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Wheat and faba bean intercropping and cultivar impacts on morphology, disease, and yield

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Abstract

Modern agriculture relies heavily on synthetic fertilizer and pesticide inputs. Pressure is increasing to find alternatives that reduce such inputs. In comparison to monocultures, intercropping can reduce plant diseases and increase yield, thereby reducing inputs and maximizing land use efficiency. However, knowledge gaps remain regarding which crop and cultivar combinations maximize such benefits. Here, we grew two wheat (*Triticum aestivum* L.) and six faba bean (*Vicia faba* L.) cultivars in monoculture and intercrops over three seasons and measured plant morphology, disease prevalence, and yield. Wheat ear development was slower in monocultures but varied by cultivar and year. Wheat cultivars senesced faster in monocultures versus certain faba bean intercrop combinations. In both wheat cultivars, *Fusarium* spp. severity was higher, while yellow rust (*Puccinia striiformis* f.sp. *tritici* Westend.) was lower in monocultures versus intercropped plots but varied by year and faba bean cultivar. Chocolate spot (*Botrytis fabae* Sardiña) in faba bean was higher in the cultivar 'Louhi' when grown in monoculture. Wheat cultivars yielded higher in monoculture versus intercropped plots. Faba bean yield was higher in monocultures but depended on wheat cultivar and year. Land equivalent ratios (LER) were not affected by interactions between cultivars or years but were always above one in intercropped plots. This indicates that it is always more efficient for yield to intercrop. Our results show that the benefits of intercropping with different wheat and faba bean cultivars varied, indicating that specific goals (i.e., disease suppression and yield) should be considered when selecting wheat–faba bean cultivar combinations.

1 | INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most widely grown cereal crops in the world (Igrejas & Branlard, 2020), with an estimated 776 million tons produced globally in 2021 (Babar et al., 2022). Of leguminous crops, faba bean (*Vicia faba* L.) is one of the most important, due to its high concentrations of protein, vitamins, minerals, and antioxidants and its ability to improve soil fertility (Karkanis et al., 2018) and structure (Rochester et al., 2001; Streit et al., 2019). Production of faba bean has risen by 21% between 1994 and 2014, with a global harvest of approximately 4.1 million tons (Karkanis et al.,

Abbreviations: LER, land equivalent ratio.

2018). The importance of both wheat and faba bean has made them the subject of intensive research (Giraldo et al., 2019; Zhang et al., 2019), amongst which the benefits of intercropping have received considerable attention (Aziz et al., 2015; Jensen et al., 2020; Karkanis et al., 2018).

Intercropping is a system that involves growing different crops together simultaneously. Numerous benefits can be realized by intercropping, with increases in yield quantity and quality receiving the most attention. For example, wheat grown with leguminous crops can yield 20%–30% more versus wheat grown in monoculture (Bedoussac & Justes, 2010; Li et al., 2001). Wheat yield quality can also improve, with higher protein concentrations seen in wheat grown in tandem with faba beans (Bulson et al., 1997; Gooding et al., 2007). In contrast, faba bean grown with wheat can realize yield losses up to 21% (Fan et al., 2006; Song et al., 2007; Xiao et al., 2021), but combined total yields can be higher (Agegnehu et al., 2008).

The effects of intercropping on yield can vary based on seasonal conditions due to weather-induced shifts in competitive interactions (Gou et al., 2016). Further, it has been shown that when wheat and grain legumes are grown together, the legumes fix more nitrogen (N) from the atmosphere compared to when they are grown in monoculture, while the wheat takes up a disproportionate amount of N (Jensen et al., 2020). Such complementary competitive and facilitative interactions can reduce synthetic N inputs by 100–200 kg ha^{-1} (Jensen et al., 2010) and potentially cut global fossil fuel-based synthetic N fertilizer use between 5%–26% (Jensen et al., 2020; Xiao et al., 2018).

Disease resistance and severity can be changed by intercropping. A meta-analysis showed that growing wheat and faba bean together can reduce damage caused by yellow rust (*Puccinia striiformis* f.sp. *tritici* Westend.) in wheat by 34% and damage by chocolate spot (*Botrytis fabae* Sardiña) and brown rust (*Uromyces viciae-fabae* var. *viciae-fabae* J. Schröt.) in faba bean by 39% and 36%, respectively (Zhang et al., 2019). Growing wheat with rye (*Secale cereale* L.), clover (*Trifolium pratense* L.) or mustard (*Sinapis alba* L.) can reduce damage caused by brown rust (*Puccinia triticina* Erikss.) (Vilich-Meller, 1992) and *Fusarium graminearum* Schwabe (Drakopoulos et al., 2021). Nonetheless, evidence for similar effects on wheat, intercropped with faba bean remains scant or nonexistent. If substantial reductions in disease severity can be realized in wheat–faba bean intercropping systems, pesticide use could be (partially) curtailed (Van Der Werf & Bianchi, 2022). However, it is important to take into account that the effects of mixed cropping on disease suppression can vary from year to year based on weather conditions (Fernández-Aparicio et al., 2011). It remains unknown how interactions between cultivars and yearly climatic variations could affect disease suppression in intercropping systems.

Despite accumulating evidence demonstrating the positive effects of wheat–faba bean intercropping, there remain substantial knowledge gaps concerning which wheat and faba bean cultivars can be suitably paired to maximize yield and disease resistance (Mamine & Farès, 2020). Importantly, the benefits of intercropping wheat with faba bean may not be consistent across cultivars due to differences in plant morphological characteristics (Ajal & Weih, 2022; Nelson et al., 2021). Generally, intercropping can change the morphological characteristics of wheat, such as tiller production, number of ears, and leaf N concentrations (Zhu et al., 2016). Such changes to wheat morphology in response to intercropping can impact yield (Berghuijs et al., 2020).

Variation in traits between different cultivars of the companion crop could alter yield. For example, faba bean cultivars that are shorter and have a lower leaf area index can generate less interspecific light competition (Nelson et al., 2021), while wheat cultivars that grow taller generally compete and perform better in mixtures with faba bean (Haymes & Lee, 1999). Lodging (i.e., bending over of the stems towards the ground) in wheat can be reduced with the selection of an intercrop with the proper traits (Nelson et al., 2021; Timaeus et al., 2022). In general, selecting crop traits that generate less niche overlap allows for more efficient resource use (Ajal et al., 2021). Mixed legume-cereal stands can have lower evaporation due to a more complex canopy structure and thereby better drought tolerance (Tsubo & Walker, 2004). Specific traits that influence stand and canopy structure in intercropping systems can sometimes better regulate or reduce humidity, thereby reducing disease incidence (Boudreau, 2013; Ma et al., 2019). However, when grown in combination with wheat, faba bean nutrient content tends to be dictated by the faba bean cultivar and not by intercropping with or without wheat (Ajal & Weih, 2022). Therefore, potential benefits of mixed cropping rely on cultivar-specific trait complementarity between specific wheat and faba bean cultivars.

Core Ideas

- Intercropping can increase yield, reduce synthetic inputs, and suppress diseases compared to monocultures.
- Two wheat and six faba bean cultivars were grown in intercropped versus monoculture plots over 3 years.
- Impacts on plant morphology, disease severity, and yield quality and quantity were measured.
- Intercropping showed both positive and negative effects that varied by cultivar and year.
- Wheat–faba bean cultivars must be carefully chosen to maximize goals such as disease suppression and yield.

