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Which pea traits for agroecological weed management in pea-wheat intercrops. A simulation study

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ABSTRACT

Context: Intercropping pea (*Pisum sativum* L.) with cereals is a promising lever to reduce weed infestation and damages. A large phenotypic diversity exists in pea which could be used for breeding varieties adapted to intercropping and weed management.
Objective: We aimed to identify, depending on cropping system and weed flora, (1) the key pea parameters (traits) that drive crop production and weed control in pea intercropped with wheat (*Triticum aestivum* L.), (2) optimal combinations of pea and wheat parameter values, and intercrop management techniques, to maximise these goals.
Material and methods: Virtual experiments were run, using 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 model includes five winter pea and three winter wheat varieties. Virtual varieties (5 pea and 10 wheat) were created by randomly combining variety-parameter values according to a Latin Hypercube Sampling (LHS) plan, respecting parameter ranges and 2-by-2 Pearson correlations observed in real varieties. 3600 cropping systems were simulated following another LHS plan, combining pea and wheat varieties, crop rotations and management techniques in nine contrasting situations (e.g., conventional, organic, no-till, type of weed flora). Simulated data were analysed with classification and regression trees (CART). Another simulation plan followed the same method, but pea was grown as a sole crop.
Results: Intercropping reduced pea yield loss due to weeds (by 30% for the least weed-tolerant varieties, e.g. Enduro) and field infestation (by 14% for the least weed-suppressive varieties, e.g., 886–1). We highlighted (1) key pea parameters (e.g., biomass allocation to leaves until full maturity, increased plant width per unit biomass when shaded, frost tolerance) and (2) how to combine them to maximise potential yield and weed suppression. The combination of parameter values that increase light interception (when shaded, allocate a larger proportion of biomass to leaves, grow taller and wider per unit biomass, shift leaves upwards) fitted to most contexts. Other combinations were specific to particular systems (e.g., a large superficial root system to leave less soil moisture for superficial weed seeds only works in no-till).
Conclusions: A high pea yield in weed-infested intercrops needs a pea variety with a high yield potential, a weed-suppressive wheat variety and weed-preventive management techniques.
Implications: Our results are pointers for breeding varieties to regulate weeds in intercrops, and rules for farmers to choose pea varieties, depending on the production goal, the intercropped wheat variety and the cropping system. Further research needs to link pea parameters to variables routinely measured in breeding programmes.

1. Introduction

Weeds are very harmful to crop production (Oerke, 2006) though essential for biodiversity in agricultural landscapes (Blaix et al., 2018). As herbicide use must be reduced because of environmental and health issues, weed management strategies must be completely overhauled to leave out herbicides, which are usually highly efficient and easy-to-use. For this, it is necessary to combine multiple and mostly preventive management techniques, each of which is partially effective (Liebman and Dyck, 1993; Liebman and Gallandt, 1997). Among these techniques, intercropping, i.e., growing different crop species simultaneously, has been reported to allow a better weed control (Weisberger et al., 2019).

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In particular, cereal–legume intercrops improve weed control compare to sole legumes (Verret et al., 2017; Gu et al., 2021). In addition, such mixtures improve crop production (Kiær et al., 2009; Bedoussac et al., 2015), land and resource use efficiency (Pelzer et al., 2014; Xu et al., 2020), and disease control (Boudreau, 2013).

To date, intercropping is still a niche production in most European countries. In France for instance, cereal–legume intercrops cover only 1% of arable area at national scale (more than 5% in some departments) but they are particularly associated with organic farms and feed autonomy of livestock farms (Yan et al., 2025). They thus contribute to herbicide-use reduction and to another key challenge in agriculture, i.e., the need to increase plant-based protein production (Hristov et al., 2024). Pea (*Pisum sativum* L.) and wheat (*Triticum aestivum* L.) are two particular interesting candidates for intercropping, as respectively the most grown grain legume (166 405 ha, 52% of grain legume area in 2024) and cereal (4 215 574 ha, 50% of cereal area) in France (Agreste, 2025).

Weed suppression is the ability of a crop to reduce weed biomass and/or weed seed production (Mason et al., 2007; Worthington and Reberg-Horton, 2013; Zerner et al., 2016). The other component of crop competiveness against weeds is tolerance against weeds (hence, "weed tolerance"), i.e., the ability to reduce yield loss in the presence of weeds (Goldberg, 1990; Lemerle et al., 2006; Zerner et al., 2016). The traits that make pea competitive against weeds have been investigated in sole-crop pea (Jacob et al., 2017; Colbach et al., 2022). Identifying the traits that promote weed regulation in pea–wheat intercropping is more complex. These traits result from the balance of competition, complementarity, cooperation, and compensation between the species, called "the 4 C approach" (Justes et al., 2021). This should ensure a higher resource capture compared to sole crops, thereby hampering weed growth (Liebman and Dyck, 1993; Corre-Hellou et al., 2011).

Interspecies interactions are usually disregarded during crop breeding, whether with companion crops or weeds (Francis et al., 1978; Kammoun et al., 2021; Kiær et al., 2022). Moreover, screening all possible combinations of crop lines in intercropping field experiments would be next to impossible because it would require testing many variety combinations in many pedoclimates, weed-flora contexts or cropping systems. It is also notoriously difficult to correctly estimate crop yield loss due to weeds in fields because it is next to impossible to ensure a continuously weed-free control to measure potential yield (Colbach et al., 2020c) as well as a homogeneous weed-infested test. Even if models are an imperfect representation of reality, they (particularly mechanistic process-based ones) make it easier to identify limiting factors, relevant crop traits and ideotypes, and to account for interactions between genotype, environment and cropping system (Jeuffroy et al., 2014). Models also make it easier to discriminate the two components of weed competitiveness, i.e., weed tolerance and weed suppression.

The objective of the present study was to use a mechanistic crop-weed model to identify (1) the key pea and wheat traits (corresponding to model parameters) and (2) pea and wheat ideotypes (i.e., theoretical ideal crop plants, Martre et al., 2015) that make their intercrops competitive against weeds, in different management scenarios. As intercropping is more beneficial for the less competitive pea than for the highly competitive wheat (McDonald, 2003; Corre-Hellou et al., 2011; Gu et al., 2021), the present study voluntarily focused on the performance of pea in the intercrop. The focus was also on the resource for which crops and weeds compete the most in temperate fertilised cropping systems, i.e., light (Wilson and Tilman, 1993; Perry et al., 2003; Colbach et al., 2023). Model parameters considered here are traits that are independent of environmental conditions (Tardieu, 2003). They only vary with the species and/or crop variety and characterize their intrinsic properties. For example, plant height per unit biomass at flowering onset in unstressed conditions (i.e., non-limiting resources and absence of competition by neighbouring plants) is a constant parameter value for a given species/variety, in contrast to plant height at flowering onset, which depends on growing conditions.

We ran virtual experiments with actual and virtual pea and wheat varieties in contrasting cropping systems to identify (1) the most influential pea parameters that drive intercrop yield and weed harmfulness, and (2) optimal combinations of pea and wheat parameter values for yield, weed tolerance and weed suppression. These parameters and combinations were determined (1) irrespective of the associated wheat variety and cropping system to identify generalist pea ideotypes, and also (2) depending on the intercropping designs and associated wheat variety/traits to identify specialist ideotypes adapted to contrasting conditions. Adaptation to other crop-management techniques was already investigated in a previous study (Colbach et al., 2022) and was ignored here.

In order to evaluate weed impacts on crop production and biodiversity, the model used in this study needed to simulate multi-annual and multi-species weed–crop dynamics from cropping system and pedoclimate. For this, the FLORSYS model was chosen as one of the most complete model (see reviews by Freckleton and Stephens, 2009; Colbach et al., 2021). There are other process-based models that simulate intercrops, sometimes in much more detail, but most are annual bi-species models, none of which consider weeds and few go beyond light partitioning between constituent species to include effects on morphological plasticity and/or of most management techniques (Gaudio et al., 2019; Meunier et al., 2022).

2. Material and methods

2.1. Principle

The simulation plan aimed to evaluate the impact of pea and wheat variety parameters and intercrop management techniques on intercrop performance in a large range of contrasting cropping systems, weed floras and weather years, albeit from the same region and with the same soil, in order to identify the most influential pea parameters, intercrop management techniques and combinations thereof to ensure high intercrop yields in weedy conditions. We conducted a global sensitivity analysis (i.e., varying factors simultaneously, Saltelli et al., 2000), adapting the method from our previous simulation studies on sole-crop pea (Colbach et al., 2022) and sole-crop wheat (Lebreton et al., 2025).

First, a range of contrasting varieties was parameterized for FLORSYS (step 1 in Fig. 1). These included actual varieties parameterized from experiments and literature (step 1.1) as well as virtual varieties to extend the range of parameter values and combinations thereof to identify directions for future crop breeding (2.3.1). The approach was akin to variety testing by crop breeders, with different conditions and evaluation criteria, except that many more cropping systems, weed flora conditions and evaluation criteria were used here than in field tests.

In step 2 of Fig. 1, intercrops combining these pea and wheat varieties were tested with different weed floras, intercrop management and weather conditions. Considering the many traits and management options and their ranges of variation, it is impossible to build a complete structured simulation plan, such as a factorial experimental plan. Instead, a set of nested space-filling designs was used (2.3): (1) nine situations contrasting in terms of cropping-system types and weed floras were created in step 2.1 because pea varieties respond differently to management techniques and weed species, (2) for each situation, Latin Hypercube Sampling (LHS) was used to build a space-filling design of 400 cropping systems whose rotations and management techniques had to respect the type of cropping system practices (step 2.2), (3) these systems were simulated over a dozen years and repeated with five different weather scenarios (step 2.3, 2.3.3).

