Optimal species proportions, traits and sowing patterns for agroecological weed management in legume-cereal intercrops

Pierre Lebreton, Laurent Bedoussac, Catherine Bonnet, Etienne-Pascal Journet, Eric Justes, Nathalie Colbach

European Journal of Agronomy 159 (2024) 127266

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Optimal species proportions, traits and sowing patterns for agroecological weed management in legume–cereal intercrops

Pierre Lebreton [a], Laurent Bedoussac [b], Catherine Bonnet [c,d], Etienne-Pascal Journet [c,e], Eric Justes [c,1], Nathalie Colbach [a,*]

[a] Agroécologie, INRAE, Institut Agro, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, Dijon F–21000, France
[b] AGIR, Univ Toulouse, ENSFEA, INRAE, Castanet-Tolosan, France
[c] AGIR, Univ Toulouse, INRAE, Castanet-Tolosan, France
[d] current address: DYNAFOR, Univ Toulouse, INRAE, Castanet-Tolosan, France
[e] LIPME, Univ Toulouse, CNRS, Castanet-Tolosan, France

ARTICLE INFO

Keywords:
Intercrop
Weed
Model
Yield loss
Yield gap
Sowing pattern
Sowing density
Species trait
Agroecology

ABSTRACT

Intercropping, i.e., growing several species in the same field for a major part of their growing periods, often improves yield and weed control, but their performance greatly varies across situations. The aim of this study was to evaluate the effects of bi-species legume–cereal intercrops on weed dynamics and their impact on crop production, in the absence of nitrogen or water stress, via simulations with FlorSys. This individual-based 3D model simulates daily crop–weed seed and plant dynamics over the years, from cropping system and pedoclimate, focusing on competition for light. The study tested seven species proportions in two species mixtures (wheat–faba bean and barley–pea) and nine spatial sowing patterns in three species mixtures (triticale–faba bean, wheat–faba bean, wheat–pea), in both cases comparing the intercrops with the corresponding sole crops (controls). Intercrops and controls were inserted into rotations and simulated over 30 years and repeated with 10 climate scenarios from South-Western France, either with or without weeds. The simulations showed that: (1) the intercrops that best controlled weeds were barley–pea and triticale–faba bean, (2) the spatial pattern alternating one cereal row with one legume row as well as the 67 %-cereal–33 %-legume and 100 %-cereal–50 %-legume species proportions were those that maximised yields and minimised losses due to weeds, (3) the weed biomass in intercrop was greater than or equal to that of the sole cereal, and less than that of the sole legume, and (4) legumes benefitted more from intercropping than cereals because cereals are more competitive against weeds. Intercrop yield was best when combining species with contrasting shading responses (etiolated with stockier plants, leafy with stemmier plants) but early and good plant emergence was essential, particularly for weed suppression.

1. Introduction

Weeds are very harmful to crop production (Oerke, 2006) but provide ecosystem services such as trophic resources for pollinators or better physical soil properties (Blaix et al., 2018). As herbicide use must be reduced because of environmental and health issues, we need new weed management strategies that replace the highly efficient and easy-to-use herbicides. For this, it is necessary to combine multiple and mostly preventive management techniques, which, individually, are only partially effective (Liebman and Dyck, 1993; Liebman and Gallandt, 1997). Among these techniques, crop diversification plays a key role, both in time (cover crops, crop succession) and in space (variety mixtures, intercropping, crop pattern in the landscape) (Weisberger et al., 2019). Among the different types of intercropping – several species cultivated in the same field for a major part of their growing periods – mixtures of two annual arable crops are the most widespread and their many advantages have been demonstrated notably for yield (Kiær et al., 2009; Bedoussac et al., 2015; Raseduzzaman and Jensen, 2017), land and resource use efficiency (Pelzer et al., 2014; Xu et al., 2020) and weed control (Verret et al., 2017; Gu et al., 2021). These

* Corresponding author.
E-mail address: Nathalie.Colbach@inrae.fr (N. Colbach).
[1] Current address: CIRAD, Persyst Department, Montpellier, France.

https://doi.org/10.1016/j.eja.2024.127266
Received 30 April 2024; Received in revised form 18 June 2024; Accepted 23 June 2024

benefits are assumed to result from the final balance of competition, complementarity, cooperation, and compensation between the species as named "the 4 C approach" by Justes et al. (2021) which ensure a higher resource capture compared to sole crops, thereby hampering weed growth (Liebman and Dyck, 1993; Corre-Hellou et al., 2011).

Studies on intercrops or weeds are usually based on field experiments or surveys of farmers' fields. Despite the undeniable advantages of these approaches, they suffer from severe limitations when it comes to investigating yield loss due to weeds (Colbach et al., 2020b). Notably, they often disregard long-term effects even though weed seeds survive for many years in the soil (Lewis, 1973). This weed seed bank makes weed management particularly difficult as today's operations will also have an impact on future crops when weed seeds emerge from the soil (those that survived these operations or that were produced by plants surviving the operations). Moreover, field studies usually investigate intercrops in a single pedoclimate and floristic context even though those contexts significantly influence weed dynamics and cropping-system performance. Meta-analyses attempt to overcome this limitation to the detriment of process analysis. Another solution is to extrapolate existing field experiments through simulations, notably with process-based models (Colbach et al., 2020b). This approach allows testing cropping-system prototypes designed by experts such as farmers or scientists (Colbach et al., 2021). Simulations can test more factors (and their interactions) and systems over longer durations than field experiments, with (1) different contexts (soils, climate, weed floras etc), (2) faster results and (3) in the case of mechanistic (process-based) models, an easier access to a great number of state variables for understanding the causes of the simulated effects. The latter is particularly interesting when aiming to investigate the 4 C processes proposed to understand intercropping (Justes et al., 2021).

The present study applied such a model-based approach to investigate the performance of different species combinations, species proportions and sowing patterns of annual–cereal–legume intercrops. Performance was evaluated in terms of yields and competitivity against weeds, discriminating tolerance to weeds, i.e., the ability to produce a higher crop yield or a lower yield loss in the presence of weeds (e.g., Lemerle et al., 2006), and weed suppression, i.e., the ability of a crop to reduce weed biomass and/or weed seed production (e.g., Mason et al., 2007). The study also aimed to identify the key crop species traits that drive potential yield, weed tolerance and weed suppression in intercrops. The evaluated intercrops and cropping systems originated from field experiments and participatory workshops with farmers to account for their contraints and questions and work with realistic cropping systems.

The model used for the simulations was the process-based FlorSys, which is a virtual field on which weed seed banks and crop–weed canopies grow, reproduce and survive at a daily time-step over several years or decades, depending on crop management and weather (Colbach et al., 2021). FlorSys is to date the most complete crop–weed model in terms of the range and precision of arable crop management techniques (Section 2.3.5), biophysical processes (Section 2.3.3), crop and weed species (Section 2.3.1) as well as weed impacts on crop production and biodiversity (Section 2.3.6) (Chantre and González-Andújar, 2020; Colbach et al., 2021). FlorSys particularly presents many of the features required to model intercrops and heterogeneous multispecies canopies, i.e., a 3D individual-based representation of the canopy (Gaudio et al., 2019) and the most important of Justes et al.'s (2021) 4C processes (see details in Section 2.3.4). The model also includes the effects of management variables (Section 2.3.5), among which sowing density. The latter is essential to discriminate the effects of the 4 C processes from that of changes in sowing densities.

2. Material and method

2.1. Principle

The study tested seven species proportions in two annual cereal–legume intercrops and nine spatial sowing patterns in two separate experimental designs, with several species combinations per design. The first design was also tested with two options of mechanical weeding to evaluate crop damage and weed suppression. The intercrops were inserted into cropping systems which were based on rotations and management plans designed during participatory workshops with farmers to make the systems realistic and adapted to farmers' production contexts (Section 2.2). In both designs, each intercrop was compared with its two corresponding sole crops (controls), without any other changes in the rotation, to assess yield gaps due to intercropping. Intercrops and controls were simulated over 30 years with the virtual-field model FlorSys (Section 2.3) to account for long-term effects resulting from the weed seed bank, and repeated with 10 climate scenarios acting as repetitions (Section 2.4.1). Simulations were run either with or without weeds to compute weed impacts on crop production (Section 2.3.6). To go beyond the limited number of species combinations tested here, a trait analysis was carried out to link species and intercrop traits to intercrop performance (Section 2.4.3).

2.2. Data origin and simulation plans

Two datasets were created based on cropping systems with annually intercrops co-designed during the Reduce (www.inrae.fr/actualites/reduce-projet-reduire-lusage-pesticides-agriculture) and Micmac projects (Bonnet et al., 2021) by farmers and researchers in participatory workshops and then conducted on the INRAE Toulouse-Auzville experimental station. Based on these systems, we designed two simulation plans to study the effects of species proportions in the intercrops (hence "species proportions" design), and of spatial sowing patterns (hence "sowing patterns" design).

2.2.1. The "Species proportions" design

The systems adapted from Reduce were based on a four-year rotation of six cash crops, including two cereal–legume intercrops: barley (*Hordeum vulgare* L.)–pea (*Pisum sativum L.*) sown in mixed rows, and wheat (*Triticum aestivum* L.)–faba bean (*Vicia faba* L.) sown in separate rows (system I_BP_WF in section B.1 in supplementary material online). The rotation was barley–pea / camelina (*Camelina sativa* L.) / maize / wheat–faba bean / buckwheat (*Fagopyrum esculentum* Mönch) / soybean, with camelina and buckwheat grown during the same cultural years as the intercrops.

Eight additional systems were designed on that basis: four sole-crop control systems with either the cereal or the legume instead of the intercrop (C_b_w, C_w_p, C_b_f, C_p_f, labelled with the initials of the sole-crop controls) and four other rotations replacing one of the sole-crop crops with an intercrop (I_BP_w, I_b_WF, I_BP_f, I_p_WF, with lowercase and uppercase intials of the sole-crop and intercropped species, respectively). For the intercrops, seven species proportions were tested, combining sowing densities relative to sole-crop densities ranging from 33 % to 100 %, with either an additive or substitutive design (Table 1). In barley–pea intercrops, species were sown on the same row in a single sowing operation. In wheat–faba bean intercrops, species were sown intoo separate alternate rows (3 wheat rows vs 1 faba-bean row) in two successive sowing operations.

The combinations of the rotations and the species proportions resulted in 39 cropping systems (4 controls + 5 × 7 proportions). Each was tested twice, with either a rotary hoe or a tine harrow for mechanical weeding, resulting in a total of 78 systems for the "Species proportions" design. There were no herbicides. Two crops of the rotation were irrigated (camelina and soya), and the fields were mouldboard-ploughed every four years before maize (for more details, see section

Table 1
The sowing density proportions of legumes (L) and cereals (C) tested in the intercrops of the "Species proportions" design and simulated with FlorSys. Sowing densities in sole-crop crops were 36, 90, 210 and 360 seeds/m^2 for faba bean, pea, barley and wheat, respectively.

Intercrop design	Relative sowing density			Label
	Total	Cereal	Legume	
Additive	133 %	100 %	33 %	100C33L
	150 %	100 %	50 %	100C50L
	150 %	50 %	100 %	50C100L
	133 %	33 %	100 %	33C100L
Substitutive	100 %	33 %	67 %	33C67L
	100 %	50 %	50 %	50C50L
	100 %	67 %	33 %	67C33L

B.1 online).