We conducted a field trial with two wheat cultivars (Lavett and Quintus) and six faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in monocultures and single pairing mixtures (i.e., one wheat cultivar with one faba bean cultivar) over three growing seasons in order to test the following hypothesis: Wheat and faba bean morphological characteristics, disease severity, and yield quality and quantity will change in monoculture versus intercropped plots, with these effects being dependent upon cultivar and year. Specifically, we expect disease severity to be lower and yield quality and quantity to be higher in intercropped versus monoculture plots.

2 | MATERIALS AND METHODS

2.1 | Experimental site

The experiment was located in Kraggenburg, Noordoostpolder, Flevoland, The Netherlands (52° 39′ 50.9″ N 5° 51′ 55.0″ E) on a commercially certified organic/biodynamic farm. A 1–6 crop rotation (i.e., wheat is planted every 6th year) is practiced with, among others, potato (*Solanum tuberosum* L.), onion (*Allium cepa* L.), wheat with clover (*Trifolium repens* L.) as a cover crop, carrots (*Daucus carota* L.) and alfalfa (*Medicago sativa* L.) in the typical rotation scheme. The fertilization strategy is based on the decomposition of crop and cover crop remnants, as well as coarse, stable goat, and cattle manure. No other fertilizer is added. The land was reclaimed from the former Zuiderzee (Southern sea) in the 1940′s. The soil is considered a fertile, light, low-lying, young marine silty fluvisol soil (Tóth et al., 2008, https://www.isric.org/explore/), fairly high in calcium carbonate and the horizons remain poorly developed. In autumn, conservation tillage is practiced, using an "eco-plough" (Rumptstad Industries BV) (Bavec, 2014). The soil composition at a 0- to 30-cm depth consists of ~ 22% sand, 51% silt, and 18% clay, with 2.3% soil organic matter content, 7.4 pH, 1220 g total N kg^{-1}, 0.9 mg plant available P kg^{-1}, and 88 mg plant available K kg^{-1}. Based on the nearest Royal Netherlands Meteorological Institute in Marknesse, the mean daily temperatures during the duration of the experiment were 10.9°C, 10.8°C, and 11.2°C in 2018, 2019, and 2020, respectively. Total annual precipitation was 618, 753 and 767 mm in 2018, 2019, and 2020, respectively. More details on annual temperatures and precipitation during the course of the experiment can be found in Table S1.

2.2 | Experimental design

The experiment was established on March 26, 2018 and ran until August 19, 2020. Two wheat cultivars were used: Lavett (Agrifirm, The Netherlands) and Quintus (Wiersum Plant Breeding, The Netherlands) and six faba bean cultivars: Columbo (DLF Seed Science, Denmark), Fuego (Wiersum Plant Breeding, The Netherlands), Kontu (Boreal Plant Breeding, Finland), Louhi (Boreal Plant Breeding, Finland), Taifun (Wiersum Plant Breeding, The Netherlands), and Tiffany (Wiersum Plant Breeding, The Netherlands).

Lavett is known to be susceptible to *Fusarium* spp. infection (Timmermans et al., 2009) and has been considered as the standard variety chosen for organic agriculture due to its yield (~6 ton ha^{-1}) and high baking quality (Osman et al., 2015, 2016). Quintus has a relatively high yield (~5 ton ha^{-1}) (Strazdiņa & Fetere, 2017) and is considered to be highly resistant to drought, *Fusarium* spp., yellow and brown rust and produces high-quality flour suitable for baking (https://wiersum-plantbreeding.nl/en/wheat/quintus/).

Of the faba bean cultivars, Columbo has a relatively higher protein and lower tannin content than most other cultivars, remains in flower longer (~ 27 days), and has good resistance to lodging and grows shorter (~ 124 cm) (http://www.dlf.com/system-pages/download-product-leaflet-with-settings/other/columbo-41200701.aspx?LanguageID=LANG1&PDF=true&LeftRightMargin=-23&TopBottomMargin=1&Filename=COLUMBO.pdf). Fuego yields relatively well overall, has a relatively high protein content (~28%) (Skovbjerg et al., 2020), has demonstrated high resistance to chocolate spot disease and lodging, and has a long flowering period of ~ 30 days. It matures in about 130 days (Olle et al., 2019), but has shown only moderate resistance to rust (Bundessortenamt, 2020). Kontu is an early flowering and maturing cultivar (~107 days) with a relatively low yield, but a high protein content (*circa* 31%) (Skovbjerg et al., 2020; Stoddard & Hämäläinen, 2011). Louhi is a very early, relatively high-yielding, short variety with small seeds and good lodging, chocolate spot and *Ascochyta* resistance (http://www.agrolitpa.lt/Product/seeds/spring-cereals/field-bean/LOUHI/). Taifun has moderate disease resistance, yield, and protein content (~ 29%) (Skovbjerg et al., 2020), while Tiffany has moderate resistance to rust and chocolate spot, but a relatively high crude protein and overall yield (Bundessortenamt, 2020).

Across the 3 years of the trial, the sowing/harvest dates were March 26, 2018/July 30 2018, April 2, 2019/August 22, 2019, and March 27, 2020/August 19, 2020, depending on weather conditions and crop development. The wheat and faba bean cultivars were grown in monocultures and in one-on-one crosses between all wheat and faba bean cultivars (i.e., each wheat species was grown with each faba bean cultivar). Plots measuring 1.5 (6 rows by 25 cm between rows) by 10 m were distributed across the field in a randomized complete block design with the 20 treatments (two wheat monocultures, six faba bean monocultures, and 12 intercrop combinations (i.e., two wheat cultivars grown with each of the six faba bean cultivars) replicated three times. In 2018 and 2019–2020, a net area of 1.5 by 8 m and 1.5 by 8.5 m was harvested, respectively. Harvesting of the faba bean, wheat and the mixture of both in the intercropped plots was done using a Wintersteiger Delta harvesting machine.

Each year, in accordance with the crop rotation scheme outlined at the beginning of section 2.1, the entire experiment was conducted in a different field within the commercial wheat crop on the same farm. The experimental plots were bordered on all sides by at least a 3 m buffer of the commercial wheat crop with ~ 50 m between the locations of the different fields. Given the close proximity and the relative homogeneity of the soil due to its relatively recent reclamation status, intra-field effects were likely negligible. Plots were sown using a customized machine from Wageningen University & Research Field Crops Lelystad. The crops were sown in intercrops to a depth of approximately 3–4 cm with 25 cm between rows. Wheat and faba bean sowing density in monoculture was 300 seeds m^{-2} and 30 seeds m^{-2}, respectively, except the faba bean cultivars 'Louhi' and 'Kontu', which were sown at a density of 40 seeds m^{-2}. In mixed stands, wheat sowing density was 100 seeds m^{-2}, while faba bean sowing density remained the same. Wheat sowing density differed between monoculture and intercropped plots because early season growth is rapid and many companion crops can be outcompeted before sufficient establishment. To reduce initial wheat competition, the sowing density in intercropped plots was reduced to 33% of that in a wheat monoculture.

2.3 | Morphological characteristics

Wheat and faba bean plant height were assessed on July 5, 2018, July 11, 2019, and July 23, 2020 when senescence of the wheat crop had begun (stages GS71–GS85 on the Zadoks scale according to Fowler, 2018). The average canopy height at three locations was assessed within each plot. Wheat ear development was assessed on May 30, 2018, June 13, 2019 and June 16, 2020 on five plants per plot on a 1–5 scale using an adaptation of Zadoks scale: 1 = GS41 (flag leaf extending), 2 = GS43–45 (ear visibly developing in flag leaf), 3 = GS47–49 (flag sheath opening; first awns visible), 4 = GS51–57 (ear emerging), 5 = GS59 (ear fully emerged) (Fowler, 2018). Wheat crop senescence was measured on July 3, 2018, July 25, 2019, and July 23, 2020 on five plants per plot on a 1–5 scale: 1 = completely green, 5 = completely yellow), which corresponds to stages GS71–GS85 on the Zadoks scale (Fowler, 2018). On May 23, 2018, the average number of internodal flowers on 10 faba bean plants per plot was estimated.