LHS was used in steps 1.2 and 2.2 because it is the best compromise to explore the whole space of possible input combinations with the fewest simulation runs (McKay et al., 1979). Step 2.1 improved the efficiency of space filling for cropping systems even more, by concentrating space filling to the range of input combinations that were the most pertinent for major arable cropping system types of temperate

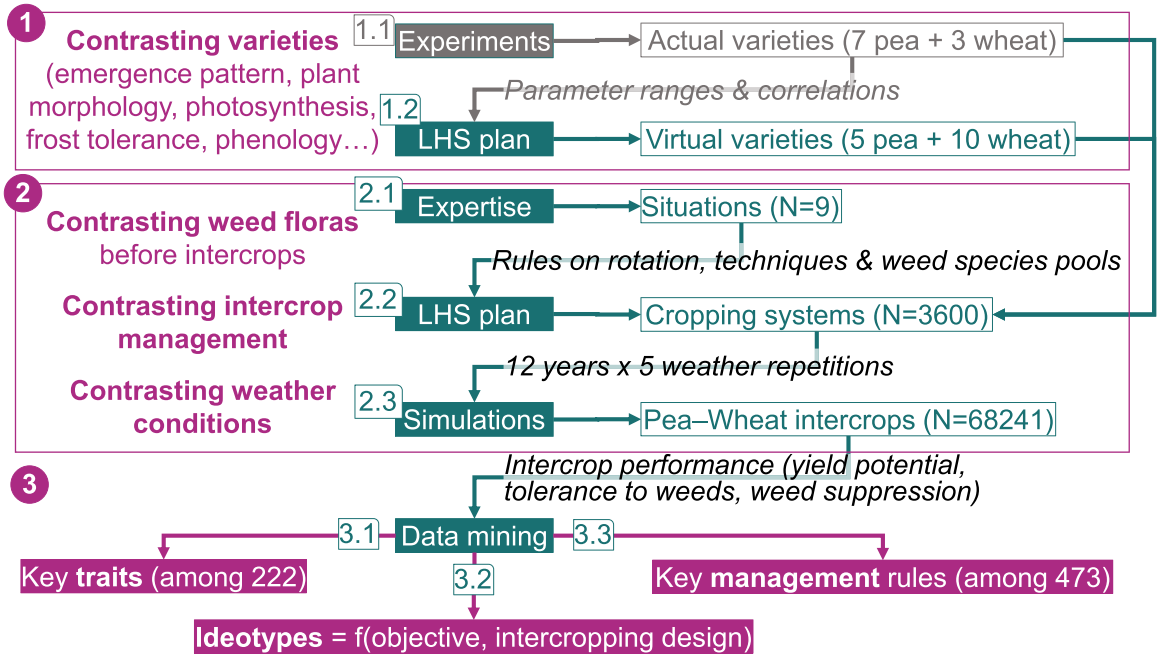


Fig. 1. Flowchart summarizing the three steps, with their objectives (in purple), substeps (blue-green boxes) and their outputs (white boxes), conducted in this study to identify key crop traits, crop ideotypes and key management techniques for weed management in pea–wheat intercrops, using simulations with the FLORSYS model (Colbach et al., 2021). Step 1.1 and part of step 1.2 were conducted previously (Munier-Jolain et al., 2014; Colbach et al., 2022). LHS refers to Latin Hypercube Sampling.

conditions.

In the last step (step 3 of Fig. 1), simulated intercrops were analysed with data mining techniques (2.4) to identify key crop traits (step 3.1), pea–wheat ideotypes (step 3.2) and key management techniques (step 3.3). Data mining (or machine learning) is particularly adapted to explore simulation plans as the ones used here, with many interacting inputs. Indeed, they provide non-parametric analysis methods, allowing heterogeneous data sets with numerous and interacting inputs as long as the learning data set is large enough (Villa-Vialaneix et al., 2012). Classification and Regression Trees (Breiman et al., 1984) were preferred to Random Forests (Breiman, 2001) as they not only allow ranking inputs according to their impact on outputs, but also input combinations, which are needed to identify crop ideotypes.

To assess the impact of intercropping on pea or wheat varieties in terms of yields, competiveness vs their companion crop, weed tolerance and weed suppression, the simulations of step 2.3 were repeated by replacing the intercrop by either pure pea or pure wheat (2.3.4). Average variety performance in intercrops vs sole crops were plotted to identify which varieties over- or underperformed in intercropping relatively to the mean variety pool (2.4.2).

2.2. *The virtual field FlorSys*

FLORSYS is a virtual field on which cropping systems can be experimented, producing a large range of virtual measurements of crop, weed and environmental state variables (Gardarin et al., 2012; Munier-Jolain et al., 2013, 2014; Colbach et al., 2014a, 2014b, 2021; Pointurier et al., 2021). The main steps are summarized below and further details can be found in section A in the supplementary material online. The FLORSYS3_03072020 version was used here.

2.2.1. *Weed and crop life cycle*

The input variables of FLORSYS consist of (1) a description of the simulated field (daily climatic conditions, latitude and soil characteristics); (2) all the crops (including intercropping and cover crops) and management operations in the field, with dates, tools and options; and (3) the initial weed seed bank, which is either measured on soil samples or estimated from regional flora assessments (Colbach et al., 2016). These 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, combining approaches from functional-structural plant models (FSPMs) and "big leaf" models to allow for multispecies heterogeneous canopies and applicable to dozens of contrasting species (Colbach et al., 2021; Gaudio et al., 2022). As in FSPMs, each crop and weed plant is positioned after emergence and represented in 3D but with the same representation regardless of species. This resulted in a cylinder (above ground) on top of a spilled cone (below ground), in which biomass, leaf area and root-length density are distributed along height and depth. Space is discretized with voxels (3D pixels) in which plants compete for resources as in "big leaf" models: in a given voxel, a given plant absorbs photosynthetically active radiation (PAR) depending on the incident PAR on top of the voxel, the plant's leaf area in the voxel and the species extinction coefficient relatively to the leaf areas and extinction coefficients of all other plants with leaves inside this voxel. The photosynthesized biomass also depends on air temperature, as does respiration. Biomass is allocated among compartments (leaves, stems, seeds, roots) and the plant volume increases, depending on species potential and shade-response parameters. At plant maturity, weed seeds are added to the soil seed bank; crop seeds are harvested to determine crop yield. Nitrogen stress is disregarded in the present model version, and water stress only considered for pre-emergent processes as the necessary submodel is still work in progress.

Despite these limits, FLORSYS integrates examples of the 4 C processes proposed to describe plant × plant interactions in the context of intercropping (Justes et al., 2021). Competition is included for (1) the main resource for which crops and weeds compete in temperate conditions, i.e., light, and, to a lesser degree, (2) for water when emerged plants leave less water for still emerging plants. However, plant–plant competition for water and nitrogen as well as nitrogen fixation were

disregarded. Complementarity corresponds to the spatio-temporal differentiation in niches. It is included in FLORSYS by differentiating plant cohorts depending on their emergence date and representing each plant in 3D, with its particular biomass, plant height and width, leaf area and root length density. This also allows including compensation when one of the intercrop crop species emerges or grows badly and the other crop species occupies the empty niches. Finally, cooperation is when the modification of the environment by one species is beneficial to the others. It occurs in FLORSYS when the light interception of climbing species is improved by the physical support of neighbouring species, but also when one of the intercrop species controls weeds that would be harmful for the other crop. But increased soil-resource availability was disregarded.

2.2.2. The species and varieties included in FLORSYS and their parameters

The model version used here was parameterized for 26 common and contrasting annual weed species (section A.5 of the supplementary material online). In addition to pea and wheat, the model includes 30 other crop species, consisting of cash crops as well as cover and forage crop species. This diversity is essential to simulate crop rotations into which intercrops must be included to take into account the effect of past crops on the soil conditions (e.g., structure, water content) and weed seed bank present at the onset of the intercrop as well as the after-effects on subsequent crops.

Crops and varieties are characterized by a set of 222 parameters driving germination and emergence (22 parameters), photosynthesis and biomass production (9), potential plant morphology and shade response at 11 key stages from emergence to full maturity (145), root

Table 1
Key features of the simulation study for assessing pea and wheat varieties.

