

For the design and optimization of diversified cropping systems to maximize their services, precise planning is essential. This includes the selection of appropriate cultivars, along with considerations such as proper sowing dates and sowing densities. Cultivar choice is reported to play a pivotal role in optimizing functional complementarity in intercropping (Ajal et al., 2021; Demie et al., 2022; Kammoun et al., 2021). However, not all cultivars provide positive interaction in the mixture in terms of final grain yield (Paul et al., 2024). For example, in barley and pea intercropping, none of the five barley cultivars exhibited a positive effect in mixtures compared to when they were cultivated in monoculture (Hauggaard-Nielsen & Jensen, 2001). However, several studies have shown that selecting the right cultivars can lead to higher production in intercropping compared to sole crops (Demie et al., 2022; Yu et al., 2016). This emphasizes the potential for cultivar combinations to optimize intercropping systems. Therefore, a deeper mechanistic understanding of various cultivars is crucial to elucidate the connections between cultivar phenotype characteristics and optimizing functional complementarity in intercropping.

Plant traits that enhance complementary effects, minimize competition between species in the mixture, and thereby increase total productivity are crucial considerations as cultivars in designing intercropping. In particular, having similar phenology but different morphology, or vice versa, in cereal/legume mixtures leads to temporal and/or spatial niche complementarity (Demie et al., 2022). For instance, in pea and barley intercropping, having barley with a root system highly competitive for soil nitrogen sources and pea with a medium competitive root system capable of obtaining enough soil inorganic nitrogen are favorable traits, among others (Hauggaard-Nielsen & Jensen, 2001). When choosing cultivars for mixtures, it is crucial to look at various plant traits such as height, vigor, light absorption, leaf area, canopy structure, tillering, ground cover, nutrient use, stability, and disease resistance (Baxevanos et al., 2017). Among other cultivar traits, plant height has frequently been cited as a factor contributing to intercropping complementarity (Demie et al., 2022). In particular, when shorter dominant species (such as cereals) are combined with taller dominated species (such as legumes), higher productivity in the system is observed (Paul et al., 2024; Weih et al., 2022). Therefore, during selection, it's important to consider how a trait affects not just the target crop yield but also the partner crops in the mixture. For instance, while lodging resistance is important for peas grown as a sole crop, it's less critical when they're intercropped with barley due to the mechanical support provided by barley (Karpenstein-Machan & Stuelpnagel, 2000). Hence, there is a need for innovative research to establish criteria and conditions for selecting multiple plant species collectively as plant teams for intercropping.

The majority of cultivars available on the market are bred for monoculture rather than intercropping systems (Bančič et al., 2021; Bourke et al., 2021; Louarn et al., 2020). In the process of selecting the best-performing genotypes, current breeding programs primarily emphasize pure stands, thereby overlooking potential interspecific interactions and complementarity effects among multiple species. Hence, the best-performing cultivar in monoculture may not necessarily show the same level of performance in intercropping scenarios (Baxevanos et al., 2017; Kammoun et al., 2021; Paul et al., 2024). For this reason, it is imperative to establish exclusive breeding programs aimed at developing cultivars specifically adapted for intercropping, focusing on their performance within the mixture rather than in monoculture. Throughout this selection process, it is crucial to carefully choose multiple species as a cohesive team, ensuring they are ideally suited to the targeted environment and management practices.

Intercropping, a traditional practice spanning thousands of years, remains poorly understood agronomically in many parts of the world. With research in this field trailing behind that of monoculture, there's a need for further investigation to develop intercropping systems suitable for modern farming. However, due to the complexity and site-specific nature of interactions among multiple factors in intercropping, local experimentation with various crop combinations over multiple seasons is necessary. A deeper understanding of intercropping systems will boost adoption rates among farmers, offering more efficient resource utilization compared to monocropping. Given the diverse advantages of intercropping and the environmental challenges posed by current farming practices, continued research into multi-cropping systems is essential for fostering sustainable agriculture in the future.

1.6 Thesis objectives and outline

As evidenced above, crop mixtures offer numerous advantages compared to monocultures, although the mixture effect very much depends upon the careful selection of cultivars, environmental factors, and management practices. To address this knowledge gap, we conducted a series of large field experiments to evaluate the mixture effect and the mixing ability of multiple spring wheat and faba bean cultivars in two different densities and three different growing environments. In particular, the selected cultivars of both species share similar maturity for simultaneous sowing and harvesting while differing in their plant heights, allowing for observation of the impact of cultivar height on mixture performance. This thesis aims to showcase the beneficial impact of crop mixtures, particularly in terms of compensation, as well as explore how the mixture effects of different cultivars influence early crop development and final grain yield compared to monoculture.

In **Chapter 2**, We quantified the compensation of various cultivars of spring wheat and faba bean grown both as sole crops and intercrops in an environment with low crop emergence. Specifically, we hypothesized that compensation is higher in mixtures than in monocultures. Our observations confirmed a significant increase in overall compensation in mixtures. Surprisingly, this higher compensation in the mixtures originated from the weak competitor, faba bean. This finding underscores the importance of choosing diverse cropping systems over monocultures to achieve higher compensation, especially in challenging environments.

In **Chapter 3**, we initially hypothesized that the spring wheat/faba bean crop mixture would positively influence crop emergence during early growth stages. We examined various contributing factors, including the specific cultivars of spring wheat and faba bean, environmental conditions, and sowing densities, to understand this early-stage mixture effect. Additionally, we explored the dominance of spring wheat over faba bean within the mixture and how this dominance evolved over time. Our findings indicated a positive mixture effect for both species, with spring wheat initially dominating faba bean without suppressing its emergence (compared to faba bean emergence in monoculture) at around 23 days after sowing. This early dominance of spring wheat ultimately led to stronger performance in later growth stages, showing a consistently increasing trend over time. Understanding the mechanisms behind early domination and its evolving intensity can enhance the development and management of diversified cropping systems, promoting sustainable agriculture.

In **Chapter 4**, we assessed the mixing ability of ten spring wheat and two faba bean cultivars to determine the most productive mixtures in terms of total grain yield across three growing conditions and two sowing densities. Subsequently, we investigated the contributing factors (such as spring wheat cultivar, faba bean cultivar, environmental conditions, and sowing densities) towards this later-stage mixture effect. Additionally, we examined the correlation between the plant height of spring wheat cultivars and the total grain yield in the mixtures. Our findings revealed a complex interaction effect of multiple factors with cultivars, emphasizing the significance of cultivar selection tailored to the specific environment and management practices. The results can assist in identifying or developing suitable spring wheat cultivars specifically tailored for intercropping systems.

Finally, in **Chapter 5**, we synthesize and discuss the results obtained from the preceding chapters. This comprehensive analysis provides insight into the overarching patterns, relationships, and implications derived from our research on the compensation dynamics, mixture effects at early and later growth stages, and spring wheat/faba bean cultivar interactions in multiple cropping systems and management practices.

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2 Compensation in cereal-legume crop mixtures

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Abstract

The increasing environmental variability due to climatic change poses a significant threat to the stability of future agricultural production. Crop diversity has been shown to enhance stability, and a key mechanism in this diversity-stability relationship is thought to be compensation, i.e., the ability of a system to regain functionality in response to losing parts of its structure. However, quantitative evidence for compensation linked to diversity is currently scarce. To test if compensation is higher in more diverse systems, we conducted a field experiment comparing the compensation of spring wheat and faba bean grown in sole crops, i.e., monoculture, and grown together as an intercrop. We quantified the compensatory growth of crop biomass in response to naturally varying loss of plant density of spring wheat, relative to sowing density. Our findings revealed greater compensation in mixtures than in monocultures. Spring wheat dominated the mixture, but the higher compensation in the mixture stemmed predominantly from the weaker competitor, faba bean, as competition from spring wheat relaxed. For future research, we suggest to focus on crop traits enabling high compensation ability and the relationship between compensation and stability.

Keywords

Crop mixture, Complementarity, Diversity, Competition release, Compensation

2.1 Introduction

Increasing climatic variability is expected to be responsible for significant yield instability in future crop production (Lesk & Anderson, 2021; Vesco et al., 2021; Webber et al., 2020). As weather extremes are forecast to become more pronounced and unpredictable (AghaKouchak et al., 2020), it is urgent to consider approaches that stabilize crop performance and buffer against environmental fluctuations. Greater plant diversity has been shown to result in greater stability of primary production, for example in binary species mixtures of arable crops (Raseduzzaman & Jensen, 2017), cultivar mixtures (Reiss & Drinkwater, 2018), short-term multi-species mixtures of cover crops (Elhakeem et al., 2021), and in grassland communities (Tilman et al., 2001, 2006). Various mechanisms may underly the observation of higher stability of primary production in more diverse communities. For example, diversity is known to reduce the incidence of pests and diseases (Finckh et al., 2000; Ratnadass et al., 2012; Reiss & Drinkwater, 2018), e.g. through dilution effects, thereby decreasing variability of primary production in response to variable pest occurrence. Also, diversity is often supposed to maintain overall stability through higher compensation (Creissen et al., 2013; Rao & Willey, 1980). Compensation is a phenomenon closely related to the 'insurance hypothesis' of diversity, which states that diversity insures ecosystems against declines in their functioning because many species provide greater guarantees that some will maintain functioning even if others fail (Yachi & Loreau, 1999). Using the insurance hypothesis as a framework, Reiss & Drinkwater (2018) explain increased stability in cultivar mixtures by compensation, providing an example in which “cultivar-specific mortality in an early drought allows better adapted cultivars to exploit this additional space”. As already Yachi & Loreau (1999) pointed out, however, competitive release is only one component of compensation, as there are multiple ways of generating asynchronicity of species responses.

Generally, compensation can be defined as a process through which a system restores its normal functionality after disturbance or stress (Döring & Elsalahy, 2022). An aspect of compensation not incorporated in the model by Yachi & Loreau (1999) is the observation that it also occurs in non-diverse systems, such as monocultures (Wilson et al., 2003). Compensation is expected to be higher in species mixtures than in monocultures, because different species respond differently to external stresses, where the failure of one species is likely to be compensated through complementary resource utilization and a release from the competitive pressures of other species (Creissen et al., 2013; Peoples et al., 2009). For example, after being affected by Hurricane Mitch in Central America and Hurricane Ike in Cuba, farmers noted significantly less damage in intercropping systems (Altieri & Nicholls, 2012), with losses estimated at only 50% in intercropped fields compared to 90–100% in sole crop fields (Rosset et al., 2011).

So far, however, little attention has been given to quantifying the compensation in diversified cropping systems (Döring & Elsalahy, 2022). To determine the drivers and causes of compensation, it is therefore vital to quantify the compensation of different partners in multiple cropping systems. This would then help to better understand the multifunctional performance of crop diversification and predict overall system stability, especially in response to biotic and abiotic stresses.

Here, we conducted a field experiment aimed at quantifying the compensation of multiple spring wheat (SW) and faba bean (FB) cultivars grown as sole crops and intercrops. In particular, we tested the hypothesis that compensation of biomass growth against loss of plant density is higher in mixtures than in monocultures. The experiment involved evaluating the compensation of twelve SW entries and two FB cultivars in monoculture and intercropping against naturally occurring loss of plant individuals in the field. In other words, loss of plant density was hypothesized to be compensated by increased per-plant growth due to relaxed competition.

As legumes are known as weak competitors (Döring, 2015) and cereals are known to dominate in mixtures with legumes (Paul et al., 2023; Yu et al., 2016), a higher compensation was expected to stem from spring wheat in the mixture, e.g. due to increased tillering of the remaining plants. While our findings did indeed reveal greater overall compensation in mixtures compared to monocultures, this compensation was surprisingly not contributed by spring wheat, but by the weaker competitor, faba bean.

2.2 Material and Methods

A large field experiment was carried out in the year 2020 at the research station Campus Klein-Altendorf (CKA) of the University of Bonn, Germany. This conventionally managed research station is located in Rheinbach at 50°36'North, 6°59'East, and at an altitude of 186 m above sea level (a.s.l.), about 40 km south of Cologne. The site is characterized by a fertile Haplic Luvisol with a loamy silt soil texture. An average of 10.3 °C and 669 mm annual temperature and annual rainfall were observed between 1991 and 2020 at CKA. In the topsoil (0-30cm), 1.14%, 0.12%, and 2.8 kg ha^{-1} of total organic carbon, total nitrogen (N), and mineral N concentration at the start of the growing season were measured (for further details, see Paul et al., 2023).

A randomized complete block design was used with four replicates to test the effects of four experimental factors, namely, Factor A: cropping system, with the substitutive equiproportional mixture (i.e., replacement design mixed within a row) of SW and FB being compared with the respective monocultures; Factor B: FB cultivars (cv. Mallory and cv. Fanfare); Factor C: twelve SW entries, with ten SW cultivars (Anabel, Chamsin, Jasmund, KWS Starlight, Lennox, Quintus, Saludo, Sonett, Sorbas, and SU Ahab) and two 5-component equiproportional mixtures of these SW cultivars (for full details, see Paul et al., 2023); and Factor D: two sowing densities, namely 120% and 80% of the recommended sole crop densities (400 seeds m^{-2} for SW and 45 seeds m^{-2} for FB). Each of the 320 experimental plots was 10 m long and 1.5 m wide, with 6 rows and a 21 cm distance between rows. We sowed FB at 6 cm depth and SW at 3 cm depth on top of the FB rows (Paul et al., 2023).

To quantify compensation against loss of spring wheat density, we first determined plant density in all plots by counting emerged plants m^{-2} about 23 days after sowing (DAS), and measured crop aboveground biomass (dry matter, DM, in t ha^{-1}) about 82 DAS (full details, Paul et al., 2023) from monocultures and mixtures, manually separating SW from FB in the mixture samples.

We calculated compensation in the monoculture for SW and FB at a particular plant density (D) (**Eqn. 2.1**) and across all relative densities between 0 and 1 (**Eqn. 2.2**) as the difference between the actual biomass in the monocultures and the hypothetical biomass with no compensation (Döring & Elsalahy, 2022).

$$c'(\mathrm{D}) = \mathrm{f(D)} - \mathrm{n(D)} = \frac{\mathrm{kD}}{1+\mathrm{aD}} - \frac{\mathrm{kD}}{1+\mathrm{a}} \qquad (2.1)$$

$$C_{mono} = \frac{\mathrm{k}}{\mathrm{a}}\left(1 - \frac{1n(1+a)}{a}\right) - \frac{k}{2(1+\mathrm{a})} \qquad (2.2)$$

where c´(D) is the compensation function, f(D) is a non-linear density function that relates plant biomass B to density, and n(D) is a linear no-compensation function that simulates a proportional decrease of biomass with each unit of D decreasing from 1. Here, k and a are parameters estimated from **Eqn. 2.1**. C_{mono} is the overall compensation in monoculture across all relative densities from 0 to 1 (**Fig. 2.1A**).

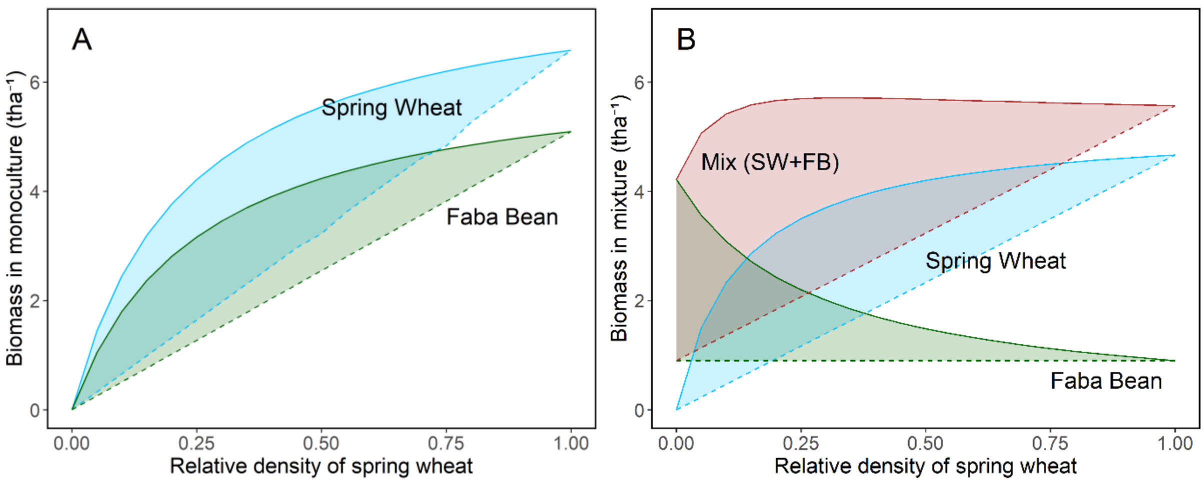

Figure 2.1. Examples of crop biomass (in DM tha^{-1}) compensation against loss of density, in a spring wheat entry (blue) and faba bean entry (green) with their sum (pink) in monoculture (A) and in the mixture (B). Here, SW is the partner with a variable relative density between 0 to 1, and FB is the fixed partner with a relative density of 0.5. Broken lines represent the no-compensation functions; solid lines represent modelled biomass yield with compensation fitted to observed data; and compensation is represented by the difference between the two lines (shaded areas).

Compensation is supposed to take place against a varying loss of the SW density due to biotic or abiotic stresses. To estimate this compensation for SW and FB biomass in the mixture, we considered FB density to be fixed density and SW density as variable. That means for each unit of density change for SW, the density of FB remains constant. In the field experiment, empirical variability of density of FB was nearly constant (mean 25.9 and SD 2.8) compared to density of SW (mean 126.7 and SD 50.6). Specifically, we calculated

$$c'_{SW}(D_{SW}) = \frac{k_{SW}D_{SW}}{1+a_{SW}D_{SW}} - \frac{k_{SW}D_{SW}}{1+a_{SW}} \qquad (2.3)$$

$$c'_{FB}(D_{FB}) = \frac{k_{FB}D_{FB}}{1+a_{FB}D_{SW}} - \frac{k_{fb}D_{FB}}{1+a_{FB}} \qquad (2.4)$$

$$C_{SW\_mix} = \frac{k_{SW}}{a_{SW}}\left(1 - \frac{ln(1+a_{sw})}{a_{sw}}\right) - \frac{k_{sw}}{2(1+a_{sw})} \qquad (2.5)$$

$$C_{FB\_mix} = \frac{k_{FB}D_{FB}ln(1+a_{FB})}{a_{FB}} - \frac{k_{FB}D_{FB}}{1+a_{FB}} \qquad (2.6)$$

$$C_{mix} = C_{SW\_mix} + C_{FB\_mix} \qquad (2.7)$$

where c'_{sw} is the compensation function for SW in the mixture with SW relative density (D_{sw}) from 0 to 1, and c'_{FB} is the compensation function for FB in the mixture with variable SW relative density (0 to 1) and fixed FB relative density (0.5; **Fig. 2.1B**). Here, k and a are parameters estimated from **Eqn. 2.3** for SW and **Eqn. 2.4** for FB. C_{mix} (**Eqn. 2.7**) is the sum of the corresponding integrals of these functions, i.e., the overall compensation in the mixture of SW and FB, across all relative densities of SW from 0 to 1 and fixed at 0.5 for FB.

To quantify the effect of mixtures on compensation in comparison to their respective monocultures, we used an index commonly used for assessing mixture effects, the land equivalent ratio (LER) (**Eqn. 2.8**), and its components, the partial LER (PLER), and applied this concept to the calculated compensated biomass. This was done by dividing the compensation of each partner in the mixture by the compensation in monocultures, **Eqn. 2.8** (Willey & Rao, 1980)

$$LER = PLER_{SW} + PLER_{FB} = \frac{C_{SW\_mix}}{C_{SW\_mono}} + \frac{C_{FB\_mix}}{C_{FB\_mono}} \qquad (2.8)$$

where C_{SW_mix} and C_{FB_mix} are the compensation of SW and FB in the mixture, defined by **Eqns. 2.5** and 2.**6**, respectively, and C_{SW_mono} and C_{FB_mono} are the compensation of SW and FB in monoculture as defined by **Eqn. 2.2**. Higher or lower efficiency of intercropping over monocultures is indicated by the LER value being larger or smaller than 1, respectively (Dariush et al., 2006).

In addition, we used the net effect ratio (NER; Li et al., 2023) (**Eqn. 9**) as a further commonly used index to quantify the extent of mixture effects on compensation, with

$$NER = \frac{C_{SW\_mix}+C_{FB\_mix}}{(p_{SW}*C_{SW\_mono})+(p_{FB}*C_{FB\_mono})} \quad (2.9)$$

Where p_{SW} and p_{FB} are the relative proportions of SW and FB in the mixture, i.e. 0.5.

We examined the mixture effects on compensation, testing PLER against 0.5 and LER and NER against 1 with a simple t-test by using cultivars as replicates.

2.3 Results

To evaluate the effect of the mixtures and compare the compensation in intercropping against compensation in monocultures, we calculated LER and NER on the biomass compensation of SW and FB. In general, on average of all cultivars (SW and FB cultivars), intercrops showed significantly higher compensation than sole crops, with a LER of 1.17 and NER of 1.13 (**Tab. 2.1**). Additionally, we observed a 28% higher PLER of FB compensation compared to the PLER of SW compensation. However, comparing the compensation of the individual species in different cropping systems, we observed that the mean compensation of SW biomass was 62% higher (C_{mono} of SW was 1.90) in the monoculture and 19% higher (C_{mix} of SW was 1.17) in the mixture compared to the FB compensation for biomass (C_{mono} and C_{mix} of FB were 0.94 and 0.79; **Tab. 2.1**).

Table 2.1. Overall mean compensation on average of all cultivars (SW and FB cultivars) in t ha^{-1} in the monocultures (C_{mono}), mixtures (C_{mix}), partial land equivalent ratios (PLER), land equivalent ratios (LER), and net effect ratio (NER) for the mean compensation of spring wheat and faba bean; differences from 0.5 for PLER and differences from 1 for LER and NER according to simple t-test at p<0.01 (**) and p<0.001 (***) or non-significant (ns).

Species	C_{mono}	C_{mix}	PLER	LER	NER
Spring Wheat	1.90	0.94	0.50^{ns}	1.17^{***}	1.13^{**}
Faba Bean	1.17	0.79	0.67^{***}		

In the mixture, the mean biomass compensation of SW cultivars with FB cultivar Mallory was 1.07 tha^{-1} and with Fanfare 0.84 tha^{-1} (**Fig. 2.2A**). However, we did not observe any significantly higher SW compensation in the mixture compared to the monoculture with both FB cultivars (**Fig. 2.2A**). The mean biomass compensation of both FB cultivars was significantly, on average, 26% higher in the mixture (0.73 tha^{-1} for Mallory and 0.84 tha^{-1} for Fanfare) compared to the FB biomass compensation of both cultivars in the monocultures (0.54 tha^{-1} for Mallory and 0.62 tha^{-1} for Fanfare; **Fig. 2.2B**). In FB, we did not observe any negative compensation of biomass in the monoculture or in the mixture (**Fig. 2.2B**).

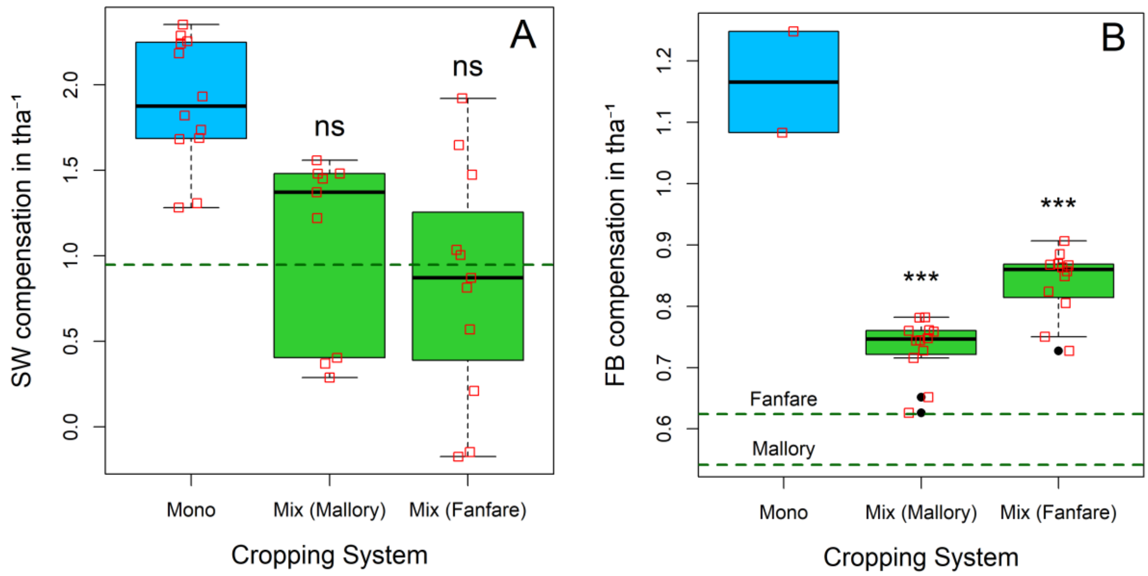

Figure 2.2. The overall compensation (C; t ha^{-1}) of twelve SW entries at monoculture, in a mixture with FB cultivar Mallory and FB cultivar Fanfare (A); the overall compensation of two FB cultivars at monoculture and in a mixture with twelve SW entries (B). The overall compensation in monocultures (blue boxes) was calculated by Eq. (2.2) at relative densities from 0 to 1, and the overall compensation in the mixture (green boxes) was calculated by Eq. (2.5) at relative densities from 0 to 1 for SW and a fixed relative density of 0.5 for FB. The dashed line represents the expected compensation in the mixture compared to monoculture; Significance levels (at p<0.001 (***) and non-significant (ns), t-test) refer to differences between observed and expected compensation in the mixture.