2.4 | Disease severity

Brown and yellow rust (*Puccinia triticina* and *Puccinia striiformis* f.sp. *tritici*, respectively) infection severity in wheat was assessed on July 6, 2018, June 27, 2019, and July 9, 2020 on 10 randomly chosen plants per plot on a 1–9 scale (1 = dead due to infection, 9 = no sign of infection) (McNeal et al., 1971). *Fusarium graminearum* infection severity in wheat was assessed on June 29, 2018 and July 9, 2020 by counting the number of plants that showed bleaching of and/or pink and yellow spore formation on the spikelets in two central rows of each plot (2 × 10 m) to eliminate edge effects. Chocolate spot (*Botrytis fabae*) and brown rust (*Uromyces viciae-fabae* var. *viciae-fabae*) disease severity in faba bean were assessed on July 9, 2020 on 10 randomly chosen plants per plot on a 1–9 scale (1 = dead due to infection, 9 = no sign of infection) (Olle et al., 2019).

2.5 | Yield quantity and quality

After harvest (see section 2.2 for dates and details on the machine used), wheat and faba bean grains were hand cleaned using mesh sieves. In the case of intercropped plots, wheat and faba bean grains were separated from one another using a subsequent series of sieves with decreasing mesh size so that the yield (ton ha^{-1}) of each crop could be determined individually. A combined yield of wheat and faba bean (ton ha^{-1}) was also calculated in the intercropped plots. Percentage protein content (total N multiplied by 6.38) in faba beans was determined in 2018 and in wheat in 2018–2020 using the Kjeldahl method (Latimer, 2016) at Ghent University, Belgium. In 2018–2019, shortly after harvest and milling, the percentage moisture in wheat was determined in a cereal drying oven at Wageningen University and Research, The Netherlands. The land equivalent ratio (LER) was calculated by adding up the partial land equivalent ratios (PLER) of wheat and faba bean yield to determine whether intercropped plots overall yielded better or worse than monocultures (Bedoussac et al., 2015; Willey & Osiru, 1972). The LER was calculated as follows:

$$\begin{aligned}\text{LER} &= \frac{\text{intercropped plot wheat yield}}{\text{mean wheat monoculture yield}} \\ &+ \frac{\text{intercropped plot faba yield}}{\text{mean faba monocolture yield}} \\ &= \text{PLER wheat} + \text{PLER faba},\end{aligned}$$

where an LER of >1 indicates over yielding and an LER <1 indicates under yielding relative to monocultures. In other words, an LER >1 indicates that a greater area of land would be needed to grow the respective monocultures to produce the same total yield than when the crops are intercropped.

2.6 | Statistical analyses

All response variables were analyzed using general linear mixed effects models using R software (R Core Team,

2020) with the packages lme4/lmerTest (Bates et al., 2015; Kuznetsova et al., 2017). Wheat cultivars (Lavett and Quintus), faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) and year (growing seasons 2018, 2019, and 2020; when variables were measured in more than 1 year; see Materials and Methods and analysis of variance [ANOVA] table footnotes for details) were considered fixed effect and block was considered a random effect. When a wheat response variable was considered, ANOVAs were conducted to detect differences between the monocultures of the two wheat cultivars and their responses when intercropped with each faba bean cultivar across years. This means that the categories of the fixed factor "wheat" were: Lavett monocultures, Quintus monocultures, and then each of the wheat cultivars grown in pairs with each of the six faba bean cultivars (resulting in 14 categories). Similarly, faba bean cultivar response variables from monocultures were compared to responses when grown intercropped with each of the two wheat cultivars across years. This means that the categories of the fixed factor "faba bean" were: monocultures of each of the six faba bean cultivars and then each of the faba bean cultivars grown in pairs with each of the two wheat cultivars (resulting in 18 categories). All interactions between wheat cultivars, faba bean cultivars and years were included in the models.

Restricted maximum likelihood estimation was used to produce an unbiased estimate of variation and covariation between and within blocks (Patterson & Thompson, 1971) and Kenward–Roger degrees of freedom approximation was used to reduce bias introduced by a relatively small sample size (Kenward & Roger, 1997). When significant effects were detected between treatments, data were subjected to posthoc tests (Day & Quinn, 1989) using the emmeans/multcomp packages in R (Hothorn et al., 2012; Lenth, 2019) with Tukey HSD (honestly significant difference) adjustment for multiple comparisons. All data were transformed as necessary to meet the model assumptions (see ANOVA tables for details). Wheat height and senescence data from 2020 and brown rust data from 2019 were dropped from further analyses due to missing data points.

3 | RESULTS

3.1 | Morphological characteristics

Intercropping interactions between cultivars had very limited effects on wheat and faba bean morphological characteristics. The full results of the ANOVAs, degrees of freedom, and means ± standard errors for wheat morphological characteristics can be found in Tables 1, S2, and S3, respectively, and for faba bean morphological characteristics can be found in Tables 2, S4, and S5, respectively. There was a significant

TABLE 1 Results of analysis of variance (ANOVAs) on the effects of intercropping different wheat cultivars (Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to wheat monocultures across 3 years (2018, 2019, and 2020) and their interactions on wheat morphology, disease presence, and yield quantity and quality.

	Ear development[a]	Senescence[a,c,d]	Plant height[a,c,d]	Brown rust[a,c,e]	Yellow rust[a]	*Fusarium* spp.[a,c,e]	Moisture content[b,c,d]	Protein content	Yield (ton ha^{-1})[a]
Wheat cultivar (W)	23.6 (**<0.001**)	11.0 (**0.002**)	19.0 (**<0.001**)	0.7 (0.393)	2.4 (0.128)	1.2 (0.282)	0.3 (0.567)	4.6 (**0.036**)	6.6 (**0.012**)
Faba bean cultivar (F)	1.4 (0.225)	5.6 (**<0.001**)	4.1 (**0.002**)	0.7 (0.624)	1.7 (0.122)	4.5 (**<0.001**)	17.6 (**<0.001**)	19.1 (**<0.001**)	15.2 (**<0.001**)
Year (Y)	4.4 (**0.015**)	39.2 (**<0.001**)	5.6 (**0.022**)	16.3 (**<0.001**)	1.4 (0.252)	45.6 (**<0.001**)	126.3 (**<0.001**)	16.3 (**<0.001**)	12.6 (**<0.001**)
W × F	3.8 (**0.002**)	1.8 (0.112)	1.3 (0.293)	0.8 (0.596)	1.1 (0.373)	1.9 (0.104)	0.2 (0.978)	0.6 (0.739)	0.6 (0.696)
W × Y	13.5 (**<0.001**)	9.7 (**0.003**)	3.1 (0.086)	5.5 (**0.023**)	5.9 (**0.004**)	0.8 (0.389)	4.0 (0.051)	0.1 (0.917)	5.8 (**0.005**)
F × Y	3.7 (**<0.001**)	1.2 (0.335)	3.3 (**0.007**)	0.8 (0.565)	3.4 (**<0.001**)	3.1 (**0.012**)	3.1 (**0.011**)	1.6 (0.098)	2.5 (**0.007**)
W × F × Y	2.0 (**0.031**)	1.6 (0.166)	0.4 (0.891)	0.8 (0.596)	1.1 (0.405)	1.1 (0.383)	0.3 (0.917)	0.2 (0.996)	0.6 (0.805)

Note: Values shown are *F*-values (*p*-values). Significant *p*-values < 0.05 are shown in bold. Degrees of freedom can be found in Table S2.