A. The nine expert-based situations for structuring the simulation plan (details in supplementary material in section B.1 online). Differences highlighted in grey

Situation	Rotation	Crop management	Weed flora
1	**Intercrop, wheat, oilseed rape**	**Conventional**	**26 annuals**
2	Same as ①	① with mechanical weeding and more tillage	Same as ①
3		② without pesticides or organic fertilizer	
4		① without tillage	
5	① without oilseed rape	Same as ①	
6	① with barley		
7	⑥ with sunflower, maize		
8	Same as ①		6 harmful
9			6 harmful dicots

B. The three designs for intercropping pea and wheat (details in section B.3 online)

Design	Density (relative to usual pure-crop density)		
	Total	Pea	Wheat
Incomplete	6–90%	3–71%	2–72%
Substitutive	90–110%	18–89%	17–83%
Additive	110–489%	29–322%	16–250%

C. The five key indicators for assessing an intercrop or a variety (details in section A.8 online)

Annual indicator	Unit	Origin	Scale	Assessment of
Potential yield	t/ha	Weed-free simulation	Species	Yield potential
Field infestation	t/ha	Weed-inclusive simulation	Field	Weed suppression
Yield loss	%	(actual– potential yield) / potential	Species	Weed tolerance
Actual yield	t/ha	Weed-inclusive simulation	Species	Combined species result
Actual yield	MJ/ha	Weed-inclusive simulation	Field	Total outcome

system (13), frost damage after emergence, during vegetative growth and reproduction (12), seed production (4) and phenology (17). Most parameters were estimated per variety, except for some belowground processes whose parameter values were determined per species (section A.6 online). Further parameters describe processes specific for weeds, e.g., seed dormancy and *in situ* mortality in the soil. The parameter values were estimated in previous studies (for pea, see Colbach et al., 2022; for wheat, see Lebreton et al., 2025), from experiments (greenhouse, garden plots, fields ….), other models and literature. A summary of the parameter origins is given in section A.6 online, the detailed list with the range of variations for pea, wheat and other species is included in section F.3 online.

2.2.3. Effect of cultural techniques

Life-cycle processes depend on the dates, options and tools of management operations (tillage, sowing, herbicides, mechanical weeding, mowing, harvesting), in interaction with weather and soil conditions on the day the operations are carried out (section A.7 online). For instance, weed plant survival probabilities are calculated deterministically (i.e., without any random effect) depending on management operations, biophysical environment as well as weed morphology and stage; the actual survival of each plant is determined stochastically (i.e., including some random variability) by comparing this probability to a random probability. The effect of crop and variety choice is included indirectly, via biological processes such as plant-plant competition for resources (2.2.1) and via the choice of techniques for managing the crop.

2.2.4. Indicators of crop production, crop competitiveness and weed services

In addition to the daily state variables describing crops, weeds and the soil, FLORSYS simulates crop yield as well as annual indicators assessing weed impacts on crop production and biodiversity (Mézière et al., 2015; Colbach et al., 2020a) (see section A.8 online). The indicators analysed in the present study (Table 1.C) were potential yield (from weed-free simulations) and actual yield (from weed-infested simulations) as well as crop yield loss, as the relative crop yield difference of simulations with and without weeds. In the case of intercrops, these variables were considered separately for each crop species of the intercrop as well as at the field scale. In the latter case, energy yield (MJ/ha) resulting from multiplying the grain yield simulated by FLORSYS by its energy content (a crop parameter) (Mézière et al., 2015) was analysed to allow adding pea and wheat yields.

In addition, we analysed field infestation, i.e., the daily weed biomass averaged from crop sowing to crop harvest. Weed tolerance and weed suppression correspond to reduced yield loss and reduced field infestation, respectively. Finally, two indicators of weed contribution to biodiversity were included. Among the two FLORSYS indicators of wild plant biodiversity, weed species richness was chosen, which corresponds to the number of weed species with at least one plant during the current year (from harvest to harvest). Weed contribution to feeding domestic bees was chosen among the seven FLORSYS indicators of functional biodiversity, resulting from the daily number of weed flowers weighted by their pollinating value following fuzzy logic, and averaged during the bees' feeding season.

2.2.5. Domain of validity

FLORSYS was evaluated ("validated") with independent field data on weed short and long-term dynamics at French national scale, over a large range of existing arable cropping systems (section A.9 online). It showed that crop yields, daily weed species densities and, particularly, densities averaged over the years were generally well predicted and 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). The model is able to discriminate not only species but also varieties of a given species. For instance, Pearson correlations between observed and simulated aboveground biomasses, plant heights or leaf areas were 0.83, 0.91 and 0.96, respectively, in a weed-infested variety experiment (section A.9.2 online). Crop yield losses higher than those reported in previous field studies mostly resulted from the simulation plan. This does not adapt practices to simulated weed floras and interannual weather variability (as farmers or trial managers would do), 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).

2.3. Simulation plan for virtual experiments

2.3.1. Actual and virtual pea and wheat varieties

The actual winter pea and winter wheat varieties were parameterized from experiments and literature in previous studies (step 1.1 of Fig. 1). To date, five varieties (including two spring varieties) and two unregistered genotypes have been parameterized for pea (Colbach et al., 2022, section A.6.1 online) and three registered varieties for winter wheat (Caphorn, Cézanne, Orvantis; Munier-Jolain et al., 2014, section A.6.3 online). Here, these were completed with virtual winter varieties (5 pea and 10 wheat) to extend the range of variability in varieties and traits (2.3.1). Hence, the term "varieties" also refers to virtual varieties and to genotypes that have not yet been registered in the variety catalogue.

The virtual pea varieties had already been created by Colbach et al. (2022) and the virtual wheat varieties were added here. The values of the 222 species parameters of 2.2.2 were randomly chosen inside [0.9 minimum value, 1.1 maximum value] observed for each parameter on actual varieties (sections F.3 and F.4 online) based on Latin Hypercube Sampling (using the randomLHS() function of package lhs of R (R Core Team, 2023) (step 1.2 of Fig. 1). For parameters estimated per species (e.g., e.g., base water potential, additional seedling mortality in compacted soil), values were drawn inside [0.8 value, 1.2 value]. To avoid biological nonsense, sampling was constrained using the LHScorcorr() function of package pse (Pearson method, 0.05 accepted deviance, heuristic-determined number of iterations based on hypercube size) with correlations among parameters, i.e., 2-by-2 Pearson correlation coefficients established for the 222 parameters either on the seven parameterized pea varieties or the three wheat varieties with corr() of package Hmisc. Drawn parameter values needed to be logical, e.g., the proportion of non-dormant seeds could not exceed 1, or the minimum temperature for photosynthesis could not exceed the optimum one. Moreover, each time a pea-wheat intercrop was grown in a simulation, flowering timing was forced to ensure that pea was fully mature at crop harvest, regardless of the variety or the simulated weather. Simulations therefore disregarded photoperiod-dependency in pea varieties.

As fewer actual varieties were used to create the virtual varieties in wheat than in pea (3 vs. 7), parameter values varied less among wheat varieties (median coefficient of variation = 0.06, inter-quartile CV variation: 0.03–0.15, section A.6.5 online) than among pea varieties (median CV = 0.21, inter-quartile CV variation: 0.09–0.39). The moderate Pearson correlations found among pea parameters (including virtual varieties, median correlation coefficient $r = 0.26$, section B.2 online) showed that parameter values were not chosen totally randomly (as was the case for management techniques, see 2.3.2) and reflects the biological correlations among variety characteristics that were introduced by constraining the LHS via parameter correlations. The same was true for wheat parameters (results not shown).

2.3.2. Contrasting cropping systems including pea–wheat intercrops

In step 2.1 (Fig. 1), nine situations were chosen (Colbach et al., 2022) to determine rules for diversifying intercrop management and weed floras (Table 1.A), the latter by changing the crops preceding the intercrop and/or feeding particular weed species pools into the model. Briefly, the reference situation was based on a 3-year rotation (combining oilseed rape, pea-wheat intercropping and wheat, in any order), conventional management (including tillage, mineral fertilizer

and herbicides) and a weed species pool typical of Burgundy consisting of 26 contrasting annuals. The other situations varied in terms of rotation length (2-year, without wheat; 4-year, adding barley; 6-year, moreover adding sunflower and maize), crop management (complete, adding mechanical weeding; organic, moreover intensifying tillage, deleting herbicides and replacing mineral by organic fertilizer; no-till, replacing tillage by glyphosate) or weed species pool (the six most harmful weed species, the six weed species that contributed to feeding bees).

The cropping systems (400 per situation) were built in step 2.2 (Fig. 1) by randomly choosing management techniques (including pea and wheat varieties) based on Latin Hypercube Sampling (with randomLHS() of the lhs package of R and respecting the constraints of each situation (e.g., no tillage in the no-till situation, no herbicides in organic systems). Dates and options of management operations (e.g., seed density, seed depth and interrow width for sowing; depth, speed and tool for tillage) were randomly chosen for each crop of the rotation (see ranges in section B.1 online) but respecting agronomic logic (e.g., winter wheat could not be sown in spring, no tillage after crop sowing).

Pea and wheat sowing densities in intercrops were drawn in the same ranges as in sole crops (25–115 seeds/m^2 and 100–488 seeds/m^2, respectively, section B.1 online) simulated in the previous study (Colbach et al., 2022). Over all situations, 26% of the intercrops presented relative total sowing density of 100% (± 10%), corresponding to substitutive designs (Table 1.B). Relative total intercrop sowing densities were calculated by adding the intercrop pea sowing density divided by the standard sole-pea density (70 seeds/m^2) and the intercrop wheat sowing density divided by the standard sole-wheat density (290 seeds/m^2). These sole-crop densities correspond to the median densities from the previous sole-crop study of Colbach et al. (2022). 36% of the intercrops were additive designs whose relative total density exceeded 110% and the rest were "incomplete" designs with a relative total density of less than 90%. The latter corresponded to unconventional situations which experts would discard but were kept here to identify the most detrimental conditions. Relative pea and wheat sowing densities ranged from a median 33% and 32% for respectively pea and wheat in the incomplete design, through 51% and 49% in the substitutive design, to 68% and 65% in the additive design, with large variations for each of the three designs (Table 1.B). The maximum relative total sowing density in additive designs was 489%, which experts would usually not recommend, but which could be beneficial in terms of weed management.