2.2.2. The "Sowing patterns" design

The Micmac-inspired systems of the "Sowing patterns" design were based on a six-year rotation including three cereal–legume intercrops: durum wheat (*Triticum durum* Desf.)–faba bean, wheat–pea and triticale (*Triticosecale*)–faba bean (system I_all in section B.2 in supplementary material online). Soft wheat was used in the simulations instead of durum wheat, to have the same wheat–faba bean intercrop in the two simulated designs. Moreover, durum wheat is not yet parameterized in FlorSys (Section 2.3.1). The competitive abilities of soft and durum wheats are sufficiently close so that the species exchange had no impact on the competitive ability of the tested intercrops. The complete rotation was sunflower (*Helianthus annuus* L.)–soybean (*Glycine max* (L.) Merrill) / triticale–faba bean / wheat–pea / sunflower–soybean / wheat–pea / wheat–faba bean.

Eight controls were added, each replacing one intercrop by one of its constituent crops in sole crop all else being equal. Nine spatial sowing patterns were tested for the I_all intercrop (Fig. 1): eight alternated different numbers of cereal and legume rows, and the last mixed both cereals and legumes inside each row. The sowing design was substitutive: the relative sowing density of each intercropped species was 50 % of its sole-crop sowing density, and interrow width remained unchanged. Thus, the density of each species on the row varied according to the spatial pattern: as the number of rows of a species increased, its density on the row and per linear metre decreased.

In total, the "Sowing patterns" design included 18 cropping systems (1 × 9 patterns + 9 controls). Weed management relied on mechanical weeding and herbicides (details in section B.2 online).

2.3. The virtual field FlorSys

FlorSys is a virtual field on which cropping systems can be experimented with a large range of state variables describing crop, weed and environment (Gardarin et al., 2012; Munier-Jolain et al., 2013, 2014; Colbach et al., 2014a, 2014b; Pointurier et al., 2021). It has been widely used for a variety of questions (see examples in Colbach et al., 2021) and evaluated with contrasting cropping systems and pedoclimates (Section 2.3.7). Below only key information is detailed to understand the methodology used for this simulation work, further information is given in section A online.

2.3.1. The parameterized species

The model is currently parameterized for 30 frequent and contrasting annual weed species and 33 crop species, including cash crops as well as cover crop species and forage crop species, and can thus simulate intercrops (see section A.4 online). One of the crops of the "Species proportions" design, buckwheat, is not yet included in FlorSys. A similar parameterized species in terms of seasonality, growth duration and morphology was used instead (i.e., mustard, *Sinapis alba* L.). This will not have any impact on the competitive ability of the tested intercrops. Similarly, durum wheat was replaced by soft wheat in the "sowing patterns" design (Section 2.2.2).

2.3.2. Input variables

The input variables of FlorSys consist of: (1) a description of the simulated field (daily weather, latitude and soil characteristics), (2) all the crops (including intercrops, cover crops and undersown crops), (3) management operations in the field, with dates, tools and options, and (4) the initial weed seed bank, which is either measured on soil samples or estimated from regional flora assessments. Section B online lists these inputs for the two designs simulated in the present study.

2.3.3. Weed and crop life-cycle

The input variables influence the annual life cycle of annual weeds and crops, with a daily time-step. Pre-emergence stages (surviving, dormant and germinating seeds, emerging seedlings) are driven by soil structure, temperature and water potential. The crop–weed canopy is represented in 3D, with each crop and weed plant schematized as a cylinder (above ground) and another cylinder on top of a spilled cone (below ground), into which biomass, leaf area and root lengths are distributed. This is a compromise to use the same generic plant representation for any annual crop and weed species (Section 2.3.1) while being precise enough to simulate plant–plant competition for resources and to discriminate not only species but also varieties (Colbach et al., 2022).

Post-emergence processes (e.g., photosynthesis, respiration, growth,

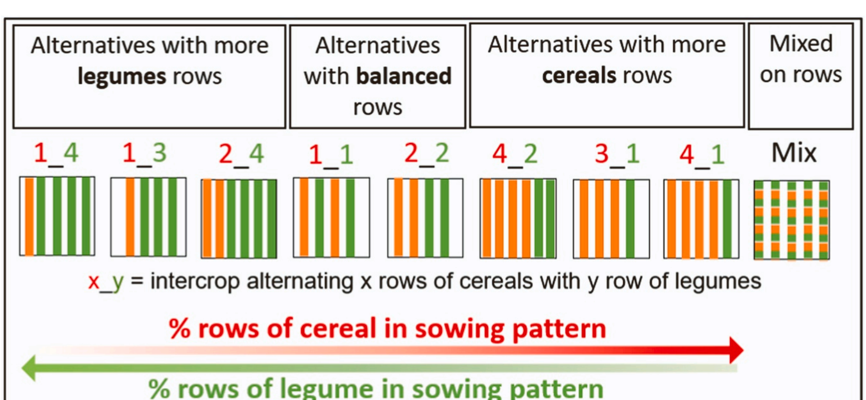

Fig. 1. The different sowing patterns tested for legume–cereal intercrops in the simulations with the "sowing patterns" design, with legume rows in green and cereal rows in orange. Note that sowing densities and interrow widths were the same, whatever the sowing patterns (Pierre Lebreton 2023).

shade response) are driven by light availability and air temperature. New biomass is allocated among plant compartments, resulting in cylinder growth and leaf area increase, depending on species and shading intensity. For instance, shaded plants tend to etiolate (i.e., increased plant height per unit biomass), their leaves become thinner and larger (i.e., increased leaf area per unit leaf biomass) and their leaf area shifts upward (see section A.3.3 online). At plant maturity, weed seeds are added to the soil seed bank while crop seeds are harvested to determine crop yield.

2.3.4. The plant-plant interactions relevant for intercropping

Nitrogen stress was disregarded in the present model version, and water stress only considered for pre-emergent processes. In other words, the present simulations considered that both nitrogen and water were non-limiting after plant emergence. Indeed, light is the resource for which weed and crop plants mostly compete in temperate arable cropping systems (Colbach et al., 2023). Despite these simplifications, the key processes for intercropping (Justes et al., 2021) are included in FlorSys. Competition happens among plants with similar spatio-temporal presence and is the result of all processes that occur when one species has a greater ability to use limiting resources. In FlorSys, plant-plant competition is limited to light. Complementarity occurs when plants grown together have different requirements for abiotic resources in space, time or form. In FlorSys, it results from considering daily emergence cohorts for each simulated species and complementary plant structures of the intercropped species in the individual-based 3D canopy.

Cooperation happens when the modification of the environment by one species is beneficial to the other(s). In Florsys, cooperation among intercrop species occurs when one intercrop species controls weeds to the benefit of other intercrop species. Compensation happens when the failure of one species is compensated by the other(s) because they differ in their sensitivity to abiotic stress. In FlorSys, compensation is possible when one intercrop species emerges or grows badly because of weather events and weed competition and the other intercrop species occupy the empty niche by growing wider, with more leaf area and root lengths. Though the cylinder-based plant structure does not specifically represent details such as individual cereal tillers, it simulates the outcome of such processes, e.g., by widening cylinders of plants in canopy gaps or by slimming and increasing them in case of dense shading canopies.

2.3.5. Effect of management techniques

Life-cycle processes depend on the dates, options and tools of management techniques (tillage, sowing, herbicides, mechanical weeding, mowing, harvesting, irrigation), in interaction with weather and soil conditions on the day the operations are carried out (see section A.5 online). For instance, weed plant survival probabilities are calculated deterministically depending on management operations, biophysical environment as well as weed morphology and stage; the actual survival of each plant is determined stochastically by comparing this probability to a random probability.

2.3.6. Indicators of weed impact on crop production and biodiversity

FlorSys simulates crop yield as well as a set of indicators assessing weed impacts on crop production and biodiversity (Mézière et al., 2015; Colbach et al., 2020a). The present work focused on two indicators of weed harmfulness for crop production, i.e., crop yield loss due to crop–weed competition for light, and field infestation by weed biomass. Indicators were produced at the scale of the cash crops, i.e., there were two output values per year with double crops (e.g., year 1 of the rotation of the "Species proportions" design, section B.1 online).

2.3.7. Domain of validity

Several short-term studies checked that the FlorSys submodels correctly predicted key state variables such as weed emergence abundance and timing (Colbach et al., 2006), light penetration into the canopy (Munier-Jolain et al., 2013) or seed movements during tillage (Colbach et al., 2000) and whether the model was able to discriminate species and varieties in terms of growth and plant morphology (Lecuyer, 2009). Moreover, FlorSys was evaluated with independent field data on weed long-term dynamics at French national scale, over a large range of existing arable cropping systems with limited nitrogen and water stress. It showed that crop yields, daily weed species densities and, particularly, weed densities averaged over the years were generally well predicted and well ranked as long as a corrective function was added to keep weeds from flowering during winter at more southern latitudes (Colbach et al., 2016; Pointurier et al., 2021). This evaluation showed that the model's prediction quality is adequate for the model's purpose, i.e., to predict orders of magnitude and to rank various cropping systems, crop species and varieties as well as weed species. Higher crop yield losses than those reported in field studies mostly resulted from the simulation plan. This plan does not adapt practices to simulated weed floras and interannual weather variability in order to discriminate the effect of crop species and management practices on weeds from the effect of weeds on the choice of crops and practices (Colbach and Cordeau, 2018) as farmers or trial managers would do.

However, the observed data covering South-Western France used in the previous FlorSys evaluation was imprecise and did not include any multiannual weed dynamics observations. An additional evaluation was thus carried out here to check the model's adequacy for the particular conditions of Toulouse (details in section A.7 online). Data from the Micmac field trial was used, which included the intercrop scenario I_all described in Section 2.2.2 and two sole-crop rotations, all three with two different fallow management options and replicated three times. The weeds inside these 18 fields were monitored several times a year from 2010 to 2018. The statistical criteria used to evaluate the prediction quality of FlorSys were those chosen and adapted by Colbach et al. (2016) to account for the model's complexity and the variability in weed observations. The results showed that the model also worked satisfactorily in the Toulouse region.

2.4. Simulations

2.4.1. Running the virtual experiments

In total, we simulated 96 cropping systems, 78 systems from the "Species proportions" design, and 18 from the "Sowing patterns" design. Each cropping system was simulated twice with FlorSys, once starting with a regional weed species pool consisting of 30 annuals, and once without weeds. The weed-free simulation produced potential yields and the difference between the weed-free and weed-inclusive simulations allowed estimating the crop yield loss due to weeds. To maximise the differences between crop species and cropping systems, the density of the initial weed flora pool was voluntarily high (i.e., approx. 44000 seeds/m^2 corresponding to 125 mg seeds/m^2) and weed-control operations were not adapted if the weed densities rose during the simulations. This also avoided confounding effects of intercrops on weeds with effects of weed floras or weather on cropping systems.