2.4 Discussion

In this study, we quantified and compared the biomass compensation of SW and FB in different cropping systems (intercropping vs. monocultures) in response to a reduction in plant density in one of the partners (wheat). Previous research has found theoretical (Yachi & Loreau 1999) and empirical evidence that greater species diversity leads to higher stability of primary productivity (Tilman et al., 2006). While compensation has been suggested as a mechanism to lead to increased stability, and thus, higher compensation was expected for intercrops compared to sole crops, compensation in systems of varying diversity, including monocultures has so far rarely been quantified.

Based on the LER and NER on compensation (Table 2.1), our analysis shows that intercrops did indeed compensate more than monocultures. In our experiment, wheat plants suffered from early mortality, reducing wheat plant density in some plots and thereby its competitive pressure. Faba bean, on the other hand, was unaffected by such early mortality. As a general mechanism explaining this observation, different species in the mixture may respond differently to external disturbances (Creissen et al., 2013). When one partner in the crop mixture fails, the other partner compensates through release of competitive pressure effectively utilizing additional space and resources available

(Creissen et al., 2013; McLaren & Turkington, 2011; Reiss & Drinkwater, 2018). Therefore, two different species in intercropping generate higher compensation than in single plant species-based monoculture.

In a cereal-legume crop mixture, cereals are known as the stronger competitors (Paul et al., 2023; Yu et al., 2016) in comparison to the legumes. Because cereals contribute more to the biomass of the mixture, it was expected that the observed positive effect of the SW-FB crop mixture over monocultures would stem primarily from SW rather than FB. In contrast, we observed that the overall positive effect of mixtures arose mainly from compensation in FB, especially due to competitive pressure release from the dominant partner SW. Although the removal of dominant species often leads to increased biomass by releasing subordinate species from competition (McLaren & Turkington, 2011), in our case, this competitive release was so strong that compensation through the subordinate partner (FB) was higher in the mixture than from the dominant partner (SW). On the other hand, SW did not compensate significantly more in the mixture with both FB cultivars than in monoculture (intercropping vs. monocultures).

In conclusion, higher compensation was observed in crop mixtures, predominantly driven by both FB cultivars compensation. Therefore, we highlight the importance of selecting more diverse cropping systems over monocultures to obtain higher overall compensation, particularly in challenging environments marked by biotic and abiotic stresses in the future. Additionally, as further research, we recommend quantifying crop compensation across different genotypes to select for higher compensation and enhance overall yield stability by effectively buffering against environmental fluctuations. One of the limitations of the present study is its focus solely on biomass compensation, warranting future research to also quantify and compare compensation at different life cycles, particularly for final grain yield. Moreover, it is important to explore correlations between multiple plant traits and compensation levels to better understand the dynamics of compensation and stabilize the overall agricultural production system.

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Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Data collection was performed by MP and DD, data curation was done by all authors, and data analysis was conducted by MP, TD. The first draft of the manuscript was written by MP, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The dataset generated during the current study is available as electronic supplementary material.

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3 Effects of spring wheat / faba bean mixtures on early crop development

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Abstract

Aims. Intercropping cereals and grain legumes has the potential to increase grain yield in comparison to the respective sole crops, but little is known about mixture effects at the early crop developmental stage. In cereal legume mixtures, the cereal is usually the dominating partner. We aimed to find out when domination starts, which factors may enhance early domination, and if there is a legacy effect of early domination on later growth stages.

Methods. We set up field trials at a low input conventional site in 2020 and an organic site in 2020 and 2021. Treatments included all possible monocultures and 1:1 mixtures of twelve spring wheat (SW) entries, and two faba bean (FB) cultivars. All combinations were each sown in two sowing densities. To measure the effect of the mixture on early crop development, we counted crop emergence (plant m-2) at ~23 days after sowing (DAS) and crop biomass dry matter at ~52 and ~82 DAS.

Results. We found positive mixture effects on SW emergence at the conventional site and on SW and FB emergence at the organic site in 2021. Spring wheat was the dominating partner in all three environments; SW domination, without suppressing FB, was already noticed at emergence at the conventional site. There, a small head start of SW at emergence favored dominance at later growth stages and lead to superiority over FB in terms of plant biomass.

Conclusions. Understanding early dominancy as observed here may help managing competition in mixture to enhance complementarity and improve productivity.

Keywords

Above ground biomass, asymmetric competition, compensation, diversification, early dominance, interspecific competition

3.1 Introduction

Intercropping, i.e. the mixed cultivation of crop species, is recognized as a pathway towards more sustainable agriculture (Brooker et al., 2015; Li et al., 2020; Lithourgidis et al., 2011; Maitra et al., 2021; Malézieux et al., 2009), because it has the potential to outperform monocropping in several aspects. In particular, intercropping has been found to improve resource use efficiency (Hauggaard-Nielsen et al., 2008, 2011), increase above ground biomasses (Cardinale et al., 2007; Rauber et al., 2001; Trydeman Knudsen et al., 2004), provide favorable habitat for beneficial organisms (Potts et al., 2003), reduce weeds, diseases and insect pests (Aziz et al., 2015; Bedoussac et al., 2015; Lithourgidis et al., 2011; Lopes et al., 2016), and assist farmers to deal with adverse and unpredictable weather condition due to climate change (van Zonneveld et al., 2020; Waha et al., 2018). Moreover, cereal legume mixtures are known for complimentary use of nitrogen (N) sources due to symbiotic N_2 fixation (SNF) from the atmosphere by legumes (Peoples et al., 2009). Most studies on mixtures have concentrated on final (grain) yield which integrates growth dynamics between species over the whole growing period. In contrast, only a few studies have investigated the degree of interaction between intercrops that may already be detected at a very early growing stage (Bellostas et al., 2003; Benincasa et al., 2012; Elsalahy et al., 2021), such as at crop emergence and the carry-on effects of mixing from early to later growth stages(Luo et al., 2021).

Crop emergence, i.e. the emergence of the shoot from a germinated seed through soil, is the first essential stage in the life cycle of plants because this process often affects components of plant fitness (Verdú & Traveset, 2005) and determines the future crop performance both at the individual (plant) and the population (crop stand) level. Presumably the final yield benefit of cereal legume crop mixture compared to their monocrops could not appear without earlier below- and aboveground competition and/or facilitation processes. In barley and pea intercropping, for example, the reduction in yield of pea has been found likely to be induced in early growth stages (Tofinga et al., 1993). However, the exact proportion and direction of the mixture effects on that early growing stage are currently largely unknown.

Seed germination and seedling emergence are influenced by the combination of different biotic and abiotic factors. Different studies show that germination and early crop establishment are affected by a range of factors, including temperature and soil water availability (T. Luo et al., 2018; Tribouillois et al., 2016), soil characteristics such as soil bulk density and the presence of soil crusts (Briggs & Morgan, 2011; Soureshjani et al., 2019), as well as the identity and density of neighboring seeds and seedlings (Fenesi et al., 2020; Leverett et al., 2016, 2018; Tielbörger & Prasse, 2009). Some studies demonstrate that the acceleration of germination is most likely influenced by the presence of a competitive neighborhood (Dyer et al., 2008; Orrock & Christopher, 2010). The entire soil chemistry related to early root and shoot growth could change due to volatile organic compound emission from the germinating seed coat (Fincheira et al., 2017; Tielbörger & Prasse, 2009) and thus affect their neighbors. However, the growth dynamics in a crop mixture depend on the balance between competitive (Renne et al., 2014; Tielbörger & Prasse, 2009) and facilitative interactions (Orrock & Christopher, 2010; Schiffers & Tielborger, 2006) between seedlings. Indeed, facilitation was observed to enhance seedling survival, especially in extreme weather events such as harsh winters where low temperatures constrain alpine tree regeneration and growth (Batllori et al., 2009). By accelerating or reducing the emergence rate, crop mixtures might have a decisive role on plant biomass in the early growth stage, and thereby also on the balance of competition among partners at later growth stages.

Crop mixtures of cereals and grain legumes have a high potential of increasing the system productivity compared to the respective sole crops (Xiao et al., 2018). In general, in such crop mixtures, cereals have been shown to gain a higher relative yield than grain legumes (Xiao et al., 2018; Yu et al., 2016). However, estimating the final yield as an overall growth dynamic is obviously insufficient for drawing conclusions about lifetime dominancy over the whole growing stage of the cereal over the legume. It is currently unknown when the domination (i.e. relative higher proportion of biomass in the mixture) of the cereal over the legume starts, in particular, whether this domination is evident already at an early growing stage. Further, it is not known if there is a legacy of early dominance (if any) on later performance of the crops. It is important to understand the competitive balance between the two intercropping partners at an early growing stage because this may play a major role in determining productivity in mixtures. To understand the complexity of crop mixtures and predict their productivity and the relative performance of the partners, it is vital to study the entire life cycle of the interacting plants from crop emergence. Our goal was therefore to look at the early dynamic of cereal legume interaction in the mixture and its effect on the future crop developmental stage.

We therefore conducted an experiment to test the mixture effect of spring wheat/ faba bean crop mixtures of emerging seedlings in three different environments. In particular, we tested the following four hypotheses: (H1) There is a positive mixture effect of spring wheat/faba bean crop mixture at the early growing stage (emergence); a positive mixture effect, i.e. higher crop emergence in mixture than in the respective monocultures, may occur due to higher relative emergence of SW or FB or both partners in the mixture. (H2) The early mixture effect depends on factors such as SW cultivar, FB cultivar, environment, and sowing density; (H3) Domination of SW in the mixture can be observed already at crop emergence; here, by domination we mean that the relative proportion of dominating partner in the mixture is higher compared to the other partner; (H4) There is a legacy of early mixture effects on later growth stages as measured by crop biomass, i.e. the strength of domination of one partner over the other at crop emergence is carried over to later stages.

3.2 Material and Methods

3.2.1 Experimental Site

The field experiment was carried out in three environments, namely in one year (2020) at Campus Klein-Altendorf (CKA) and in two years (2020 and 2021) at Wiesengut (WG), both research stations of the University of Bonn, Germany. These three environments are referred to as CKA2020, WG2020, and WG2021. Campus Klein-Altendorf is a conventionally managed research station located at 50°36'North, 6°59'East, and at an altitude of 186 m above sea level (a.s.l.) in Rheinbach, about 40 km south of Cologne. The site is characterized by a fertile Haplic Luvisol with a loamy silt texture. Wiesengut, an organically managed research station, is located at 50°47'North, 7°15'East at an altitude of 65 m a.s.l. in the lowland of the river Sieg near Hennef. The soil type is a Haplic Fluvisol with a silt loam texture on gravel layers, and fluctuating groundwater level. Compared to CKA, total organic carbon (C_t) and total N (N_t) concentrations in the soil were higher at WG. Mineral N (N_{min}) concentrations in 2020 were higher at CKA than at WG, and the latter site, higher in 2021 than in 2020 (**Table 3.1**).

Table 3.1. Total soil organic carbon (C_t), total nitrogen (N_t), and mineral N concentrations in three soil layers (0-30cm, 30-60cm, 60-90cm) at sowing at Campus Klein-Altendorf (CKA) and Wiesengut (WG). Mean and standard deviation (s.d.) are provided.

Soil depth [cm]		**CKA 2020**			**WG 2020**			**WG2021**
		C_t [%]	**N_t [%]**	**Mineral N [kg ha^{-1}]**	**C_t [%]**	**N_t [%]**	**Mineral N [kg ha^{-1}]**	**Mineral N [kg ha^{-1}]**
0-30	Mean	1.14	0.12	2.80	1.35	0.13	1.39	3.42
	s.d.	0.051	0.004	0.22	0.052	0.006	0.26	0.72
30-60	Mean	0.56	0.07	1.32	0.75	0.09	0.39	1.28
	s.d.	0.078	0.004	0.14	0.051	0.004	0.11	0.44
60-90	Mean	0.35	0.06	1.60	0.40	0.06	0.18	1.25
	s.d.	0.029	0.003	0.18	0.057	0.006	0.06	0.55

The average annual temperature and annual rainfall at the experimental sites was 10.3 °C and 669 mm at CKA, and 10.7 °C and 732.8 mm at WG between 1991 and 2020, respectively. In April and May, the most relevant months for early crop development of the spring sown trial crops, precipitation was relatively low in 2020, but higher in 2021 with an average temperature mean at both sites (**Fig. S3.1**). Soil temperature at 15 cm soil depth during April and May was higher in 2020 (15.52°C at WG and 12.28°C in CKA) compared to 2021 (10.14°C in WG).

3.2.2 Experimental Design

Each of the three field experiments was performed as a randomized complete block design with four replicates and four experimental factors. Factor A compared the mixture of spring wheat (SW) and faba bean (FB) with the respective monocultures. In the mixtures, both crop species were mixed in a substitutive equiproportional mixture (i.e. replacement design) within the row during sowing. Factor B was the FB cultivar with two levels (cv. Mallory and cv. Fanfare). Factor C had 12 levels of different SW entries, using ten spring SW cultivars (**Table 3.2**) and two 5-component equiproportional mixtures of these SW cultivars. To increase the level of functional diversity, two groups of cultivars mixtures were created by dividing the SW cultivars according to their plant height scores. Scores of SW cultivars were obtained from official national variety lists provided by the German Federal Plant Variety Office (Bundessortenamt 2019). Group 1 contained five cultivars with diverse plant height scores (standard deviation (s.d.) = 2.4), whereas Group 2 contained five cultivars with more similar plant height scores (s.d. = 0.8) (**Table 3.2**). The required amounts of seeds for each cultivar within the group were calculated separately according to their seed weight (thousand kernel weight, TKW), germination percentage (GP) (**Table S3.1**), plot area, and sowing density (**Equation S3.3**). Finally seeds of the five cultivars were mixed homogeneously before sowing. Although two 5-component equiproportional group mixtures is discussed here as SW entries, no significant effect of those groups on crop emergence were observed and will not be discussed further in this paper.

Table 3.2. Ten spring wheat cultivars and two mixed groups of spring wheat cultivars with their characteristics scores based on a 1-9 scale according to German Federal Plant Variety Office (Bundessortenamt 2019). High and low figures (score 9 and score 1, respectively) indicate that the cultivar shows the character to a high, or low degree, respectively.

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**

Factor D varied the sowing density and had two levels, 120% and 80% of the recommended sole crop densities (%RD) of 400 seed m^{-2} for SW and 45 seed m^{-2} for FB (**Table 3.3**). Spring wheat and faba bean were mixed in a 1:1 ratio that means for the high density in the mixture 50% of the high density of SW monoculture was mixed with 50% of the high density used FB monoculture, and low density mixture consisted of 50% of the low density used for SW monoculture and 50% of the low density used for FB. In total, the experiment included 76 treatments per block and both crops, SW and FB. The monocultures of FB were doubly replicated to stabilize comparisons with the numerous mixtures. This resulted in 320 plots for each of the three field trials.

Table 3.3. Faba bean and spring wheat seed densities in the monocultures and the mixtures for two levels of sowing density.

Relative rate/	**Seeds in Monoculture (seed m^{-2})**		**Seeds in Mixture (seed m^{-2})**	
Species	**80%**	**120%**	**80%**	**120%**
Faba bean	36	54	18	27
Spring wheat	320	480	160	240

3.2.3 Management Practices

After harvesting the pre-crop (**Table 3.4**), the soil was ploughed once (30 cm depth, with a moldboard plough) in WG and twice (7 and 10 cm depth, with a chisel plough) in CKA, and the seedbed was prepared with a rotary harrow at both sites. The single plot size was 1.5 m × 10 m with 6 rows and 21 cm row to row distance. Faba bean was sown first, at 6 cm depth; to maintain the appropriate FB sowing density, a direct seeding machine type Hege 95 B was used and optimized by rotation setting according to sowing density (**Table S3.2**). Thereafter, SW was sown directly over FB with a Hege 80 seeder at 3 cm soil depth. No seed treatment was performed on FB or SW before sowing. The trials were run with no use of chemical fertilizers, herbicides, or pesticides. In both years, mechanical weeding was carried out twice (3 and 5 weeks after sowing) using a hoe, and once four weeks after sowing with a harrow.

Table 3.4. The three environments, pre-crops, sowing dates, and measurements of faba bean and spring wheat in the intercropping experiment.

Environment	Pre-crop	Sowing date		Crop Emergence Counting (plant m^{-2})	Biomass Cut (DM in t ha^{-1})	
		Faba bean	Spring Wheat		First	Second
CKA 2020	Winter barley	25th March	26th March	22th April	20th May	17/19th June
WG 2020	Red clover grass	28/29th March	29th March	20th April	20th May	15/16th June
WG 2021	Red clover grass	3rd March	3rd March	20th April	18th May	21/23th June

3.2.4 Measurements

In order to monitor the emergence and early growth of the crop, crop emergence (plant m^{-2}) was measured by counting plants on defined areas (**Fig. 3.1**) per plot about 23 days after sowing (DAS), and biomass measurements (dry matter, DM, in t ha^{-1}) were performed twice about 52 and 82 DAS, respectively; the exact times in days after sowing (DAS) are reported in **Table 3.4.** For all measurements, 1 m long sections from the 3rd and 4th rows of the plots were chosen after discarding 1 m for biomass and 3 m from the 3rd rows and 4 m from the 4th rows for crop emergence from the edge to avoid potential edge effects. Counting of emerged seedlings and the first biomass cut was performed from one side of the plot whereas a second biomass cut was performed from another side of the plot (**Fig. 3.1**).

During the first biomass cut, 12 selected treatments (all FB monocultures, FB mixtures with SW cultivars Lennox and SU Ahab, and SW monocultures with cultivars Lennox and SU Ahab; which makes 48 plots in total out of 320 plots per site) were taken to manage work load of the large field trial. During both biomass cuts, both crop and weed aboveground biomasses were taken at the base. Fresh biomass samples from the sole crops were manually separated into weeds and crops; samples from the intercrops were separated into weeds, SW, and FB before further processing. Biomass dry weight (t ha^{-1}) of the samples was obtained by oven-drying at 105°C until weight constancy.

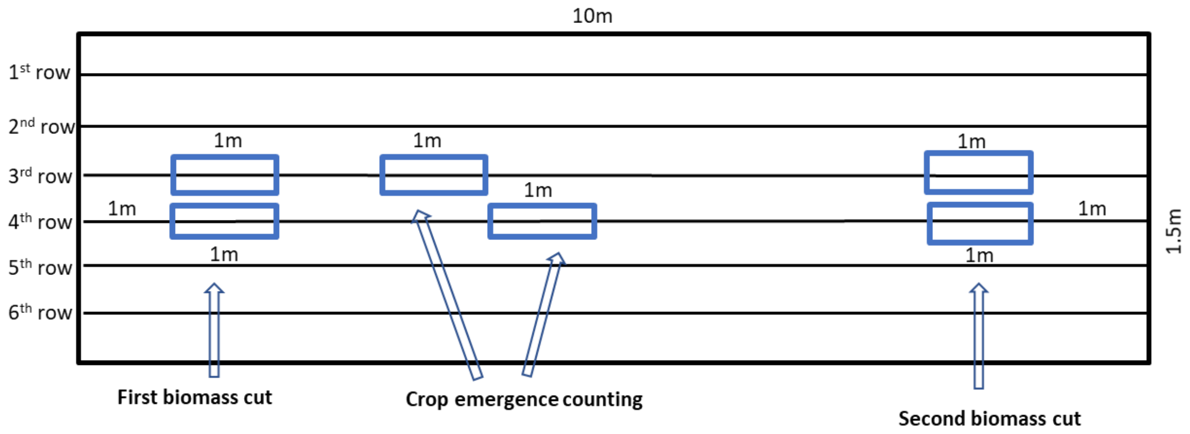

Figure 3.1. Schematic illustration of a single plot showing the locations where the individual measurements were taken.

3.2.5 Data Processing and Calculations

To quantify the effect of the mixture in comparison to the monocultures, land equivalent ratio (LER), and partial LER (PLER) were calculated for the both first and second crop biomass cut. The LER of a mixture measures the relative land area that is required for the crop monocultures to produce the same biomass as observed in the mixture; it was calculated as the sum of the PLERs of the two species (**Equations 3.1 and 3.2**) in the mixture by using **Equation (3.3)** (Willey & Rao, 1980).

$$PLER_{SW} = Wheat_{mix} / Wheat_{mono} \quad (3.1)$$

$$PLER_{FB} = Bean_{mix} / Bean_{mono} \quad (3.2)$$

$$LER = PLER_{SW} + PLER_{FB} \quad (3.3)$$

where $Wheat_{mono}$ and $Bean_{mono}$ are the biomass of SW and FB in monoculture and $Wheat_{mix}$ and $Bean_{mix}$ are the biomass of each crop in the mixture. An LER value > 1 indicates an advantage of intercropping over monocropping, while LER < 1 indicates that intercropping reduces the biomass of the components in comparison to the monocultures (Dariush et al., 2006).

We also applied the same concepts to crop emergence data to quantify the effect of mixture on emergence in comparison to the monocultures. In particular, we calculated partial emergence equivalent ratio (PEER) of SW and FB by dividing the number of emerged crop plants in the mixture by the number of emerged crop plants in monocultures (**equations 3.4 and 3.5**). Emergence equivalent ratio (EER) was calculated as the sum of the PEERs of the two species by using **Equation (3.6)**.

$$PEER_{SW} = \text{number of wheat plants in mix/number of wheat plants in monoculture} \quad (3.4)$$

$$PEER_{FB} = \text{number of bean plants in mix /number of bean plants in monoculture} \quad (3.5)$$

$$EER = PEER_{SW} + PEER_{FB} \quad (3.6)$$

The emergence equivalent ratio is the analogous to the germination ratio (GR) used in Elsalahy et al. (2021), but refers to emergence rather than germination.

To measure the competitive ability of intercrops, to identify the dominant partner producing relative higher proportion of biomass in the mixture than the other partner and to indicate the degree of dominance, a simple competitive ratio (CR) is considered. CR refers to the ratio of the PLERs of the two partners in the intercropping (Willey & Rao, 1980), and, by analogy, to the ratio of the PEERs. Competitive ratio (CR) was only calculated for the second crop biomass cut.

$$CR_{SW} \text{ on emergence} = PEER_{SW} / PEER_{FB} \quad (3.7)$$

$$CR_{SW} \text{ on biomass} = PLER_{SW} / PLER_{FB} \quad (3.8)$$

3.2.6 Statistical Analyses

Partial land equivalent ratio (PLER) and Partial emergence equivalent ratio (PEER) were non-normally distributed according to the Shapiro-Wilk test and the variances between the groups were homogeneous according to Fisher's F test which was complemented by graphical assessments. As we observed the data were non-normally distributed, non-parametric tests were performed in most of the cases. In particular, we examined the mixture effects at the early growth stage by using a two-sided Wilcoxon signed-rank test against PEER above 0.5. In a substitutive mixture, a PEER values > 0.5 for individual partners (SW and/or FB) means a positive mixture effect on crop emergence on that respective partner. Dominance of one partner over the other at emergence as well as at later biomass was assessed by comparing the two partners using a two-sided Wilcoxon test of PLER and PEER. For multiple comparisons between different factors, non-parametric Kruskal-Wallis test was used followed by Dunn test with Bonferroni correction.