The low Pearson correlations among simulated crop management techniques confirmed that the LHS plan indeed allowed decorrelating management variables: the highest correlations were found among rotation descriptors, with a median correlation of only 0.09 (section B.2 online). Moreover, correlations between pea or wheat parameters and crop management techniques were negligible, confirming that our simulation plan was adequate to avoid confusing effects of crop management and variety characteristics. This means, among others, that sowing dates and densities did not depend on pea or wheat varieties.

2.3.3. Simulation length and weather repetitions

The 9 × 400 cropping systems were simulated over 12 consecutive years to assess long-term effects and repeated with five weather series consisting of randomly chosen records from the INRAE Dijon weather station (47.3°N,5.0°E, INRAE Climatik database, 1987–2013). Mean annual temperature was 11°C, total annual precipitation 768 mm (details in section B.4.1 online), and the soil consisted mostly of clay and silt (41% clay, 54% silt, 5% sand). The resulting combination of cropping systems (3600), years (12) and weather series (5) resulted in a database of 216 000 lines, among which 68241 concerned pea–wheat intercrops. Even though all simulations started with one the three same initial seed banks (Table 1.A), the contrasting cropping systems and the different weather series selected for different weed communities over time, ensuring that these 68241 intercrops were exposed to very different weed seed banks at the time of their sowing.

2.3.4. Discriminating crop–crop interactions from crop–weed interactions

The simulations of step 2.3 (Fig. 1) succeeded in producing differences in intercrop production and weed (dis)services across situations. For instance, yield loss due to weeds varied from an average of 20% in situation 9 starting with only 6 dicot weeds beneficial for bees to 75% in the 2-year situation 2 (section C.1 online). To better understand plant–plant interactions and to discriminate pea–wheat competition from crop–weed competition or intraspecies competition, step 2.3 was actually run four times: (i) as described previously to estimate pea and wheat yields in the presence of weeds, (ii) replacing all intercrops by either pea or (iii) wheat sown at the same density as in the intercrops (iv) or at the standard sole-crop sowing densities (pea only), to evaluate weed suppression and yield loss due to a companion crop. All four series were also simulated without weeds to estimate potential yields and yield loss due to weeds, which was calculated as (yield from weed-free simulation – yield from weedy simulation) / (yield from weed-free simulation). The final database thus included 272 964 lines from weedy simulations, resulting from 68241 intercrops from four simulation series (intercrops, sole pea or sole wheat at same densities as in intercrops, sole pea at standard density,). The 272 964 weed-free data were used to calculated yield loss, which was then added to the weed database.

2.4. Statistics

The analysed response variables (performance indicators) were yield potential (yield from weed-free simulations), actual yield (from weedy simulations), weed tolerance (the opposite of yield loss due to weeds) and weed suppression (the opposite of field infestation by weed biomass) of all years with pea–wheat intercrops (N = 68241). These were analysed as a function of pea and wheat variety parameters as well as management techniques of the intercrops and any other crops of the rotation. We did not use any of the indicators commonly used in intercrop studies (e.g., Land Equivalent Ratio) (Bedoussac and Justes, 2011) as our aim was not to assess the advantage of intercropping vs. sole cropping but to identify optimal combinations of crop parameters for weed management.

The analysis and the presentation of the results focused on pea varieties and parameters as there were more actual varieties included in FLORSYS for pea than for wheat, making the virtual varieties more robust. Moreover, the behaviour of pea varieties and parameters in sole-crop has been investigated in our previous simulation study (Colbach et al., 2022), making it possible to analyse how far this behaviour changes in intercrops compared to sole crops.

2.4.1. Identify the most influential simulation factors with classification and regression trees

To identify which simulation factors influence the indicators, classification and regression trees (CART) (Breiman et al., 1984) were run with the library mvpart (De'ath *et al.*, 2014). The trees (see example in Fig. 2) predict a continuous response variable (here, the performance indicators) from a set of discrete or continuous predictor variables (here, our simulation factors, i.e., situation, pea-variety and wheat-variety parameters, crop management techniques). The data set is successively split into two subsets along a threshold value of the predictor in order to maximize the difference between subsets. Branches are combinations of predictor values that lead to predictions contained in leaf nodes.

Predictors (including surrogate variables that would split the data set exactly as the primary splitting predictor variables, see section D.1 online) were ranked according to their Variable Importance (VIP), i.e., a proxy of the indicator variability explained by the predictor (section D.2 online). To assess the contribution of predictor types (pea parameters, wheat parameters, intercrop management techniques, other-crop techniques, situation, i.e., regional weed flora pool and cropping-system type), relative partial R^2 were calculated for each type, dividing the

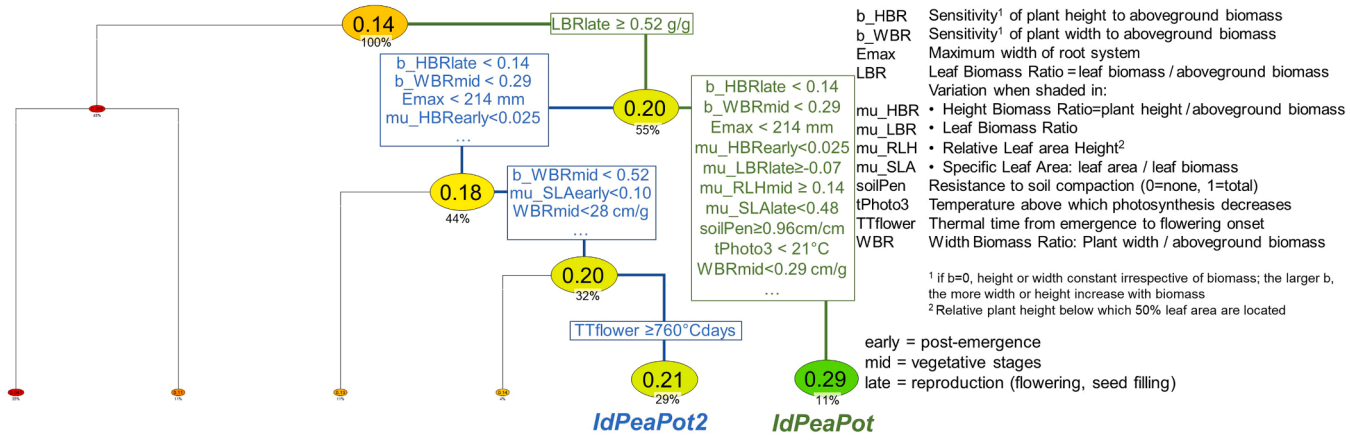


Fig. 2. Example of a classification and regression tree (CART) analysing potential pea yield (response variable) in pea-wheat intercrop from weed-free simulations as a function of pea parameters (see Table 4 for further explanations). The highlighted branches show the two best ideotypes, *IdPeaPot* (also in Table 4) and *IdPeaPot2*. Boxes show examples of predictors and thresholds for splitting branches (only for the two highlighted branches), sorted from the most to least influential predictors based on Variable Importance (VIP). Leaves (at the bottom of the tree) and nodes show indicator values normed to [0 =lowest yield,1 =highest yield of simulated data set]; leaves are coloured from red (lowest yield) to green (highest yield). Percentages below nodes show the proportion of individuals that fall into that node. The root node at the top of the tree has 100% since the dataset has not been split yet. (Nathalie Colbach 2023).

VIP summed over all predictors belonging to the type by the VIP summed over all predictors, excluding surrogates. This corresponds to the proportion of total CART R^2 explained the different predictor types.

2.4.2. Impact of intercropping on pea-variety performance

To rank pea varieties, the performance indicators were analysed in a linear model using the lm() function of R package stats (R Core Team, 2016), as a function of pea variety, wheat variety, situation (nine levels), year since simulation onset, their interaction as well as weather repetition. Average indicator values per pea variety were compared using the emmeans() function of package emmeans and a Tukey test to account for the unbalanced data set.

To assess the impact of intercropping on pea performance, the same four indicators were analysed with the same linear model and the same comparison of means, but using the data from the sole-crop control simulations (2.3.4). The mean indicator values per pea variety from pea–wheat intercrops were then plotted against the values from sole-crop pea, and the gaps with the y = x line analysed.

2.4.3. Identify pea ideotypes with classification and regression trees

Classification and regression trees (CART) were again used to identify pea ideotypes (i.e., optimal combinations of pea parameter values) for different selection targets in pea-wheat intercrops. The selection targets aimed to maximise potential and actual yields, as well as weed tolerance and weed suppression. To do so, CARTs were run, using only pea parameters as descriptor variables. The best branches of each CART were selected, i.e., those with the highest average yields (see example in Fig. 2). These branches described the generalist pea ideotypes that maximised performance in intercrops, regardless of the associated wheat variety, cropping-system type and crop management.

In raw CART outputs, the branch splits sort varieties with rules such as optimal *parameter value* < *threshold* vs *parameter value* ≥ *threshold*. To improve readability, the ideotype tables (e.g., Table 4) show optimal parameter ranges, i.e. *[min, threshold[* when low parameter values improve variety performance, or *[threshold, max]* when high parameter values are needed, with *min* and *max* the minimum and maximum parameter values observed on (actual and virtual) varieties. Moreover, based on past interactions with breeders (e.g., Lebreton et al., 2025), these ranges were compared to the parameter values of actual varieties.