[a]Data ln(x) transformed before analysis.

[b]Data arcsin[sqrt(x)] transformed before analysis.

[c]Measured in 2018.

[d]Measured in 2019.

[e]Measured in 2020: when no letters given, measured in all years.

TABLE 2 Results of analysis of variance (ANOVAs) on the effects of intercropping different wheat cultivars (Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to faba bean monocultures across 3 years (2018, 2019, and 2020) and their interactions on faba bean morphology, disease presence, and yield quantity and quality.

	Plant height	Internode flowers[a,b]	Chocolate spot disease[c]	Brown rust[c]	Protein content[b]	Yield (ton ha^{-1})
Wheat cultivar (W)	24.8 (**<0.001**)	0.2 (0.853)	1.4 (0.251)	0.9 (0.417)	0.1 (0.928)	98.7 (**<0.001**)
Faba bean cultivar (F)	53.9 (**<0.001**)	81.2 (**<0.001**)	5.3 (**0.001**)	2.8 (**0.034**)	21.1 (**<0.001**)	34.4 (**<0.001**)
Year (Y)	65.1 (**<0.001**)	NA	NA	NA	NA	46.3 (**<0.001**)
W × F	1.4 (0.197)	0.7 (0.716)	4.1 (**<0.001**)	0.6 (0.829)	0.8 (0.615)	0.8 (0.614)
W × Y	2.3 (0.067)	NA	NA	NA	NA	2.5 (**0.046**)
F × Y	2.0 (**0.042**)	NA	NA	NA	NA	4.6 (**<0.001**)
W × F × Y	1.0 (0.489)	NA	NA	NA	NA	2.0 (**0.020**)

Note: Values shown are *F*-values (*p*-values). Significant *p*-values < 0.05 are shown in bold. Degrees of freedom can be found in Table S4. NA, not applicable.
[a]Data ln(x) transformed before analysis.
[b]Measured in 2018.
[c]Measured in 2020: when no letters given, measured in all years.

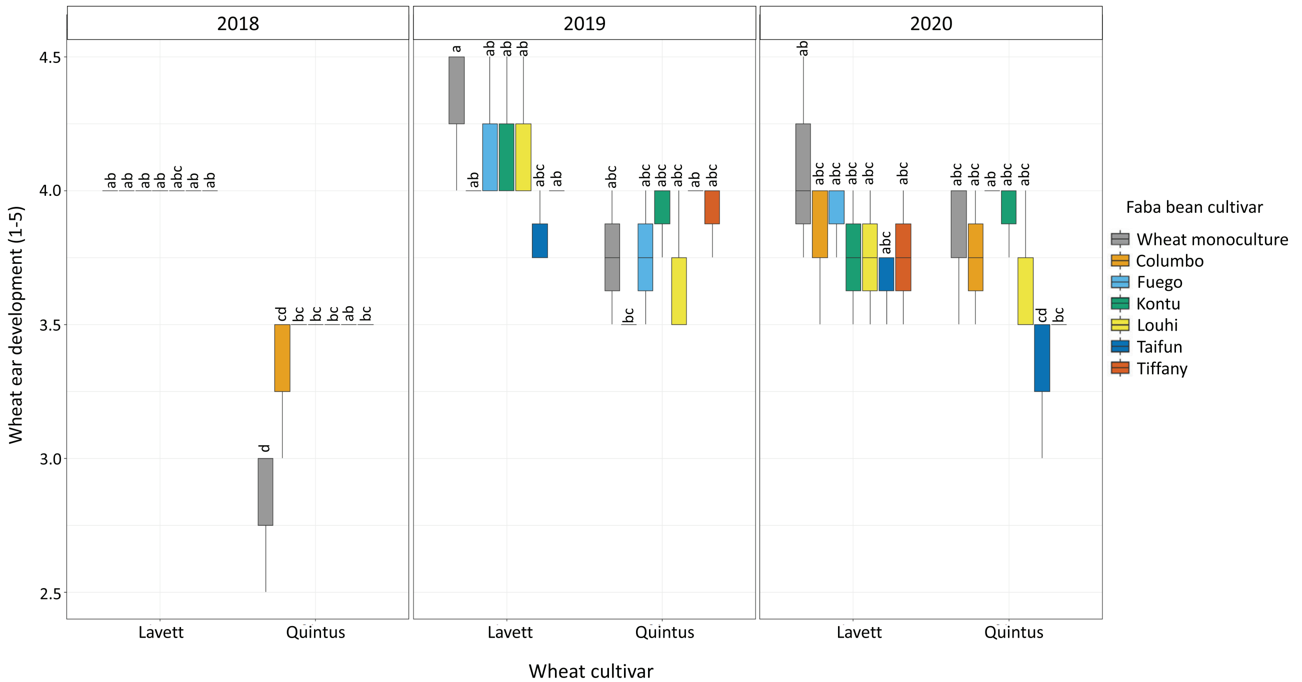

FIGURE 1 The effect of intercropping different wheat cultivars (Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to wheat monocultures across years (2018, 2019, and 2020) on wheat ear development (adaptation of Zadoks scale: 1 = flag leaf extending, 2 = ear visibly developing in flag leaf, 3 = flag sheath opening; first awns visible, 4 = ear emerging, 5 = ear fully emerged). Across all years, groups of bars topped with different lowercase letters differ at $p \leq 0.05$ (Tukey's honestly significant difference). Bars show the first and third quartiles above and below the medians, respectively (i.e., line inside each bar), the minimum and maximum values (i.e., tips of whiskers) and the outliers (i.e., dots outside whiskers). Analysis of variance (ANOVA) results and degrees of freedom are shown in Tables 1 and S2, respectively.

wheat cultivar × faba bean cultivar × year interactive effect on wheat ear development (Table 1) because in Quintus wheat ear development was slower in monocultures versus intercropped plots in 2018 (except when intercropped with Columbo), but this effect disappeared in 2019 and 2020 (Figure 1). In 2020, Quintus grown with Fuego showed faster ear development than when grown with Taifun, but since this was based on a single data point, this effect cannot be robustly assessed (Figure 1). There was a significant faba bean intercrop × year interactive effect on wheat plant height (Table 1). Overall, compared to monocultures, intercropped wheat plants of both cultivars grew ~6 cm taller, but only in 2018 (Table S3). Differences in faba bean height in monoculture and intercrops were detected (Table 2), with plants ~8 cm shorter in the latter (Table S5), but these differences could not be assessed with posthoc tests due to missing data points and resultant rank deficiency in the statistical models. There was a significant faba bean cultivar × year interactive effect on the senescence of wheat plants (Table 1). Senescence was faster in both wheat cultivars in both 2018 and 2019 when grown in monoculture versus when intercropped with Columbo, Fuego, or Kontu (Table S3). Overall, faba bean internode flowers were not affected by interactions between wheat cultivars (Table 2).