All scenarios were simulated over 30 years, repeating the basic rotation pattern over time to assess long-term effects. Each was repeated with ten weather series consisting of 30 randomly chosen annual records from the Toulouse-Auzeville weather station (provided by the INRAE Climatik platform) to evaluate the systems' robustness. Weather repetitions also allow for variations resulting from the stochastic processes included in the model, for instance when determining actual plant survival from deterministic survival rates (Section 2.3.5)

The simulations were carried out with the 2022 version of FlorSys (Pointurier et al., 2021), considering that water and nitrogen were non-limiting after plant emergence. Plant–plant interactions therefore only consider competition for light as well as plant-seed competition for water during germination and pre-emergent growth (see Section 2.3.3).

2.4.2. Yield indicators calculated from the simulations

For each crop of every cropping system and weather repetition, yield loss due to weeds was calculated as:

$$\textit{Yield loss due to weeds}(\%) = \frac{\textit{Yield in weed\_free simulation} - \textit{yield in weed\_infested simulation}}{\textit{Yield in weed\_free simulation}} \quad (1)$$

To evaluate the impact of intercrops vs sole-crop crops on crop production, the gap between the yield of each species grown in an intercrop and its expected yield was calculated based on its sole-crop yield (grown during the same year and weather repetition in the same rotation) and its sowing density in the intercrop relative to its density as a sole crop:

$$\textit{Expected yield}\ \left(MJ \middle/ m^2\right) = \textit{sole crop yield}\left(MJ \middle/ m^2\right) \cdot \textit{relative sowing density}\left(\frac{seeds/m^2}{seeds/m^2}\right) \quad (2)$$

$$\text{Yield gap due to intercropping}(\%) = \frac{\textit{Yield in intercrop}(MJ/m^2) - \textit{Expected yield}(MJ/m^2)}{\textit{Expected yield}(MJ/m^2)} \quad (3)$$

A positive yield gap means a better yield per species in the intercrop than in the sole crop, and vice-versa for a negative yield gap. If the yield gap is calculated with yields from weed-free simulations, it evaluates the effect of a companion crop on the species yield. If the gap is computed from weed-inclusive simulations, it also includes possible benefits for the species yield from weed suppression by the companion crop.

2.4.3. Statistical analysis

The analysed data sets were very large, with thumber of observation ranging from 2000 for intercrop-scale variables in the "sowing patterns" design to 12600 for species-scale variables in the "species proportions" design. Consequently, linear models can be used without issues about homoscedacity or normality of residuals (Pek et al., 2018).

To evaluate the effects of crop species, species proportions and sowing patterns of intercrops, the yield gaps as well as the indicators of weed impacts on crop production (weed-free and weed-infested yields, yield loss due to weeds, field infestation by weeds) were analysed with linear models including factors and covariables using the lm() function of R (R Core Team, 2022) for the "species proportions" (Eq. 4) and "sowing patterns" designs (Eq. 5):

$$Indicator_{syr} = \beta_0 + Crop_{sy} + Species\_proportion_s + Mechanical\_weeding_s + \beta_{year} \cdot Year_y + Crop_{sy} \times Mechanical\_weeding_s + Crop_{sy} \times Species\_proportion_s + \beta_{crop} \cdot Year_y + \beta_{mech\_weeding} \cdot Year_y + \beta_{proportion} \cdot Year_y + Weather\_repetition_r + \varepsilon_{syr} \quad (4)$$

$$Indicator_{syr} = \beta_0 + Crop_{sy} + Sowing\_pattern_s + \beta_{cer} \cdot Linear\_density\_Cer_{sy} + \beta_{leg} \cdot Linear\_density\_Leg_{sy} + \beta_{year} \cdot Year_y + \beta_{cer\_leg} \cdot Linear\_density\_Cer_{sy} \cdot Linear\_density\_Leg_{sy} + \beta_{crop} \cdot Year_y + \beta_{pattern} \cdot Year_y + \beta_{cer\_year} \cdot Linear\_density\_Cer_{sy} \cdot Year_y + \beta_{leg\_year} \cdot Linear\_density\_Leg_{sy} \cdot Year_y + Weather\_repetition_r + \varepsilon_{syr} \quad (5)$$

where $Indicator_{syr}$ is the yield gap or indicator predicted by FlorSys for cropping system s in year y and weather repetition r, using only years with intercrops or their sole-crop controls (for indicators other than yield gaps). $Crop_{sy}$, $Species\_proportion_s$, $Mechanical\_weeding_s$, $Sowing\_pattern_s$ and $Weather\_repetition_r$ are, respectively, the effects of crops (Wheat–faba bean…), species proportions (33C100L …), mechanical weeding (rotary hoe…), sowing patterns (1_4 …), and weather repetition (repetition1 …) on the analysed indicators. $Linear\_density\_Cer_{sy}$ and $Linear\_density\_Leg_{sy}$ are the density of seeds (seeds/m) sown per linear meter on a cereal or legume row in the "sowing patterns" design. β_0, β_{year}, β_{cer} and β_{leg} are intercept and regression coefficients for quantitative variables (year, cereal density and legume density). The other β regression coefficients (e.g., β_{crop}, β_{cer_year}…) denote interactions between one of these quantitative variables and other variables.

The contribution of the various explanatory variables to explaining the variability in indicator values or yield gaps was assessed using partial R^2 based on type-III sum of squares. This was followed by a comparison of lsmeans (Lenth, 2016) (or means for the "sowing patterns" design) with a least-significant-difference test to compare different crops, types of mechanical weeding, species proportions and sowing patterns two-by-two. Levels were then grouped with the Tukey method to adjust p-values via the cld() function. All analyses were performed with R software version 4.2.2 (R Core Team, 2022).

To identify which species traits drove species yields in sole crops and intercrops, a stepwise regression of species yield was run as a function of species traits and sowing densities. The traits were the seven FlorSys parameters most similar to those used by MacLaren et al. (2023) to link species yields in intercrops to species traits in a large range of tropical intercrops. These traits were (1) specific leaf area (after emergence, during vegetative growth, during reproduction) which reflects how a plant invests leaf biomass to intercept light, (2) plant height per unit above-ground biomass (at the same three stages) which reflects how tall a plant grows from a given amount of biomass, and (3) maximum plant height. Except for specific leaf area, the trait values of the target species were divided by those of its companion species to illustrate relative occupation of space. In sole crops, these relative trait values were 1. The regression was carried out with PROC GLMSELECT of SAS. Inputs were added sequentially, by adding effects that at each step produced the smallest value of the Schwarz Bayesian information criterion (SBC) statistic and stopping when adding any effect increased the SBC statistic again. SBC results in more parsimonious models, with less risk of overfitting, than the Akaike's information criterion (AIC). The final model was chosen among the successive models as the one that yielded the lowest predicted residual sum of square with cross validation.

Species yield was also analysed as a function of all 104 parameters used by FlorSys to describe the species-inherent environment-independent characteristics of species (e.g., plant height per unit biomass at flowering onset, base temperature for germination, light use efficiency), regardless of cropping system, year and weather repetition. All 104 traits were included both in absolute values (e.g., seed weight of the species) and relatively to its companion species (e.g., seed weight of the target species divided by the seed weight of its companion species). Relative sowing densities, separate vs mixed rows, weather repetition, year, location × type of mechanical weeding were also used as regression inputs.

The same analysis was also carried out at the canopy scale, analysing yields of sole crops and intercrops as well as their infestation by weed biomass as a function of canopy traits, using both mean trait values of the crop canopy, and interspecies variation therein. For mean canopy trait values of the intercrop, we used the principle of the Community Weighted Mean from ecology (Lavorel et al., 2008):

$$Mean\_Trait_{AB} = \frac{density_A \cdot trait_A + density_B \cdot trait_B}{density_A + density_B} \quad (6)$$

where $density_A$ and $density_B$ are the sowing densities (seeds/m^2) of species A and B, respectively, in a given cropping system and year, and where $trait_A$ and $trait_B$ are the values of a given trait (e.g., seed weight) for species A and B, respectively. The unit of $Mean\_Trait_{AB}$ is the same as that of the crop trait. For interspecies variability in canopy traits, the inter-plant coefficient of variation in parameter values was used (and not the inter-species coefficient of variation):

$$var\_trait_{AB} = \frac{density_A \cdot (trait_A - Mean\_Trait_{AB})^2 + density_B \cdot (trait_B - Mean\_Trait_{AB})^2}{density_A + density_B} \quad (7)$$

$$CV\_trait_{AB} = \frac{\sqrt{var\_trait_{AB}}}{mean\_trait_{AB}} \quad (8)$$

If CV_trait_{AB} is nil, the constituting species A and B are identical for the considered trait. The larger CV_trait_{AB} is, the more the intercrop differs in terms of traits, particularly when both species have similar plant densities. The analysis also included data from control sole crops corresponding to the intercrops, with $Mean\_Trait_{AB} = trait_A$ and $CV\_trait_{AB} = 0$.

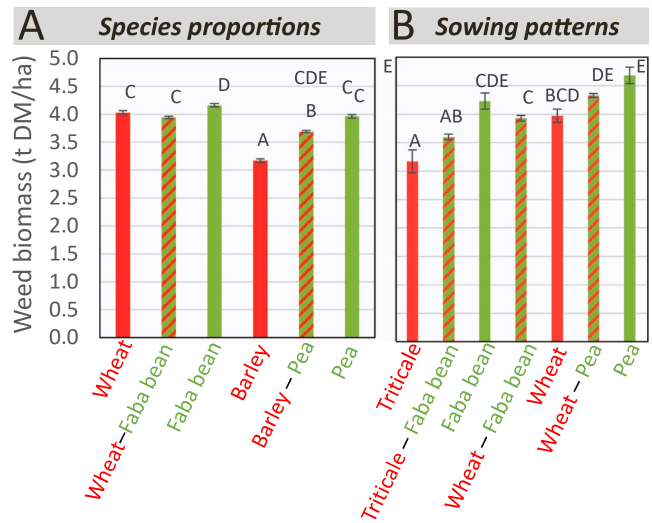

Fig. 3. Weed biomass in intercrops (hatched) and in the corresponding sole crops with legumes in green and cereals in red for the "Species proportions" (A) and "Sowing patterns" (B) designs. For a given graph, bars with the same letter are not significantly different at p=0.05 (Tukey tests after analysis of variance) (Pierre Lebreton 2023).