Further CARTs were run to identify pea ideotypes adapted to different intercropping designs and/or associated wheat varieties. To adapt ideotypes to a given intercropping design (additive, substitutive, or incomplete), only the simulated intercrop data corresponding to that designs was used. To adapt to wheat varieties, wheat parameters were also used as descriptor variables.

Ideotypes were labelled starting with *Id* and the species (*Pea* or *Wheat*), followed by a suffix indicating the selection aim (*Pot, Yield* or *Tol* for potential yield, actual yield or weed tolerance) or the intercropping design (*Add, Sub* or *Inc* for additive, substitutive and incomplete designs).

2.4.4. Identify the most influential management techniques in intercrops

The key intercrop management techniques were those with the highest Variable Importance (VIP) in the trees of 2.4.1. For these, probabilities that indicators such as potential pea yield or pea tolerance to weeds in intercrops increases when an intercrop management variable (e.g., pea sowing density in intercrop) increases were calculated. To do this, for a given management variable, the relative number of data points that were sorted into the tree branch with the higher indicator value was calculated at each tree node where the variable was used to split the data set, and then summed over all tree nodes (section D.2.5 online). For each variable, the results table also summarize the mean biophysical causes for its effects on the analysed indicators, based on the processes included in the model.

The effects of rotation and management of other crops were also included in the analyses but only presented in supplementary material F.2 online as the present paper aims to focus on intercrops only.

3. Results

3.1. Major factors impacting yield and competitivity against weeds

3.1.1. Pea varieties were more influential than wheat varieties for intercrop yield

Potential yield (from weed-free simulations) of pea-wheat intercrop was more influenced by pea-variety parameters than wheat-variety parameters (proportion of R^2 explained by pea and wheat parameters = 0.24 and 0.08, respectively, Table 2). This was not because pea contributed more to intercrop yield than wheat (mean pea and yields in intercrops = 21 and 75.7 10^3 MJ/ha, respectively) but because pea yield in intercrops varied more than wheat yield (relative variation calculated as (3rd quartile – 1st quartile)/mean = 161% vs 106%, section C.2.2 online). The pea yield inside the intercrop was also the indicator that depended the most on pea-variety parameters whereas potential wheat

Table 2
Contribution of simulation factors to explaining indicators of intercrop yield and weed harmfulness in years with pea-wheat intercrops. Relative partial R^2 (coloured from white = 0 to yellow = 1) from classification and regression trees calculated from Variable Importance Predictors (VIP) relatively to total VIP. Yield loss due to.

Type of variables	Potential (weed-free) yield			Actual weed-infested yield			Yield loss due to weeds[$]			Field infestation
	Total intercrop	Pea in intercrop	Wheat in intercrop	Total intercrop	Pea in intercrop	Wheat in intercrop	Total intercrop	Pea in intercrop	Wheat in intercrop	
	High ← Impact of crops → Low									
	Low ← Impact of weeds → High									
Pea parameters	0.24	0.42	0.19	0.20	0.36	0.05	0.09	0.20	0.03	0.02
Wheat parameters	0.08	0.08	0.16	0.07	0.05	0.12	0.05	0.06	0.06	0.04
Intercrop techniques	0.57	0.31	0.47	0.49	0.33	0.52	0.49	0.48	0.51	0.35
Other-crop techniques	0.10	0.19	0.19	0.24	0.26	0.31	0.36	0.26	0.41	0.60
Initial weed seed bank	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total R^2	0.60	0.60	0.63	0.43	0.50	0.43	0.34	0.35	0.31	0.31

[$] Values < –100% were disregarded because they occurred when potential yield was close to zero and did not allow a correct calculation of loss.

yield was roughly equally influenced by wheat-variety and pea-variety parameters. But the two species grew best in different conditions as illustrated by the negative correlation between their weed-free sole-crop yields (r = –0.29, section C.3 online). Overall, the most influential factor was intercrop management (partial R^2 = 0.57, Table 2), e.g., tillage, sowing and harvesting dates, sowing densities and patterns (3.4).

3.1.2. Weed tolerance and suppression depended mostly on crop rotation and management

The more a performance indicator depended on weeds, the lower the influence of varieties was (Table 2): in contrast to potential and actual yields, yield loss due to weeds and, particularly, field infestation, depended almost entirely on management and initial weed seed bank. In other words, the impact of pea varieties was lower for weed tolerance (i.e., yield loss reduction) and negligible for weed suppression (i.e., field infestation reduction), in contrast to potential and actual yields. Weed-related biodiversity (e.g., weed species richness, weed-based trophic resources for insects or birds) did not depend on either pea or wheat varieties (results not shown) and was not investigated further in this paper. Total R^2 values were lower for actual yield, yield loss and field infestation than for potential yield, pointing to more "noise", due to complex interactions among simulation factors, notably interactions between crop parameters and crop management techniques.

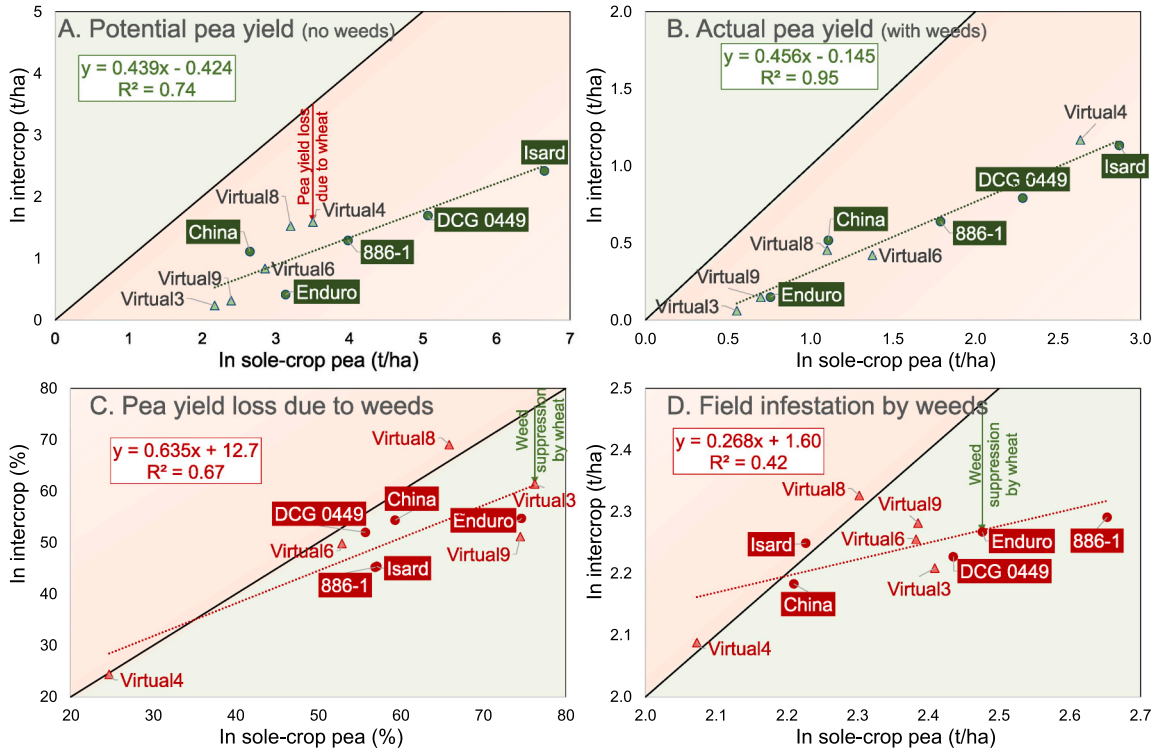


Fig. 3. Pea variety ranking in pea-wheat intercrops and in sole-crop pea. A. Potential (weed-free) pea yield, B. Actual (weed-infested) pea yield, C. Pea yield loss due to weeds, D. Field infestation by weeds. Expected Marginal Means after analyses of variance (see section C.2.1 online) of yields, yield losses and field infestations from years with intercrops from the 3600 cropping systems × 5 weather repetitions simulated with FLORSYS over 12 years in the intercropping simulation experiment and from years with sole-crop pea from the control simulation experiment with the same sowing densities as in the intercrop. Broken lines show linear regressions fitted to data points, continuous lines are y = x. Areas shaded in green (respectively red) show benefits (respectively detriments) due to intercropping (Nathalie Colbach 2025).

3.2. Pea varieties differ for their response to competition

3.2.1. Among pea varieties, yield varies more than competiveness against weeds

In average over all simulations, potential pea yield in intercrop varied ten-fold according to the pea variety (Fig. 3.A), with Virtual3 being the least productive and Isard the most productive variety. Actual pea yield even varied twenty-fold, from the least productive Virtual3 to the most productive Virtual4 (Fig. 3.B).

Weed tolerance and suppression varied much less among pea varieties. Pea yield loss due to weeds varied only approximately four-fold, from the most tolerant Virtual4 to the least tolerant Virtual3 (Fig. 3.C). Field infestation only increased by 10% from the most suppressive Virtual4 to the least suppressive Virtual8 (Fig. 3.D). This is consistent with the low effect of pea varieties on weed suppression reported in 3.1.