In addition, to detect interactions and dependencies of mixture effects from other trial factors, the multifactorial trial was subject to analysis of variance (ANOVA), although most of the data significantly deviated from normal distribution as the robustness of ANOVA is proven under application of non-normally distributed data (Schmider et al., 2010). When the sample size is reasonably large and equal, the ANOVA's F test is robust enough to deal with moderate departures from normality (Sainani, 2012; Winer et al., 1991). Even with extreme deviations from normality, a sample size of approximately 80 is sufficient to run a parametric test t-test; Lumley et al., 2002). Here, we conducted ANOVA, to test the effects of the mixture on cultivar spring wheat, cultivar faba bean, environment, and sowing density. In the first step, a model was prepared considering all possible interactions between those four factors. Non-significant factors or interactions were iteratively removed from the model to improve model performance according to Akaike's Information Criterion (AIC) (Burnham et al., 2011). The final model included two independent variables spring wheat cultivar and environment, and their interaction.

We assumed a legacy of early mixture effects on later biomass. To verify this, we tested for a correlation (Pearson) and linear regression model between the competitive ratio (CR) at emergence and CR at later crop biomass. All statistical analyses were conducted in RStudio version 1.4.1106 (*R Core Team., 2020*).

3.3 Results

3.3.1 Mixture effects at the early growth stage

Although the expected crop emergence (100% of sown plants, based on densities shown in **Table 3.3**) was the same in the three environments, the observed emergence was highly different between the three trials (**Table 3.5**). At CKA2020, the observed SW emergence was much lower for both densities compared to the other two environments (WG2020 and WG2021, **Table 3.5** and **Fig. 3.2**). Compared to the expected crop emergence, the observed SW emergence at CKA2020 in monoculture was 46.1% at low density and 46.2% at high density. In some plots the counted number of crops was higher than the calculated number of sown seeds (**Fig. 3.2**), probably due to slight technical inaccuracies of the sowing machine in placing the seeds within the row.

Table 3.5: Mean values for observed crop emergence (number m^{-2}) of faba bean and spring wheat (monocultures and mixtures) for the three environments depending on the sowing density (low density: LD and high density: HD). Within each column, environments with different letters are significantly different according to the Dunn test with Bonferroni correction.

Environments	Faba Bean				Spring Wheat			
	Monoculture		mixture		Monoculture		mixture	
	LD	HD	LD	HD	LD	HD	LD	HD
CKA2020	33.0a	51.5a	16.7a	25.9a	147.5c	222.0c	88.8c	128.0c
WG2020	32.6a	50.3a	16.5a	25.7a	264.0b	387.5b	130.7b	197.0b
WG2021	29.3a	45.1b	16.8a	23.6b	287.2a	404.1a	147.4a	219.6a

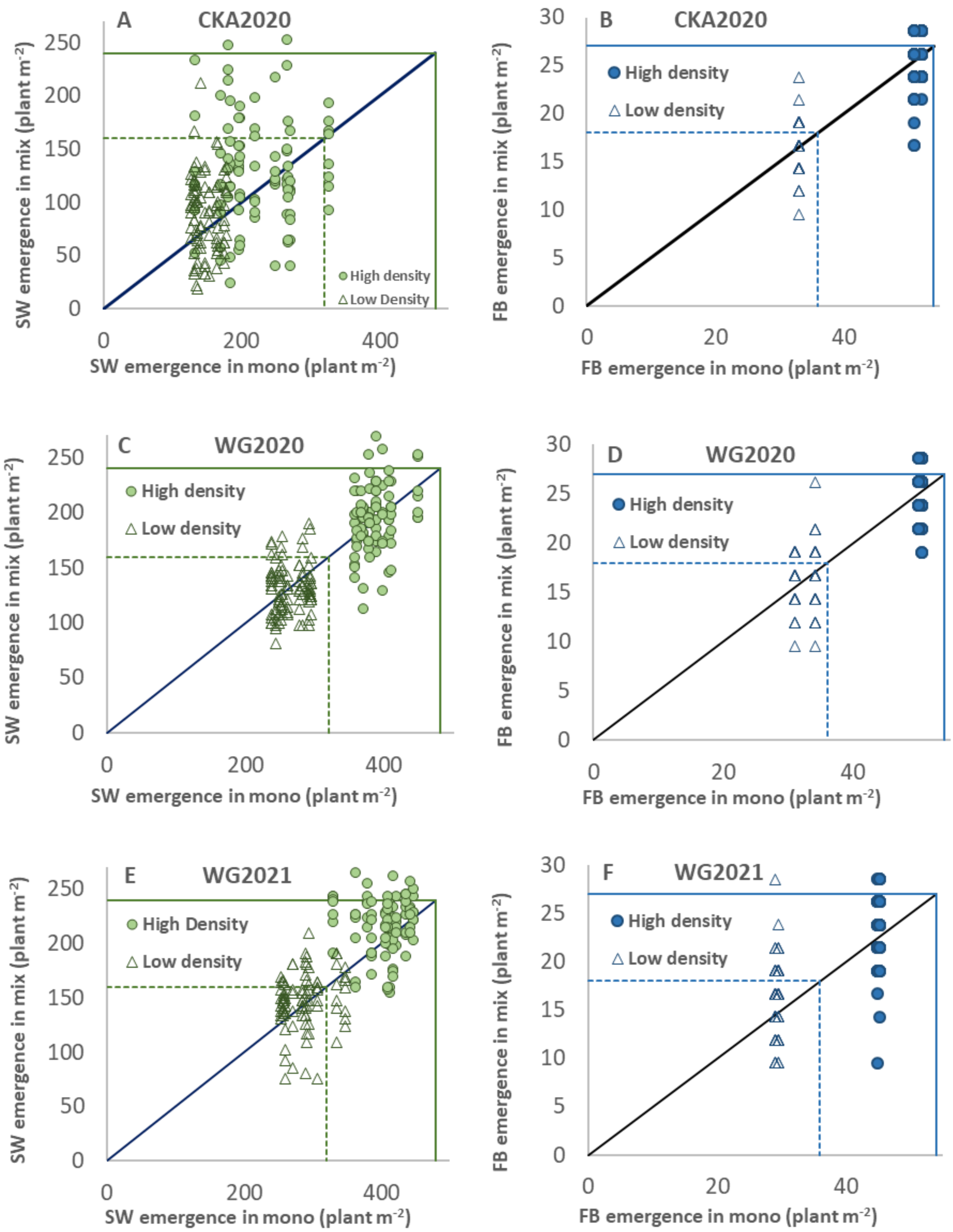

Figure 3.2. Crop emergence (plant m^{-2}, each symbol representing one plot) of spring wheat (SW, panels A, C, and E, green symbols) and faba bean (FB, panels B, D, and F, blue symbols) in monocultures (mono) and mixtures (mix) for high (filled circles) and low (open triangles) sowing densities in the environments CKA2020 (A, B), WG2020 (C, D) and WG2021 (E, F). Points above the black diagonal (PEER = 0.5) indicate higher crop emergence in the mixture than in monoculture. Sown high and low densities are represented by solid and dashed lines, respectively.

In mixture, the observed SW emergence at CKA compared to the expected SW emergence was comparatively higher than in monoculture. We observed a high variation of SW emergence at CKA2020 compared to the other two environments (WG2020 and WG2021; **Fig. 3.2A**). At the environment WG2021, a relatively low FB emergence was noticed compared to the expected emergence (in monoculture 83.3% and 81.4% for high density (HD) and low density (LD), respectively; and in mixture 86.2% and 94.7% in LD and HD, respectively; **Table 3.5** and **Fig. 3.2F**).

Depending on the trial, we marked positive mixture effects already at crop emergence (PEER> 0.5) about 23 days after sowing (DAS) (**Table 3.6**). In particular, the mixture effect was consistently positive for SW at both densities at the environment CKA2020 where the observed SW emergence was low (**Table 3.5**). At WG2021, the mixture effect was positive for both species (FB and SW) and both densities (LD and HD) where the observed FB emergence was low. That means although the observed crop emergence in general was lower in both cropping systems (mixture and monoculture) than what was sown, the observed emergence was much lower in monoculture than mixture. Neither species nor densities showed any positive effect at WG2020 (**Table 3.6**).

Table 3.6: Mean values for partial emergence equivalent ratio (PEER) of faba bean and spring wheat for three environments depending on sowing density; differences from 0.5 according to Wilcoxon test at p<0.01 (**) and p<0.001 (***) or non-significant (ns).

Environments	Faba Bean		Spring Wheat	
	LD	**HD**	**LD**	**HD**
CKA2020	0.51^{***}	0.50^{ns}	0.61^{***}	0.61^{***}
WG2020	0.51^{ns}	0.51^{ns}	0.50^{ns}	0.51^{ns}
WG2021	0.57^{***}	0.52^{***}	0.52^{**}	0.54^{***}

3.3.2 Dependence of mixture effects on other experimental factors

The mixture effect at the crop emergence stage may depend on different other factors, such as SW cultivar, FB cultivar, sowing density, environment, and their interactions. To find out which of these had a significant effect on potential mixture effects, a full model ANOVA was conducted considering all possible interactions between those four factors (**Table S3.3**). Step by step all non-significant factors and interactions between those factors were removed from the model to improve model performance according to Akaike's Information Criterion (AIC). The final model included two independent variables SW cultivar and environment, and their interaction (**Table 3.7**).

Table 3.7: The AIC-selected final ANOVA model for emergence equivalent ratio (EER) with spring wheat (SW) cultivar and environment, and their interaction; df: degrees of freedom.

Source of variation	df	Mean Square	F-value	P-value
SW cultivar	11	0.14	3.53	<0.001***
Environment	2	0.50	12.56	<0.001***
SW: Environment	22	0.14	3.47	<0.001***

Comparatively higher divergence of SW emergence equivalent ratios (EER) was observed at CKA2020 than at WG2020 and WG2021 (**Fig. 3.2** and **3.3**). At CKA2020, SW cultivar Lennox showed significantly higher crop emergence in the mixtures than monocultures, across both bean cultivars. On the other hand, the SW cultivars Anabel and Quintus showed significantly lower crop emergence in the mixture than monocultures. At WG2021, SW cultivar SU Ahab showed significantly higher crop emergence than SW cultivar Jasmund. No significant effect of SW cultivar was observed at WG2020.

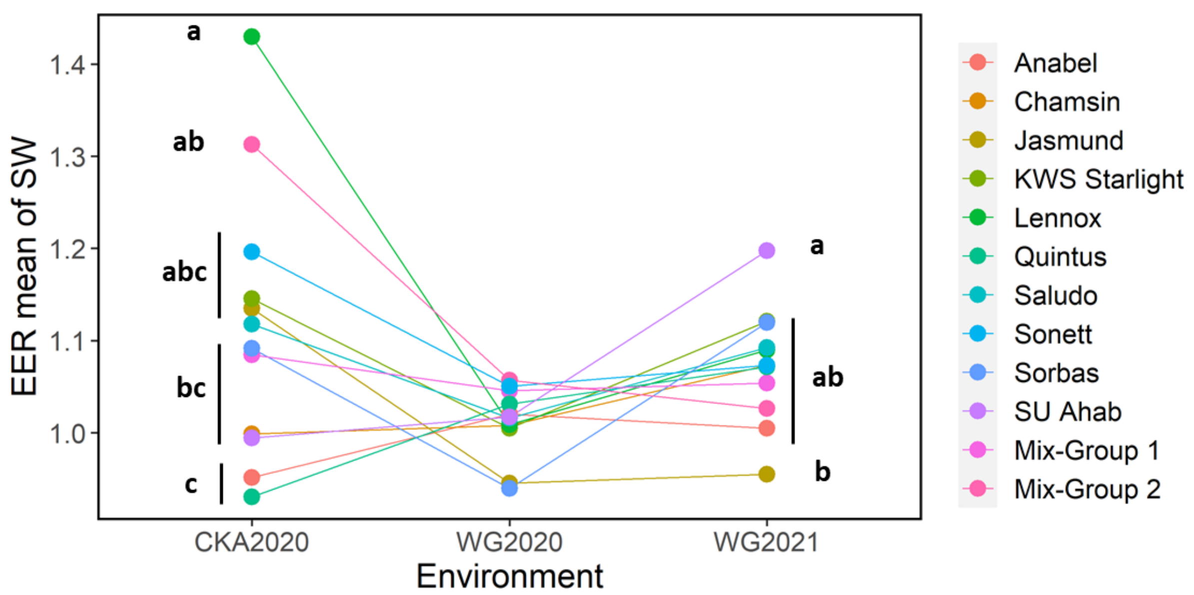

Figure 3.3. Mean of emergence equivalent ratio (EER) of 12 levels of different spring wheat entries (ten cultivars and two 5-component mixtures of these wheat cultivars) in three different environments. Within each environment, SW cultivars with different letters are significantly different according to Tukey's HSD test.

3.3.3 Spring wheat dominance at the early stage

At the environment CKA2020, domination of SW over FB was already observed at crop emergence (**Fig. 3.4A**), as the mean partial emergence equivalent ratio (PEER) of SW was 0.11 higher than FB mean PEER (Wilcoxon test; P< 0.001). This level of domination of SW over FB at CKA2020 increased over time (**Fig. 3.4B and 3.4C**). The PLER mean difference between SW and FB at CKA2020 increased to 0.4 (Wilcoxon test; P< 0.001) at about 52 DAS and to 0.50 (Wilcoxon; P< 0.001) at about 82 DAS.

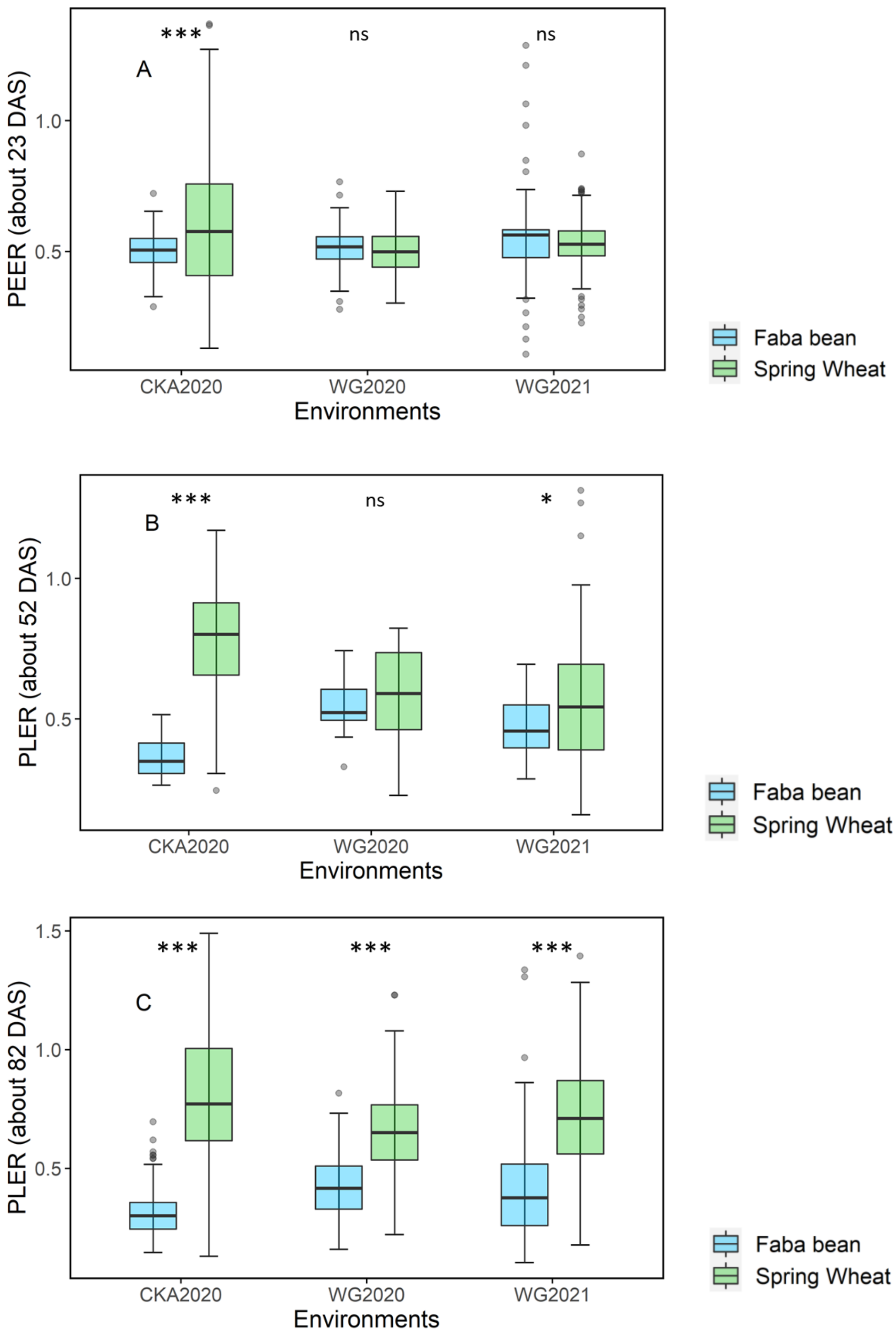

Figure 3.4. Comparison between faba bean (blue boxes) and spring wheat (green boxes) partial emergence equivalent ratio (PEER; A) about 23 days after sowing (DAS) and the partial land equivalent ratio about 52 DAS (PLER, B) and about 82 DAS (C) in the three environments. Significant differences were indicated according to

Wilcoxon test at P<0.05 (*) and P<0.001 (***) or non-significant (ns). PEER was calculated by Eq. (3.4) and Eq. (3.5); PLER was calculated by Eq. (3.1) and Eq. (3.2).

Although no significant PEER mean differences between SW and FB were observed during the early developmental stage at WG2020 and WG2021, the SW domination over FB changed over time for these environments (**Fig. 3.4**). At WG2021, a significant mean difference between SW and FB was first observed about 52 DAS (PLER mean difference 0.11; $P < 0.05$) which increased by about 82 DAS to a PLER mean difference of 0.31 $P < 0.001$; **Fig. 3.4B and 3.4C**). On the other hand, at WG2020, a highly significant mean difference between SW and FB PLER was only observed after about 82 DAS (PLER mean difference of 0.25; $P < 0.001$; **Fig. 3.4C**).

3.3.4 Legacy of early mixture effects on later biomass

In cereal legume crop mixtures, the cereal is known to be a dominant partner by achieving a higher relative yield than grain legumes. However, it is not known if the degree of early cereal domination affects its domination at later biomass production, i.e. if there is any legacy of early mixture effects on later biomass. To estimate the legacy effect, SW competitive ratio (CR_{SW}) was calculated by **Eq. (3.7)** and the relationship between CR_{SW} at emergence vs. later CR_{SW} was tested with linear regression. There was a strong linear relationship between the two CR_{SW} values at CKA2020 for both densities ($P < 0.001$, **Fig. 3.5** and **Table 3.11**), i.e. the higher the proportion of SW early on in SW-FB mixtures, the higher was its dominance later in the season. In addition, dominance, as measured by the CR_{SW}, increased over time. In the two other environments (WG2020 and WG2021) and two densities (high and low), only a weak significant correlation was observed, which at WG2020 for high density was significant at $p < 0.05$ (**Table 3.11**).

Table 3.11. Summary of the linear regression model (lm) of spring wheat competitive ratio (CR_{SW}) at PLER (about 82 days after sowing) against CR_{SW} at PEER (about 23 days after sowing) for three environments depending on sowing density.

Environments	Densities	Linear regression (CR_{SW} at PLER ~ CR_{SW} at PEER)			
		df	Slope	St. error of slope	Multiple R^2
CKA2020	High	90	1.48	0.23	0.31***
	Low	88	1.77	0.25	0.36***
WG2020	High	92	1.05	0.46	0.05*
	Low	92	0.06	0.35	0.00
WG2021	High	84	0.24	0.56	0.00
	Low	86	0.26	0.94	0.01

Significance codes: ***= P< 0.001, **= P< 0.01, * = P< 0.05 and ns = not significant.

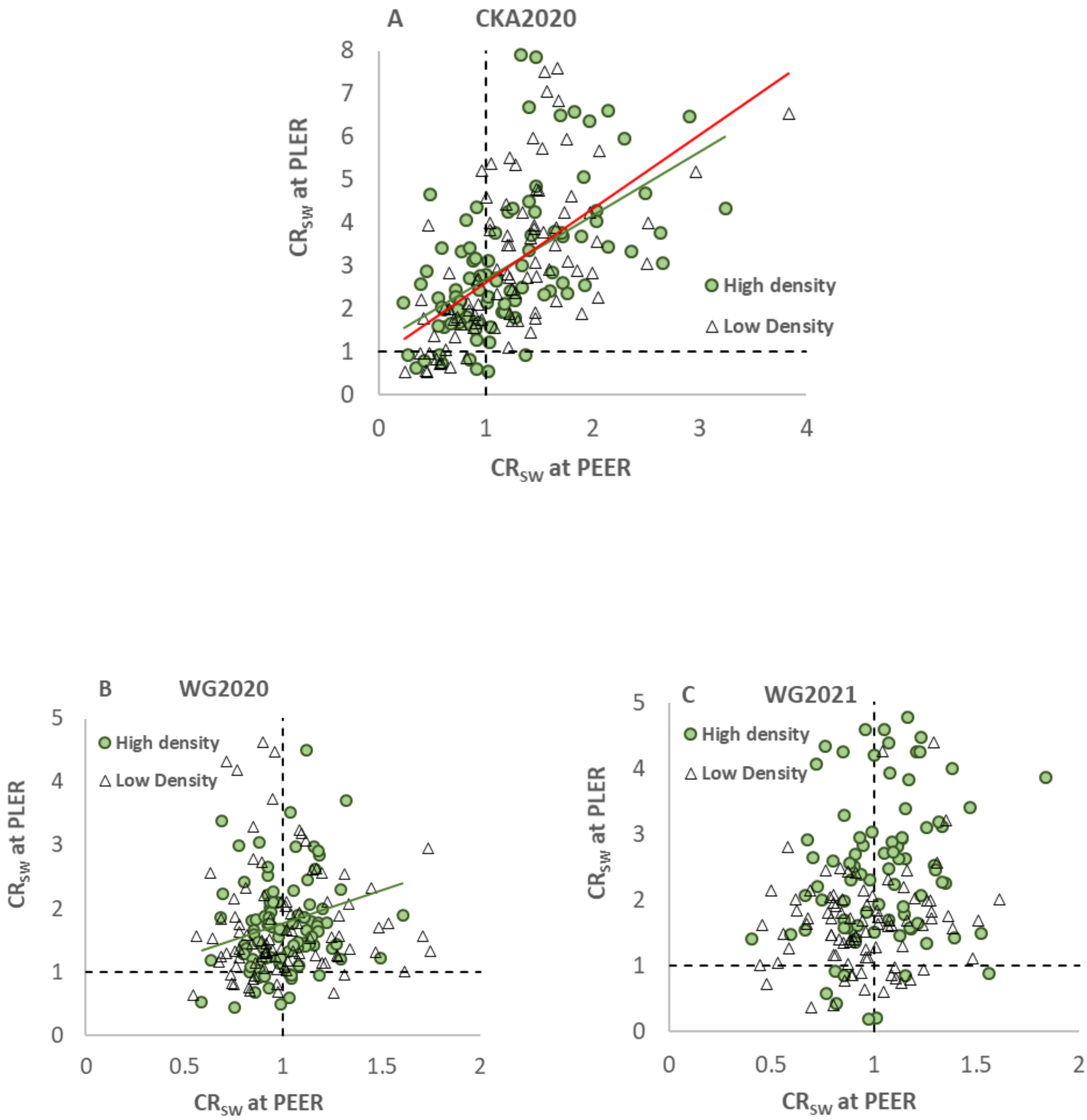

Figure 3.5. Spring wheat competitive ratio (CR_{SW}) at PLER (about 82 DAS) against CR_{SW} at PEER (about 23 DAS) for high (filled circles) and low (open triangles) sowing densities in three environments CKA2020 (A), WG2020 (B) and WG2021 (C). The regression lines of high and low densities are represented by red and green lines, respectively. The regression line was only added for significant linear relationships according to the linear regression model (Table 3.11). SW competitive ratio (CR_{SW}) was calculated by Eq. (3.7) and Eq. (3.8). At CR=1 (dashed lines), neither of the two partners dominates the mixture.