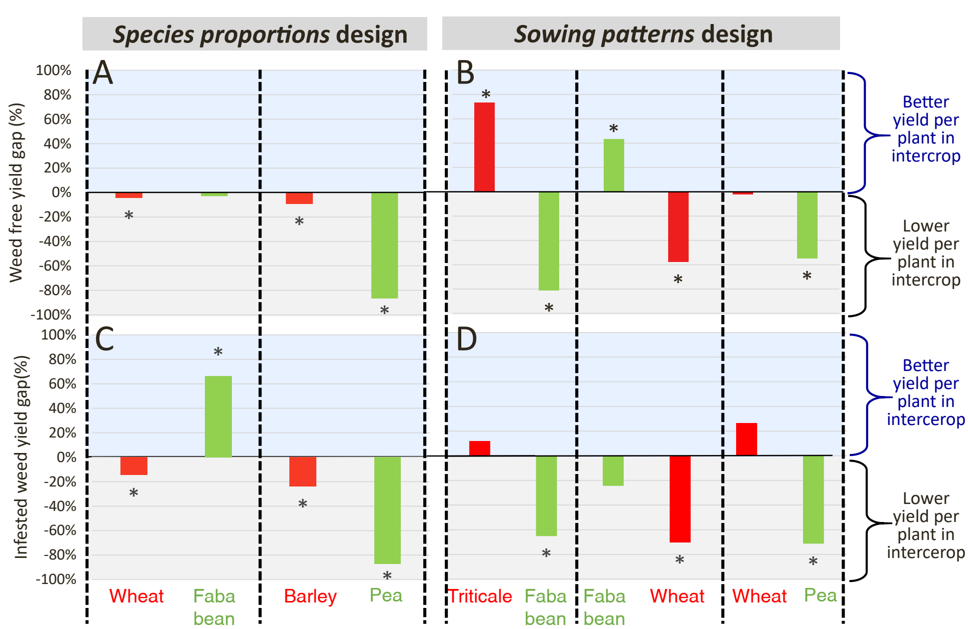

Fig. 2. Relative variation in yield per plant in intercrops compared with sole crops (yield gap) in the absence (A and B) or presence (C and D) of weeds based on simulations run with FlorSys in conditions with unlimiting nitrogen and water after plant emergence. *: yield gaps are significantly different from zero at p=0.05 (least-significant-difference test after analysis of variance) (Pierre Lebreton 2023).

3. Results

3.1. Species performance in intercrops compared with sole crops

3.1.1. Intercropping can reduce the yield per plant

In weed-free simulations with the "Species proportions" design, in average over all species proportions and weeding options, the yield gap between intercrops and sole crops was negative for all species except faba bean (Fig. 2.A). In other words, adding a companion crop reduced the yield per plant in all species except faba bean.

Wheat–faba bean intercrops were also grown in the "Sowing patterns" design, with similar but more contrasted results: wheat yield per plant was even lower in intercrops than in sole crop in the "Sowing patterns" vs "Species proportions" design whereas faba bean yield per plant was significantly better in intercrops than in sole crops (Fig. 2.B). Triticale was another species whose yield per plant increased in intercrops.

The "Sowing patterns" design also showed that the yield gap depended on the companion species. Faba bean was more competitive than pea against wheat (wheat yield gap with faba bean < gap with pea in Fig. 2.B) and triticale was more competitive than wheat against faba bean (faba bean yield gap < 0 with triticale but > 0 with wheat). Triticale was actually the only cereal with a positive yield gap (+73 %).

3.1.2. Weed control is better in intercrops than in sole crop legumes

In the "Species proportions" design (Fig. 3.A), field infestation by weed biomass was higher in sole-crop cereals than in sole-crop legumes, with barley as the least infested crop at 3.2 t DM/ha and sole faba bean as the most infested at 4.2 t DM/ha. Weed biomass was significantly lower in intercrops than in sole legumes, and higher than in or similar to sole cereals. Of the two intercrops, the barley–pea controlled weeds better than wheat–faba bean (3.7 and 3.9 t DM/ha, respectively).

The results of the "Sowing patterns" design were similar (Fig. 3.B), with the weediness of the intercrops comparable to that of sole cereals, and less than that of sole legumes. Of all the species tested, triticale as a sole crop had the best weed control at 3.2 t DM/ha, while legumes had an approximately 30 % higher weed biomass. As a result, intercropping faba bean with triticale reduced weed biomass (compared to sole faba bean) more than with wheat. Conversely, intercropping wheat with pea increased weed biomass (compared to sole wheat) more than with faba bean.

In both designs, weed-infested legume yields were similar as or better than expected in those intercrops whose weed biomass was as low as in the sole cereals (i.e., wheat–faba bean vs wheat).

3.1.3. Legumes benefit more from the weed-suppressive effect of the intercrops

In both designs, yield loss due to weeds in sole crops tended to be lower in cereals (particularly, barley and triticale) than in legumes. Only legumes benefitted from the weed suppression due to intercropping of Section 3.1.2. Indeed, in both designs, yield loss due to weeds was lower for intercropped vs sole-crop legumes (–13 % and –16 % on average for pea and faba bean, respectively) but similar or higher for cereals (~0 %, +6 % and +18 % for wheat, barley and triticale, respectively, Fig. 4.A and B).

The lower weed-induced yield loss could cancel out or reduce the negative yield gap for legumes due to the companion crop. This was the case for faba bean and, to a lesser degree, pea in the "Species proportions" design (weed-infested yield gaps of Fig. 2.C > weed-free gaps of Fig. 2.A). But in the "Sowing patterns" design, this only worked for faba bean intercropped with triticale (weed-infested yield gap in Fig. 2.C > weed-free gap of Fig. 2.A) but not when either faba bean or pea were intercropped with the less weed-suppressive wheat. Conversely, the increased weed-induced yield loss of triticale in intercrops vs sole crop (+15 % Fig. 4.B) was cancelled out by its large positive yield gap (+73 %, Fig. 2.B), resulting in a negligible yield gap in weed-infested simulations (Fig. 2.D).

3.1.4. Which species are the most competitive?

Species could be ranked in terms of their competitiveness against companion crops based on yield gaps in weed-free simulations (triticale > faba bean > wheat > pea, Fig. 2.A and B), weed suppression in intercrops based on field infestation (triticale > wheat > faba bean > pea, Fig. 3), and tolerance to weeds based on weed-induced yield loss in sole crops (triticale > wheat ~ faba bean ~ pea, Fig. 4.A and B). Barley roughly ranked between triticale and wheat, with a lower weed-induced yield loss than wheat (Fig. 4.A) but no positive yield gap in weed-free simulations (Fig. 2.A), in contrast to triticale.

3.2. Effect of mechanical weeding on crop damage and weed control

In weed-free simulations, the choice of the mechanical-weeding tools did not impact yields in barley–pea intercrops with their mixed rows (section C.3 online). Conversely, wheat yields were better with the tine harrow and faba bean yields with the rotary hoe. In other words, in the intercrop with separate rows for wheat and faba bean, hoeing damaged wheat plants more than harrowing and vice-versa for faba bean.

Hoeing was slightly better at controlling weeds, but only in the wheat–faba bean intercrop. The better weed control cancelled out the higher damage to wheat plants, and there was no more difference in wheat yield in weed-inclusive simulations. Conversely, the reduction in faba bean yield with tine harrow was even larger in relative terms in the presence of weeds (–9 % vs –14 %) because of the lesser weed control by harrowing.

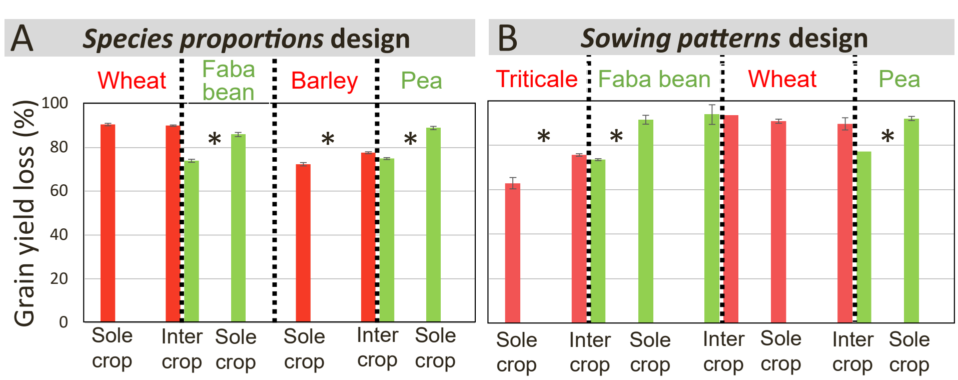

Fig. 4. Grain yield loss due to weeds (cereals in red, legumes in green) of species grown in intercrops or as a sole crop. *: yield losses are significantly different at p=0.05 in sole crop vs intercrop (Least-significant-difference test after analysis of variance). Vertical bars are standard-errors (Pierre Lebreton 2023).

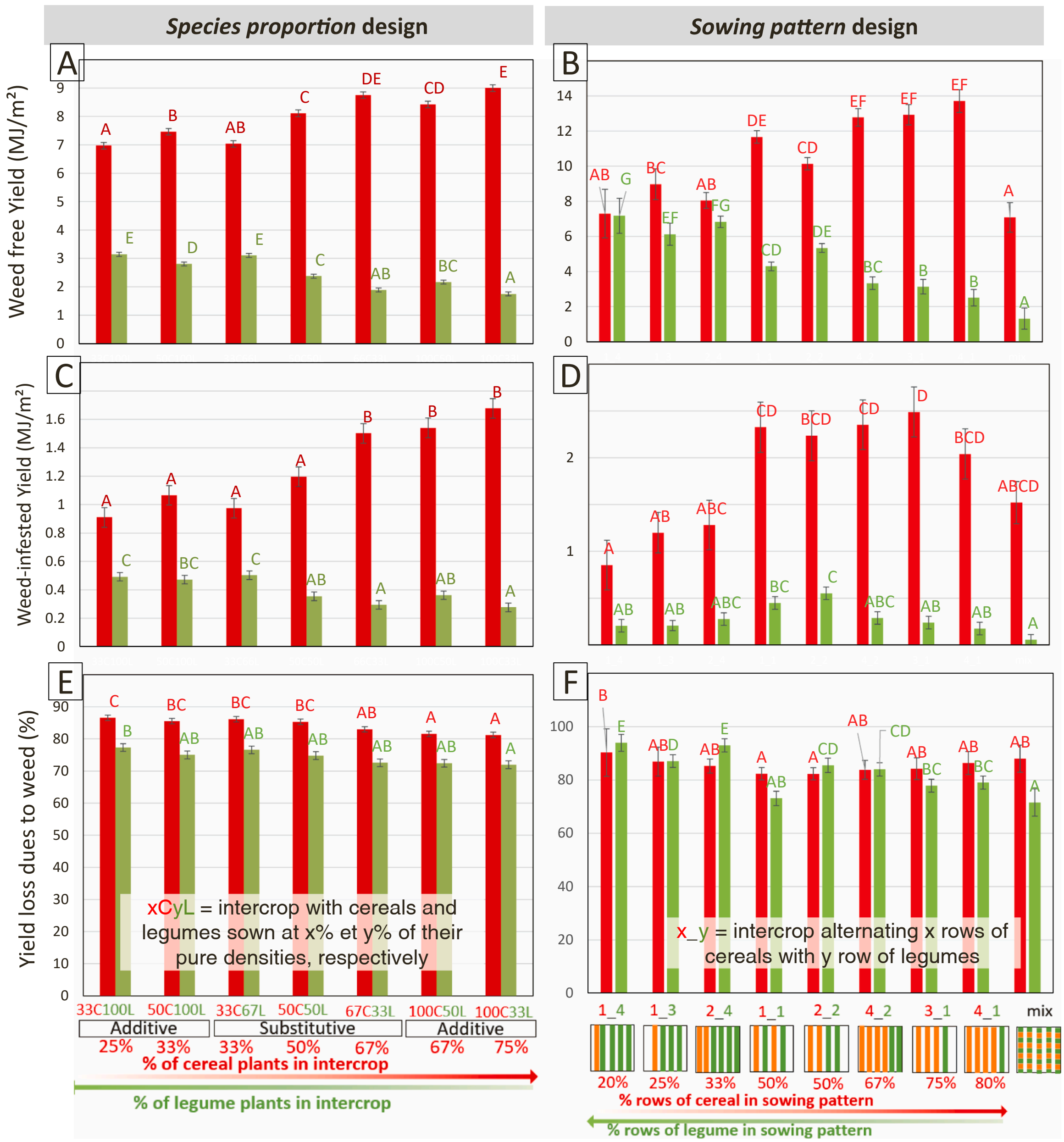

Fig. 5. Effect of species proportions (A, C and E) and sowing patterns (B, D and F) of cereal–legume intercropping on yield in the absence (A et B) and the presence of weeds (C and D), and on yield losses due to weeds (E and F), all in the absence of nitrogen and water stress after plant emergence. Cereal (in red) or legume yields (in green) with the same letter are not significantly different at p=0.05 (Tukey test after analysis of variance) (Pierre Lebreton 2023).