3.2.2. The less a pea variety was competitive, the more Intercropping improved weed tolerance

Pea–wheat intercrops tolerated and suppressed weeds better than sole pea crops though the benefit varied with the pea variety (Table 3). In average over all simulations, pea yield loss due to weeds was 8% lower in intercrops than in sole pea crops sown at their usual sowing density (51% vs 59% in Table 3), and even 20% lower for some of the least weed-tolerant pea varieties (Enduro, Virtual9). Conversely, the most weed-tolerant and suppressive variety Virtual4 did not benefit from intercropping, with similar weed-caused yield losses in both sole pea and pea-wheat intercropping.

The benefits of intercropping for weed suppression were even larger when its pea yield losses were compared to sole pea sown at the same density as the pea in the intercrops (Fig. 3.C). Then, losses dropped by 16% in average and up to 26% for the least weed-tolerant varieties (Table 3). Field infestation by weeds (which depended less on varieties, Table 2) decreased by 10% for the least weed-suppressive varieties such as 886–1 in intercrops (average = 8%), compared to sole pea (Fig. 3.D). The decrease in intercrop infestation compared to sole wheat was only 3% in average (section C.2.5 online). The beneficial effect of intercrops on weed suppression was visible even in the following crops of the rotation: intercropping reduced field infestation by 8% in average over all other crops (section C.2.2 online).

3.2.3. Wheat is more competitive than pea

Pea yield in weed-free intercrops decreased by 28–81% depending on the pea variety (average 55%) compared with sole pea crops (Fig. 3.A, Table 3), even when pea sowing densities were the same in both cases. This represents the yield loss of pea due to wheat, which was similar to the yield loss due to weeds (39–81%, average = 67%) observed in sole pea (Table 3). The most competitive pea variety against wheat (i.e., with the lowest weed-free yield loss due to wheat) was Virtual4, the least competitive ones Enduro, Virtual3 and Virtual9 (Table 3). The latter were also the least weed-tolerant varieties, with the largest weed-caused yield loss in sole pea, whereas Virtual4 was also the most weed-tolerant variety.

Pea yields in intercropping decreased with increasing intercrop wheat yields: wheat yield (t/ha) = 3.22 – 0.509 pea yield (t/ha) (R^2=0.51, section C.4 online). Isard was the only variety presenting a pea yield larger than expected from the associated wheat yield (approx. +1 t/ha). Wheat yield loss due to pea was much lower (20–50%, average = 30%) than its reciprocal (28–81%, average 55%). As for pea, the wheat varieties with the highest yield loss due to weeds (VirtualA and VirtualD) were also those with the highest yield losses due to pea (respectively 47% and 50% in weed-free fields, section C.2.5 online).

3.2.4. Contrasting winning pea variety profiles in intercrops

Isard and Virtual4 presented the best weed-infested yield, both in intercrops and in sole-crop pea (Fig. 3.B), but these resulted from different strategies. Isard presented the highest potential weed-free yield (Fig. 3.A) but a medium yield loss due to weeds (Fig. 3.C) and wheat (Table 3). Conversely, Virtual4 excelled in interspecies competition,

Table 3
Pea yield loss due to weeds and wheat, in sole pea and pea-wheat intercropping. Sole pea was either sown at the same density as in the intercrop, or at the usual pea sowing density. Estimated Marginal Means calculated after analyses of variance of pea yield loss due to weeds and *t*-tests at p = 0.05. Pea yield loss due to wheat was calculated as relative differences of mean pea variety yields in intercrops vs sole pea sown at the same density as in the intercrop, from simulations without and with weeds. Cells were coloured from green (lowest yield loss in table) through yellow to red (highest loss).

Pea variety[$]	Pea yield loss due to weeds (%)						Pea yield loss due to wheat (%)	
	Pea intercropped with wheat		Pea as sole crop					
			Same density		**Usual** density		Without weeds	With weeds
China	55	c	66	d	59	e	46	31
DCG 0449[§]	52	d	62	f	53	h	43	33
Enduro	54	c	81	a	74	b	81	62
886-1	46	f	66	d	57	f	51	32
Isard	45	f	63	e	55	g	54	42
Virtual3	61	b	81	a	77	a	77	71
Virtual4	24	g	39	g	26	i	28	11
Virtual6	50	e	62	f	54	hg	49	33
Virtual8	69	a	71	c	67	d	43	41
Virtual9	51	ed	77	b	72	c	81	58
min	24		39		26		28	11
mean	51		67		59		55	41
max	69		81		77		81	71

[$] "Varieties" comprise registered varieties, unregistered genotypes from our genotype collection and virtual varieties created by combining parameter values randomly selected inside the parameter range measured on real varieties or genotypes.
[§] Name used in previous publications (Colbach et al., 2022), now IPIP200490 (Hohenheimer Pink Flower), after the collection was updated during the Peamust project (www.peamust-project.fr)

both against weeds and wheat, which compensated for its medium potential yield (Fig. 3.A). Finally, despite being the second-best wheat-competitive variety (Table 3), Virtual 8 showed a low weed-infested yield in intercrops (Fig. 3.B), resulting from its low weed tolerance (high weed-caused yield loss in pure pea, Fig. 3.C) and medium yield potential (Fig. 3.A).

3.2.5. *A high weed tolerance does not always mean a high weed suppression*

High weed tolerance did not always come with a high weed suppression (i.e., a low field infestation). For instance, variety 886–1 was very weed-tolerant in both sole-crop pea and intercrops (Fig. 3.C) but was the least weed-suppressive variety in sole-crop pea and the second-least one in intercrops (Fig. 3.D). Conversely, the second-most weed-suppressive variety, China, was among the least weed-tolerant varieties (Fig. 3.C).

The variety ranking revealed differences between real and virtual varieties. In weed-free simulations, the varieties with the highest yield were real ones, Isard and DCG 0449, both in intercrops and sole-crop pea whereas the worst varieties were virtual ones (Fig. 3.A). Conversely, the worst varieties in terms of weed tolerance or suppression in sole pea were real varieties (Enduro and 886–1 in Fig. 3.C and D, respectively).

3.3. *Which combinations of pea parameters are the best for yield and weed suppression?*

The analyses for tracking ideal varieties revealed a series of contrasting ideotypes whose parameter profiles varied with the selection goal (e.g., yield potential vs weed suppression), the target species (pea vs wheat vs both) and intercropping design. The following sub-sections explain how the ideotypes were defined (i.e., optimal parameter value ranges, differences in parameter ranges with existing varieties, 3.3.1), which selection targets (i.e., weedy yield, Sections Sections 3.3.2 and

Table 4

Generalist pea ideotypes: optimal combinations of pea parameters for maximising weed tolerance as well as pea yield in pea-wheat intercrops, in weed-free (potential yield) or weed-inclusive simulations (actual yield) in systems with unlimiting nitrogen availability identified with classification and regression trees (see example of *IdPeaPot* in Fig. 2). Ideal parameter ranges (between brackets) were compared to existing varieties (in bold, if ideal range differs from 90% of existing parameter range). Cells were coloured according to parameter impact on variety performance: in green, increased performance, in red, trade-offs (i.e., potentially decreasing performance but correlated to beneficial characteristics) and/or having no influence in the tested systems; in white: parameter ranges covered by actual varieties. Only the parameters that were among the 10 most influential ones for at least one pea-related indicator, and whose Variable Importance Predictor cumulated over all indicators ≥ 0.01 for yields, and ≥ 0.001 for weed tolerance (complete results in section F.6-8 online).