3.4 Discussion

3.4.1 Mixture effects at the early development stage

Because of the small size of the young plants and the short time of coexistence for the two species it is reasonable to expect that at the early crop developmental stage there is a lack of interference and therefore a neutral mixture effect. In contrast to this expectation, however, this study showed clear evidence of positive mixture effects at this stage in some of the trial environments. In two out of three environments, we observed higher crop emergence in spring wheat/faba bean mixtures compared to their respective monocultures. The strongest mixtures effects were found in those environment-crop combinations where absolute crop emergence was low (**Fig 3.2A; Tables 3.5, 3.6**), but we were unable to identify the exact reasons for spring wheat emergence being low at CKA2020. Although in this environment SW emergence was low (**Table 3.5**), its PEER was high (**Table 3.6**), i.e. higher relative SW emergence in mixtures compared to monocultures. It may be assumed that the higher SW emergence in mixtures was due to the temporal complementarity effect in resource use between SW and FB (Li et al., 2016; Xiao et al., 2018) in the very early stage of plant development (Elsalahy et al., 2021). In our field experiment, we observed that FB was slower to germinate than SW, potentially because of the (necessarily) deeper seed depth of FB (6 cm) than of SW (3 cm). In the mixture, this asynchronous germination between SW and FB may allow SW to temporarily access more resources and induce higher germination than in monoculture (Elsalahy et al., 2021).

Results also showed the same pattern of high mixture effects and low absolute emergence in the case of WG2021 where a lower FB emergence at high density and a positive mixture effect for both species was observed. These phenomena may be explainable by compensation effects in the mixture (Elsalahy et al., 2021). The mechanism of compensation means that if one of the partners in a mixture fails, the other partner takes its place; it has been shown to lead to high-yield stability in crop mixtures in response to different environmental stresses (Creissen et al., 2013). More specifically, with regard to emergence, a locally acting mortality factor that only affects one partner will reduce competition for the remaining partner and finally may induce higher emergence or survival in the mixture. A positive mixture effect was also observed at CKA2020 for FB emergence at low density.

Our results provide evidence of compensation by one species; this may be particularly important for the low emergence of species in case of climate extremes and increasing environmental stresses. However, further experiments with different combinations of other species are required to confirm the generality of our results.

3.4.2 Dependence of mixture effects on cultivar identity, environment and density

The mixture effect is an outcome from a complex combination of different factors and the interactions between them. In this study, the SW cultivars, environments and their interactions are the influencing factors of mixture effects on crop emergence. Higher differences among SW emergence were observed at the low input conventional site (CKA2020) than at the organic sites (WG2020 and WG2021). At CKA2020, the SW cultivars Lennox and Anabel and at WG2021, the SW cultivar SU Ahab showed significantly higher crop emergence in mixture than in monoculture. While the existence of mixing potential in some SW cultivars may been indicated by this finding, the identity of cultivars and the direction of their differences was not consistent across environments. Furthermore, the effect of mixture completely disappeared for all SW cultivars in WG2020.

Although a wide range of SW cultivars are currently available for monocropping, there is lack of cultivars suitable for intercropping (Bančič et al., 2021; Bourke et al., 2021; Louarn et al., 2020). Given this present lack of genotypes suitable for mixing, the experiment of SW-FB crop mixture must rely on the SW cultivars available in the market which are selected for monocultures. Yet, it has been reported that the performance in sole crop could not be considered as an index of wheat performance in mixed cropping (Kammoun et al., 2021; Tavoletti & Merletti, 2022). The final performance of intercropping depends on the combination of competition, complementarity, cooperation, and compensation between the species which has been named as "The 4C approach"(Demie et al., 2022; Justes et al., 2021). Therefore, the best cultivars for monocropping are likely not the best ones for intercropping. Furthermore, the assessment of the mixing ability of SW cultivars will depend on many further criteria beyond crop emergence, and may change in other environments. Specific breeding for intercropping tends to be particularly important at the targeted growing conditions (Annicchiarico et al., 2019), and this is likely to affect selection of SW cultivars for SW-FB mixed cropping.

3.4.3 Wheat dominates the species mixture (even) at the early stage

Although cereals are considered strong competitors in cereal-legume mixtures (Agegnehu et al., 2008; Hauggaard-Nielsen et al., 2001; Yu et al., 2016), it is not clear if the cereal domination over legumes already starts as early as crop emergence. The individual cereal plant, at this stage, is smaller than the legume, and up to this point in time, there is only short duration of coexistence for the two species in which competition could occur (Bellostas et al., 2003; Benincasa et al., 2012). In fact, however, we did observe early domination of SW in the mixture at CKA when counting emerged plants about 23 DAS (**Fig. 3.4A**). On the other hand, dominance does not necessarily mean suppression of the other partner. The relative emergence of SW was 16.4% higher than FB (**Table 3.6**) at that stage, indicating dominance, but the PEER value of FB (0.51 at LD and 0.50 at HD; **Table 3.6)** showed no reduction of FB emergence in the mixture compared to FB monoculture. The higher emergence of SW in the mixture than in the SW monoculture was observed presumably due to the complementarity effect (Xiao et al., 2018), and could be linked to asynchronous germination between the two species (Elsalahy et al., 2021). At the same time, the observed dominance of SW did not lead to the suppression of FB emergence in the mixture possibly due to the small size of the cereal, and the short time of co-growth between the two species.

At WG2021, the domination of SW started about 52 DAS with a slight suppression of FB biomass (PLER of 0.47; **Fig 3.4B**) where we also noticed low FB emergence in both the mixture and the monoculture, especially at high seed density (**Fig 3.2F**). One mechanism to explain this result could be that crop failure of FB may have relaxed competition and thereby enhanced the domination of SW in the mixture. In line with this, a study with grassland species, in which *Asteraceae* were sown together with different neighboring species, reported the dominance of these companion species to be particularly strong after a severe drought disturbance (Fenesi et al., 2020), which was linked to the failure of the weaker species. Finally, the SW dominated the mixture about 82 DAS in all three environments by suppressing FB biomass by 38%, 16%, and 18% at CKA2020, WG2020, and WG2021, respectively, compared to monoculture (**Fig 3.4C**); observed differences between the sites are potentially due to their different fertility levels. Characteristics that allowed rapid access of SW cultivars to environmental resources are likely to be the determining factors leading to the dominance at a later stage. A rapid growth because of deeper root distribution may help the cereal to access extra nutrients, especially N, and greater shoot length of the cereal may cause shading of the legume and thereby reduce its growth in crop mixture (Hauggaard-Nielsen et al., 2001; Xiao et al., 2018; Yu et al., 2016). These findings may assist farmers to manage competition in the mixture, e.g. by reducing relative sowing densities of cereals, to enhance complementarity and improve total productivity under different environmental conditions. Grain legume breeding for intercropping with higher vigour at the early growth stages may reduce the early, and thereby also the later domination of the cereal. However, further research is recommended especially under the different environmental conditions to understand the dynamics between cereal and legumes and the (early) domination of cereals over legumes.

3.4.4 Legacy of early mixture effects on later biomass

Despite the fact that the SW domination was detected at all three environments at about 82 DAS, the degree of domination was different among those three environments (**Fig 3.4C**). The higher degree of SW domination (PLER 62% higher than monoculture; **Fig 3.4C**) and a higher degree of FB suppression (PLER 38% lower than monoculture; **Fig 3.4C**) was observed at CKA2020 where we also recorded an early dominating effect of SW in the mixture about 23 DAS. That means the larger the proportion of SW seedlings early on in the SW-FB mixture, the higher SW domination and FB suppression later in the season. The domination intensity of SW for both densities exhibited a consistent expanding trend through the overall growth period at CKA2020 (**Fig. 3.5A**). It has been reported that earlier emerging seedlings of dicotyledonous sand dune annual plants tended to become larger adults (Turkington et al., 2005). In line with this, also other studies found that the strength of superiority that started at a very early developmental stage expanded as plants grew (Benincasa et al., 2012; Mangla et al., 2011; Schiffers & Tielborger, 2006). The increasing intensity of SW domination over FB was also observed at WG2020 for low density (**Fig. 3.5B**).

The early proportion between partners during crop establishment determines future development patterns in the mixture (Mangla et al., 2011). But measuring the strength and direction of interactions at multiple life history stages between cereal and legume may reveal valuable information to assess the importance of competition on community composition later on in the season. A further step would be to integrate this finding into a decision support tool to design cereal/legume intercrops by fitting the early competitive balance with future intercrop productivity.

3.5 Conclusions

Our study highlights that positive mixture effects may be detected at the early developmental stage but these mixture effects depend on the environmental conditions and selected SW cultivars. The results also suggest that SW and FB crop mixtures may also improve the ability of crop emergence to buffer environmental stresses, especially during the partial crop failure of one partner. Spring wheat domination in the mixture was noticed in all the environments. Cereals-grain legumes crop mixtures have a high potential to bring stability in productivity compared to the respective sole crops. The findings of this paper highlight the importance of early competition between intercropping partners, and its potential legacy effects on the performance of the mixture. Early competition could be managed in three different ways, namely through crop management decisions before sowing, or after sowing, or through long-term decisions via plant breeding.

With regard to decisions taken before sowing early competition could be managed, e.g. by reducing the relative density of the dominant partner or increasing the relative density of the suppressed partner, by adjusting the sowing time and sowing depth of partners, or by selecting appropriate cultivars so as to favor the weaker partner. Further, arranging the intercropping partners in alternating rows (not in mixed within row) would facilitate the management of individual partners. After sowing, it may be difficult to take crop management actions with a view to correct early dominancy. However, if the partners are known to respond differentially to within-season management of the crop, such as irrigation or mechanical weeding, the targeted application of these practices may help to balance competition between the partners. Finally, targeted breeding for intercropping is recommended as a longer-term tool to manage early competition. Grain legumes with higher vigour at the early growth stages or/and SW cultivars with lower early growth may reduce the early domination and thereby the later domination of cereal.

More generally, a better understanding of the mechanisms of early domination and its intensity changing over time may help to improve the development and management of diversified cropping systems towards sustainable agriculture.

Supplementary Materials

The following are available at https://link.springer.com/article/10.1007/s11104-023-06111-6#Sec20

Supplementary information 3.1 The total precipitation (mm) and average temperature (°C) at Campus Klein-Altendorf (CKA) in 2020 growing season (September 2019 to August 2020) and at Wiesengut (WG) in 2020 and 2021 growing season (September 2019 to August 2021) are presented as a graph. In April and May, the most relevant for early crop development, precipitation was relatively low in 2020 for both sites, but higher in 2021, **Figure S3.1** Precipitation (mm) and temperature (°C) at the experimental station Campus Klein-Altendorf (CKA) from September 2019 to August 2020 (A), precipitation (mm), and temperature (°C) at the experimental station Wiesengut (WG) from September 2019 to August 2021 (B), **Supplementary information 3.2** Thousand kernel weight (TKW) and germination percentage (GP) of two faba bean (FB) and ten spring wheat (SW) cultivars for two years, 2020 and 2021, **TableS3.1** Thousand kernel weight (TKW) and germination percentage (GP) for faba bean and spring wheat cultivars for two years, 2020 and 2021, **Supplementary information 3.3** Equations for spring wheat cultivar mixtures. Two groups of 5-component equiproportional spring wheat (SW) cultivars mixtures were created to increase the level of functional diversity. Each group contains five spring wheat cultivars. The required amount of seeds for each cultivar were calculated separately (**Equation S3.3**) and mixed homogeneously before sowing.

$$TKG * Density * (area\ per\ plot/5) / GP * 10 \qquad (S3.3)$$

Where TKG and GP are Thousand Kernel Weight (TKW) and germination percentage (GP) of the respective wheat cultivars (**Table S3.2**). Low and high density for monoculture and mixture (**Table 3.3**) were considered as density in **Equation S3.3**. Total area for each plot were divided by 5 for 5-component variety mixture to ensure the equiproportional contribution of each component among the mixture, **Supplementary information 3.4**: To maintain the appropriate faba bean seed density at sowing at monoculture, we set faba bean seeder, Hege 95 B at certain setting. For monoculture and mixture at two sowing densities, 120% and 80%, there are four machine setting, **Table S3.2** Hege 95 B rotation option according to faba bean seed density, **Table S3.3** Full model of Analysis of Variance (ANOVA) for emergence equivalent ratio (EER) considering all possible interactions between cultivar spring wheat, cultivar faba bean, environment, and sowing density.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Data collection was performed by MP and DD, data curation was done by all authors, data analysis was conducted by MP, TD. The first draft of the manuscript was written by MP, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The dataset generated during the current study is available as electronic supplementary material.

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4 Evaluation of multiple spring wheat cultivars in diverse intercropping systems

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Abstract

Re-diversifying agriculture through cereal-legume intercropping could provide higher productivity, but the cultivars and traits associated with agronomic performance of intercropping are currently unclear. Moreover, the impact of different cultivars on intercropping performance under diverse environmental and management conditions is largely unexplored. Therefore, we investigated various cultivar combinations of spring wheat (SW, *Triticum aestivum* L.) and faba bean (FB, *Vicia faba* L.) under diverse intercropping conditions, and evaluated their mixing abilities. We used variability in terms of plant height among cultivars and assessed the effects of height on total grain yield in the mixture. Twelve entries (ten cultivars and two cultivar mixtures) of SW and two cultivars of FB were sown as sole crops and all possible 1:1 species mixtures, with each of these treatments grown at two sowing densities and in three environments. Our results did not show any significant main effect of SW and FB cultivars on the total grain yield in the mixture. However, there were significant two-way interaction effects of SW cultivars with all the other factors (environment, FB cultivar, and sowing density) on the mixtures' grain yield advantage over sole crops. Spearman's rank correlation (ρ) among SW cultivars between SW yield in monoculture and total yield in mixture was variable, depending on the trial environment with ρ ranging from 0.42 (non-significant) to 0.90 ($P<0.001$). In addition, a highly significant effect of environments and crop densities on the total grain yield in the mixture was observed. A significant but weak positive correlation of SW plant height with the total grain yield in the mixture was detected in one of the three environments. We conclude that selecting a site-specific partner combination of cereals and legumes with appropriate management practices is a key element to enhance functional complementarity and improve total productivity in intercropping, though the complexity of the interactions makes this a difficult task.

Keywords

Crop mixture, crop synergy, diversification, sustainable agriculture, competition, cooperation, compensation, varietal choice

4.1 Introduction

Sustainable intensification of agriculture through cereal-legume intercropping has been shown to achieve higher productivity (Bedoussac et al., 2015; Cardinale et al., 2007; Rauber et al., 2001) while maintaining biodiversity and minimizing environmental impact compared to sole cropping. The complementary effects of nitrogen (N) use (Peoples et al., 2009), the facilitation effects regarding acquisition of different nutrients (C. Li et al., 2016; L. Li et al., 2007; Zhang and Li, 2003), and the dilution effects of host density to reduce diseases and insect pest infestation (Aziz et al., 2015; Bedoussac et al., 2015; Lithourgidis et al., 2011; Lopes et al., 2016) contribute to higher production per area in intercropping compared to monoculture (sole cropping). Different meta-analyses considering numerous studies reported a median land equivalent ratio (LER; the sum of the relative yields of component species in an intercrop as compared to their respective sole crops) up to 1.17-1.3 for cereal-legume intercropping (C. Li et al., 2023; Demie et al., 2022; Martin-Guay et al., 2018; Yu et al., 2016). That means, compared to the same area of land that was managed as sole crops, intercrop was, on average, 17 to 30% more efficient in using available land. However, this benefit of intercropping depends on the specific cultivars grown in the mixture (Demie et al., 2022) along with other factors, suggesting the importance of cultivar selection while designing intercropping (Ajal et al., 2021; Santalla et al., 2001).

According to Demie et al. (2022) who analyzed a compilation of studies on the effects of cultivars in intercropping, 85% of the LER data points of cereal/legume intercropping were greater than 1, while 15% of the specific cereal/legume cultivar combinations resulted in LER < 1. Among the studies analyzed by Demie et al. (2022) the largest LER range was reported in a study of 10 bean and two maize cultivar combinations (Santalla et al., 2001). This finding indicates the potential of cultivar selection for higher LER and thereby higher production in intercropping compared to sole crops. However, the performance of cultivars in monoculture is not necessarily correlated with the performance in intercropping (Annicchiarico et al., 2019), and the final performance of intercropping depends on the interaction between the species used in intercropping (Justes et al., 2021), as well as environments and management practices (Corre-Hellou et al., 2006; Launay et al., 2009; Moutier et al., 2022; Naudin et al., 2010). For that reason, it is important to select two or more component crops simultaneously by considering genotype × environment (GxE) and genotype × environment × management (GxExM) interactions to obtain suitable cultivars for intercropping.

As the final performance (grain yield) of intercropping is defined by multiple complementary interactions during the developmental growth stage, it is important to understand how different cultivar combinations work under diverse environmental conditions to design successful intercropping systems. For example, in cereal-legume intercropping, the cereal is a better competitor for soil inorganic N, especially under conditions of low-input cropping systems (C. Li et al., 2020), whereas the legume can exploit atmospheric N and increase the total N availability in the system (Bedoussac et al., 2015; C. Li et al., 2020). In maize-faba bean intercropping, interspecific facilitation of phosphorus (P) acquisition has been observed due to protons, malate, and citrate releases by faba bean into the rhizosphere, which mobilized insoluble soil P, notably on P-deficit soil (Li et al., 2007). Further, the more complex habitat of intercropping may provide diverse resources for beneficial organisms (Potts et al., 2003) and may also reduce pest infestation compared to monocultures (Finch and Collier, 2012). In 73% of 200 different studies, fewer disease incidences have been reported in intercropping than in monoculture due to decreased host plant availability, which altered the pathogen establishment through rain, wind, and vectors (Boudreau, 2013). In maize-pea intercropping, variability in the effect on water use efficiency has been observed depending on the growing conditions (Mao et al., 2012). Different studies (Brooker et al., 2015; Litrico and Violle, 2015; Li et al., 2014and) indicated the necessity of maximizing complementary resource use through niche differentiation while minimizing asymmetrical competition to improve the overall productivity of the intercropping system. Given the known complexity of intercropping systems, the challenge is to characterize and combine the crop traits that optimize complementary interactions under a range of diverse environmental conditions in intercropping.

Aboveground and belowground morphological, phenological, and physiological traits with relevance for this task of optimizing intercropping include plant height, growth habit, phenotypic plasticity, root architecture, root exudates, and the presence of beneficial microbes, which are responsible for increasing species synergy (Bourke et al., 2021; Brooker et al., 2015; Homulle et al., 2022; Kiær et al., 2022; Nelson et al., 2021; Timaeus et al., 2022; Zhu et al., 2015) and influencing the positive relationship between diversity and production (Kiær et al., 2022; Litrico and Violle, 2015). In a meta-analysis considering 11 studies with morphological differences in cultivar traits observed, plant height was reported to be frequently involved in intercropping complementarity (Demie et al., 2022); in particular, the authors mentioned a trend of shorter cereal cultivars being associated with higher intercropping performance. For example, in cereal-legume intercropping, less competitive cereals (lower height or growth) combined with a highly competitive legume (higher height or growth), including greater plasticity of both partners, were seen to result in higher productivity in intercropping systems (Weih et al., 2022). In wheat-pea intercropping, the competitive ability of the pea was influenced by leaf area in the early growth stage and plant height later on (Barillot et al., 2014). However, it is currently unknown in how far the effects of plant traits, in particular height, on intercropping performance are robust across different growing environments and field management conditions. For that reason, it is important to examine the mixing ability of several cultivars with contrasting plant heights across multiple environments and crop management conditions to improve the selection of cultivars for intercropping.

We therefore conducted a series of large field experiments to evaluate the mixture ability of multiple spring wheat (SW) - faba bean (FB) cultivars, with variability in terms of cultivar height, for the identification of high-yielding mixtures in three contrasting environments. To evaluate the potential advantages of intercrops, we selected two well-known indices, LER and AME (absolute mixture effect), among many others (Bedoussac and Justes, 2011; Yu et al., 2015). In this paper, we tested the following five hypotheses: The mixture effect on the total grain yield depends (H1) on SW cultivar; (H2) on FB cultivar; (H3) on the environment; (H4) on the crop management, that means interaction between species (SW X FB) and species with densities; (H5) The total grain yield in the mixture depends on plant height of the SW cultivars. The trials providing the data to test these hypotheses were large and complex; here we focus on the effects of spring wheat cultivar and its interaction with the other experimental factors. We found that mixing multiple SW-FB cultivars in diverse environments with various densities revealed complex interaction effects of different factors with cultivars. This indicates the importance of cultivar selection as well as other growing factors for the mixture performance.

4.2 Material and Methods

4.2.1 Experimental Site

The field experiment was carried out at two research stations of the University of Bonn, Germany, namely Campus Klein-Altendorf (CKA) in the year 2020 (referred to as CKA2020), and Wiesengut (WG) in the years 2020 and 2021 (referred to as WG2020 and WG2021, respectively). Campus Klein-Altendorf is a conventionally managed research station located in Rheinbach, about 40 km south of Cologne and WG is an organically managed research station located in Hennef, about 15 km east of Bonn. The average annual temperature and annual rainfall between 1991 and 2020 were 10.3 °C and 669 mm at CKA and 10.7 °C and 733 mm at WG, respectively. Higher total organic carbon (C_t) and total N (N_t) concentrations were observed in the soil (0-90cm) at WG compared to CKA (for details, see Paul et al., 2023).

4.2.2 Experimental Design

Each experiment was conducted as a randomized complete block design with four replicates and four experimental factors. Factor A comprised the cropping system, with the substitutive equi-proportional mixture (i.e., replacement design; mixed within row) of spring wheat (SW) and faba bean (FB) being compared with the respective monocultures. Factor B included the two FB cultivars (cv. Mallory and cv. Fanfare). Factor C contained twelve levels of SW entries, with ten spring SW cultivars (Anabel, Chamsin, Jasmund, KWS Starlight, Lennox, Quintus, Saludo, Sonett, Sorbas, and SU Ahab) and two 5-

component equiproportional mixtures of these SW cultivars (Group 1 contained five SW varieties similar in plant height scores, whereas Group 2 contained five SW varieties dissimilar in plant height scores; for full details, see Paul et al., 2023). Factor D consisted of two levels of sowing densities, namely 120% and 80% of the recommended sole crop densities (400 seed m^{-2} for SW and 45 seed m^{-2} for FB). At both densities, SW and FB were mixed in a 1:1 ratio, that means 50% of seeds of each species from the respective monocultures (high/low density) were mixed to get the respective density (high/low) in the mixture (Paul et al., 2023).

Table 4.1. Ten spring wheat cultivars and two mixed groups of spring wheat cultivars with their published characteristics, based on a 1-9 scale according to German Federal Plant Variety Office (Bundessortenamt 2019). High and low figures (score 9 and score 1, respectively) indicate that the cultivar shows the character to a high, or low degree, respectively. [a]: Susceptibility score.

Nr	Cultivar		Height	Ear emergence	Protein	Maturity	Brown Rust[a]	Fusarium[a]
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**

4.2.3 Management Practices

As pre-crop, winter barley and red clover grass were sown in CKA and WG (both years) respectively. The seedbed was prepared with a rotary harrow after ploughing the soil with a moldboard plough at 30 cm in WG and with a chisel plough at 7 to 10 cm in CKA. Each single plot was 10 m long and 1.5 m wide, with 6 rows and 21 cm distance between rows. We sow FB at 6 cm depth with a direct seeding machine type Hege 95 B and SW at 3 cm depth on top of FB with a Hege 80 seeder. As management practices, only mechanical weeding was carried out twice (3 and 5 weeks after sowing) using a hoe, and once four weeks after sowing with a harrow (Paul et al., 2023).

4.2.4 Agronomic, Grain Yield, and Yield Components Measurements

In order to determine the final grain yield and the correlation between grain yield and other agronomic characters, plant height, plant aboveground biomass at the flowering stage, and at full maturity stage were collected and measured before the final grain harvest from the entire plots (**Table 4.2**). To measure plant height (cm) of FB and SW, twelve random plants were selected from the 2nd to the 5th row among the six rows from the entire plot after discarding 1m from the edge to avoid potential edge effects.

Table 4.2. Measurement dates of plant height, plant aboveground biomasses (dry matter, DM) and total grain yield of faba bean and spring wheat in three environments.