3.2 | Disease severity

Intercropping had some effects on wheat and faba bean disease severity. The full results of the ANOVAs, degrees of freedom, and means ± standard errors for wheat disease severity response variables can be found in Tables 1, S2, and S3, respectively, and for faba bean disease severity response variables can be found in Tables 2, S4, and S5, respectively. There was a significant wheat intercropping × faba bean cultivar interactive effect (Table 2) because severity of chocolate spot disease (*Botrytis fabae*) in faba bean was higher in the cultivar 'Louhi' when grown in monoculture versus intercropped plots, but no other differences between wheat–faba bean cultivar combinations were detected (Table S5). There was a significant faba bean cultivar × year interactive effect on wheat *Fusarium* spp. severity (Table 1). There was a higher number of plants showing signs of infection in 2018 in monocultures versus Kontu and Tiffany intercrops and Columbo intercrops versus Fuego, Kontu, Taifun, and Tiffany, but these differences disappeared in 2020, likely because *Fusarium* spp. occurrence was so low in 2020 (Table S3). There was a significant faba bean cultivar × year interactive effect on wheat yellow rust (Table 1). In 2018, wheat yellow rust severity was lower in monoculture versus all intercropped plots, except in plots where wheat was planted with Columbo (Figure 2). These differences disappeared in 2019 and 2020 (Figure 2). Further, wheat yellow rust was lower when intercropped with 'Tiffany' in 2019 versus 2018, but this effect was not found in 2020 (Figure 2). Wheat brown rust (Table 1) and faba bean brown rust (Table 2) severity were not affected.

3.3 | Yield quantity and quality

Intercropping had some significant effects on yield quality and quantity, wheat yield, and LER for wheat and faba bean. The full results of the ANOVAs, degrees of freedom, and means ± standard errors for wheat yield quantity and quality response variables can be found in Tables 1, S2, and S3, respectively, and for faba bean quantity and quality response variables can be found in Tables 2, S4, and S5, respectively. The ANOVA results, degrees of freedom, and means ± standard error for LER and total yield can be found in Tables 3, S6, and S7, respectively. There was a significant faba bean cultivar × year interactive effect on wheat percentage moisture. In 2018, wheat percentage moisture was just under 1% higher in monoculture plots versus those intercropped with Kontu, but in 2019 wheat percentage moisture in monocultures was slightly over 1% higher compared to when wheat was intercropped with any faba bean cultivar combination (Table S3). Wheat protein content was significantly affected by faba bean intercropping (Table 1) because in both wheat cultivars protein content was lower in monocultures versus all faba bean intercropped cultivar combinations; ~9.9% versus 12.2% (Table S3). A significant faba bean cultivar × year interactive effect on wheat yield was detected (Table 1). In 2018, wheat yield in monocultures was higher than when intercropped with Fuego or Tiffany (Figure 3). In 2019, wheat monoculture yielded higher than all intercropped combinations and in 2020, monocultures only yielded higher than intercrops with Louhi (Figure 3). There was a significant wheat cultivar × faba bean cultivar × year interaction on faba bean yield (Table 2) because in 2019, yield of the faba bean cultivars Columbo, Louhi, and Kontu was higher in monoculture versus Quintus intercropped plots and the yield of Kontu was also higher in monoculture versus Lavett intercropped plots, but this effect did not manifest in 2018 or 2020 (Figure 4). Instead, in 2020, Fuego yield was higher in monoculture versus Quintus intercropped plots (Figure 4). In 2020, Louhi grown with Lavett showed a lower yield compared to Louhi grown in monoculture, but since this finding was based on a single data point, this effect cannot be robustly assessed. The LER only differed between years and was never affected by interactions between cultivars (Table 3). There was a significant wheat cultivar × faba bean cultivar effect on total yield (i.e., wheat plus faba bean combined; Table 3) because total yield was always lower in faba bean monocultures versus the corresponding intercropped paired plots (i.e., faba bean cultivar monoculture compared to plots where the same cultivar was paired with one of the wheat cultivars), but no differences were detected between wheat monocultures versus the corresponding intercropped paired plots (Figure 5). Further, when the faba bean cultivars Fuego and Tiffany were grown with Quintus, the total yield was higher compared to plots with monocultures of Lavett or in plots where Lavett was intercropped with Columbo, Kontu, or Louhi (Figure 5).

4 | DISCUSSION

Here, we explored the interactive effects of intercropping different wheat–faba bean cultivar combinations on crop

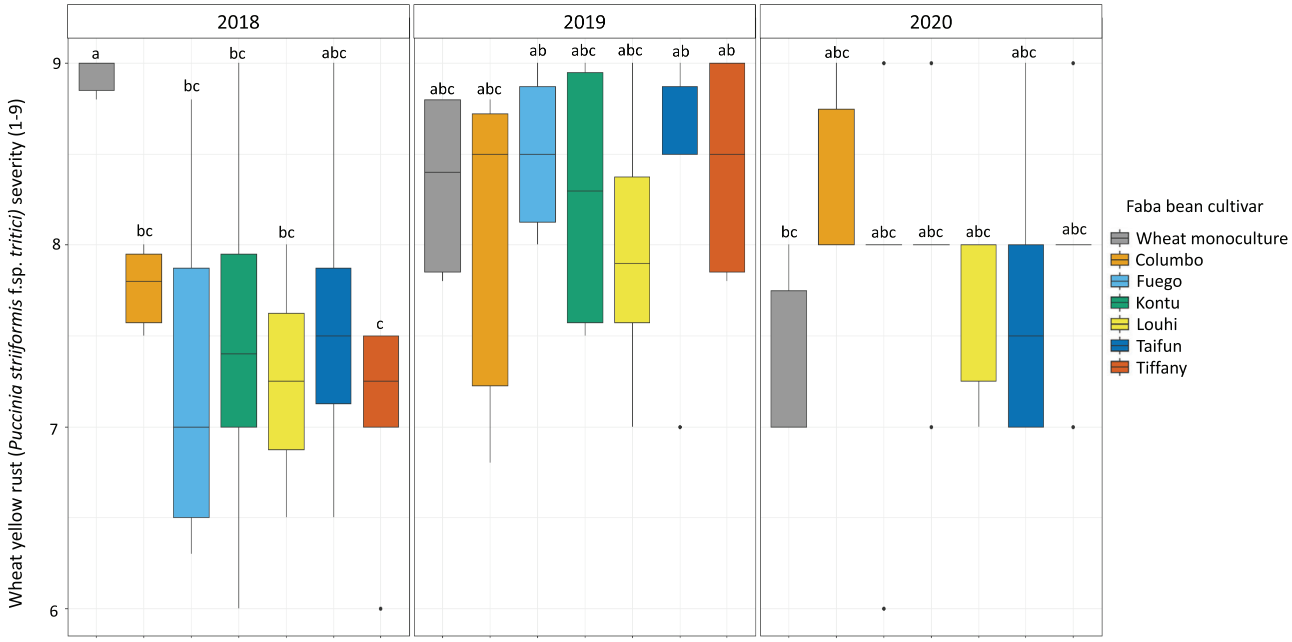

FIGURE 2 The effect of intercropping wheat (averaged across the two cultivars, Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to wheat monocultures across years (2018, 2019, and 2020) on wheat yellow rust (*Puccinia striiformis* f.sp. *tritici*) severity (scale 1–9: 1 = dead due to infection, 9 = no sign of infection). Across all years, groups of bars topped with different lowercase letters differ at $p \leq 0.05$ (Tukey'shonestly significant difference). Bars show the first and third quartiles above and below the medians, respectively (i.e., line inside each bar), the minimum and maximum values (i.e., tips of whiskers) and the outliers (i.e., dots outside whiskers). Analysis of variance (ANOVA) results and degrees of freedom are shown in Tables 1 and S2, respectively.