Pea parameters (see section **A** in supplementary material online for details) *(italics show parameters that do no vary among existing varieties)*					Ideal parameter values (and *ideotype names*) for		
	Name	Meaning		Unit	Potential yield (*IdPeaPot*)	Actual yield (*IdPeaYield*)	Weed tolerance (*IdPeaTol*)
A. Germination, emergence and establishment							
L1	*nonDormant*	Proportion of non-dormant seeds		seeds/seeds			Lower [0.91, 0.92[
L2	*g0*	Germination onset (time since rain or tillage)		°C days			Earlier [18.3, 18.9[
L3	r50	Time until 50% of final root length is reached[1]		°C days		Later [108, 122]	
L4	*gamma*	Increase of seedling mortality with seed depth		sdl·sdl^{-1}·logmm^{-1}			Less [0.30, 0.31[
L5	*betaCompact*	Seedling mortality due to soil compaction		seedling/seedling			More [0.86, 0.87]
L6	se_LA	Variability of leaf at emergence		cm^2		Similar [0.43, 1.96]	
L7	RGR	Relative growth rate (emergence)		cm^2/°Cday		Faster [0.015,0.026]	
B. Above-ground plant morphology in unshaded conditions							
L8	maxHeight	Maximum plant height		cm		Smaller [94, 141[	**Smaller [91, 96[**
L9	b_WBRmid	Heterogeneity of plant width [2]	vegetative	none	Less [0.21, 0.29[		
L10	b_HBRlate	Heterogeneity of plant height [2]	reproduction	none	Less [0.12, 0.14[		
L11	WBRmid	Plant width per biomass ratio WBR	vegetative	cm/g	Narrower [9.8, 12.9[		
L12	WBRlate		reproduction	cm/g		Similar [9.3, 22.7[	
L13	LBRearly	Leaf biomass ratio	emergence	g/g		Similar [0.76, 0.78]	**Leafier [0.78, 0.79]**
L14	LBRlate		reproduction		**Leafier [0.52, 0.55]**	Similar [0.27, 0.55[	
L15	RLHearly	Relative leaf area height RLH (high values indicate leaves at plant top)	emergence	cm/cm		Lower [0.51, 0.58[	
L16	RLHmid		vegetative			Lower [0.48, 0.55[	
C. Shade response (parameter > 0: increase in morphology variable, < 0: decrease variable)							
L17	mu_HBRearly	Plant height per biomass ratio HBR	emergence	none	Smaller [–0.01, 0.025[	Smaller [–0.01, 0.072[	
L18	mu_WBRlate	Plant width per biomass ratio WBR	reproduction	none		Wider [0, 0.22[	
L19	mu_LBRmid	Leaf biomass ratio LBR (leaf biomass/total above-ground biomass)	vegetative	none	Leafier [–0.04,–0.004]		
L20	mu_LBRlate		reproduction	none	Leafier [–0.07, 0.06]	Leafier [–0.25, 0.06]	
L21	mu_RLHmid	Median Relative leaf area height (high values indicate leaves at plant top)	vegetative	none	**Higher [0.14, 0.16]**	Higher [0.083, 0.16]	
L22	mu_RLHlate		reproduction	none		Similar [–0.07, 0.31]	
L23	mu_SLAearly	Specific leaf area SLA (leaf area/leaf biomass)	emergence	none		Lower [0.035, 0.06[	**Lower [0.035,0.037[**
L24	mu_SLAlate		reproduction	none	Lower [0.40, 0.48[		**Higher [0.74, 0.75]**
D. Root system							
L25	Emax	Maximum root-system width		cm	Narrower [213, 214[		Wider [283, 301]
L26	rateCyl	Relative thickness of surface layer with high root density[3]		cm/cm	Thicker [0.24, 0.26]	Thicker [0.14, 0.26]	
L27	soilPen	Resistance to soil compaction (0=none, 1=total)		cm/cm	Better [0.96, 1.00]	Better [0.86, 1.00]	
E. Temperature sensitivities							
L28	tFrostLate1	Max temperature for biomass loss via frost reproduction)		°C			Lower [–0.04,–0.03[
L29	tPhoto3	Temperature above which photosynthesis decreases		°C	**Lower [20, 21[**	Lower [20, 26[	
F. Varieties answering to the rules					Isard	Isard Virtual4	Virtual4
G. Intercrop performance							
L30	Potential pea yield in pea-wheat intercrops from weed-free simulations (t/ha)				2.44	2.37	1.60
L31	Actual pea yield in pea-wheat intercrops from weed-inclusive simulations (t/ha)				1.14	1.35	1.16
L32	Intercrop infestation by weeds (t/ha)				2.2	2.3	2.1

3.3.3) and methods (i.e., co-select the two intercrop species, 3.3.4) worked best. They summarized a series of ideotypes adapted to the three intercropping designs (Sections Sections 3.3.5 and 3.3.6), identifying the winning strategies for a given goal (e.g., to maximise pea yield, the pea and wheat ideotypes should both precede weeds, but the pea ideotype must increase leaf area at the top of the canopy whereas the intercropped wheat should maximise ground cover).

3.3.1. Pea ideotypes are defined by a combination of rules on parameter values

With the help of the classification and regression trees (CART), optimal combinations of pea parameter values maximising pea yield (with or without weeds) in pea-wheat intercrop were identified (see example in Fig. 2). The pea ideotypes were defined as a combination of rules defining pea parameter values and corresponded to the best CART branches, i.e., those with the highest yields. Table 4 lists the ranges of parameter values corresponding to these ideotypes, and compares them to the ranges of the existing pea varieties.

Pea ideotype *IdPeaPot* maximised potential (weed-free) pea yield in intercrops regardless of the associated wheat variety or intercrop management. It was defined by 13 major parameter rules, most of which determine above-ground plant morphology in shaded and unshaded conditions (9 rules), followed by below-ground morphology (3 rules). The most important feature of *IdPeaPot* (the first splitting rule in Fig. 2) was its ability to allocate a large proportion of above-ground biomass to leaves even during reproduction (leaf biomass ratio during reproduction LBRlate in [0.52, 0.55] g/g in line L14 of Table 4). The real pea varieties tested here had a much lower leaf biomass ratio, with only 10% of their parameter range fitting this rule (bold L14).

In addition, *PeaPot*'s height and width were homogeneous irrespective of plant biomass, particularly after emergence and during vegetative stages, respectively (L9 and L10). Plants could be narrower per unit biomass than real varieties (L11), which avoided damage by mechanical weeding. When shaded by neighbour plants (among which wheat), *IdPeaPot* plants shifted their leaves upward (positive values in L21), and reduced biomass allocation to leaves less (or even increased it) than real varieties) (L19 and L20). Leaves became thinner and larger in shaded *PeaPot*, but less than in most real varieties (L24). Shaded *IdPeaPot* plants also etiolated but less than real varieties (L17). Almost all these characteristics increase light interception and shading of neighbour plants by increasing leaf area and positioning it above neighbours. Note that the afila (semi-leafless) vs. leafy character was never significant in Table 4.

Roots should grow well in compacted soil (L27) and root density biomass had to be concentrated close to soil surface (large L26). This ensured that *IdPeaPot* plants left less superficial soil moisture for the germination of other species growing in the field. But the root system needed to be limited in size (L25), which left more biomass for above-ground plant compartment, again to intercept more light and shade neighbours more. Finally, *IdPeaPot* did not photosynthesize well at temperatures above 21°C (L29).

Among the tested real and virtual varieties, only Isard fitted all these rules (Table 4.F). This is consistent with the large average potential yield of Isard in Fig. 3.A. The second-best generalist high-potential ideotype was the opposite of *IdPeaPot* for all rules of Table 4.F: e.g., where the latter required a leaf biomass ratio exceeding 0.52 g/g, the former needed a ratio lower than 0.52 g/g (Fig. 2). The only exception was the high biomass allocation rate to leaves during reproduction, which was common to both ideotypes. The associated potential pea yield was approximately 20% less than for *IdPeaPot* (1.9 t/ha, section F.6 online). In other words, judicious combinations of variety traits could cancel out deleterious effects of individual traits, but only to some degree.

3.3.2. Ideotypes for maximising yield potential and weed tolerance differ

When weeds were added to the simulations, the best pea ideotype for pea–wheat intercropping was not entirely the same (*IdPeaYield* in Table 4). *IdPeaYield* and the potential-maximising *IdPeaPot* were most similar in terms of shading response (L17 to L24), root system (L25 to L27) and temperature sensitivity (L29). Their main difference occurred immediately after emergence, with *IdPeaYield* needing to grow faster than most real varieties (L7), allocate as much biomass to leaves (L13), and distribute its leaf area lower along plant height (L15). *IdPeaYield* resulted in a better weed-infested pea yield than *IdPeaPot* (L31), but in a slightly lower yield potential (L30). Again, the second-best ideotype for high yield was the exact opposite of the best performer *IdPeaYield* (sections D.3 online), with roughly 20% less yield (line L2 vs L1 in Table 5).

Weed-suppressive and weed-tolerant variety rules were very different from those driving yield (Table 4). The only common feature of *IdPeaTol* vs. *IdPeaPot* was the need to allocate a higher proportion of biomass to leaves though for *IdPeaTol*, this was crucial after emergence (L13). Otherwise, the emphasis of *IdPeaTol* was very much on improving its own emergence, with earlier germination (L2) and less seedling mortality (L4), or reducing weed emergence, via a wider root system that left less soil water for weed germination and pre-emergent growth (L25). Note that all these parameters were constant for existing varieties (parameter names in italics in Table 4) and varied here only in virtual varieties. Some beneficial traits such as early germination (L2) came at a price, with more dormancy (L1). In other words, earliness trumped final density. *IdPeaTol* indeed had lower field infestation than the other two ideotypes (L32), as well as a lower yield difference due to weeds (L30–L31). But its yields were also lower (L30 and L31).

Among the tested pea varieties, two fitted the *IdPeaYield* rules, Isard and Virtual4 (Table 4.F). The latter also fitted the *IdPeaTol* rules and was the variety with the lowest yield loss due to weeds in Fig. 3.C. As Isard fitted the rules of both *IdPeaPot* and *IdPeaYield*, this meant that different characteristics of the variety were relevant, depending on the environment, i.e., the presence of only wheat (in *IdPeaPot*) or both wheat and weeds (*IdPeaYield*).

3.3.3. Targeting weed-infested yield works best

The previous two sections showed that selecting to maximise weed-infested pea yield in pea–wheat intercrops produced the best pea ideotypes, with the highest pea yields in the presence of weeds and a high yield potential (Table 4.G). Selecting for the best potential yield or for the best weed tolerance resulted in low tolerance and potential, respectively, and thus finally in lower weedy yields. Selecting for wheat yields or wheat weed-tolerance only improved these indicators, but neither pea indicators nor weed suppression: e.g., wheat yield was multiplied by 2.5 but pea yield divided by 4 and field infestation increased by 2% compared to a pea-yield focused selection (section C.5 online). Selecting for intercrop indicators was similar to selecting for pea indicators. The following analyses focused on ideotypes selected for maximum weedy pea yields.

3.3.4. Co-selecting pea and wheat varieties improves pea and intercrop performance

The ideotypes of Table 4 correspond to generalist winners that performed best, regardless of the intercrop management or intercropped wheat varieties. If the pea ideotypes were selected together with the wheat ideotypes, i.e., if the CART were built using both pea and wheat parameters, all performance indicators improved (though not consistently for wheat). Potential and weedy pea yields were multiplied by approx. two-three in the two best branches (lines L3 vs L1, and L5 vs L2 in Table 5), and field infestation by weeds was more than halved.