Environment	Plant height[a] [cm]	Plant aboveground biomass [DM in t ha^{-1}]		Total grain yield[b] [t ha^{-1}]
		First sampling[a]	Second sampling[b]	
CKA2020	17th June	17/19th June	30th June	4th August
WG2020	15th June	15/16th June	29th June (Block I)[c]	6th August
			31th June (Block II, III, IV)	
WG2021	21th June	21/23th June	4th August (Block I)	13th August
			8th August (Block II, III, IV)	

[a]: at flowering; [b]: grain filling stage (2020) or full maturity (2021); [c]: although sampling dates were (slightly) different between blocks as reported here, we did not detect any significant block effects on the tested response variables.

The aboveground biomass cuts were performed at the flowering stage at one side of the plot after discarding 1m from the edge and at the grain filling (2020) or full-maturity stage (2021) at the middle part of the plot. During both biomass cuts, 1m long sections from the 3rd and 4th rows of the plots were chosen and total aboveground biomasses were harvested at the base. Fresh biomass samples from the vegetative stage were manually separated into weeds, SW, and/or FB depending on the cropping system and oven dried at 105°C until weight constancy to obtain biomass dry weight (t ha^{-1}). The biomass samples from the full-maturity stage were stored to air dry. The total grain from dried samples was oven dried at 105°C until weight constancy to get grain dry weight (t ha^{-1}).

To measure the final grain yield per plot, the entire plots were harvested with a 'Wintersteiger' harvester at CKA and with a 'Hege plot combined 140' harvester at WG at the full-maturity stage. After harvesting with these combine harvesters, the grains were cleaned from weed seeds and separated into SW and FB in case of mixed samples with a grain separator. Finally, the entire grain after separation was weighted and a small portion of the total grain was oven dried at 105°C until weight constancy to get the total grain dry weight (t ha^{-1}).

4.2.5 Data Processing and Calculations

The absolute mixture effect (AME) was used to calculate the difference between the observed grain yield in the mixture with the average grain yield in the monoculture (Elsalahy et al., 2021) for SW and FB. The sum of the AME of SW and FB (**Equations 4.1 and 4.2**) was used to calculate the total AME in the mixture for both cultivars by using **Equation (4.3)**

$$AME_{SW} = Wheat_{mix} - (Wheat_{mono} /2) \quad (4.1)$$

$$AME_{FB} = Bean_{mix} - (Bean_{mono}/2) \quad (4.2)$$

$$AME = AME_{SW} + AME_{FB} \quad (4.3)$$

where $Wheat_{mix}$ and $Bean_{mix}$ are the total dry matter grain yield of SW and FB in the mixture and $Wheat_{mono}$ and $Bean_{mono}$ are the total dry matter grain yields of both species in the monoculture. The positive or negative effect of intercropping on grain yield over monocultures was indicated by the positive or negative value of AME whereas intercropping has no effect on the total grain of the components in comparison to the monocultures when the AME value equals 0.

The land equivalent ratio (LER) was used to calculate the efficiency of intercropping compared to the monocultures by measuring the relative land area that was required for the crop monocultures to produce the same grain yield as observed in the mixture. The sum of the partial land equivalent ratios (PLERs) of SW and FB (**Equations 4.4 and 4.5**) was used to calculate the LER in the mixture by using **Equation (4.6)** (Willey and Rao, 1980).

$$PLER_{SW} = Wheat_{mix} /Wheat_{mono} \quad (4.4)$$

$$PLER_{FB} = Bean_{mix} /Bean_{mono} \quad (4.5)$$

$$LER = PLER_{SW} + PLER_{FB} \quad (4.6)$$

The LER value Higher or lower than 1 indicates intercropping has higher or lower efficiency compared to monocultures, whereas intercropping having no effect on land use efficiency was indicated by the LER value equaling 1 (Dariush et al., 2006).

4.2.6 Statistical Analyses

To test the mixture effects on spring wheat cultivar, faba bean cultivar, environment, and sowing density, a multifactorial analysis of variance (ANOVA) was carried out on total grain yield in sole crops and in mixtures, and on AME and LER of total grain yield of SW and FB followed by Tukey HSD test. Absolute mixture effect (AME) was normally distributed, and LER was non-normally distributed according to the Shapiro-Wilk test. In addition, the variances between the groups of both AME and LER were not always homogeneous according to the Bartlett test, which was complemented by graphical assessments. Despite these deviations we performed a parametric ANOVA test due to the robustness of ANOVA (Sainani, 2012; Schmider et al., 2010). Especially when the sample size is reasonably large and equal, ANOVA is found to tolerate modest violations of normality and/or homogeneity (Lumley et al., 2002; Winer et al., 1991). Here, a full model was conducted considering all possible interactions between all factors, and non-significant factors/ interactions were removed gradually according to Akaike's Information Criterion (AIC; Burnham et al., 2011). The final model included all significant factors and interactions between them. In cases when data was strongly non-normal and could not be normalized by transformations, non-parametric Kruskal-Wallis test was used followed by Dunn test with Bonferroni correction for multiple comparisons. To verify the correlation between grain yield and plant height, we tested for a correlation using Pearson correlation coefficient (PCC) and linear regression model between the total grain yield as well as SW and FB grain yield with SW cultivar height. Spearman's rank correlation (ρ) was calculated across SW entries for SW yields in monoculture against SW yields in mixture and against total mixture yields. For each of the three environments, this was done both for the four individual combinations of FB cultivar (Mallory, Fanfare) and density (high, low), and for the average across these four combinations. All statistical analyses were conducted in RStudio version 1.4.1106 (*R Core Team., 2020*).

4.3 Results

4.3.1 Total grain yield in monoculture

On average of all factors (two sowing densities, and three environments), KWS Starlight was the highest performing, and Sorbas, one of the tallest cultivars among others, was the lowest performing SW cultivar in terms of grain yield in the monoculture (**Table 4.3**). However, a change in the performance ranking of SW cultivars was observed when individual environments were considered. For instance, SW cultivar Chamsin, which was the one of the lowest yielding cultivars on average of all other factors, was one of the highest yielding cultivars in CKA2020. In contrast, SW cultivar Sorbas, one of the tallest cultivars among others (height score 7), consistently gave a significantly lower yield in all three environments in monoculture (**Table 4.3).**

Table 4.3: Mean of spring wheat and faba bean dry matter grain yield (t ha^{-1}) of the three environments (CKA2020, WG2020, and WG2021) and on the average of three environments in monoculture. Within each column, environments with different letters are significantly different according Tukey HSD test.

Species	Cultivars	Average of three environments	Trial environment		
			CKA2020	WG2020	WG2021
Spring Wheat	KWS Starlight	3.18^{a}	3.69^{ab}	3.12^{a}	2.72^{ab}
	Saludo	2.95^{ab}	3.31^{cd}	2.70^{bc}	2.84^{a}
	SU Ahab	2.94^{ab}	3.75^{a}	2.67^{bcd}	2.41^{bc}
	Lennox	2.93^{ab}	3.47^{abcd}	2.57^{bcde}	2.70^{ab}
	Sonett	2.92^{ab}	3.26^{d}	2.84^{b}	2.67^{ab}
	Mix-Group 2	2.92^{ab}	3.52^{abcd}	2.68^{bcd}	2.59^{ab}
	Quintus	2.82^{b}	3.42^{bcd}	2.52^{cde}	2.55^{ab}
	Jasmund	2.79^{b}	3.60^{abc}	2.73^{bc}	2.14^{cd}
	Anabel	2.75^{b}	3.30^{cd}	2.42^{de}	2.52^{ab}
	Mix-Group 1	2.75^{b}	3.31^{cd}	2.47^{cde}	2.46^{bc}
	Chamsin	2.65^{bc}	3.70^{ab}	2.47^{cde}	1.84^{d}
	Sorbas	2.36^{c}	2.87^{e}	2.32^{e}	1.86^{d}
Faba bean	Mallory	1.74	3.87^{a}	1.16^{a}	0.27^{b}
	Fanfare	1.67	3.40^{b}	1.17^{b}	0.49^{a}

4.3.2 Overall mixture effect on total grain yield (AME and LER)

To evaluate the effect of the mixture and compare the yield in intercropping with regard to monocultures, we calculated AME and LER on the total grain yield (**Equations 4.3** and **4.6**). In general, on the average of all other factors (two FB cultivars, two sowing densities, and three environments), intercrops showed higher average land-use efficiency and positive grain yield than sole crops, with a mean grain LER of 1.08 and a grain yield AME of +0.28 t ha^{-1} (**Table 4.4**). However, depending on the environment, we observed variability in the mixture effect on total grain yield. For instance, at the environment CKA2020, we observed mostly negative mixture effects, with negative grain AME and neutral to low grain LER, except for SW cultivars Quintus, Anabel and Chamsin. In contrast to CKA2020, the mixture effect was mostly positive for all SW cultivars in the two other environments (WG2020 and WG2021), except for Anabel and Mix-Group 2 on grain LER at WG2021. Among the two environments at WG, we observed comparatively higher grain AME and grain LER at WG2020 (AME and LER were 0.56 and 1.21) than at WG2021 (AME and LER were 0.43 and 1.05, respectively; **Table 4.4**).

Table 4.4: Average absolute mixture effect (AME in t ha^{-1}) and land equivalent ratio (LER) of twelve SW entries on total grain yield on the average of all other factors (two FB cultivars, two sowing densities, and three environments) and at the three trial environments; sorted by LER average.

Cultivars	Average across all factors[a]		CKA2020[b]		WG2020[b]		WG2021[b]	
	AME [t ha^{-1}]	LER	AME [t ha^{-1}]	LER	AME [t ha^{-1}]	LER	AME [t ha^{-1}]	LER
Mix-Group 1	0.34	1.13	-0.15	0.98	0.67	1.28	0.51	1.13
KWS Starlight	0.23	1.10	-0.41	0.89	0.60	1.19	0.51	1.21
Sorbas	0.26	1.10	-0.19	0.99	0.50	1.22	0.46	1.09
Quintus	0.37	1.09	0.03	1.02	0.53	1.18	0.56	1.05
Anabel	0.31	1.09	0.04	1.03	0.66	1.28	0.22	0.95
Sonett	0.27	1.09	-0.18	0.98	0.56	1.22	0.42	1.06
Chamsin	0.30	1.09	0.01	1.00	0.66	1.27	0.23	1.01
Lennox	0.29	1.05	-0.05	1.00	0.38	1.10	0.56	1.04
Jasmund	0.25	1.07	-0.22	0.94	0.62	1.22	0.34	1.06
SU Ahab	0.27	1.07	-0.23	0.94	0.57	1.22	0.46	1.04
Saludo	0.28	1.06	-0.28	0.94	0.44	1.18	0.69	1.07
Mix-Group 2	0.24	1.03	-0.03	1.00	0.56	1.19	0.19	0.91

[a]: two FB cultivars, two sowing densities, and three environments.: [b]: on average across FB cultivars and sowing densities

4.3.3 Dependence of mixture effects on experimental factors and their interactions

Different experimental factors, such as SW cultivar, FB cultivar, sowing density, environment, and interactions among those factors, may be responsible for determining the total grain yield in the mixture in relation to yield in the sole crops. To find out which of these factors played a significant role in potential mixture effects, a full model ANOVA was conducted on AME and LER of total grain yield, considering all possible interactions between those experimental factors. The AIC-best model (see methods) includes all the main effects and the two-way interactions and excludes the three-way interaction among those factors (**Tables 4.5** and **4.6**).

The SW cultivars and the FB cultivars, which were selected based on their contrasting characteristics of plant height, did not show any significant main effect on the total grain yield in the mixture (**Tables 4.5** and **4.6**). On average across densities and FB cultivars, Spearman's rank correlation between SW yields in monoculture and SW yield in the mixtures across all 12 cultivars was highest in WG2021 (ρ=0.867, $P<0.001$), but lower in WG2020 (ρ =0.685, $P<0.05$), but not significant for CKA2020 (ρ = 0.43, $P>0.1$). Similarly, the correlations among three environments varied when SW yields in monoculture were compared against total grain yield (SW and FB) in the mixture, which were ρ=0.89 ($P<0.001$), 0.51 ($P<0.1$), and 0.43 ($P>0.1$), for WG2021, WG2020, and CKA2020, respectively. When rank correlations across SW cultivars were determined for separate levels of the factors FB cultivar and sowing density, results were comparable (data not shown).

Although the main effect of cultivar on AME and LER was not significant for both species, significant two-way interactions of cultivars with all the other factors (cultivar of other species, environment, and density) on AME were noticed (**Table 4.5**). In particular, there was a significant interaction effect between cultivar choice among the two species (SW cultivar x FB cultivar) on the relative performance of the mixture compared to monocultures. This indicates the importance of the interaction effect of SW and FB species, including the effect of cultivars. However, there were no significant three-way or higher interactions.

Table 4.5. The AIC-selected final ANOVA model for absolute mixture effect (AME) on total grain yield (t ha^{-1}; DM) with considering all possible interactions between spring wheat (SW) cultivar, faba bean (FB) cultivar, environment, and sowing density; df: degrees of freedom.

Source of variation	df	Mean square	F-value	P-value
SW cultivar	11	0.08	0.63	0.801^{ns}
FB cultivar	1	0.20	1.66	0.199^{ns}
Density	1	4.79	40.17	0.000***
Environment	2	25.65	215.05	0.000***
SW cultivar: FB cultivar	11	0.27	2.23	0.012*
SW cultivar: Density	11	0.36	3.01	0.000***
SW cultivar: Environment	22	0.35	2.94	0.000***
FB cultivar: Density	1	0.75	6.30	0.012*
FB cultivar: Environment	2	0.84	7.02	0.000***
Density: Environment	2	0.75	6.28	0.002**

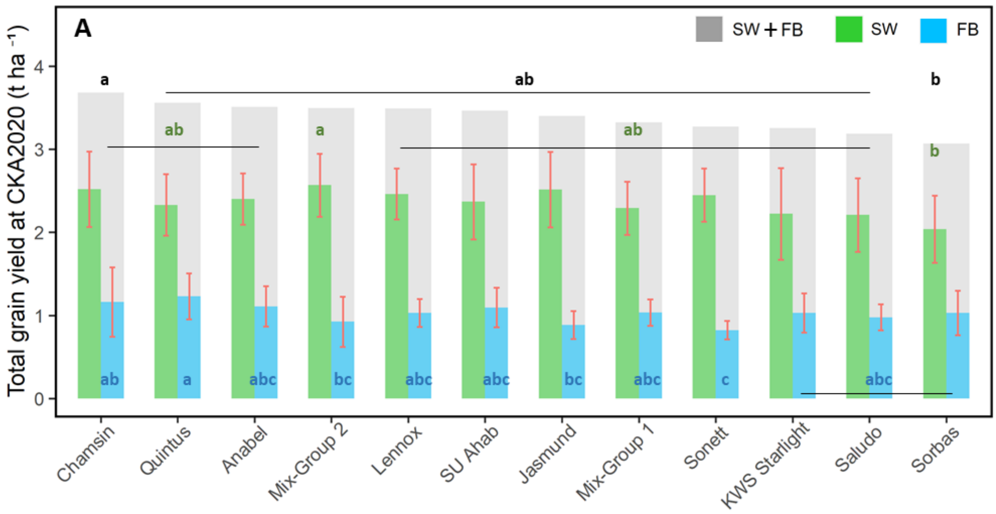
Significance codes: ***= P< 0.001, **= P< 0.01, * = P< 0.05 and ns = not significant.

Table 4.6. The AIC-selected final ANOVA model for land equivalent ratio (LER) on total grain yield (t ha^{-1}; DM) with considering all possible interactions between spring wheat cultivar, faba bean cultivar, environment, and sowing density; df: degrees of freedom.

Source of variation	df	Mean square	F-value	P-value
SW cultivar	11	0.03	0.60	0.833^{ns}
FB cultivar	1	0.01	0.24	0.619^{ns}
Density	1	0.32	6.85	0.009**
Environment	2	2.72	57.48	0.000***
SW cultivar: FB cultivar	11	0.08	1.70	0.070^{ns}
SW cultivar: Density	11	0.08	1.73	0.063^{ns}
SW cultivar: Environment	22	0.06	1.29	0.169^{ns}
FB cultivar: Density	1	0.38	8.04	0.005**
FB cultivar: Environment	2	0.09	1.92	0.147^{ns}
Density: Environment	2	0.08	1.67	0.190^{ns}

Significance codes: ***= P< 0.001, **= P< 0.01, * = P< 0.05 and ns = not significant.

Despite the fact that the total and individual SW and FB grain yields were not significantly different among the twelve SW entries on the average of two FB cultivars, three environments, and two densities ($p > 0.05$; **Fig. S4.1**), the result was different when each environment was observed separately (**Fig. 4.1**). As the ANOVA model on grain AME and LER showed a highly significant difference between the three environments ($P < 0.001$, **Table 4.5** and **Table 4.6**), the environment played a significant role in determining the final grain yield in the mixture.



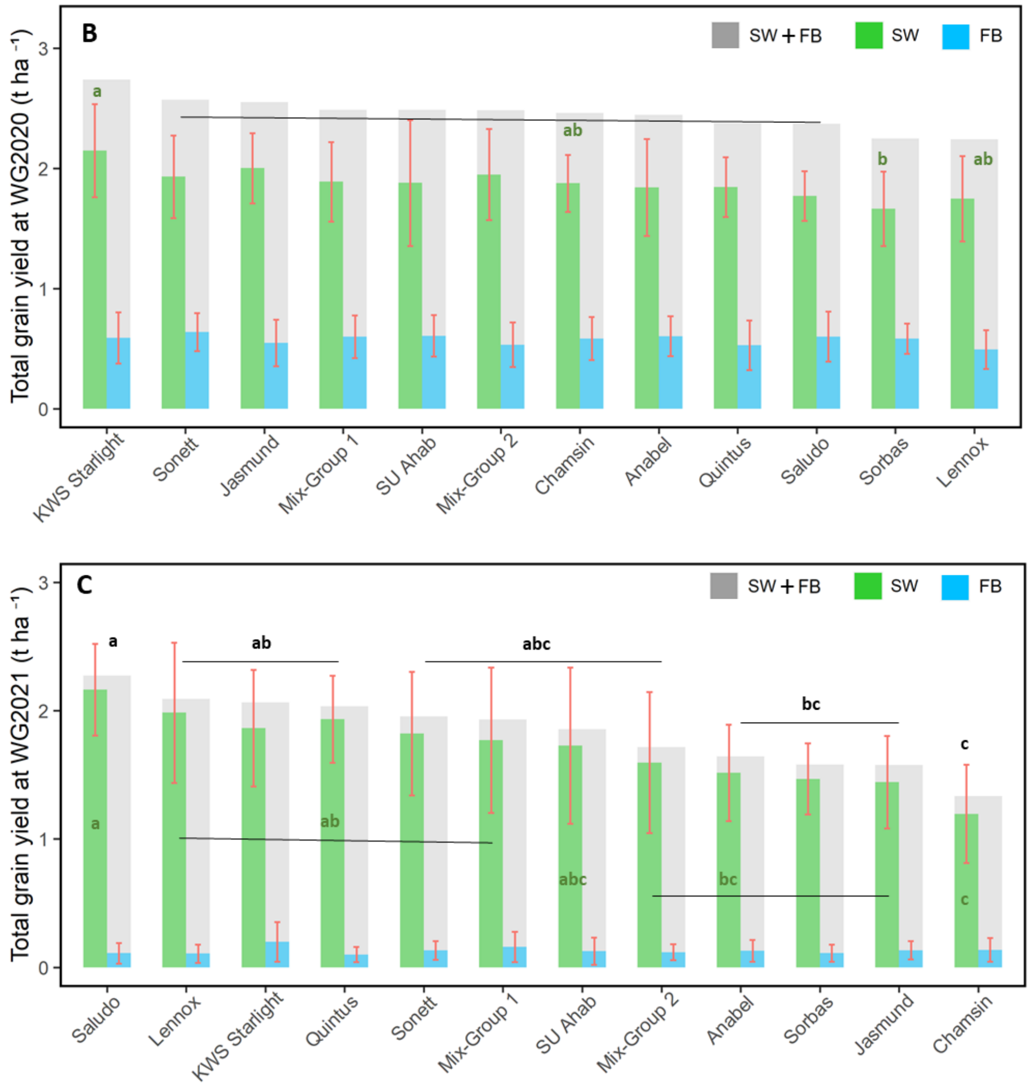


Figure 4.1. The mean of total grain yield (t ha^{-1}, grey bar) which is then also separated into the two fractions of spring wheat (green bar) and faba bean (blue bar) grain yield in dry matter (DM) in the mixtures in three environments CKA2020 (A), WG2020 (B) and WG2021 (C) for twelve SW entries (ten cultivars and two 5-component mixtures of these wheat cultivars). Within each environment, the different letters on the total grain yield (black letters), or the fractions of spring wheat (green letters) and faba bean (blue letters) grain yield indicate significant differences (Tukey's HSD test, P > 0.05); same letters within a fraction indicate no significant differences were found according to Tukey's HSD test; the vertical bars represent the standard deviation.

Similar to the main effect of environments, there was a highly significant interaction effect of the environment with both species' cultivars and density, but only on grain AME ($P < 0.001$, Table 4.5). In particular, SW cultivars showed a change in the performance ranking considering the individual environment (Fig. 4.1). For instance, in CKA2020, the total and individual SW and FB grain yields were significantly different among the twelve SW entries according to Tukey's HSD test (Fig. 4.1A). The SW cultivar Chamsin and the SW entry Mix-Group 2 (created by taking 5 SW varieties dissimilar in plant height; Paul et al., 2023) were giving significantly higher total grain yield and SW grain yield, respectively, whereas the SW cultivar Sorbas resulted in significantly lower yield in both total and SW grain yield in the mixture. The SW cultivars Quintus and Sonett were associated with significantly higher and lower FB grain yields in the mixture, respectively (**Fig. 4.1A**).

Contrary to CKA2020, the SW entries only significantly differ for the SW grain yield in the environment of WG2020 (**Fig. 4.1B**). A significantly higher SW grain yield for the cultivar KWS Starlight (2.1 t ha^{-1}) and a significantly lower SW grain yield for the cultivar Sorbas (1.7 t ha^{-1}) were observed at WG2020 (**Fig. 4.1B**). In the environment WG2021, the total (SW+FB) grain yield and SW grain yield were significantly different among the twelve SW entries according to Tukey's HSD test (**Fig. 4.1C**). The SW cultivar Saludo was responsible for providing a significant maximum total and SW grain yield (2.3 and 2.2 t ha^{-1}) in WG2021. Contrary to CKA2020, where the SW cultivar Chamsin was responsible for a significantly higher total grain yield (3.7 t ha^{-1}**;** **Fig. 4.1A**), it was producing a significantly lower total grain yield (1.3 t ha^{-1}) as well as a lower SW grain yield (1.2 t ha^{-1}) in the environment of WG2021 (**Fig. 4.1C**).

Similar to the environmental main and interaction effects with cultivars, the main effect of crop management, that is, sowing density, was highly significant on both grain AME and LER (SW+FB; **Tables 4.5** and **4.6**), but the interaction effect was only significant on grain AME (except FB x density was significant on both AME and LER; **Table 4.6**). Particularly, the two-way interaction between both species (SW and FB) and density was highly significant on the AME of total grain yield in the mixture ($P < 0.001$, **Table 4.5**).

We can see this at high sowing density (120% of recommended sowing density), where some SW varieties were consistently giving higher and lower total grain yields across both FB cultivars (**Fig. 4.2A**), on the contrary at low sowing density. In particular, SW cultivars KWS Starlight and SU Ahab were more productive with both FB cultivars (2.94 and 2.89 t ha^{-1} with Mallory; 2.99 and 3.01 t ha^{-1} with Fanfare), whereas SW cultivars Sorbas and Chamsin were less productive with both FB cultivars (2.50 and 2.62 t ha^{-1} with Mallory; 2.43 and 2.55 t ha^{-1} with Fanfare; **Fig. 4.2A**).