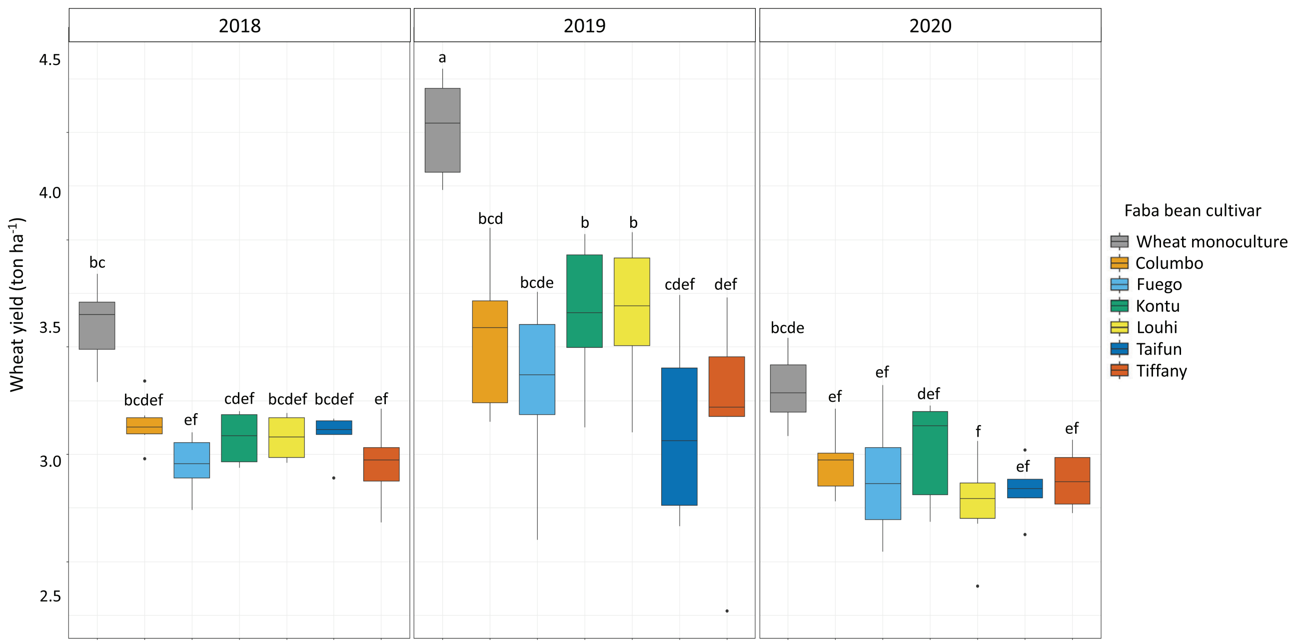

FIGURE 3 The effect of intercropping wheat (averaged across the two cultivars, Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to wheat monocultures across years (2018, 2019, and 2020) on wheat yield. Across all years, groups of bars topped with different lowercase letters differ at $p \leq 0.05$ (Tukey's honestly significant difference). Bars show the first and third quartiles above and below the medians, respectively (i.e., line inside each bar), the minimum and maximum values (i.e., tips of whiskers) and the outliers (i.e., dots outside whiskers). Analysis of variance (ANOVA) results and degrees of freedom are shown in Tables 1 and S2, respectively.

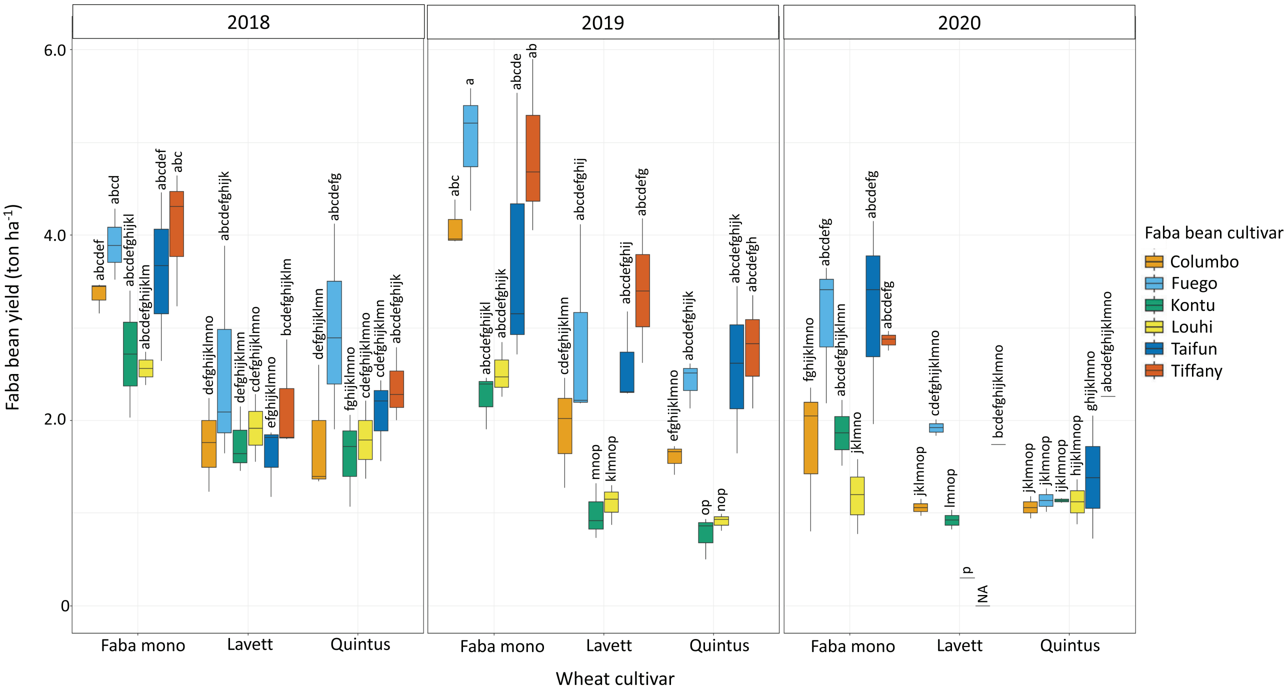

FIGURE 4 The effect of intercropping different wheat cultivars (Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to faba bean monocultures across years (2018, 2019, and 2020) on faba bean yield. Across all years, groups of bars topped with different lowercase letters differ at $p \leq 0.05$ (Tukey's honestly significant difference). Bars show the first and third quartiles above and below the medians, respectively (i.e., line inside each bar), the minimum and maximum values (i.e., tips of whiskers) and the outliers (i.e., dots outside whiskers). Analysis of variance (ANOVA) results and degrees of freedom are shown in Tables 2 and S4, respectively. Faba mono, faba bean monocultures.

TABLE 3 Results of analysis of variance (ANOVAs) on the effects of intercropping different wheat cultivars (Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to wheat and faba bean monocultures across 3 years (2018, 2019, and 2020) and their interactions on the land equivalent ratio (LER) and total yield (wheat and faba bean combined). Values shown are F-values (*p*-values). Significant *p*-values (<0.05) are shown in bold. Degrees of freedom can be found in Table S6.