3.3. Which species proportions and sowing patterns to optimise intercrops?

3.3.1. High cereal proportions control weeds but also disturb legume production

In the "Species proportion" design, the cereal yield was best with at least 67 % of cereals in the intercrop, both in the absence and presence of weeds (Fig. 5.A and C). Similarly, the legume yield was highest when the legume proportion exceeded 67 %. Note that in the absence of weeds, the densest design (50C100L) produced less legume yield than the other two high-legume designs (33C100L and 33C67L, Fig. 5.A). A similar tendency was observed for cereal yield, which was slightly lower in the densest high-cereal design (100C50L) than the other two high-cereal designs (67C33L and 100C33L). Yield loss due to weeds decreased in both crop species when the proportion of cereals in intercrops increased, and vice-versa increased when the proportion of legumes increased (Fig. 5.C). The same applied to weed biomass, regardless of the intercropped species (section C.4.2 online).

Actually, in additive designs, weed-free yields of the majority crop (cereals in 100C33L and 100C50L, legumes in 33C100L and 50C100L) were much lower than their expected yields based on sole-crop yield and relative sowing densities (Fig. 6.A and B). This was the most visible for the least competitive crop (i.e., pea), which was moreover mixed on rows with the cereal, and the least visible for the most competitive one (i.e., faba bean), which was sown on separate rows. In substitutive designs, the yields of the most competitive species (cereals, faba bean) were similar to or slightly better than expected yields. The same was true for minority crops in additive designs (legumes in 100C33L and 100C50L, cereals in 33C100L and 50C100L). But pea yields were always lower than expected yields.

In summary, weed-free intercrop species yields were mostly linked to their sowing densities. Additive designs favoured the yields per plant of

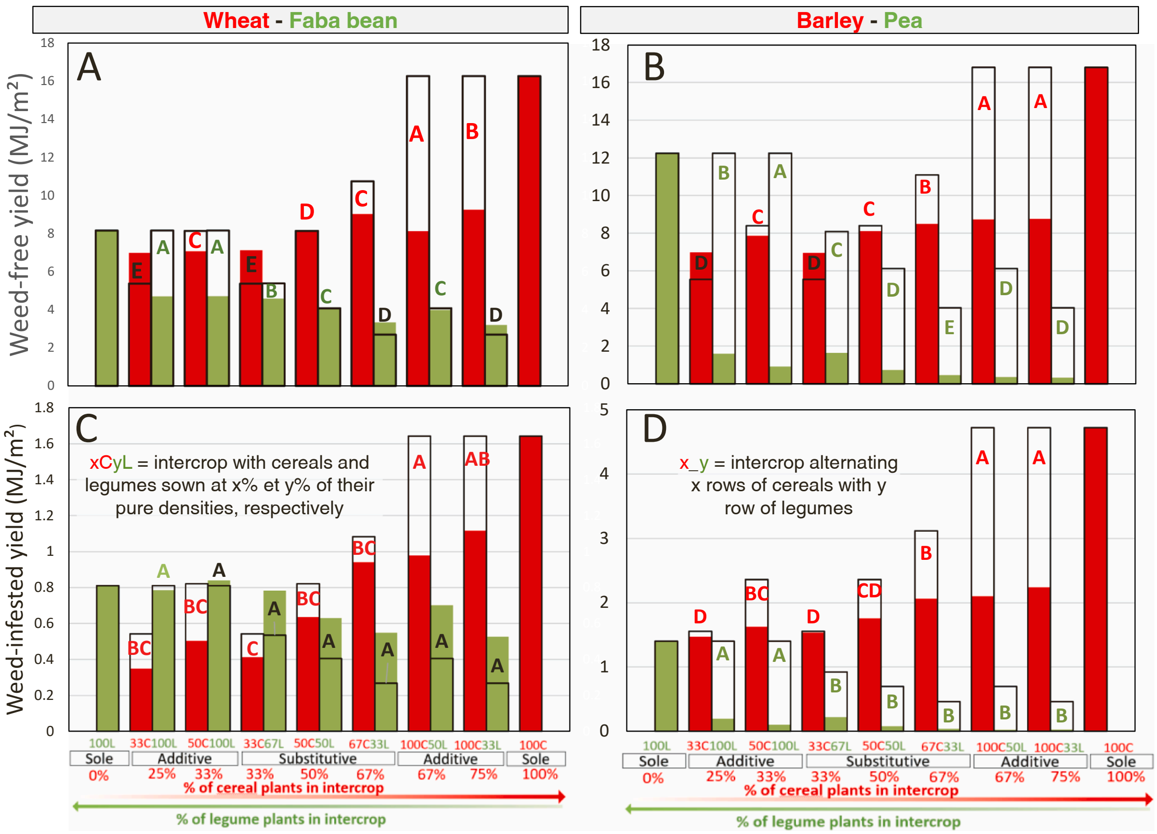

Fig. 6. Effect of species proportions of cereal–legume intercropping, in the presence (A and B) and absence (C and D) of weeds, on cereal (red bars) and legume yields (green bars) in intercropping (full bars). Empty bars show yields expected based on sole-crop yields and intercropping sowing densities, in the absence of nitrogen and water stress after plant emergence. Red and green letters show cereal and legume yields that were worse than expected, black letters show yields that were better than expected; yield gaps (difference between full and empty bars) labelled with the same letter are not significantly different at p=0.05 (Tukey test after analysis of variance, section C.4.1 online) (Pierre Lebreton 2023).

minority crops (particularly of highly competitive ones) more than majority crops. In the presence of weeds, the situation changed for the better for legumes and for the worse for cereals (Fig. 6.C and D). Competitive legumes such as faba bean benefitted the most, with much better yields than expected in high-cereal mixtures.

3.3.2. Row patterns matter the most for less competitive species

In the "sowing pattern" design, the weed-free cereal yield increased with the proportion of cereal rows in the intercrop, and decreased with the proportion of legume rows (Fig. 5.B), even though sowing densities remained constant. In other words, a higher proportion of cereal rows means that the same amount of cereal seeds was sown into more rows while the same amount of legume seeds was sown into fewer rows. This translated into a lower on-row cereal density and a higher on-row legume density. Both cereal and legume yields were lowest for the on-row mixtures.

But the results depend on the species choice (Fig. 7.A-C). When the most competitive cereal (triticale) was mixed with the most competitive legume (faba bean), yields varied very little across sowing patterns (Fig. 7.A). The only exception was the on-row mixture where yields were the lowest of all patterns.

When a less competitive cereal (wheat) was mixed with the most competitive legume, results changed (Fig. 7.B) and were more similar to the global effect of Fig. 5.B. Cereal yields increased and legume yield decreased with the proportion of cereal rows, and the on-row mixture was again the worst (Fig. 7.B). Legume yields were better and cereal yields worse than expected when there were more cereal than legume rows (4_2, 3_1, 4_1). When the less competitive cereal was mixed with the least competitive legume (pea), yields varied similarly with the proportion of cereal rows (Fig. 7.C). But cereal yields were now better than expected with the high proportion of cereal rows, and legume yields were always worse than expected.

3.3.3. Balanced species row patterns reconcile production and weed control the best

In the presence of weeds, the pattern effect changed (Fig. 5.D). Cereal yields were best when there were as many cereal rows as legume rows (1_1, 2_2) or up to three times more cereal rows than legume rows (4_2 or 3_1). Legume yields also were best with equal legume and cereal rows. Indeed, yield loss due to weeds tended to be the lowest for these patterns (Fig. 5.F). For legume yield loss, the proximity of wheat plants was essential, demonstrated by the lowest yield loss for the pattern alternating one legume vs one cereal row (1_1) and the on-row mix.

In the presence of weeds, the pattern effect at the species scale (Fig. 7.D-F) was similar to the general effect of Fig. 5.D, i.e., cereal yields were best when there were as many or slightly more cereal rows than legume rows, and legume yields were best with equal row proportions, regardless of the species (Fig. 7.D-F). The species choice mostly influenced weed-infested yield gaps: legumes benefitted the most from intercropping when mixed with a more competitive cereal, with yields nearly similar to (faba bean with triticale, Fig. 7.D) or even better than expected yields (pea with wheat, Fig. 7.F). When the legume was mixed with a less competitive cereal (faba bean with wheat), both had larger yield gaps in weed-infested than weed-free fields (Fig. 7.E).