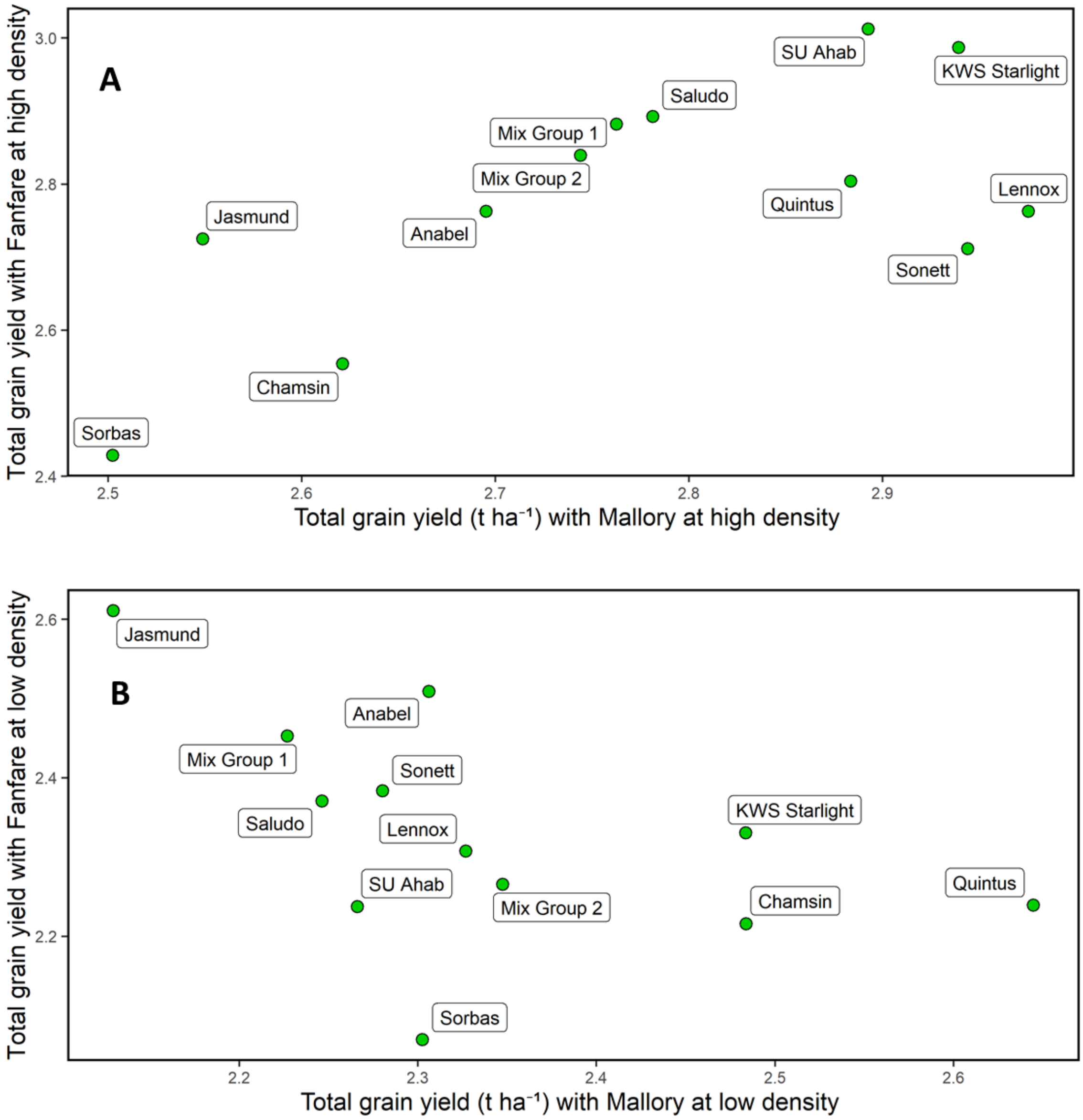


Figure 2. The mean total grain yield (t ha^{-1}, in DM) in the mixtures with two faba bean cultivars, Mallory against Fanfare at high density (HD, A) and at low density (LD, B) on the average of the three environments (CKA2020, WG2020, and WG2021) for the twelve spring wheat entries.

On the other hand, SW cultivars did not show any consistency among FB cultivars in terms of total grain yield at low sowing density (80% of recommended sowing density; Fig. 4.2B). In particular, SW cultivar Jasmund, which was the lowest yielding cultivar with FB cultivar Mallory (2.13 t ha^{-1}), was the highest yielding cultivar with FB cultivar Fanfare (2.61 t ha^{-1}). In addition, SW cultivar Quintus, which was the highest yielding cultivar with FB cultivar Mallory (2.64 t ha^{-1}), was one of the cultivars with lower yields when combined with FB cultivar Fanfare (2.24 t ha^{-1}; Fig. 4.2B).

As the SW cultivars showed inconsistency in total grain yield among the environments, sowing densities, and FB cultivars, a rank system was applied to the grain AME and grain LER of three environments to summarize the overall performance of twelve SW entries in the mixture compared to the monocultures (Fig. 4.3). The SW entry Mix-Group 1 (created by taking 5 SW varieties similar in plant height; Paul et al., 2023) ranked first on both AME and LER by having a higher average AME (0.34 t ha^{-1}) and the highest average LER (1.13) in three environments (Table 4.5). In the following, the three moderate-height (scored 3 to 5 on Bundessortenamt 2019) SW cultivars Quintus, Anabel, and Chamsin ranked in the next positions (except Quintus for LER; Fig. 4.3), which were also the cultivars resulting in positive AME at all three environments, especially at CKA2020. The last positions were ranked by the two tallest (scored 7 on Bundessortenamt 2019) SW cultivars, Saludo and Sorbas (except Sorbas, which ranked fourth for LER), followed by the SW entries Mix-Group 2 due to lower average rand for AME and LER in three environments (Fig. 4.3).

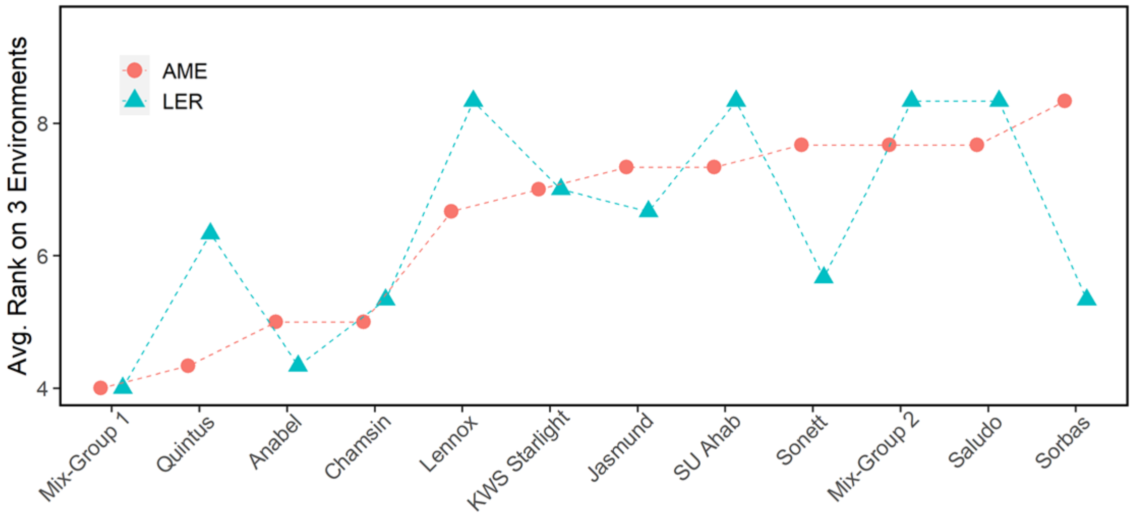


Figure 4.3. Average rank on the absolute mixture effect (AME) and land equivalent ratio (LER) of total grain yield (t ha^{-1}, in DM) in the mixtures in three environments (CKA2020, WG2020, and WG2021) for twelve spring wheat entries (ten cultivars and two 5-component mixtures of these wheat cultivars). A lower rank number indicates higher AME/LER compare to a higher rank number.

4.3.4 Grain yield in mixture and SW height

As a tendency of moderate height SW cultivars (Quintus, Anabel, and Chamsin) ranking first and taller SW cultivars (Saludo and Sorbas) ranking last was observed (Fig. 4.3 and Table. 4.4), we hypothesized that there is a correlation between SW height (at the flowering stage) and total grain yield in the mixture. To estimate the degree of correlation, the dependency between total grain yield (t ha^{-1}) in mixture vs. SW plant height (cm) was calculated with linear regression (Table 4.7). A significant linear relationship between SW height and total grain yield was observed at WG2021 for both FB cultivars (P

< 0.05 for Mallory and P < 0.01 for Fanfare, Fig. 4.4 and Table 4.7). No correlation was observed in the two other environments (CKA2020 and WG2020; Fig. S4.2A, S4.2B, and Table 4.7).

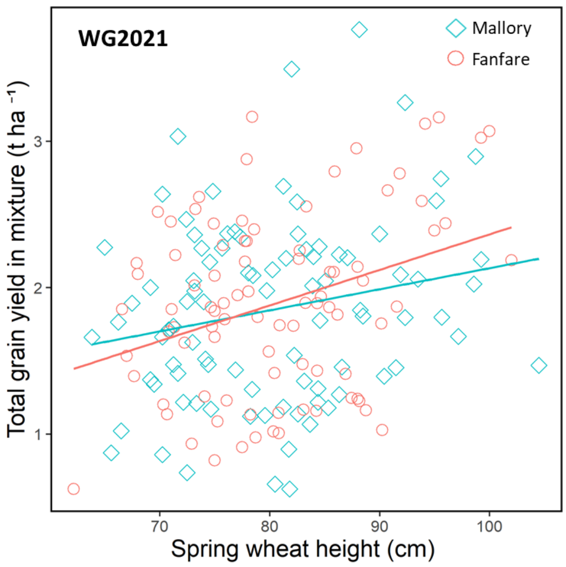


Figure 4.4. Total spring wheat and faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (at the flowering stage; cm) for faba bean cultivars Mallory (blue diamonds) and Fanfare (orange circles) in the mixtures in WG2021. The regression lines of Mallory and fanfare are represented by blue and orange lines, respectively.

Table 4.7. Summary of the linear regression model (lm) of total spring wheat and faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for three environments depending on faba bean cultivars.

Environments	FB cultivars	Linear regression (Total grain yield in mix ~ SW height in mix)			
		df	Slope	St. error of slope	Multiple R^2
CKA2020	Mallory	91	-0.01	0.01	0.11
	Fanfare	90	-0.00	0.01	0.00
WG2020	Mallory	93	0.01	0.01	0.01
	Fanfare	92	0.01	0.01	0.02
WG2021	Mallory	87	0.01	0.01	0.04*
	Fanfare	86	0.02	0.01	0.11**

**: P< 0.01, *: P< 0.05 and ns: not significant.

The correlation that was observed between SW height and total grain yield (SW+FB; Fig. 4.4) could be caused by SW grain yield and/or FB grain yield in the mixture. To understand the root cause of this correlation, individual linear regression was calculated between SW grain yield vs. SW height (Fig. 4.5 and Table 4.8) and FB grain yield vs. SW height (Fig. 4.6 and Table 4.9) in the mixture. Among the three environments, we observed a correlation between SW height and SW grain yield with both FB cultivars only at WG2021 at the significant level of 5% (P < 0.05, Fig. 4.5 and Table 4.8).

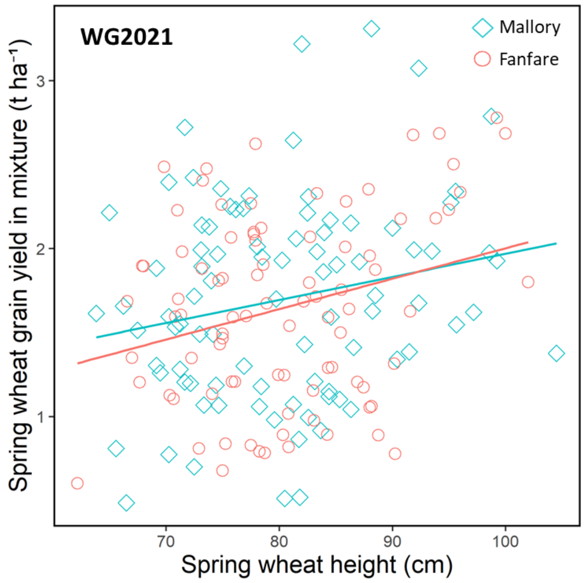


Figure 4.5. Spring wheat grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for faba bean cultivars Mallory (blue squares) and Fanfare (orange circles) in the mixtures in WG2021. The regression lines of Mallory and fanfare are represented by blue and orange lines, respectively.

Table 4.8. Summary of the linear regression model (lm) of spring wheat grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for three environments depending on faba bean cultivars.

Environments	FB cultivars	Linear regression (SW grain yield in mix ~ SW height in mix)			
		df	Slope	St. error of slope	Multiple R^2
CKA2020	Mallory	91	-0.01	0.01	0.01
	Fanfare	90	0.01	0.01	0.01
WG2020	Mallory	93	0.01	0.01	0.01
	Fanfare	92	0.00	0.01	0.01
WG2021	Mallory	87	0.01	0.01	0.04*
	Fanfare	86	0.02	0.01	0.07*

**: P< 0.01, *: P< 0.05 and ns: not significant.

Not only SW height showed a significant relationship with SW grain yield (**Fig. 4.5** and **Table 4.8**) but also it showed a significant relationship with FB grain yield at the environment WG2021 (**Fig. 4.6** and **Table 4.9**). Among two FB cultivars, the taller cultivar Fanfare grain yield was weakly (R^2 = 0.1) correlated with SW height at P < 0.01 (**Fig. 4.6** and **Table 4.9**). No correlation was observed in the two other environments (CKA2020 and WG2020) and also with the shorter FB cultivar Mallory (**Fig. S4.4**).

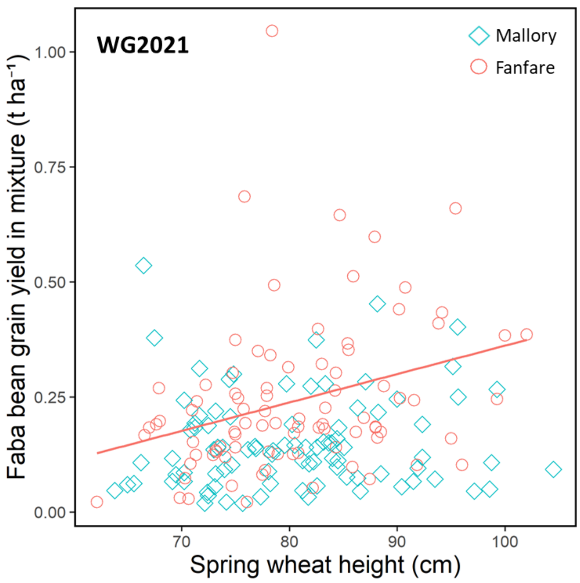


Figure 4.6. Faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for faba bean cultivars Mallory (blue squares) and Fanfare (orange circles) in the mixtures in WG2021. The regression lines of Mallory and Fanfare are represented by blue and orange lines, respectively.

Table 4.9. Summary of the linear regression model (lm) of faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for three environments depending on faba bean cultivars.

Environments	FB cultivars	Linear regression (FB grain yield in mix ~ SW height in mix)			
		df	Slope	St. error of slope	Multiple R^2
CKA2020	Mallory	91	-0.00	0.01	0.00
	Fanfare	90	-0.01	0.01	0.02
WG2020	Mallory	93	0.00	0.00	0.00
	Fanfare	92	0.00	0.00	0.01
WG2021	Mallory	87	0.00	0.00	0.00
	Fanfare	86	0.01	0.00	0.10**

**: P< 0.01, *: P< 0.05 and ns: not significant.

4.4 Discussion

4.4.1 General overview

In this study, we analyzed the mixing ability of SW cultivars in intercropping with three different factors (FB cultivars, density, and environment). In contrast, the cropping system (intercropping vs. monoculture) was not considered as an experimental factor, as the comparison between intercropping and monocultures was contained in the AME and LER; our main aim was to observe the variation of intercropping performance within cultivars, depending on environment and crop management. To provide variability in terms of the cultivars' effect in intercropping, we selected cultivars that vary in plant height, as this trait was previously identified as being potentially important in driving species interactions in intercropping systems (Demie et al. 2022), and is regularly reported in official variety descriptions. In particular, to create the variability, we selected SW and FB cultivars with contrasting characteristics of plant height (among other traits), and the association between height and total grain yield in the mixture was evaluated. In addition, we calculated AME and LER to compare the total grain yield in intercropping in comparison to the monocultures. As a result, based on the grand mean of AME and LER (**Table 4.3**), intercrops were on average 8% more efficient and had a 0.28 t ha^{-1} greater yield than expected from monocultures. Other findings support this result (C. Li et al., 2023; Demie et al., 2022; Yu et al., 2016), which indicated that on a limited area of land, in general, intercropping is a more efficient cropping system than sole crops.

4.4.2 Spring wheat cultivar performance: intercropping vs. monocultures

Many cultivars are currently available for monoculture, but are not bred for intercropping (Bančič et al., 2021; Bourke et al., 2021; Louarn et al., 2020). Various studies have shown that a cultivar's performance in monoculture cannot reliably be used as an index in intercropping (Baxevanos et al., 2017; Kammoun et al., 2021; Tavoletti and Merletti, 2022). Therefore, the best cultivars in monoculture are not necessarily the best in intercropping (Demie et al., 2022). For this reason, it is necessary to compare the total grain yield in two cropping systems to correlate SW cultivars' performance in intercropping with monocultures. Our results, based on a large set of cultivars, supports this view, since correlations between performance in monoculture and in mixture were sometimes quite low, and non-significant (at CK2020). Accordingly, there some changes in the performance ranking of SW cultivars between sole crop and mixture (**Table 4.3; Fig. 4.1**). However, in contrast to this result, we found good agreement of SW cultivar ranking between monoculture and mixture at WG2021. This variability of agreement between sole crops and mixtures across environments suggests that there are at least some environments in which cultivar choice for intercropping cannot rely on performance evaluation in monocultures. Therefore, confirming findings of earlier studies, our study shows that it is recommendable to select site-specific SW cultivars for future mixed cropping systems based on their performance in the mixture, rather than in monoculture.

4.4.3 Dependence of total grain yield on multiple factors in the mixture

The total grain yield in the mixture is affected by a range of factors, such as the cultivars of the mixed species, climatic and soil conditions in multiple environments, cropping practices such as sowing densities, and the interactions between those factors (Corre-Hellou et al., 2006; Launay et al., 2009; Moutier et al., 2022; Naudin et al., 2010). In this study, we conducted an ANOVA on AME and LER to determine the influencing factors of the mixture on total grain yield. We observed significant effects of a few factors (which will be discussed later as the main effect of this factor) as well as two-way interactions between multiple factors. No significant three-way interactions were detected in this study.

The main effects of cultivars (SW and FB) were not significant for AME and LER on the total grain yield in the mixtures ($p > 0.05$). One possible explanation is that there is a lack of cultivars to select for crop mixtures (Bančič et al., 2021; Bourke et al., 2021; Louarn et al., 2020). Given the present lack of cultivars suitable for mixing, the selected cultivars, which were mainly bred for monoculture, have no significant main effect on mixture. Another possible explanation is the interaction of cultivars with other factors. No main effect of cultivars was observed due to multiple two-way interaction effects of cultivars with the environment, other species, and density (**Table 4.5**). Those interaction effects are normally complex and depend on numerous factors, like the availability of nutrients, soil-climatic conditions, and cultivars of the companion species (Bedoussac et al., 2015), which could suppress the main effect of cultivars that are mainly bred for monoculture, not for intercropping.

In contrast to the main effect of cultivars, different growing environments had a highly significant effect ($P < 0.001$) on the relative performance of the total grain yield in the mixture in comparison to the sole crops (**Tables 4.5** and **4.6**). The main reasons for yield variability in three growing environments are year-to-year weather variation and contrasting soil conditions at two locations (CKA and WG). Specifically, at WG, higher precipitation was recorded in 2021 compared to 2020. In addition, higher soil water and lower N availability were observed at the organic site (WG) compared to the conventional site (CKA; for details, see Paul et al., 2023). Based on the numerous findings for cereal/legume intercropping (Bedoussac et al., 2015; Chen et al., 2018; Corre-Hellou et al., 2006; Hauggaard-Nielsen and Jensen, 2001; Mao et al., 2012; Naudin et al., 2010), there are differences in intercrop performance depending on the nitrogen and water availability in the system, as well as interactions among those environmental factor. In particular, intercrops are more suited to low N availability due to a high level of complementary N use between the two species (Bedoussac et al., 2015; Bedoussac and Justes, 2011). Accordingly, we found generally higher mixture effects on the organically managed site WG than at the conventionally managed site CKA.

Similar to the environmental effect, sowing density also had a profound influence on the growth dynamics and total productivity of intercropping (Werf et al., 2021; Yu et al., 2015). As explained by some studies, higher grain yields were reported in mixtures at higher total densities than the optimal sole crop density (Neumann et al., 2007; Yu et al., 2016) due to resource complementarity between intercrops (Barker and Dennett, 2013). As the two species are not exactly competing for the same resources at the same time, there are more resources available for some cultivars that performed better at high sowing density. These findings, in line with other studies (Corre-Hellou et al., 2006;

Moutier et al., 2022; Naudin et al., 2010; Pelzer et al., 2012; Yu et al., 2016), indicate the importance of growing environments and sowing densities on the total productivity of intercropping.

In contrast to the main effect, the interaction effect of multiple factors was only significant for grain AME and not for grain LER (except for the FB × density interaction effect which was significant on both; **Tables 4.5** and **4.6**). On grain AME, significant to highly significant two-way interaction effects were recorded between the two species' cultivars, environment, and density. For instance, the SW cultivar × FB cultivar interaction effect was significant for the total grain yield in the mixture ($P < 0.05$), which was contrary to the main effect of species (SW cultivar and FB cultivar). This result indicates that the mixture effect depended more on the combined choice of cultivars as SW-FB plant teams than the cultivar identity of individual species.

Niche differentiation, created by the two species, improves the use of both soil mineral N and atmospheric N, as well as water use efficiency and light interception (Bedoussac et al., 2015; Demie et al., 2022). Additionally, it has been reported that the presence of one species (root exudates of maize) can enhance the performance of other species (increase nodulation and N_2 fixation by faba bean; Li et al., 2016). Multiple SW cultivars with diverse characteristics, for example, diverse plant heights, determine the level of positive or negative synergy that interacts with the FB cultivars. The final performance is determined by the combination of competition, complementarity, cooperation, and compensation between the cultivars of two species in the mixture (Justes et al., 2021). This species x species interaction, with the effect of cultivars, could be stronger than that of single species (Kammoun et al., 2021). This finding suggests the need to pay attention to the combined cultivar selection for both species while designing crop mixtures.

Our results also indicated that different SW and FB cultivars react differently under multiple environmental conditions ($P < 0.001$). This is evidenced by the SW cultivar Chamsin, which gave the highest total grain yield in CKA2020 (low input conventional site) but the lowest in WG2021 (organic site) compared to the other SW cultivars (**Fig. 4.1**). This result is supported by other findings in that different cereal cultivars respond differently to shoot and root growth at low and high nitrogen available condition (Górny, 2001). Such differences may be amplified in the presence of another species under interspecific growing conditions in an intercropping system. In particular, poor growth of one partner in one environment may result in stronger suppression exerted by the intercropping partner, while stronger growth in a different environment may moderate such asymmetric competition. These ideas are in accordance with Moutier et al. (2022), who concluded that N availability in the growing conditions strongly influenced the interaction between wheat and peas in intercropping. Nevertheless, the results of this study indicated that combined cultivar selection should be conducted within a targeted environment to enhance the response to selection.

Additionally, in relation to the sowing density, SW entries displayed a broad range of reactions to the mixtures with respect to the total grain yield. For example, at high sowing density, some SW cultivars like KWS Starlight and SU Ahab were consistently more productive, while Sorbas and Chamsin were consistently less productive with both FB cultivars (**Fig. 4.2).** On the other hand, at low sowing density, SW cultivar Quintus was the highest productive cultivar only with FB cultivar Mallory, and Jasmund was the highest productive cultivar only with FB cultivar Fanfare. The reason behind this is that the contrasting characteristics of different cultivars react differently to resource use complementarity under different sowing densities (Hauggaard-Nielsen and Jensen, 2001). For example, some pea cultivars were able to reach a higher potential yield at lower plant densities due to their greater branching ability (Barillot et al., 2014; Spies et al., 2010). Specifically, SW cultivars are well known for their compensation ability through tillering at variable sowing densities (Kammoun et al., 2021). This finding indicates the need to pay attention to cultivar-specific characteristics, specially the branching ability of cultivars, during selection for intercropping. In contrast to the current study, it is recommended for future studies to consider the branching ability of different cultivars when evaluating the suitability of cultivars under competitive intercropping conditions.