	LER[a]	Total yield
Wheat cultivar (W)	1.1 (0.304)	197.9 (**<0.001**)
Faba bean cultivar (F)	0.6 (0.719)	19.0 (**<0.001**)
Year (Y)	26.9 (**<0.001**)	115.4 (**<0.001**)
W × F	0.5 (0.790)	2.0 (**0.035**)
W × Y	0.9 (0.395)	1.7 (0.153)
F × Y	1.2 (0.296)	2.5 (**0.006**)
W × F × Y	1.2 (0.324)	0.7 (0.800)

Note: Values shown are *F*-values (*p*-values). Significant *p*-values < 0.05 are shown in bold. Degrees of freedom can be found in Table S6.
[a]Data ln(x) transformed before analysis.

morphology, disease severity, and yield quality and quantity in an organic cultivation system over 3 years. Of the morphological characteristics, wheat ear development was slower in monocultures of Quintus in 2018, but this effect disappeared in 2019 and 2020 and both wheat cultivars senesced faster when grown in monocultures versus in certain faba bean intercrop combinations. In both wheat cultivars, *Fusarium* spp. and yellow rust, disease severity was higher and lower, respectively, in monocultures compared to certain intercropped plots, but this effect varied by year. Chocolate spot in faba bean was higher in the cultivar Louhi when it was grown in monoculture versus when intercropped. Collectively, both wheat cultivars in monoculture sometimes outperformed wheat–faba bean intercropped cultivar combinations, but this effect varied by year. Faba bean yield was higher in monoculture for certain cultivars (e.g., Columbo,

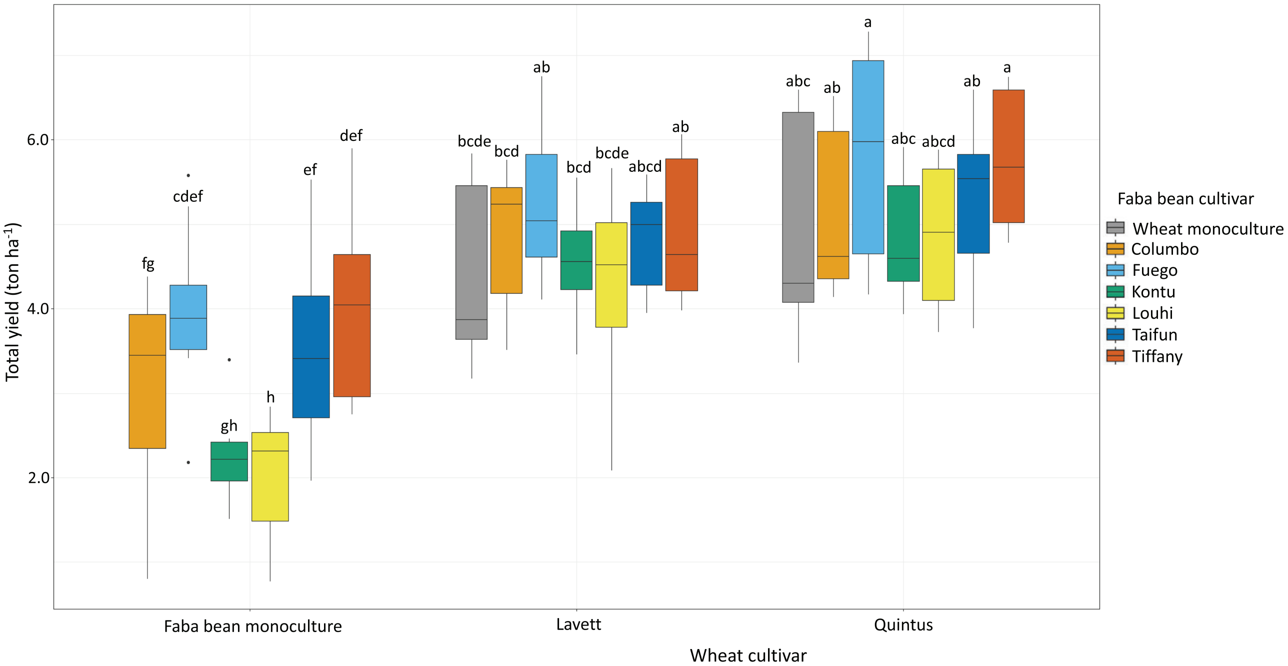

FIGURE 5 The effect of intercropping different wheat cultivars (Lavett and Quintus) with different faba bean cultivars (Columbo, Fuego, Kontu, Louhi, Taifun, and Tiffany) in comparison to wheat and faba bean monocultures across years (2018, 2019, and 2020) on total yield in faba bean and wheat monocultures and intercropped plots. Groups of bars topped with different lowercase letters differ at $p \leq 0.05$ (Tukey's honestly significant difference). Bars show the first and third quartiles above and below the medians, respectively (i.e., line inside each bar), the minimum and maximum values (i.e., tips of whiskers) and the outliers (i.e., dots outside whiskers). Analysis of variance (ANOVA) results and degrees of freedom are shown in Tables 3 and S6, respectively.

Fuego, Louhi, and Kontu), but this effect was dependent on wheat cultivar and year. Total yield was nearly always lower in faba bean monocultures versus intercropped plots, but no differences were seen between wheat monocultures and plots intercropped with the same wheat cultivar, while some wheat-faba bean cultivar combinations yielded better than others. Below we discuss the potential ramifications of our findings for grain–legume intercropping systems.

4.1 | Morphological characteristics

In partial support of our hypothesis, certain morphological characteristics were affected by intercropping in a cultivar-specific manner. Wheat ear development in Quintus was slower in monocultures versus intercropped plots (with the exception of Columbo) in 2018, but this effect did not manifest in 2019 or 2020. This may have been due to the exceptionally wet and warm weather in May 2018 (Table S1), which could have facilitated wheat ear development in intercropped plots due to higher N availability caused by enhanced faba bean-*Rhizobium* spp. symbioses (Neugschwandtner et al., 2015). In 2018 and 2019, both wheat cultivars senesced faster in monocultures than when intercropped with Columbo, Fuego, and Kontu. Rapid ear development and delayed senescence in wheat and faba bean intercropped stands could help synchronize harvest time when specific cultivar combinations are considered, which is important for improving efficiency in intercropping systems (Carr et al., 1995; Horwith, 1985). However, this remains to be tested for these specific wheat-faba bean cultivar combinations. Further, although the height of the wheat and faba bean plants did not change based on interactions between cultivars, both wheat cultivars were shorter (in 2018) and all cultivars of faba bean were taller in monocultures versus intercropped plots across all years. Faba bean plants grew taller to better procure resources to bolster seed set, likely because they were not being outcompeted by wheat (Aziz et al., 2015). On the other hand, wheat plants may have grown taller when intercropped due to favorable climatic conditions in 2018, which led to higher nitrogen input from faba beans, as mentioned above. These differences in height may have been partially responsible for the generally higher yield in both wheat and faba bean monocultures versus intercrops (but see below for discussion on the influence of faba bean and wheat cultivar and year interactions on faba bean yield).

These findings highlight the need to select crops and cultivars with appropriate height combinations to achieve the desired yield outcomes (Elmore & Jackobs, 1984; Raouf et al., 2003). However, wheat in monocultures may have grown shorter and yielded more because sowing density of wheat in monocultures was higher versus intercropped plots (i.e., 300 versus 100 seeds m^{-2}). Future studies should carry out measurements on morphological traits at multiple time points per growing season and seek to disentangle how intercropping effects on morphological characteristics of specific cultivars could lead to differences in yield quantity and quality.