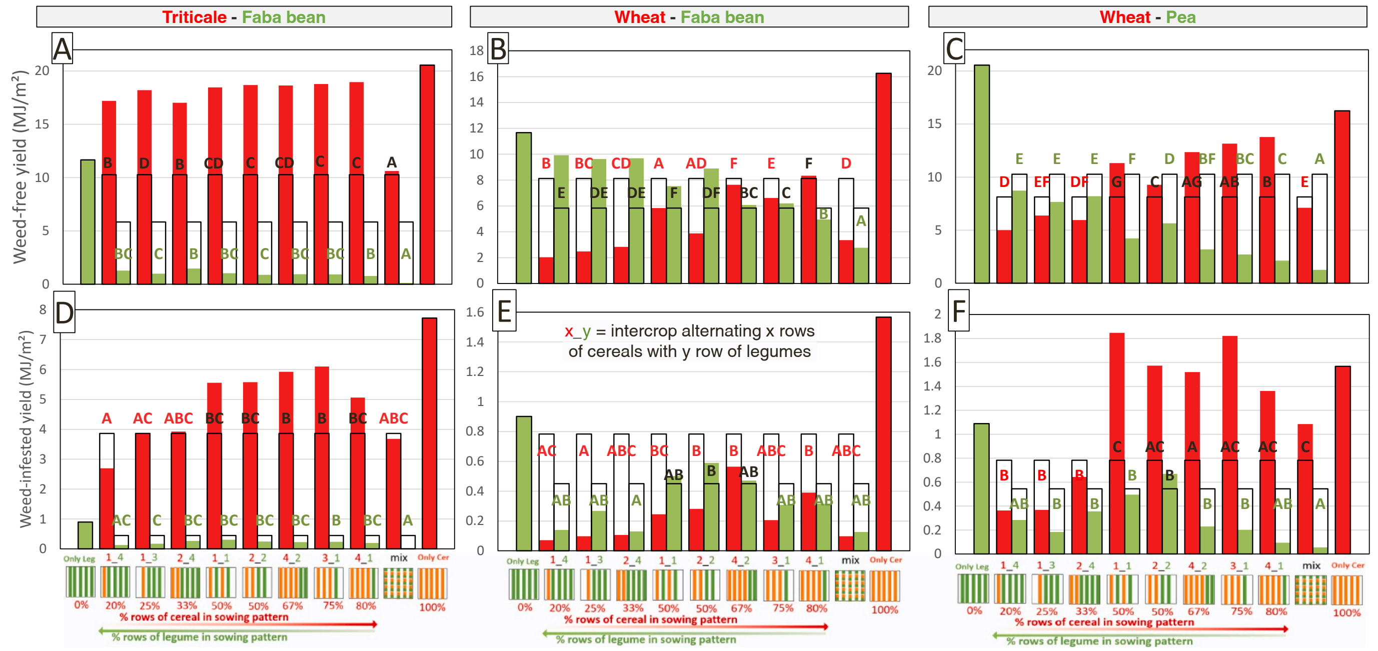

Fig. 7. Effect of species patterns in cereal–legume intercropping (50 %–50 % substitutive mixture) in the presence (A–C) and absence (D–F) of weeds, on the on cereal (red bars) and legume yields (green bars) in intercropping (full bars). Empty bars show yields expected based on sole-crop yields and intercropping sowing densities, in the absence of nitrogen and water stress after plant emergence. Red and green letters show cereal and legume yields that were worse than expected, black letters show yields that were better than expected; yield gaps (difference between full and empty bars) labelled with the same letter are not significantly different at p=0.05 (Tukey tests after analysis of variance, section C.4.1 online) for cereals (red letters, bars and lines) and legumes (green letters, bars and lines) (Pierre Lebreton 2023).

3.4. The intercrop traits driving crop production and weed suppression

3.4.1. Long crop growth and complementarity in height and leaf biomass drive intercrop yield

When the species yield was analysed with the same traits as in MacLaren et al.'s study (MacLaren et al., 2023), species yield increased with its specific leaf area and with its height (maximum plant height and plant height per unit biomass) relatively to its companion species (section C.6 online). However, when all species traits were used, other traits were more influential and explained a larger part of variability (the R^2 doubled).

A good yield, whether in sole crops or in intercrops, was first due to a high sowing density (regression coefficient = 0.0225 MJ·m-2/plants·m-2 in line 9 of Table 2.A). Yield also increased with the duration of crop growth resulting from a late flowering (positive coefficient in line 2) and the ability to increase plant height per unit above-ground biomass when shaded, notably during reproduction (line 3).

In intercrops, the yield of a given species increased if its seeds were heavier than those of its companion species (line 4) and its shading response was stronger. The higher yielding species increased plant width per biomass during reproduction more than its companion (line 5), and it shifted its leaf area more towards the plant top from vegetative stages onwards (lines 6 and 7). However, if it started flowering earlier than its companion, its yield decreased (line 8).

The field yield (intercrop yield or sole-crop yield) was mostly linked to cereals, as shown by the positive correlation with cereal sowing density (line 14 in Table 2.B). Legume density had no significant effect. Field yield was mainly due to the highest yielding crop. Indeed, the most influential crop community traits driving field yield were very similar to the species traits (Table 2.B vs A). This analysis also showed that above-ground biomass was more important than below-ground root-system (negative coefficient of root-system extension speed in line 3 in Table 2.B).

Intercrop yield benefitted from a large inter-plant variability in plant height or biomass allocation to leaves, particularly during reproduction: yield was positively correlated to shade-driven increases in height biomass ratio and leaf biomass ratio (lines 11 and 12). Inter-plant variability was detrimental if it concerned flowering timing (line 9) or plant width (line 10): these two traits should be similar for intercropped species.

3.4.2. Early, high and homogeneous crop establishment is essential to suppress weeds

Crop yield loss (section C.6 online) and field infestation depended less on canopy traits (very low R^2 in Table 2.B). A good weed suppression needs an early germination (short germination lag in line 2) and similar (low) pre-emergent seedling mortality (line 8). In contrast to yield, flowering should be early (positive coefficient in line 6) to leave less time for weeds to grow. Heterogeneous (top-heavy) leaf area distribution along plant height is also helpful (line 4). Variability in frost sensitivity during reproduction was not a problem as the tested species were generally frost-tolerant.

In average, intercrops were more weed-suppressive than sole crops (lines 16–17 vs 15), particularly with on-row mixtures. All else being equal, tine harrow destroyed weeds more than rotary harrow (lines 19 vs 18). The higher weed biomass in wheat–faba bean for tine harrow vs rotary hoe in Section 3.2 was thus most likely due to the bigger damage to faba bean (and thus a lesser weed suppression via competition) than to a lower weed destruction.

4. Discussion

4.1. Using a mechanistic model to understand and explore intercrops

In the present study, the FlorSys simulation model was used to explore a wide range of species proportions and sowing patterns for cereal–legume intercrops over several years or decades and with different weather series, which is impossible in the field. The model structure and the proposed virtual experimental design allowed a better understanding of the interactions within the cereal–legume–weed

Table 2

The crop traits and management techniques that drive yield potential and weed suppression in legume–cereal intercrops and their corresponding sole crops. Regression coefficients of stepwise regressions analysing yields at the canopy scale (A) or the species scale (B) and field infestation (columns) as a function of weather repetition (not shown), crop parameters at the canopy scale (A) or the species scale (B) and intercrop management (lines). Cells are in green (respectively red) if an increase in mean parameter value or coefficient of variation increases (respectively decreases) intercrop performance (i.e., large yields, or low field infestation). Empty cells and unlisted parameters point to correlations that were not significant at p=0.05. For further results, see section C.6 online.

A. At the species scale (N=25515)

	Species traits	Unit	Weed-free species yield (MJ/m²)
Species (absolute) trait value			
1	Base temperature	°C	–1.58
2	Thermal ime from emergence to flowering onset	°C days	0.00433
3	Increase in Height Biomass Ratio§ if shade – reproduction	no unit	1.34
Species trait value relative to companion species (species value / companion value)			
4	Seed weight		1.60
5	Increase in Width Biomass Ratio§ if shaded – reproduction		18.8
6	Increase in Relative Leaf Area Height if shaded – vegetative		1.85
7	Increase in Relative Leaf Area Height if shaded – reproduction		2.47
8	Thermal ime from emergence to flowering onset		–5.08
Crop management			
9	Sowing density	plants/m²	0.0225
10	Sole crop	yes (1) vs no (0)	2.28
11	Intercrop with separate rows	yes (1) vs no (0)	–1.09
12	Intercrop with on-row mixture	yes (1) vs no (0)	–1.18
13	R^2		0.68

B. At the canopy scale (N=15846)

Canopy traits and crop management			Weed-free field yield (MJ/m²)	Field infestation (t/ha)
	Name	Unit		
Mean value per canopy (sole crops or intercrop) weighted by species plant densities				
1	Base temperature	°C	–0.501	
2	Germination lag	°C days		0.0429
3	Speed of vertical root-system growth	mm·day	–2.99	
4	Heterogeneity of vertical leaf area distribution* – vegetative	no unit		–0.107
5	Duration of plantlet stage	°C days	–0.0608	
6	Thermal time from emergence to flowering onset	°C days	0.00328	0.0005
Inter-plant coefficient of variation in intercrop (standard-deviation / mean parameter value)				
7	Thermal time from germination to mid-elongation during emergence		26.2	
8	Seedling mortality increase with seed depth			2.56
9	Thermal time from emergence to flowering onset		–40.7	
10	Increase in Width Biomass Ratio§ if shade – reproduction		–35.6	
11	Increase in Height Biomass Ratio§ if shade – reproduction		5.43	
12	Increase in Leaf Biomass Ratio# if shade – reproduction		0.949	
13	Maximum temperature for frost-driven biomass loss – reproduction			–0.792
Crop management				
14	Cereal sowing density vs sole-cereal density	$plants \cdot m^{-2}/plants \cdot m^{-2}$	0.0799	
15	Sole crop	yes (1) vs no (0)		0.178
16	Intercrop with separate rows	yes (1) vs no (0)		–0.016
17	Intercrop with on-row mixture	yes (1) vs no (0)		–0.161
18	"Species props" design with rotary hoe	yes (1) vs no (0)		0.096
19	"Species props" design with tine harrow	yes (1) vs no (0)		–0.107
20	"Sowing patterns" design	yes (1) vs no (0)		0.010
R^2			0.73	0.10

* A value close to zero means uniform leaf area distribution. High values mean top-heavy plants.

§ Plant width or height vs above-ground plant biomass

Leaf biomass vs above-ground plant biomass

complex by discriminating several simultaneously occurring interactions: (1) effects linked to species, intercropping (simulations with intercrops vs. sole crops, all else being equal) and weeds (simulations with weeds vs. no weeds, all else being equal), (2) yield production (evaluated in weed-free simulations), tolerance to weeds (i.e., reduced yield loss due to weeds) and weed suppression (i.e., reduced field infestation by weed biomass), (3) yield reduction due to lower sowing densities in the intercrops, yield losses due to competition from more competitive companion crops, yield losses due to competition from weeds, and yield gains due to weed suppression by more competitive companion crops.

Finally, the trait-based structure of FlorSys allowed going beyond rankings of crop species or species combinations in terms of crop production and weed control, by identifying the key crop traits responsible for these classifications. This knowledge made it possible to establish more generic rules on how to combine crop species in intercrops.

4.2. A model that produces results consistent with field observations

It is essential to bear in mind that, despite their many advantages, models are only a simplified representation of reality, whose results depend on the model's predictive quality. To check this, FlorSys was evaluated in previous studies using independent field observations from different regions, over several years (Colbach et al., 2016; Pointurier et al., 2021) and again here. This evaluation showed that FlorSys predicted weed dynamics and crop yields well enough to compare cropping systems and species, and that the high yield losses seed here resulted from the simulation plan with its high initial weed infestation and non-adaptation of cropping systems to simulated weather and weeds (Section 2.3.7).

All the simulations were carried out considering that nitrogen and water were non-limiting after plant emergence. Although these conditions are not entirely comparable with real-life situations, they are close to those encountered in many temperate climate field crop systems with mineral fertilizers. In these conditions, light is the main resource for which crops and weeds compete (Colbach et al., 2023). Despite the many simplifications included in the FlorSys model, the main conclusions of the present study concur with those obtained by various meta-analyses (Gu et al., 2021) and literature reviews (Bedoussac et al., 2015), i.e.: (1) a dominant effect of the choice of species in the intercrops, (2) a weak effect of sowing patterns, (3) a limited effect of species sowing proportions, (4) a better weed control in additive intercrops dominated by cereals, (5) a stronger competitivity for cereals than for legumes, and (6) a weed infestation in intercrops similar to that of sole cereals and lower to that of sole legumes. For further details, see section D online.