All in all, the total grain yield in the mixture depends on the choices of cultivars, species, growing environments, and sowing densities, as well as the interaction among those factors. Although the effects of intercropping are complex to conclude from these short field experiments, our results indicate that to obtain transgressive overyielding in intercropping, crop mixtures need to be fine-tuned to available cultivars, growing conditions, and production systems through reorientation of agriculture (Li et al., 2023). As correlations between SW cultivar performance in monoculture vs. intercropping were variable, and weak at least in one environment (section 4.4.2), the necessity of a specific breeding program for intercropping is suggested and already indicated by several authors (Annicchiarico et al., 2019, 2021; Finckh, 2008; Lamichhane et al., 2018; Tavoletti and Merletti, 2022). By doing so, it is recommended to consider the complex interaction effects of cultivar traits with other species, environmental factors, and managemental actions to select suitable SW cultivars for targeted intercropping design for breeders and farmers.

As different SW cultivars react differently under different environmental and managemental conditions, generalization of cultivar performance in intercropping is rather difficult, as reported by several studies (Baxevanos et al., 2017, 2020; Bedoussac et al., 2015; Timaeus et al., 2022). However, to get a general overview of SW cultivar performance in the mixture, we applied a rank system to AME and LER. As a result, based on AME and LER rank, we observed that SW cultivars with moderate height (Quintus, Anabel, and Chamsin) gave a relatively higher total grain yield, while tallest SW cultivars (Saludo and Sorbas) gave a relatively lower grain yield (with some deviation on rank LER; **Fig. 4.3)** in the mixture. Indeed, a tendency of shorter cereal cultivars towards higher intercropping performance has been observed (Demie et al., 2022). Specifically, shorter oat cultivars have been reported to be most compatible for intercropping with vetch (Baxevanos et al., 2020). The reason behind this is that cultivar relative height has been widely known in plant competition for light partitioning (Barillot et al., 2014; Launay et al., 2009; Louarn et al., 2020) and nutrients. Particularly taller cultivars can disturb grain filling and contribute to greater competitive ability of smaller one (Annicchiarico et al., 2019; Hauggaard-Nielsen and Jensen, 2001; Keddy, 1990). These results can provide valuable guidance for selecting SW cultivars for sowing in diverse intercropping systems. Furthermore, we suggest that future research needs to analyze a different set of SW cultivars on a multi-environmental trial under diverse management conditions to verify the pattern of SW cultivars performance in intercropping.

4.4.4 Association of grain yield with the crop cultivars' height

While short plant height has been a breeding target during several decades of cultivar improvement, it is also known to play a critical role in plant competition (Borg et al., 2018; Weih et al., 2022). Specially, in the mixture, homogeneous height among the intercropping species is suggested to maintain a balanced proportion (Bowden et al., 2001; Dai et al., 2012) and equal light interception (Barillot et al., 2014). In this study, the plant height of SW cultivars positively (but weakly) affected the total grain yield, as well as the SW grain yield at WG2021 among three environments (**Figs. 4.4, 4.5**). On the other hand, only the yield of the taller FB cultivar (Fanfare) was positively correlated with SW height in the mixture (**Fig. 6**). The reason behind this may be that a taller plant height of legume species frequently contributes to greater competitive ability, particularly when they tend to be at competitive disadvantage (Annicchiarico et al., 2019). Because of the higher light interception, which is correlated to the relative height of the two components in the mixture (Barillot et al., 2014; Launay et al., 2009; Louarn et al., 2020), legume species are reported to have higher resource acquisition and nodule production (Annicchiarico et al., 2021). For example, the tall structure of pea cultivars is reported to be positively associated with competitive ability towards barley due to greater competition for light and nutrients (Hauggaard-Nielsen and Jensen, 2001). These results can provide guidance for selecting important traits of cultivars when designing mixtures to maximize resource acquisition and intercrop performance. Moreover, as a limitation of this experiment, future research needs to include systematic investigation and categorization of other plant traits, such as leaf area, and root architecture, to optimize complementarity between two species in mixed cropping.

4.5 Conclusions

This study shows an overall yield advantage for mixtures compared to their respective monocultures. However, the selected SW cultivars for intercropping did not always correlate with monoculture in terms of total grain yield. These finding highlights that the performance of selected SW cultivars in the mixture cannot be predicted from their performance in monoculture. Although no significant main effect of SW and FB cultivars on mixture performance was observed, the significant cereal cultivar × legume cultivar interaction indicates the importance of combining species selection as a plant team for successful intercropping design. Furthermore, other growing factors (environment and density) and their two-way interactions with cultivars also played a significant role in the performance of crop mixtures. Therefore, when designing intercropping, it is important to select both component crops simultaneously in targeted environments with appropriate densities to enhance the mixture's performance.

A slight tendency of moderate-height SW cultivars towards higher intercropping performance and the tallest SW cultivars towards lower performance has been observed. The height of SW cultivars was positively correlated with total grain yield, SW grain yield, and FB grain yield in the mixture in one of the three environments. However, this correlation between SW height and FB yield was only significant for the taller FB cultivar Fanfare. The results could help to identify or design suitable spring wheat cultivars for intercropping systems, in particular by selecting moderate-sized SW cultivars for higher mixture performance and taller FB cultivars for higher competitive ability. However, further studies on more diverse genotypes and growing conditions with diverse management systems should be conducted to optimize intercropping systems.

Supplementary Materials

This is available at https://www.sciencedirect.com/science/article/pii/S1161030123002927#sec0115

Figure S4.1 The mean of total grain yield (t ha^{-1}, grey bars) of spring wheat (SW; green bars) and faba bean (FB; blue bars) in the mixtures on the average of the three environments (CKA2020, WG2020, and WG2021) and two densities (high and low) for twelve SW entries (ten cultivars and two 5-component mixtures of these wheat cultivars); vertical bars represent the standard deviation. No significant difference was observed among SW entries for SW grain yield, FB grain yield, and total grain yield according to the Dunn test with Bonferroni correction, **Figure S4.2** Total spring wheat and faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (at the flowering stage; cm) for faba bean cultivars Mallory (blue diamonds) and Fanfare (orange circles) in the mixtures in two environments CKA2020 (A), and WG2020 (B), **Figure S4.3** Spring wheat grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for faba bean cultivars Mallory (blue squares) and Fanfare (orange circles) in the mixtures in two environments CKA2020 (A), and WG2020 (B), **Figure S4.4** Faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for faba bean cultivars Mallory (blue squares) and Fanfare (orange circles) in the mixtures in two environments CKA2020 (A), and WG2020 (B).

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Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Data collection was performed by MP and DD, data curation was done by all authors, data analysis was conducted by MP, TD. The first draft of the manuscript was written by MP, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The dataset generated during the current study is available as electronic supplementary material.

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5 General Discussion

5.1 Designing experiments for intercropping research

For a successful intercropping study, careful consideration of experimental design and proper management of intercrops before and during cultivation are essential. In particular, the selection of compatible crop species, cultivar traits suited to intercropping, planting densities, and spatial arrangements are crucial determinants of intercrop performance (Bedoussac et al., 2015) and represent the primary research challenges of this study.

Compatible crop species for intercropping are those that exhibit complementary effects on each other, minimizing competition due to their diverse aboveground and belowground structures (Brooker et al., 2015). For example, combining cereals with legumes provides significant potential for developing energy-efficient production systems (Bedoussac et al., 2015; Cardinale et al., 2007; Rauber et al., 2001). However, careful selection of different cultivars in a cereal-legume crop mixture is essential to enhance their complementarity, particularly by considering their compatibility with environmental conditions and management systems. An important selection criterion is plant architecture, such as height. Plant height has been recognized as a crucial factor due to its role in plant competition within intercropping systems (Barillot et al., 2014; Demie et al., 2022) and is regularly reported in official variety descriptions. The selection criteria must consider not only the impact of a specific trait on the target crop yield but also its potential effects on the companion crop. Therefore, we selected cultivars of both spring wheat and faba bean with contrasting characteristics of plant height (among other traits, **Chapter 3**; **Table 3.2**) to provide variability in terms of the cultivars' effect on intercropping.

In addition to cultivar selection, the densities, spatial arrangement of species, whether in row or strip intercropping, and the ratio of each species in the mixture significantly determine the success of the intercrops. Specifically, the response to plant density in intercropping is still not clearly understood. It has been documented that intercropping provides greater advantages in terms of yield compared to monoculture when the overall plant density in intercrops surpasses that of each individual crop (Neumann et al., 2007; Yu et al., 2016), as a result of the complementarity between species (Barker & Dennett, 2013). The challenge lies in determining the optimal seeding rates to achieve the positive mixing effects, as higher density can also increase the competition between component species, often favoring the dominant species in the mixture (Hauggaard-Nielsen et al., 2006). On the other hand, some cereals, such as wheat, are well-known for their ability to compensate for low density through tillering (Kammoun et al., 2021). Since farmers are often interested in reducing input costs by using fewer seeds for crop production, it is important to consider this cost parameter when determining optimal seed density. Finding a low seed density that maintains the benefits of the mixture can significantly enhance cost efficiency while preserving productivity. Therefore, we have chosen two sowing densities: one that is 20% higher and one that is 20% lower than the recommended sole crop density. This means that 120% and 80% of the recommended sole crop densities of spring wheat and faba bean were mixed in a 1:1 ratio in substitutive mixtures to observe the effect of high and low density on the crop mixture (**Chapter 3**; **Table 3.3**).

It is crucial to guarantee complete synchronization of planting and ripening times for both species when planting the component crops simultaneously in the same row (mixed-row intercropping). A delay in the ripening of one species can cause yield loss in the other due to pod shattering and seed splitting, which narrows down the number of suitable cultivars for intercropping. Another challenge arises during sowing when the two species require different sowing depths. In our experiment, spring wheat was sown at a depth of 3 cm and faba bean at 6 cm, complicating the sowing process compared to usual monoculture cropping systems. In addition, when both species are harvested together, a time-consuming and labor-intensive separation process based on seed size is necessary to separate the species unless they are used together as animal feed. The presence of broken beans in the mixture, as observed in our experiment, can further complicate or even render the separation process impossible. However, this problem can be minimized through strip intercropping, where partner crops can be sown and harvested separately. Strip intercropping closely resembles row cropping, however, the land sections are sufficiently wide to accommodate machinery operations and allow for separate cultivations. Yet, this approach does not allow us to observe the effect of interspecific interaction, such as mixed intercropping, where partner species are completely blended together within rows.

Designing an effective intercropping system is always context-specific, tailored to the unique goals of the growers. Depending on the objectives, intercropping can be designed to enhance overall yield regardless of crop species, improve the yield of specific crop species, increase land-use efficiency, and boost nutrient and water use efficiency (Khanal et al., 2021). In practice, experimenting with intercropping often involves combining multiple production objectives within a single intercrop design. This creates endless possibilities for cultivar combinations that need to be tested across various sites and under diverse climate and management conditions (Borg et al., 2018; Demie et al., 2022). In addition, the complex interactions of multiple factors (cultivar × cultivar × environment × management; **Chapter 4**) further complicate the generalization of intercropping systems. To address this challenge, the first approach involves experimentally investigating various ecological mechanisms of crop mixtures and cultivar traits to anticipate how these mechanisms can be applied in mixtures. The second approach is to develop multiple process-based agroecological models capable of assessing the mixing ability of different cultivars and forecasting the performance of context-specific mixtures across various environments and management conditions (Barillot et al., 2014; Lopez & Mundt, 2000). This modeling approach may aid in defining plant ideotypes tailored for intercropping, targeting morphological traits as key factors to maximize complementarity both temporally and spatially between species in virtual simulations. By integrating these two approaches, we can address the complexity of intercropping and design more effective and context-specific intercropping systems that are beneficial for both growers and researchers. Nevertheless, our thesis solely concentrates on the first approach, which offers valuable understanding of the overall patterns, relationships, and implications on compensation dynamics (**Chapter 2**), mixture effects during early (**Chapter 3**) and later growth stages (**Chapter 4**), and interactions between spring wheat and faba bean cultivars in various cropping systems and management practices (**Chapter 3 & 4**).

5.2 Potential findings in intercropping for production practices

The primary aim of this thesis was to investigate the mixing ability of multiple spring wheat cultivars with two faba bean cultivars across various environments and crop management practices. To achieve this, we combined spring wheat cultivars with faba bean cultivars at two different densities and compared these combinations to their respective monocultures across three different environments. On average, we observed higher total grain yields in the mixtures than in monocultures (see **Chapter 4.4.1**). This indicates that intercropping is generally a more efficient cropping system than sole cropping, particularly when considering the total grain yield in the mixture. Moreover, in this experiment, the benefit of crop mixtures was already evident as early as 23 days after sowing because we observed higher crop emergence in the mixtures compared to monocultures in some environments (**Chapter 3**). In addition, both spring wheat and faba bean showed better emergence in mixtures, especially where expected emergence was low for the respective species due to locally acting mortality factors (**Chapter 3**). This indicates the strength of diversity already in the early stages of crop development, ultimately leading to greater stability. Finally, higher compensation in crop mixtures was also measured at the later growth stage (around 52 days after sowing) for crop biomass (**Chapter 2**). These findings are particularly valuable for farmers who regularly face partial crop failures due to extreme climate. As higher stability under adverse conditions has been proved to be more crucial than higher production in favorable conditions (Raseduzzaman & Jensen, 2017), intercropping could be helpful to develop a more resilient production system, particularly in case of partial crop failures under extreme weather.

In cereal-legume crop mixtures, cereals are reported as the dominant partner over legumes, especially for the total grain yield in the mixture (Agegnehu et al., 2008; Hauggaard-Nielsen et al., 2001; Yu et al., 2016). However, questions remain, such as "Does cereal dominance over legumes begin as early as the crop emergence stage?" and “Could a small head start of cereal at emergence lead to even stronger dominance over legumes at later growth stages?”. Therefore, in this experiment, we examined those questions and observed early spring wheat domination over faba bean already at the crop emergence stage in one environment without suppressing faba bean emergence (**Chapter 3**). Additionally, this early domination of spring wheat leads to a strong domination and, thereby, stronger suppression of faba bean at later growth stages. That means a small domination of cereal that was recorded at the early stage gets even stronger at the later stage with stronger suppression over the weaker partner. Yet, it has been reported that the yield efficiency of a mixture depends mainly on the performance of its weaker partner (Annicchiarico et al., 2021). Consistent with this finding, our experiment revealed that the overall positive effect of the mixture on biomass compensation was primarily due to faba bean compensation rather than spring wheat compensation (**Chapter 3**). These findings indicate the importance of legumes in the cereal-legume crop mixture to observe the overall higher mixture performance. Additionally, for total grain yield, we observed that only the grain yield of the taller faba bean cultivar, Fanfare, was positively correlated with the spring wheat cultivar height in the mixture (**Chapter 4**). This is attributed to Fanfare's greater competitive ability compared to the shorter faba bean cultivar, Mallory. Therefore, we recommend, first, measuring and managing cereal dominance at the early developmental stage as well as the later growth stage. Second, it is crucial to select species, that are subjected to severe competition, with greater competitive ability to achieve a higher positive effect from the mixture.

The total grain yield in the mixture could depend on multiple factors, like the cultivar identity of selected species, environmental conditions, and management factors. In our experiment, all those factors, either as a main effect or as an interaction effect, were significantly influencing the performance of the mixture for grain yield (**Chapter 4**). In particular, the two-way interaction between multiple factors makes generalizations about intercropping performance from these short-field experiments rather difficult. Even though it was challenging to generalize, to enhance the selection response in intercropping system, we need to understand how multiple factors influence each other. In particular, to design a better intercropping system, we suggested selecting both component species simultaneously as a plant team with appropriate densities in the targeted environment. By doing so, it is also recommended to consider the complex interactions that exist between multiple factors in the mixture. During selecting the component species as a plant team, it is important to consider different plant architectures, such as plant height (Barillot et al., 2014; Launay et al., 2009; Louarn et al., 2020), to reduce competition and increase complementarity between selected species (Annicchiarico et al., 2019; Hauggaard-Nielsen and Jensen, 2001; Keddy, 1990). To maintain a balanced proportion of cultivars in the mixture, homogeneous height between cultivars has been recommended (Bowden et al., 2001; Dai et al., 2012). In line with those findings, we observed that medium-height spring wheat cultivars ranked higher for total grain yield in the mixture than taller and shorter spring wheat cultivars (**Chapter 4**, **Fig 4.3**). Additionally, the taller faba bean cultivar exhibited a weak correlation with spring wheat height for faba bean grain yield in the mixture (**Chapter 4**, **Fig 4.6**). These findings suggest that combining medium-sized spring wheat cultivars, which reduce wheat domination, with taller faba bean cultivars, which enhance the competitive ability of faba beans, can result in a more effective mixture. This aligns with Demie et al. (2022), who observed a tendency for shorter cereal cultivars to exhibit higher intercropping performance after reviewing 69 research articles. These results could help farmers and breeders design a better intercropping system with a positive mixture effect in the future.

Currently, a wide range of cultivars are available for monocropping (Bančič et al., 2021; Bourke et al., 2021; Louarn et al., 2020), but their performance in crop mixtures has not been tested yet. In this experiment, the effect of cultivars (spring wheat) on crop emergence was recorded in only one environment (**Chapter 3**), along with the interaction effect between spring wheat and faba bean cultivars on grain yield (**Chapter 4**). However, we have not observed any significant main effect of cultivars on the total grain yield in the mixture (**Chapter 4**). This is because the selected cultivars for this experiment are mainly bred for monoculture, and the best-yielding cultivar in monoculture is not necessarily the best one for intercropping (**Chapter 4**, **Fig 4.1**). This highlights the importance of breeding cultivars specifically for intercropping to optimize resource allocation and achieve higher yields, as also mentioned by other studies (Annicchiarico et al., 2019, 2021; Finckh, 2008; Lamichhane et al., 2018; Tavoletti and Merletti, 2022). However, this raises the question, "Do we need to breed intercrops for intercropping within intercropping system?". As our result revealed low to non-significant correlations between spring wheat cultivar performance in monoculture vs. intercropping (**Chapter 4.4.2**), it is evident that a cultivar's performance in monoculture cannot reliably serve as an indicator in intercropping. Indeed, the trait that mattered the most to control mixture proportion (i.e. interaction traits) is simply not expressed in pure stands and thereby cannot be selected in pure stands. This finding aligns with other research (Baxevanos et al., 2017; Kammoun et al., 2021; Tavoletti and Merletti, 2022) advocating selecting cultivars for intercropping in an intercropping system. Therefore, for future intercropping practices, we suggest prioritizing the breeding of cultivars specifically tailored for mixed cropping, selecting them based on their performance within mixtures rather than in monoculture. This will assist farmers in designing more successful intercropping systems and enhancing the sustainability and productivity of the agricultural system through crop mixtures.

5.3 Assessment of the present study and suggestions for future research

While crop mixtures offer numerous agro-ecological benefits (**Chapter 1.1**), a major challenge in intercropping research lies in the endless possible combinations of multiple species, cultivars, and densities that would require testing across various environments. Even though we evaluated several spring wheat and faba bean cultivars at two densities in this experiment, more cultivars still need to be studied in a variety of growth environments. Therefore, further experiments should be carried out to test and validate the findings of intercropping: 1) with various species and cultivars with different plant architectures; 2) in different densities and in different proportions of each species at sowing; 3) in various soils with varying nutrient availability and weather contexts; 4) considering biotic interactions of crops with pests, pathogens, and beneficial organisms (insects, microorganisms); 5) under abiotic stresses such as heavy rain and drought; 6) examining interactions between crop mixtures and belowground diversity; and finally, 7) by combining several factors and their interactions.

In this experiment, we chose various plant heights to promote variability among a few chosen cultivars. While plant height is a crucial aspect of plant architecture due to its role in competition (Barillot et al., 2014; Demie et al., 2022), other architectural traits also play significant roles in crop mixtures (Bourke et al., 2021; Brooker et al., 2015). Future studies need to outgrow the limitation of the present experiment by incorporating systematic investigation and categorization of other plant traits, such as leaf area, earliness, and root architecture, to optimize complementarity between two species in mixed cropping (Homulle et al., 2022; Kiær et al., 2022; Nelson et al., 2021; Timaeus et al., 2022; Zhu et al., 2015). Special consideration should also be provided when selecting cultivar traits for crop mixture, as many traits are likely to interact with one another in the mixture (Borg et al., 2018).

Additionally, we considered two densities (120% and 80%), with each species mixed in a 1:1 ratio in a replacement design (i.e. mixtures are formed by replacing a given number of plants of one component by the same number of the other component; Snaydon, 1991). However, to accurately assess the impact of varying densities on mixtures and establish the optimal seeding rate, it is essential to evaluate mixtures under a finer range of sowing densities (Bedoussac et al., 2015; Neumann et al., 2007). Instead of mixing different species in equal proportions, experiments should also be conducted using various ratios of the component species. This approach will help regulate the yields of each species within the mixture (Werf et al., 2021; Yu et al., 2015). Particular attention needs to be paid to the density of dominant and dominated species (Hauggaard-Nielsen et al., 2006) in both replacement and additive designs (i.e. mixtures are formed by adding plants of one component to the number of plants of other component present in the pure stand; Snaydon, 1991). This study only addresses mixed-row intercropping systems, which could pose practical management challenges, especially in highly mechanized settings or when component crops have different requirements for fertilizers, herbicides, and pesticides. However, these problems could be minimized with strip intercropping systems (Iqbal et al., 2019), which accommodate different planting and harvesting dates of partner crops with reduce interspecific interactions between component crops than row intercropping. Therefore, dedicated research integrating multiple factors in various growing environments is needed before assembly rules can be provided to farmers and breeders for intercropping systems.

One of the primary challenges associated with intercropping systems is the post-harvest grain sorting process. Given that both species, especially in mixed-row intercropping setups, are planted and harvested simultaneously, an effective sorting mechanism ultimately determines the marketability of the intercrops (France et al., 2018; Kiær et al., 2022). In 2020, we witnessed fragmented beans in the grain mixture, primarily due to the inconsistent maturation periods of the spring wheat and faba bean, along with bruchid beetles infestation in the faba beans. This presence of broken beans complicates the separation process further (Bedoussac et al., 2015). Therefore, for future research endeavors, we propose the following recommendations: 1) breeding both intercropped species to mature concurrently, 2) developing faba bean cultivars resistant to bruchids and implementing efficient biocontrol measures against these pests, 3) modifying combined harvesters to accommodate the more delicate species, 4) establishing a grain sorting system for efficient, rapid, and cost-effective sorting of large volumes, 5) cultivating peas that are less prone to breakage, and 6) setting new quality standards for food products, such as ensuring that a baking mixture containing small quantities of beans still yield desirable baking and taste characteristics (Dabija et al., 2017). Implementation of these aforementioned strategies will significantly streamline the separation process, reducing the number of steps and overall effort required.

The benefits of intercropping systems, in comparison to monoculture, are (typically) assessed based on plant biomass (**Chapter 2 & 3**) and total grain yield (**Chapter 4**) in the mixture. However, it is important to go beyond crop yield and evaluate the additional advantages of intercropping in order to truly understand the profitability of these systems. In practice, it is typically the economic benefit rather than the biological aspect that determines which cropping systems farmers choose to implement in practice. Hence, when evaluating the benefits of intercropping compared to monoculture, it is crucial to consider the complexities involved in managing intercropping, such as the combined sowing and harvesting of intercrops, weeding, and sorting the grain mixture. These factors can lead to higher production costs compared to monocrops (Khanal et al., 2021). Furthermore, it is necessary to calculate the selling prices of individual crops separately to determine the potential economic benefits of intercrops over monocrops (Bedoussac et al., 2015). The prices of intercrops may also vary depending on the quality of the intercropped cereal grains, particularly due to higher grain protein concentration (Vlachostergios et al., 2015). Therefore, it is essential to measure the benefits of intercropping in quantitative, qualitative, and economic terms in order to accurately assess the economic profit for farmers. Without demonstrating the economic advantages of intercropping systems compared to monoculture, it is unlikely that farmers will adopt this diverse and sustainable cropping system.