4.2 | Disease severity

Our hypothesis regarding the effects of intercropping and wheat–faba bean cultivar combinations on disease severity was partially supported. Chocolate spot disease severity in the cultivar 'Louhi' was higher when grown in monoculture versus intercropped plots, which aligns with other work that has shown intercropping can suppress chocolate spot disease in faba bean (Sahile et al., 2008; Zhang et al., 2019). This effect was consistent across both wheat cultivars, indicating that intercropping this specific faba bean cultivar with wheat could effectively suppress chocolate spot disease in practice, regardless of wheat cultivar. Farmers should consider this pairing in future intercropping planting schemes. However, brown rust infection severity in faba bean was cultivar-specific, with no influence of intercropping with wheat detected. This contrasts the results of a recent meta-analysis by Zhang et al. (2019), where a marginally significant suppression of brown rust in faba bean was detected in intercropped plots. It is possible that the traits of the wheat cultivars considered here were not appropriate to change microclimate, spore dispersal or faba bean structural or chemical defense in any meaningful way that would result in disease suppression (Boudreau, 2013).

Further, wheat plants showing *Fusarium* spp. infection were more numerous in monocultures compared to some wheat–faba bean intercrop cultivar combinations (but this effect varied by year). Dispersal and subsequent infection of air-borne diseases such as chocolate spot and *Fusarium* spp. (the latter is also spread via water-splashed macroconidia) are thought to be (partially) inhibited due to changes in stand density in intercropped fields (Boudreau, 2013). In contrast, wheat yellow rust was lower in monocultures versus all wheat–faba bean intercropped plots, except when planted with Columbo, but this effect only appeared in 2018. Changes in root exudation patterns and rhizosphere interactions wrought by Columbo may have fostered enhanced systemic resistance in wheat (Doornbos et al., 2012; Olanrewaju et al., 2019). Certain morphological traits inherent to Columbo not measured here such as canopy density or leaf size could have affected the microclimate within the plot (Castro et al., 1991; Enikuomehin et al., 2010; Fernández-Aparicio et al., 2010; Guo et al., 2021). Given that these suppressive effects were dependent on year, it is likely that weather may have played a role. The drier May of 2018 may have hindered the development of yellow rust in wheat monocultures and when intercropped with Columbo (Enikuomehin et al., 2010; Fininsa & Yuen, 2002; Te Beest et al., 2008; but see Schoeny et al. (2010)). Collectively, these findings suggest that although disease suppression benefits can be realized in wheat–faba bean intercropping systems, these benefits are not always consistent between years and cultivars and certain diseases may actually proliferate. Therefore, careful consideration must be given to cultivar identity and target disease suppression when designing wheat–faba bean intercropping systems.

4.3 | Yield quality and quantity

Yield quality and quantity were sometimes affected by different wheat–faba bean cultivar combinations and/or their interactions with year. Both wheat cultivars had higher grain protein content when intercropped with all faba bean cultivars compared to monocultures, which supports the purported benefits of intercropping with faba bean due to additional atmospheric N fixation (Bulson et al., 1997; Gooding et al., 2007) and improved soil structure that allows for easier rooting and thereby resource acquisition of companion crops (Rochester et al., 2001; Streit et al., 2019). Faba bean has one of the highest N fixation rates amongst leguminous crops, which, combined with our results, suggests that it is an ideal crop to improve companion crop protein content, possibly leading to reduced N fertilizer inputs (Jensen et al., 2010). However, wheat yield was generally higher in monocultures, which contrasts other studies (Bedoussac & Justes, 2010; Li et al., 2001). As mentioned above, this may have purely been the result of higher wheat sowing densities in monoculture versus intercropped plots and pulls focus on the need to adjust seeding densities to optimize intercropping systems (Seran & Brintha, 2010). A mismatch between wheat and faba bean cultivar traits may have also decreased wheat yield in intercropped plots, possible leading to excessive competition for light or moisture (Aziz et al., 2015).

Similarly, certain faba bean cultivars yielded more in monocultures in 2019 and 2020, which aligns with previous findings (Fan et al., 2006; Song et al., 2007; Xiao et al., 2021). In part, this may have been due to the drier weather in the early months of the growing season (i.e., May and June) in 2018 relative to 2019. This could also signal a mismatch in morphological traits (e.g., height) between the wheat and faba bean cultivars considered here (Ajal et al., 2021; Nelson et al., 2021) or unfavorable interactions between cultivar morphology and soil nutrient availability (Berghuijs et al., 2020). However, usually faba bean yield did not differ between monoculture versus intercropped plots. This finding has been shown in other studies and is likely the result of trade-offs between facilitation and competition that cancel one another out (Glaze-Corcoran et al., 2020). Given that the effects of intercropping on yield varied by year and cultivar, the need to consider species and cultivar combinations and following yield assessments across multiple growing seasons with varying weather conditions is imperative.

Total yield was higher in most intercropped plots compared to faba bean monocultures, due almost entirely to the addition of wheat and not because faba bean yield increased. No differences in total yield were observed when comparing wheat cultivar monocultures to corresponding intercropped plots, but certain Quintus-faba bean cultivar combinations yielded higher than Lavett monocultures and certain Lavett-faba bean cultivar combinations. This is perhaps unsurprising, given that cultivation of 'Lavett' has been phased out in favor of its descendent, Quintus, due to higher yield in the latter (Nuijten, 2019). Finally, although the LER was not affected by interactions between cultivars and year, it was always above 1, which indicates that in order to produce the same yield per unit area of an intercropped plot, a greater unit area of land would be required. In this instance, intercropping appears to be overall more efficient compared to monocultures, independent of cultivar, which broadly aligns with the findings of other studies on grain-legume intercropping (Aziz et al., 2015; Glaze-Corcoran et al., 2020). In general, this indicates that intercropping wheat and faba bean is a more efficient use of land than growing each crop in monocultures and that these benefits are stable over multiple growing seasons with varying weather conditions. This practice should be adopted by farmers whenever possible.

5 | CONCLUSIONS

We found that intercropping different cultivars of wheat and faba bean across multiple years resulted in mixed effects on crop morphology, diseases severity, and yield quality and quantity. The effects varied between positive, negative, and neutral, indicating a highly context-specific response to intercropping. Even though interactions between wheat–faba bean cultivar combinations did not influence the LER, it was always higher than one, indicating that wheat–faba bean cultivar systems can result in increased yield efficiency independent of cultivar. Taken together, these results highlight that, dependent on the desired benefits, careful selection of cultivars is necessary when designing wheat–faba bean intercropping systems. Specifically, disease suppression varied by cultivar, but LER showed consistently beneficial yield effects independent of cultivar, suggesting that when yield alone is considered, intercropping wheat with faba bean is a better choice than monocultures. Seasonal variation also played a strong role in determining effects, indicating that weather determines the benefits or losses of intercropping. Regional climatic patterns should be taken into account when considering wheat–faba bean intercropping, especially as climate change advances. It also is not known how different soil types could influence the outcomes observed here and future studies should integrate this point. Seeding density discrepancies in wheat monocultures versus intercropped plots could have also played a roll, meaning that some conclusions, specifically regarding plant height and yield, should be interpreted cautiously. As the pressure to develop sustainable agricultural solutions increases, further research should focus on how breeding programs can develop cultivars with the traits required to maximize benefits from intercropping systems across different climates, fertilization regimes, and sowing and harvest dates.

AUTHOR CONTRIBUTIONS

Jonathan R. De Long: Data curation; formal analysis; validation; visualization; writing—original draft, writing—review and editing. **Floor van Malland**: Data curation; investigation; methodology; writing—review and editing. **Abco de Buck**: Conceptualization; funding acquisition; investigation; writing—review and editing. **Merlijn van den Berg**: Data curation; investigation; methodology; writing—review and editing.

CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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