Our trait analyses were also consistent with the results from a study with many intercrop combinations in tropical conditions (MacLaren et al., 2023). When our analysis was run with the same traits as in MacLaren et al.'s study (2023), it produced the same conclusions: species yield increased with its specific leaf area and plant height (maximum plant height and plant height per unit biomass) relatively to its companion species. However, when all species traits were used, other traits such as base temperature, seed weight or thermal time from emergence to flowering onset were more influential and explained more variability. MacLaren et al. did not use these traits and actually concluded that plant height and specific leaf area alone cannot reliably predict intercrop yields and that other traits should be explored. Our study confirmed their conclusion and demonstrated how this could be done.

4.3. Implications for intercrop management

Thanks to *in silico* experimentations with the FlorSys model, this study opens up operational prospects for choosing species combinations, species sowing proportions and sowing patterns, depending on the objectives of the intercrop and the trade-off among the yields of the intercropped species.

4.3.1. A complementary plant morphology to optimise light interception

Weed-free simulations highlighted the interspecific interactions between the two crops in the intercrops, with situations of (1) strong competition detrimental to both species (barley–pea), and (2) asymmetrical competition where one of the crops benefits from the intercrop to the detriment of the other (e.g., triticale vs faba bean, or faba bean vs wheat). The latter situation is the most common as the gain in production of one of the two crops is generally made at the expense of the other species (van der Werf et al., 2021). Indeed, competition for light is always present, and it is moreover asymmetrical, with taller plants intercepting proportionally more light than smaller ones (Schwinning and Weiner, 1998). So, light interception by one species in a closed stand inevitably comes at the expense of interception by the other species (Yu et al., 2016).

The complementarity effect on production (Justes et al., 2021), i.e. whether intercrop yields exceeded expected yields, depended very much on the species. The species-trait analysis showed that the overall intercrop yield was best in intercrops combining contrasting species in terms of shade response, with both etiolated and stocky plants as well as both leafy and stemmy plants, to maximise light interception throughout crop layers. Though, in average, only the most competitive species overyielded (or at least did not underyield) in intercrops, the crop–crop competition can be managed. The sowing density can be optimised to achieve a suitable competitive balance (Gu et al., 2021) and the radiation distribution can be modified by the spatial stand structure via species proportions, the spatial sowing pattern, or the trait composition of the intercrop. For instance, competitive equilibrium between wheat and faba bean was reached at a relative density of 50 % (50C50L in Fig. 6.A) or four cereal vs two legume rows (4_2 in Fig. 7.B), but no equilibrium was ever reached for barley–pea intercrops. Separate crop rows also minimised interspecies competition in the here tested species combination, protecting the less competitive legumes from the more competitive cereals.

This work demonstrated the relevance of the FlorSys model for analysing plant–plant interactions and the consequences of a given species in intercropping on both weed growth and intercropping performance. This means that, for a given weed flora, the model can be used to identify, through *in silico* experimentation, the best combinations of species trait values allowing the best intercropping performance.

4.3.2. Intercrop emergence and duration matter for weed control

Weed-inclusive simulations introduced many additional species (the weeds) with sometimes very diverse plant morphologies into the species mixture. Despite this, most of the previous conclusions and explanations remained true except that the less competitive legumes performed better and the more competitive cereals worse than in weed-free situations. Interestingly, intercrop traits linked to competition for light were not the main drivers of weed tolerance and/or suppression. Instead, in line with literature, a good and faster emergence of crops vs weeds (Bertholdsson, 2005; Andrew et al., 2015) and a shorter crop cycle to cut off weed growth and reproduction as in earlier varieties (Piliksere et al., 2013; Worthington et al., 2015) or spring crops (Chauvel et al., 2001) were essential.

4.3.3. What else can be done?

The simulations also showed, unsurprisingly, that weed management should not be limited to choosing intercrop composition and patterns. Mechanical weeding can greatly reduce weed pressure (Chicouene, 2020) and can be optimised to reconcile weed control and reduce crop damage, depending on the crops. Here, for instance, rotary hoe with its better weed suppression resulted in better yields in wheat–faba bean than tine harrow, despite the higher damage to wheat plants.

More importantly, while intercropping is doubtless a very efficacious lever to protect legumes from weed competition, weeds must be managed at the rotation scale to reduce weed pressure. Here, the "species proportions" design, with its many double crops (two years out of four) and summer crops (two years out of four), had a much lower weed infestation than the "sowing patterns" design, with its frequent autumn-sown sole crops or intercrops (four years out of six). Alternating sowing seasons and multiple crop sowings per year are indeed known to be the main driver for reducing and diversifying weed floras (Adeux et al., 2019; Jastrzebska et al., 2019; Weisberger et al., 2019; Neyret et al., 2020).

Finally, the cereal–legume intercrops would probably be much more advantageous in terms of yield if they were cropped in low-nitrogen conditions (Bedoussac et al., 2015; Yu et al., 2016). Indeed, high nitrogen levels were reported to intensify above-ground biomass production and competition for light, which disadvantages the uncompetitive legumes (Fujita et al., 1992). Competition for water will probably also increasingly become an issue with the increased frequency of droughts expected with climate change (Laurent et al., 2023). This is the reason why the FlorSys team is now working on including plant–plant competition for water in the model (Cournault et al., 2024).

5. Conclusion

This work highlighted the benefits of intercrops, particularly for legumes, in reducing field infestation by weeds and, consequently, weed-related yield losses, and identified generic rules for choosing species traits, proportions and sowing patterns according to the targeted objectives. This work will be extended to other intercrops (species, varieties), other management plans and in contexts with limiting water and nitrogen. The results will be used to accompany farmers and crop advisors when designing innovative cropping systems. As the study is based on simulations, intercrops can also be tested with future climate scenarios, to evaluate the resilience of the newly designed systems vs. climate change.

CRediT authorship contribution statement

Nathalie Colbach: Writing – review & editing, Supervision, Software, Project administration, Methodology, Funding acquisition, Conceptualization. **Catherine Bonnet:** Investigation, Data curation. **Laurent Bedoussac:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Eric Justes:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Etienne-Pacal Journet:** Writing – review & editing, Conceptualization. **Pierre Lebreton:** Writing – original draft, Visualization, Software, Investigation, Formal analysis.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

This project was supported by INRAE and the European Union's Horizon 2020 Research and Innovation programme via the ReMIX projet (Grant N 727217) and the Horizon Europe programme via the IntercropVALUES project (Grant N°101081973). Additional funds were provided by the French projects ANR PPR SPECIFICS (ANR-20-PCPA-0008, www6.inrae.fr/specifics/), ANR PPR MoBiDiv (ANR-20-PCA-0006, www6.inrae.fr/mobidiv/), and COPRAA supported by the Office Français de la Biodiversité (OFB) as part of the Ecophyto call on "Global approaches to limit the use of phytopharmaceuticals: Combining preventive and curative products in sectors, from farmers to consumers" launched by the French Ministries in charge of Ecology, Agriculture, Health and Research. The authors are grateful to Thibault Maillot (L'Institut Agro Dijon) for developing and implementing the method for calibrating weed seed banks with optimization algorithms.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2024.127266.

References

Adeux, G., Vieren, E., Carlesi, S., Bàrberi, P., Munier-Jolain, N., Cordeau, S., 2019. Mitigating crop yield losses through weed diversity. Nat. Sustain. 2, 1018–1026. https://doi.org/10.1038/s41893-019-0415-y.

Andrew, I.K.S., Storkey, J., Sparkes, D.L., 2015. A review of the potential for competitive cereal cultivars as a tool in integrated weed management. Weed Res. 55, 239–248. https://doi.org/10.1111/wre.12137.

Bedoussac, L., Journet, E.P., Hauggaard-Nielsen, H., Naudin, C., Corre-Hellou, G., Jensen, E., Prieur, L., Justes, E., 2015. Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. Agron. Sustain. Dev. 35, 911–935. https://doi.org/10.1007/s13593-014-0277-7.

Bertholdsson, N.O., 2005. Early vigour and allelopathy - two useful traits for enhanced barley and wheat competitiveness against weeds. Weed Res. 45, 94–102. https://doi.org/10.1111/j.1365-3180.2004.00442.x.

Blaix, C., Moonen, A.C., Dostatny, D.F., Izquierdo, J., Le Corff, J., Morrison, J., Von Redwitz, C., Schumacher, M., Westerman, P.R., 2018. Quantification of regulating ecosystem services provided by weeds in annual cropping systems using a systematic map approach. Weed Res. 58, 151–164. https://doi.org/10.1111/wre.12303.

Bonnet, C., Gaudio, N., Alletto, L., Raffaillac, D., Bergez, J.-E., Debaeke, P., Gavaland, A., Willaume, M., Bedoussac, L., Justes, E., 2021. Design and multicriteria assessment of low-input cropping systems based on plant diversification in southwestern France. Agron. Sustain. Dev. 41, 65. https://doi.org/10.1007/s13593-021-00719-7.

Chantre, G.R., González-Andújar, J.L., 2020. Decision Support Systems for Weed Management. Springer International Publishing, Cham. DOI: https://doi.org/10.1007/978-3-030-44402-0.

Chauvel, B., Guillemin, J.P., Colbach, N., Gasquez, J., 2001. Evaluation of cropping systems for management of herbicide-resistant populations of blackgrass (*Alopecurus myosuroides* Huds.). Crop Prot. 20, 127–137.

Chicouene, D., 2020. Inventory and mechanisms of cultural control practices for weed management, a review. J. Res. Weed Sci. 3, 490–528. https://doi.org/10.26655/JRWEEDSCI.2020.4.6.

Colbach, N., Adeux, G., Cordeau, S., Moreau, D., 2023. Weed-induced yield loss through resource competition cannot be sidelined. Trends Plant Sci. https://doi.org/10.1016/j.tplants.2023.08.004.

Colbach, N., Bertrand, M., Busset, H., Colas, F., Dugué, F., Farcy, P., Fried, G., Granger, S., Meunier, D., Munier-Jolain, N.M., Noilhan, C., Strbik, F., Gardarin, A., 2016. Uncertainty analysis and evaluation of a complex, multi-specific weed dynamics model with diverse and incomplete data sets. Environ. Model. Softw. 86, 184–203. https://doi.org/10.1016/j.envsoft.2016.09.020.

Colbach, N., Busset, H., Roger-Estrade, J., Caneill, J., 2014a. Predictive modelling of weed seed movement in response to superficial tillage tools. Soil Tillage Res. 138, 1–8.

Colbach, N., Busset, H., Yamada, O., Dürr, C., Caneill, J., 2006. ALOMYSYS: Modelling black-grass (*Alopecurus myosuroides* Huds.) germination and emergence, in interaction with seed characteristics, tillage and soil climate. II. Evaluation. Eur. J. Agron. 24, 113–128.

Colbach, N., Chauvel, B., Messéan, A., Villerd, J., Bockstaller, C., 2020a. Feeding pollinators from weeds could promote pollen allergy. A simulation study. Ecol. Indic. 117, 106635 https://doi.org/10.1016/j.ecolind.2020.106635.

Colbach, N., Colas, F., Cordeau, S., Maillot, T., Queyrel, W., Villerd, J., Moreau, D., 2021. The FLORSYS crop-weed canopy model, a tool to investigate and promote agroecological weed management. Field Crops Res. 261, 108006 https://doi.org/10.1016/j.fcr.2020.108006.