5.4 Does intercropping have a role in modern agriculture?

There is a common misconception that modern agriculture does not have room for intercropping (Lithourgidis et al., 2011). This belief stems from the lack of specialized varieties and machinery for intercropping available in the market, as well as the monocropping-centered farm and market system. Years of focusing on improving monocultures and limited experience with enhancing intercropping systems have overshadowed the potential of such a sustainable cropping system in modern farming practices. Beyond field research, it is essential to educate farmers about these practices, provide economic incentives for transitioning from current methods, and create new products and market systems that favor intercropping. The widespread adoption of intercropping will only happen with the support of policies, institutions, and markets that establish the social structures and norms influencing individual farmer behavior.

To make intercropping feasible in modern cropping systems, we first need to sell cultivar and species mixtures as seeds with precise amounts of each component (Finckh, 2008). However, registering diversified cultivar mixture is challenging due to Union for the Protection of New Varieties (UPOV) guidelines and EU regulations (Regulation 2100/94/EC), which require genetic uniformity. This makes it impossible to register crop mixtures containing different species (personal communication). Breeding for intercropping will not become widespread without changes in these regulatory procedures of registration for mixed cultivars release.

Secondly, the complexity of sowing, managing, harvesting, and sorting two intercrops in a mixture must be minimized through the development of new machinery (Lithourgidis et al., 2011). Currently, most mixtures are undesirable due to technological limitations in handling crop mixtures within modern cropping systems (Finckh, 2008). Therefore, agricultural engineers should develop and market highly specialized farming machinery suitable for intercropping to enhance adaptability and ease of use.

Thirdly, new markets need to be created for products produced through intercropping. While mixed grains can be easily harvested with combine harvesters, there are few buyers for these grains. Farmers often have only one option: selling as animal feed at lower prices. Creating new markets is essential to encourage farmers to adopt and ensure the profitability of intercropping. A notable example is the organic Danish buyers who have purchased mixed grains at premium prices to use them as seeds (Hauggaard-Nielsen et al., 2008). These mixed grains are preferred as seed due to their minimal damage from pests and diseases. Additionally, research has demonstrated that noodles containing 20% yellow pea flour possess desirable sensory attributes, a pleasing texture, adequate protein content, reduced glucose release, and improved protein digestibility (Dabija et al., 2017). Such research findings and the development of new markets will enhance the profitability and adaptability of intercropping systems in modern agriculture.

Fourthly, new regulations, relevant policies, and subsidies are needed to support growers transitioning from monoculture to intercropping practices (France, 2018). Governments and policymakers should promote intercropping as a diversification strategy for yield increase. For instance, China has already implemented a policy in 2022 that encourages maize/soybean intercropping and promotes the overall increase of soil nitrogen efficiency in farming (Li et al., 2023). The European Union has undertaken Horizon 2020 and Horizon Europe research programs to accelerate the development of sustainable cropping systems like intercropping between farmers and researchers. These policies should also encompass advisory services for farmers, enabling them to acquire knowledge on intercropping techniques, raising awareness about sustainable cropping systems, and building the capacity of farmers to effectively manage the complexities associated with this system.

Finally, implementing these strategies will necessitate the collaboration of large interdisciplinary teams comprising experts from various fields, including ecologists, environmental scientists, agronomists, crop scientists, soil scientists, geneticists, and crop modelers (de Leon et al., 2016). Additionally, involving farmers in the design will help ensure their needs are met regarding the complex system dynamics and the implementation of crop diversification strategies. Aare et al. (2021) recognize farmers' potential as mixture experts and suggest a farmer-to-farmer approach towards learning this diversified cropping systems. Therefore, it is imperative to engage in conversations with farmers to gain insights into these practices and subsequently conduct trials to assess their broad applicability. This approach can pave the way for innovative research and development in agriculture, ensuring sustainable support for the growing human population and the preservation of a livable environment.

Intercropping, a traditional agricultural practice that has been utilized for thousands of years, has once again demonstrated its benefits in this study. However, if the aforementioned factors are not addressed, farmers are unlikely to adopt this cropping system. Despite its widespread use in various regions of the world, intercropping remains poorly understood from an agronomic standpoint, with research in this field lagging behind that of monoculture. Intercropping systems in traditional agriculture have evolved over centuries of trial and error. If intercropping is indeed experiencing a renaissance in response to problems associated with monoculture, it should not be seen as a return to ancient peasant ways, but rather as the integration of valuable aspects of this practice into modern agriculture. This renewed interest is partly hindered by an industrialized agriculture bias and the complexity of interactions that occur in intercrops. Nevertheless, scientists must uncover and understand the precise nature of this underutilized and valuable tool, and then offer it to those who feed an increasing population on an increasingly fragile planet. Despite the complexities and challenges involved, we probably need to give intercropping much more attention in the future, especially in light of extreme climatic challenges farmers are experiencing all around the world.

5.5 Conclusion

Successful intercropping requires careful experimental design and effective management strategies, with a focus on selecting compatible crop species, cultivar traits, and planting densities tailored to specific environments. It is crucial to consider the complex interactions between multiple factors in the intercropping environment and to pay particular attention to plant architecture during species selection. Our study observed that the height of spring wheat cultivars has a slight but significant impact on intercropping performance, with moderate-sized cultivars showing higher mixture performance compared to shorter and taller ones, while taller faba bean cultivars demonstrated greater competitive ability than shorter ones. Future research should emphasize crop traits that not only enhance target crop yield but also positively affect companion crops to maximize mixture effects through complementarity. However, the performance of selected cultivars in intercropping cannot be always predicted from their performance in monoculture, underscoring the importance of species selection within intercropping systems for successful outcomes. We found that crop mixtures enhance crop emergence and result in higher plant biomass compensation, indicating greater stability under adverse conditions compared to monocultures. We also found that spring wheat dominance can begin as early as crop emergence and intensify over time, highlighting the need for early competition management through various crop management decisions before and after sowing, as well as long-term plant breeding strategies. Future research should also focus on breeding cultivars specifically for intercropping and addressing post-harvest challenges to further optimize intercropping systems.

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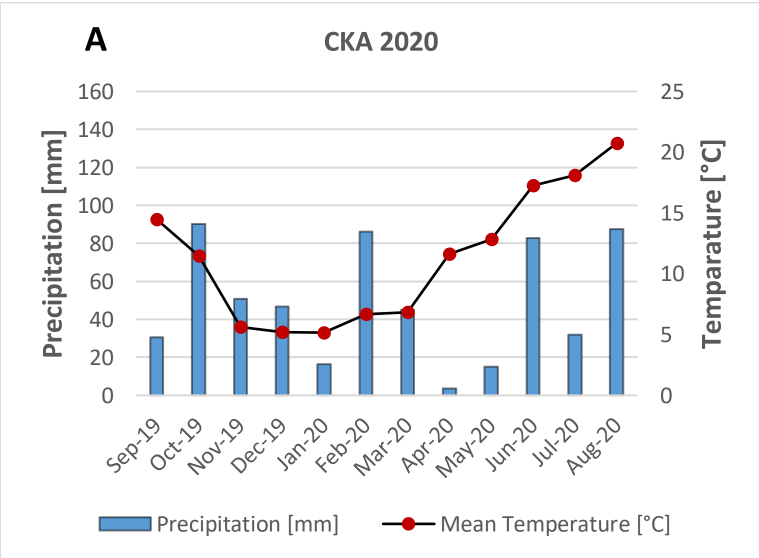
Appendix A: Supplementary material from article "Effects of spring wheat/faba bean mixtures on early crop development"

Supplementary information 3.1:

The total precipitation (mm) and average temperature (°C) at Campus Klein-Altendorf (CKA) in 2020 growing season (September 2019 to August 2020) and at Wiesengut (WG) in 2020 and 2021 growing season (September 2019 to August 2021) are presented as a graph. In April and May, the most relevant for early crop development, precipitation was relatively low in 2020 for both sites, but higher in 2021.



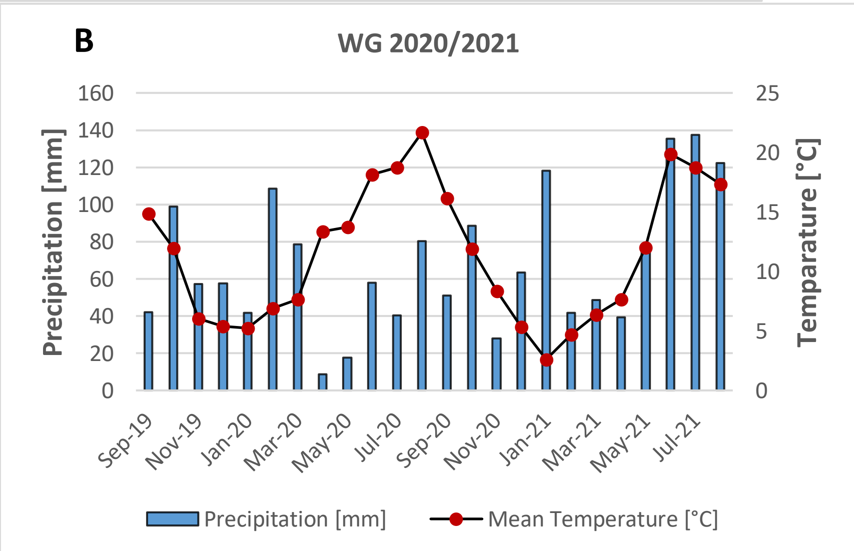


Figure S3.1. Precipitation (mm) and temperature (°C) at the experimental station Campus Klein-Altendorf (CKA) from September 2019 to August 2020 (**A**), precipitation (mm), and temperature (°C) at the experimental station Wiesengut (WG) from September 2019 to August 2021 (**B**).

Supplementary information 3.2: Thousand kernel weight (TKW) and germination percentage (GP) of two faba bean (FB) and ten spring wheat (SW) cultivars for two years, 2020 and 2021.

TableS3.1. Thousand kernel weight (TKW) and germination percentage (GP) for faba bean and spring wheat cultivars for two years, 2020 and 2021.

Variety	**Cultivar**	**TKW (g)**		**GP (%)**	
		2020	**2021**	**2020**	**2021**
Faba bean	Mallory	538	499	96	96
	Fanfare	475	431	98	93
Spring wheat	Anabel	37.6	44	94	94
	Jasmund	42.8	40.7	94	94
	Lennox	45.1	41.9	94	94
	Saludo	39.5	45.3	94	96
	Sorbas	40.7	36.2	96	97
	Chamsin	36.3	34.8	99	98
	KWS Starlight	43.9	30.7	99	99
	Quintus	43.8	48.8	92	94
	Sonett	39.1	41.9	96	97
	SU Ahab	45.2	49.1	94	94

Supplementary information 3.3: Equations for spring wheat cultivar mixtures.

Two groups of 5-component equiproportional spring wheat (SW) cultivars mixtures were created to increase the level of functional diversity. Each group contains five spring wheat cultivars. The required amount of seeds for each cultivar were calculated separately (**Equation S3.3**) and mixed homogeneously before sowing.

$$TKG * Density * (area\ per\ plot/5) / GP * 10 \qquad (S3)$$

Where TKG and GP are Thousand Kernel Weight (TKW) and germination percentage (GP) of the respective wheat cultivars (**Table S3.2**)**.** Low and high density for monoculture and mixture (**Table 3.3**) were considered as density in **Equation S3.3**. Total area for each plot were divided by 5 for 5-component variety mixture to ensure the equiproportional contribution of each component among the mixture.

Supplementary information 3.4: To maintain the appropriate faba bean seed density at sowing at monoculture, we set faba bean seeder, Hege 95 B at certain setting. For monoculture and mixture at two sowing densities, 120% and 80%, there are four machine setting.

Table S3.2. Hege 95 B rotation option according to faba bean seed density.

	Setting in Monoculture		Setting in Mixture	
	120%	80%	120%	80%
Machine setting	12/13_5/6	12/13_3/10	11/14_4/6	11/14_4/8

Supplementary information 3.5:

Table S3.3. Full model of Analysis of Variance (ANOVA) for emergence equivalent ratio (EER) considering all possible interactions between cultivar spring wheat, cultivar faba bean, environment, and sowing density.

Source of variation	df	Mean square	F-value	P-value
SW cultivar	11	0.14	03.44	0.000***
FB cultivar	1	0.01	00.21	0.644^{ns}
Density (Den)	1	0.01	00.22	0.643^{ns}
Environment (Env)	2	0.50	12.27	0.000***
Block	1	0.04	00.96	0.327^{ns}
SW: FB	11	0.04	01.01	0.436^{ns}
SW: Den	11	0.01	00.33	0.979^{ns}
FB: Den	1	0.15	03.78	0.053^{ns}
SW: Env	22	0.14	03.42	0.000***
FB: Env	2	0.02	00.50	0.605^{ns}
Den: Env	2	0.02	00.46	0.631^{ns}
SW: FB: Den	11	0.03	00.74	0.699^{ns}
SW: FB: Env	22	0.04	00.98	0.485^{ns}
SW: Den: Env	22	0.05	01.21	0.231^{ns}
FB: Den: Env	2	0.01	00.19	0.829^{ns}
SW: FB: Den: Env	22	0.03	00.79	0.744^{ns}

Appendix B: Supplementary material from article "Evaluation of multiple spring wheat cultivars in diverse intercropping systems"

Supplementary information 4.1:

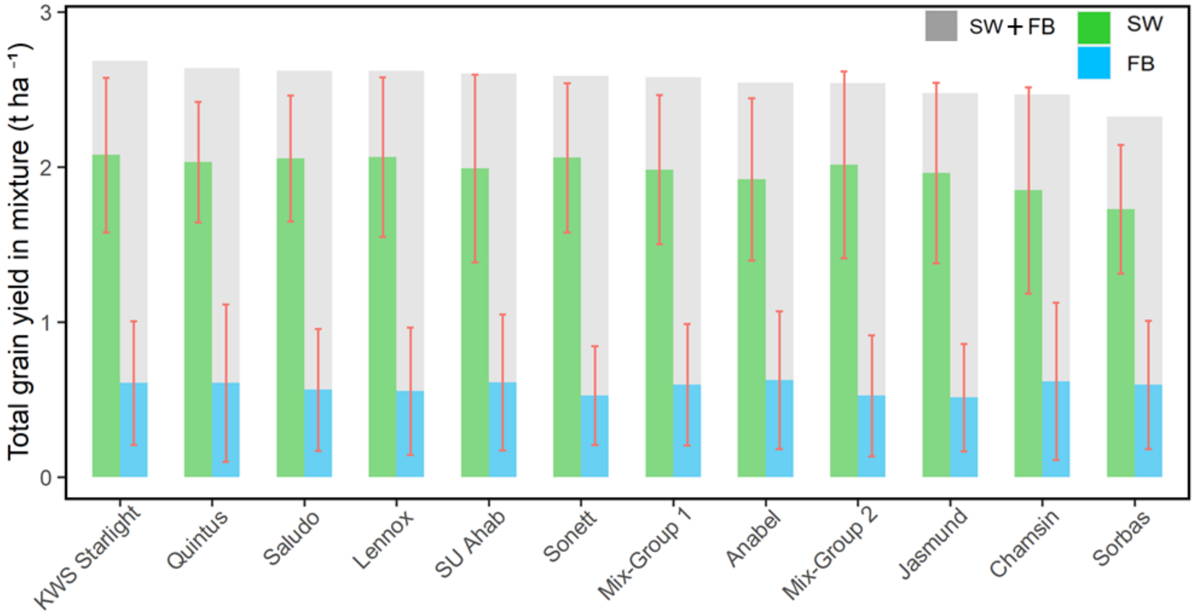


Figure S4.1. The mean of total grain yield (t ha^{-1}, grey bars) of spring wheat (SW; green bars) and faba bean (FB; blue bars) in the mixtures on the average of the three environments (CKA2020, WG2020, and WG2021) and two densities (high and low) for twelve SW entries (ten cultivars and two 5-component mixtures of these wheat cultivars); vertical bars represent the standard deviation. No significant difference was observed among SW entries for SW grain yield, FB grain yield, and total grain yield according to the Dunn test with Bonferroni correction.

Supplementary information 4.2:

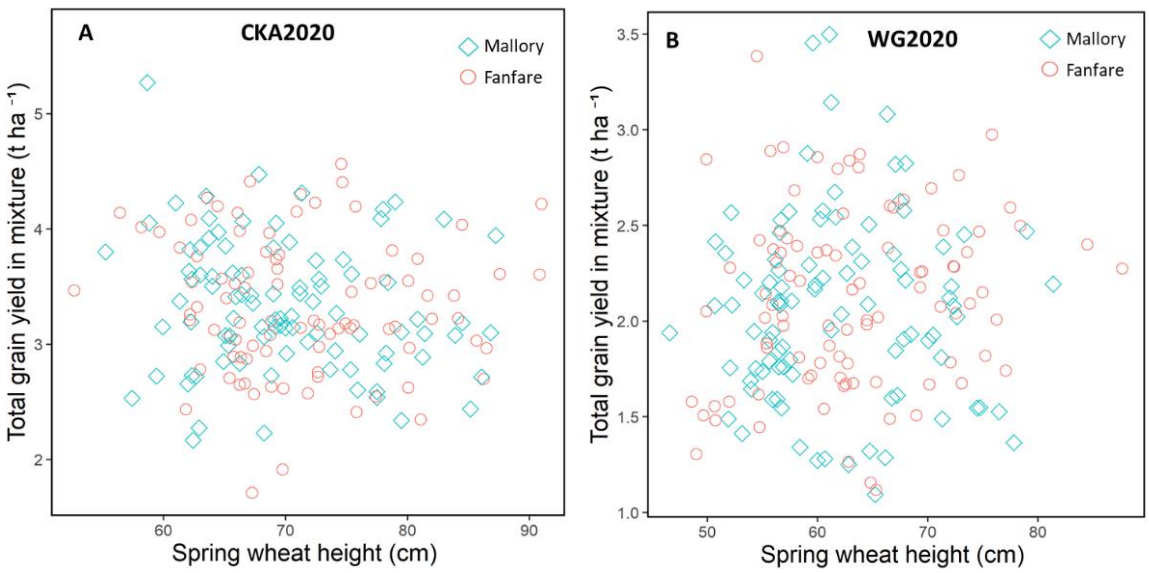


Figure S4.2. Total spring wheat and faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (at the flowering stage; cm) for faba bean cultivars Mallory (blue diamonds) and Fanfare (orange circles) in the mixtures in two environments CKA2020 (A), and WG2020 (B).

Supplementary information 4.3:

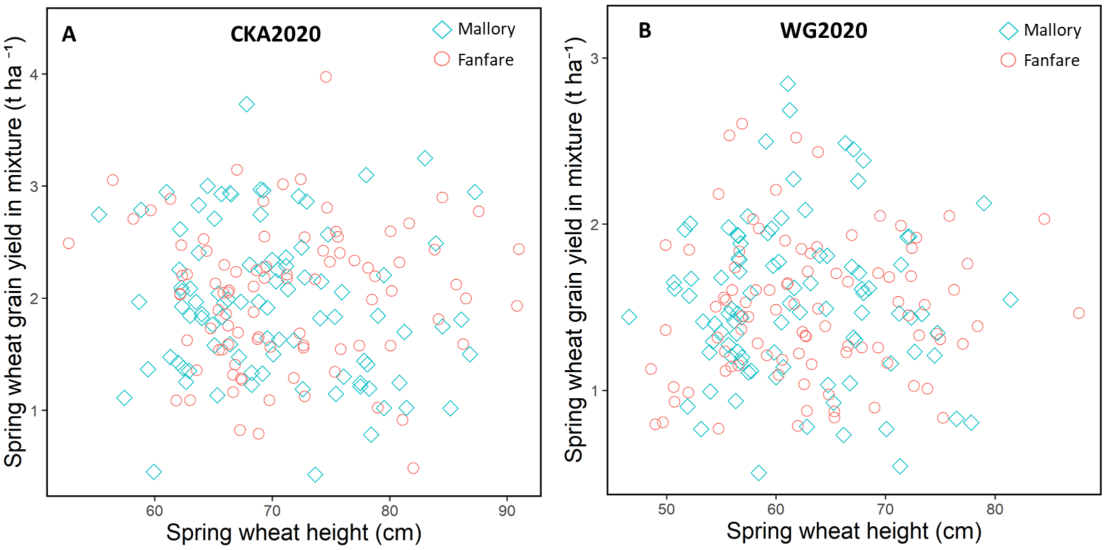


Figure S4.3. Spring wheat grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for faba bean cultivars Mallory (blue squares) and Fanfare (orange circles) in the mixtures in two environments CKA2020 (A), and WG2020 (B).

Supplementary information 4.4:

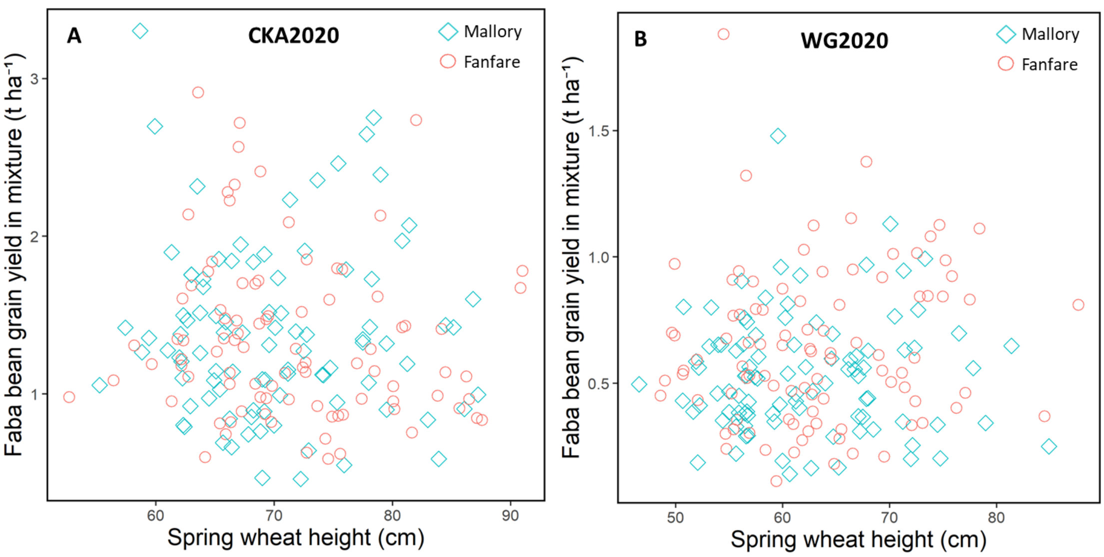


Figure S4.4. Faba bean grain yield (t ha^{-1}, in dry matter) against spring wheat plant height (cm) for faba bean cultivars Mallory (blue squares) and Fanfare (orange circles) in the mixtures in two environments CKA2020 (A), and WG2020 (B).

Appendix C: List of further publications

Conference presentations

1. **Paul, M. P**., Demie, D. T., Seidel, S. J., & Döring, T. F., (2022). Effects of spring wheat / faba bean mixtures on early crop development, *Ecology and Evolution: New perspectives and societal challenges*, 21-25 Nov 2022, Metz, France, page. 48.
2. **Paul, M.**, Krämer, J., Seidel, S. J., Rascher, U., & Döring, T. F., (2022). Crop mixture. The International Conference on Digital Technologies for Sustainable Crop Production (DIGICROP), March 28-30, 2022, Bonn, Germany. https://digicrop.de/m-paul-crop-mixture/
3. **Paul, M. P**., Demie, D. T., Jaspers, L., Vincze, J. S., Lantzerath, K. S., Caspersen, L., Seidel, S. J., & Döring, T. F., (2020). Effects of cereal-legume crop mixtures on crop and multifunctional agroecosystem performance. The International Conference on Digital Technologies for Sustainable Crop Production (DIGICROP), November 1-10, 2020, Bonn, Germany.

Contributions as co-author

1. Hadir, S., Döring, 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 and Soil. https://doi.org/10.1007/s11104-024-06742-3
2. 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 (arXiv:2312.03443). arXiv. http://arxiv.org/abs/2312.03443
3. Demie, D. T., Wallach, D., Döring, T. F., Ewert, F., Gaiser, T., Hadir, S., Kraus, G., **Paul, M. R.,** Hernandez-Ochoa, I. M., Vezy, R., & Seidel, S. J. (2024). Evaluating a New Intercrop Model Using an Extensive Spring Wheat/Faba Bean Intercrop Dataset. Available at SSRN: https://ssrn.com/abstract=4828350 or http://dx.doi.org/10.2139/ssrn.4828350 (**Reviewed**).

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