Colbach, N., Collard, A., Guyot, S.H.M., Mézière, D., Munier-Jolain, N.M., 2014b. Assessing innovative sowing patterns for integrated weed management with a 3D crop:weed competition model. Eur. J. Agron. 53, 74–89. https://doi.org/10.1016/j.eja.2013.09.019.

Colbach, N., Cordeau, S., 2018. Reduced herbicide use does not increase crop yield loss if it is compensated by alternative preventive and curative measures. Eur. J. Agron. 94, 67–78. https://doi.org/10.1016/j.eja.2017.12.008.

Colbach, N., Felten, E., Gée, C., Klein, A., Lannuzel, L., Lecomte, C., Maillot, T., Strbik, F., Villerd, J., Moreau, D., 2022. Tracking ideal varieties and cropping techniques for agroecological weed management: a simulation-based study on pea. Front. Plant Sci. 13, 809056 doi.org\10.3389/fpls.2022.809056.

Colbach, N., Petit, S., Chauvel, B., Deytieux, V., Lechenet, M., Munier-Jolain, N., Cordeau, S., 2020b. The pitfalls of relating weeds, herbicide use, and crop yield:

Don't fall into the trap! A critical review. Front. Agron. 2 https://doi.org/10.3389/fagro.2020.615470.
Colbach, N., Roger-Estrade, J., Chauvel, B., Caneill, J., 2000. Modelling vertical and lateral seed bank movements during moulboard ploughing. Eur. J. Agron. 13, 111–124.
Corre-Hellou, G., Dibet, A., Hauggaard-Nielsen, H., Crozat, Y., Gooding, M., Ambus, P., Dahlmann, C., von Fragstein, P., Pristeri, A., Monti, M., Jensen, E.S., 2011. The competitive ability of pea-barley intercrops against weeds and the interactions with crop productivity and soil N availability. Field Crops Res. 122, 264–272. https://doi.org/10.1016/j.fcr.2011.04.004.
Cournault, Q., Colbach, N., Busset, H., Matejicek, A., Souche-Suchovsky, P., Prudent, M., Moreau, D., 2024. Interspecies diversity in morphological responses to water stress: study on a panel of weed and crop species. Environ. Exp. Bot., 105825 https://doi.org/10.1016/j.envexpbot.2024.105825.
Fujita, K., Ofosu-Budu, K.G., Ogata, S., 1992. Biological nitrogen fixation in mixed legume-cereal cropping systems, 1990. In: Ladha, J.K., George, T., Bohlool, B.B. (Eds.), Biological Nitrogen Fixation for Sustainable Agriculture: Extended versions of papers presented in the Symposium, Role of Biological Nitrogen Fixation in Sustainable Agriculture at the 13th Congress of Soil Science. Springer Netherlands, Dordrecht, Kyoto, Japan.
Gardarin, A., Dürr, C., Colbach, N., 2012. Modeling the dynamics and emergence of a multispecies weed seed bank with species traits. Ecol. Model. 240, 123–138. https://doi.org/10.1016/j.ecolmodel.2012.05.004.
Gaudio, N., Escobar-Gutierrez, A.J., Casadebaig, P., Evers, J.B., Gérard, F., Louarn, G., Colbach, N., Munz, S., Launay, M., Marrou, H., Barillot, R., Hinsinger, P., Bergez, J.-E., Combes, D., Durand, J.-L., Frak, E., Pagès, L., Pradal, C., Saint-Jean, S., Werf, W. V.D., Justes, E., 2019. Modeling mixed annual crops: current knowledge and future research avenues. A review. Agron. Sustain. Dev. 39, 20. https://doi.org/10.1007/s13593-019-0562-6.
Gu, C., Bastiaans, L., Anten, N.P.R., Makowski, D., van der Werf, W., 2021. Annual intercropping suppresses weeds: a meta-analysis. Agric., Ecosyst. Environ. 322, 107658 https://doi.org/10.1016/j.agee.2021.107658.
Jastrzebska, M., Kostrzewska, M.K., Marks, M., Jastrzebski, W.P., Treder, K., Makowski, P., 2019. Crop rotation compared with continuous rye cropping for weed biodiversity and rye yield. A case study of a long-term experiment in Poland. Agronomy-Basel 9, 17. https://doi.org/10.3390/agronomy9100644.
Justes, E., Bedoussac, L., Dordas, C., Frak, E., Louarn, G., Boudsocq, S., Journet, E.-P., Lithourgidis, A., Pankou, C., Zhang, C., Carlsson, G., Jensen, E.S., Watson, C., Li, L., 2021. The 4c approach as a way to understand species interactions determining intercropping productivity. Front. Agric. Sci. Eng. 8, 387–399. https://doi.org/10.15302/J-FASE-2021414.
Kiær, L.P., Skovgaard, I.M., Østergård, H., 2009. Grain yield increase in cereal variety mixtures: a meta-analysis of field trials. Field Crops Res. 114, 361–373. https://doi.org/10.1016/j.fcr.2009.09.006.
Laurent, L., Ullmann, A., Castel, T., 2023. How abrupt changes in surface temperature impacts water cycle over France? The case study of winter bread wheat area. Total Environ. Res. Themes 8, 100079. https://doi.org/10.1016/j.totert.2023.100079.
Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field – methodology matters! Funct. Ecol. 22, 134–147. https://doi.org/10.1111/j.1365-2435.2007.01339.x.
Lecuyer, J., 2009. Paramétrage et évaluation d'un modèle de compétition culture/adventices. ENSAR,
Lemerle, D., Smith, A., Verbeek, B., Koetz, E., Lockley, P., Martin, P., 2006. Incremental crop tolerance to weeds: a measure for selecting competitive ability in Australian wheats. Euphytica 149, 85–95. https://doi.org/10.1007/s10681-005-9056-5.
Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. 69 (1), 33. https://doi.org/10.18637/jss.v069.i01.
Lewis, J., 1973. Longevity of crop and weed seeds: survival after 20 years in soil. Weed Res. 13, 179–191.
Liebman, M., Dyck, E., 1993. Crop rotation and intercropping strategies for weed management. Ecol. Appl. 3, 92–122.
Liebman, M., Gallandt, E.R., 1997. Many Little Hammers: Ecological Management of Crop-Weed Interactions. In: {C}Jackson, L.E.{C} (Eds.) Ecology in Agriculture, Academic Press, San Diego, CA.
MacLaren, C., Waswa, W., Aliyu, K.T., Claessens, L., Mead, A., Schöb, C., Vanlauwe, B., Storkey, J., 2023. Predicting intercrop competition, facilitation, and productivity from simple functional traits. Field Crops Res. 297, 108926 https://doi.org/10.1016/j.fcr.2023.108926.
Mason, H.E., Navabi, A., Frick, B.L., O'Donovan, J.T., Spaner, D.M., 2007. The weed-competitive ability of Canada western red spring wheat cultivars grown under organic management. Crop Sci. 47, 1167–1176. https://doi.org/10.2135/cropsci2006.09.0566.
Mézière, D., Petit, S., Granger, S., Biju-Duval, L., Colbach, N., 2015. Developing a set of simulation-based indicators to assess harmfulness and contribution to biodiversity of weed communities in cropping systems. Ecol. Indic. 48, 157–170. https://doi.org/10.1016/j.ecolind.2014.07.028.
Munier-Jolain, N.M., Collard, A., Busset, H., Guyot, S.H.M., Colbach, N., 2014. Investigating and modelling the morphological plasticity of weeds in multi-specific canopies. Field Crops Res. 155, 90–98. https://doi.org/10.1016/j.fcr.2013.09.018.
Munier-Jolain, N.M., Guyot, S.H.M., Colbach, N., 2013. A 3D model for light interception in heterogeneous crop:weed canopies. Model structure and evaluation. Ecol. Model. 250, 101–110. https://doi.org/10.1016/j.ecolmodel.2012.10.023.
Neyret, M., de Rouw, A., Colbach, N., Robain, H., Soulileuth, B., Valentin, C., 2020. Year-to-year crop shifts promote weed diversity in tropical permanent rainfed cultivation. Agric. Ecosyst. Environ. 301, 107023 https://doi.org/10.1016/j.agee.2020.107023.
Oerke, E.-C., 2006. Crop losses to pests. J. Agric. Sci. 144, 31–43. https://doi.org/10.1017/S0021859605005708.
Pek, J., Wong, O., Wong, A.C.M., 2018. How to address non-normality: a taxonomy of approaches, reviewed, and illustrated. Front. Psychol. 9 https://doi.org/10.3389/fpsyg.2018.02104.
Pelzer, E., Hombert, N., Jeuffroy, M.H., Makowski, D., 2014. Meta-analysis of the effect of nitrogen fertilization on annual cereal-legume intercrop production. Agron. J. 106, 1775–1786. https://doi.org/10.2134/agronj13.0590.
Piliksere, D., Strazdiņa, V., Vīcupe, Z., Jansone, Z., Legzdiņa, L., Beinarovičа, I., Kronberga, A., 2013. Cereal breeding for organic farming: crop traits related with competitiveness against weeds. Proc. Latv. Acad. Sci. 67, 272–276.
Pointurier, O., Moreau, D., Pagès, L., Caneill, J., Colbach, N., 2021. Individual-based 3D modelling of root systems in heterogeneous plant canopies at the multiannual scale. Case study with a weed dynamics model. Ecol. Model. 440, 109376 https://doi.org/10.1016/j.ecolmodel.2020.109376.
Raseduzzaman, M., Jensen, E.S., 2017. Does intercropping enhance yield stability in arable crop production ? A meta-analysis. Eur. J. Agron. 91, 25–33. https://doi.org/10.1016/j.eja.2017.09.009.
Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113, 447–455.
van der Werf, W., Zhang, L., Li, C., Chen, P., Feng, C., Xu, Z., Zhang, C., Gu, C., Bastiaans, L., Makowski, D., Stomph, T., 2021. Comparing performance of crop species mixtures and pure stands. Front. Agric. Sci. Eng. 8, 481–489.
Verret, V., Gardarin, A., Pelzer, E., Médiène, S., Makowski, D., Valantin-Morison, M., 2017. Can legume companion plants control weeds without decreasing crop yield? A meta-analysis. Field Crops Res. 204, 158–168. https://doi.org/10.1016/j.fcr.2017.01.010.
Weisberger, D., Nichols, V., Liebman, M., 2019. Does diversifying crop rotations suppress weeds? A meta-analysis. PLOS ONE 14, e0219847. https://doi.org/10.1371/journal.pone.0219847.
Worthington, M., Reberg-Horton, S.C., Brown-Guedira, G., Jordan, D., Weisz, R., Murphy, J.P., 2015. Morphological traits associated with weed-suppressive ability of winter wheat against Italian ryegrass. Crop Sci. 55, 50–56. https://doi.org/10.2135/cropsci2014.02.0149.
Xu, Z., Li, C.J., Zhang, C.C., Yu, Y., van der Werf, W., Zhang, F.S., 2020. Intercropping maize and soybean increases efficiency of land and fertilizer nitrogen use; a meta-analysis. Field Crops Res. 246 https://doi.org/10.1016/j.fcr.2019.107661.
Yu, Y., Stomph, T.-J., Makowski, D., Zhang, L., van der Werf, W., 2016. A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management. Field Crops Res. 198, 269–279. https://doi.org/10.1016/j.fcr.2016.08.001.