The pea performance was highly conditional on the intercropped wheat variety. If the best pea ideotype *IdPeaCo* was combined with wheat ideotype *IdWheatCo3* instead of *IdWheatCo*, then pea and intercrop yields dropped (by 35% and 20%, respectively) whereas wheat yield and field infestation increased by approx. 80% (L4 vs L3). In other words, *IdWheatCo3* hindered pea more than weeds, and the latter impeded pea more than wheat. Among the features favouring wheat

Table 5
Performance of the two or three best tree branches of the classification and regression trees (CART) analyzing weedy pea yield in intercrops as a function of pea parameters (all lines) and wheat parameters (all lines except L1–L2), using all pea-wheat intercrops (L1–L5) or only additive (L6–L7), substitutive (L8–L9) or incomplete (L10–L11) designs[$]. The ideotypes are described in Table 4 (L1–L2), Table 6 and sections F.6-12 online (all others). In each column, cells were coloured from green (best yield, lowest field infestation) through yellow to red (vice-versa).

	Pea ideotype	Wheat ideotype	Pea ideotype adapted to	Pea yield (t/ha)		Wheat yield (t/ha)		Weedy intercrop yield (kJ/ha)	Field infestation (t/ha)
				Weedy	Potential	Weedy	Potential		
L1	***IdPeaYield***	none	All intercropping designs	1.3	2.4	1.6	3.5	101	2.3
L2	*IdPeaYield2 (=IdPeaAdd2)*	none		1.1	2.1	1.9	4.0	84	2.4
L3	***IdPeaCo*** *(=IdPeaAdd2)*	***IdWheatCo***		4.2	5.5	0.6	0.6	196	1.1
L4		*IdWheatCo3*		2.8	3.5	1.8	2.9	158	1.9
L5	*IdPeaCo2 (=IdPeaAdd)*	*IdWheatCo2*		3.4	3.8	2.2	2.6	183	0.9
L6	***IdPeaAdd***	***IdWheatAdd***	Additive	4.9	5.7	1.3	1.3	235	0.5
L7	*IdPeaAdd2*	*IdWheatAdd2*		4.4	5.6	0.6	0.6	203	1.0
L8	***IdPeaSub***	***IdWheatSub***	Substitutive	2.9	3.0	0.6	0.9	181	0.9
L9	*IdPeaSub2*	*IdWheatSub2*		2.6	3.0	0.4	0.9	183	1.8
L10	***IdPeaInc*** *(~IdPeaYield)*	***IdWheatInc***	Incomplete	3.7	4.0	1.7	2.3	202	0.0
L11	*IdPeaInc2*	*IdWheatInc2*		3.6	4.0	2.9	2.9	205	1.0

[$] Additive, substitutive and incomplete designs present a total relative crop sowing density of 100%, 90–100% and < 90%, respectively.

growth and yield but reducing pea yield and weeds were, for instance, a faster and better emergence, wider plants, a higher leaf extinction coefficient and a lower frost sensitivity (section D.4 online).

3.3.5. *The most versatile pea ideotypes*

IdPeaAdd and *IdPeaAdd2* co-selected with wheat for additive intercropping designs were the best and most versatile pea ideotypes: they presented the best yields and lowest field infestations in additive designs (Table 5) but also regardless of intercropping design (as they were identical to *IdPeaCo2* and *IdPeaCo*) and even regardless of intercropped wheat in the case of *IdPeaAdd2* (identical to *IdPeaYield2*).

Table 6.A lists the key features of these ideotypes and how they differ from the actual pea varieties included in FLORSYS. The strategy of *IdPeaAdd* was three-fold: (1) precede weeds through fast and homogeneous plant establishment (L3, L6, L7 in Table 6.A), (2) maximise light-intercepting area (L9, L10, L12, L14, L16), particularly when shaded (L18 to L22) and/or during vegetative and reproductive stages, (3) reduce weed germination/emergence by taking away soil water with more root biomass close to soil surface (L25, L26). Among the existing varieties, only Isard fitted to these rules (L30).

For this strategy to work best, *IdPeaAdd* needed to be intercropped with wheat variety *IdWheatAdd*. The latter's strategy focused on hindering weeds but not pea: (1) precede weeds by faster and better emergence than actual wheat varieties (L1 and L3 in Table 6.B), (2) smother weeds with a better ground cover, through smaller (L7) and wider plants (L6), a downward leaf area distribution (L8) and a lower frost sensitivity (L14), (3) reduce pea shading by allocating a larger proportion of biomass to roots (L9). Only two virtual varieties followed these rules (L18).

The second pea ideotype for additive designs, *IdPeaAdd2*, focused less on reducing or preceding weed emergence (only 1 pre-emergent rule Table 6.A) and more on large and well-placed leaf area. *IdWheatAdd2* associated to *IdPeaAdd2* shared almost all weed-suppressing features with *IdWheatAdd* (L1, L6, L11 in Table 6.A).

3.3.6. *Different pea ideotypes according to the intercrop design*

The two best pea ideotypes selected for substitutive designs differed from any other ideotypes identified above. The best one, *IdPeaSub*, looked like a washed-out version of the most versatile ideotype *IdPeaAdd2* (Table 6.A), and needed a low-productive wheat companion such as *IdWheatSub* (see low yield potential in L8 in Table 5) to succeed. The second "substitutive" ideotype, *IdPeaSub2*, was the exact opposite of *IdPeaAdd* (Table 6.A), which nearly halved yields and more than tripled field infestation (L9 vs L6 in Table 5).

Incomplete designs (i.e., with a relative total density of less than 90%) needed stringent rules either for the pea variety (*IdPeaInc* in Table 6.A) or for the wheat variety (*IdWheatInc2* in Table 6.B). *IdPeaInc* was nearly the same as the generalist pea ideotype *IdPeaYield* of Table 4. The second best pea ideotype, *IdPeaInc2*, was defined by a single rule limiting shade-driven increase in plant width per biomass (L18 in Table 6.A). The associated wheat *IdWheatInc2* produced the best wheat yield of all designs and variety combinations (L11 vs other lines in Table 5). Only a virtual variety fits these rules (L18).

3.4. *The most influential intercrop management rules*

When classification and regression trees (CARTs) were used to identify the most influential intercrop management techniques (Table 7), yields and weed suppression increased with relative sowing densities. In average, the best weedy pea yield was reached with relative pea and wheat sowing densities of 0.64 seeds·m^{-2}/seeds·m^{-2}, which corresponds to an additive design of a total relative sowing density of 1.3 seeds·m^{-2}/seeds·m^{-2} (section D.4 online). Any further increase in sowing densities reduced weedy pea yield but not weedy wheat yield, which was best with an overly dense wheat (~1.1 seeds·m^{-2}/seeds·m^{-2}) and sparse pea (~0.30 seeds·m^{-2}/seeds·m^{-2}).

The most influential technique was harvest date (largest Variable Importance Predictor in Table 7). Harvest date is a proxy for a key variety parameter, i.e., flowering precocity: delayed harvesting is only beneficial for yields if it is associated with varieties that mature later. This points to the key role of flowering time, depending on the thermal time since crop emergence and daylength (Hr varieties only).

Table 7 distinguishes between pea and wheat performance, as well as between yield production and weed suppression. A final column explains the reasons for these effects. This table could guide farmers and stakeholders on how to redesign strategies for intercrop management. For instance, if the delay between the last tillage operation and intercrop sowing is increased, weedy yields, tolerance to weeds and weed suppression decrease because this delay leaves more time for weeds to emerge and establish after the last tillage destroyed all weeds that emerged during summer fallow. The effect of intercrop management techniques was more straightforward than the effect of crop parameters,

Table 6
Combinations of variety rules defining the pea and wheat ideotypes that aim to maximize weedy pea yields in pea-wheat intercrops, identified with the same method as in Table 4. Variety rules in green and red respectively improve and deteriorate pea or wheat yield and weed suppression compared to some actual varieties (in bold, if rule differs from 90% of existing parameter range); white cells show rules respected by actual varieties; empty cells refer to minor rules (Variable Importance Predictor cumulated over all pea or wheat indicators < 0.01 or < 0.005, respectively). Note that wheat rules that improve wheat yield can be detrimental for pea yield. For details, see sections F.10-12 online.

A. Combinations of beneficial PEA characteristics *(italics show parameters that do no vary among existing varieties)*				**Ideotype characteristics compared to existing varieties**					
				Additive designs		**Substitutive designs**		**Incomplete designs**	
				***IdPeaAdd*§**	***IdPeaAdd2*§**	***IdPeaSub***	***IdPeaSub2***	***IdPeaInc***	***IdPeaInc2***
L1	*Seed dormancy*			Similar			More		
L2	*Germination onset*			Similar			Earlier		
L3	Pre-emergent root growth speed (lower drought risk)			Faster	Faster	Faster	Slower	Slower	
L4	*Pre-emergent seedling loss due to seed depth*			Similar			Less		
L5	*Pre-emergent seedling loss due to soil compaction*			Similar			More		
L6	Post-emergent growth			Faster	Slower		Faster		
L7	Inter-plant heterogeneity in post-emergent leaf area			Smaller	**Smaller**	Smaller	Larger		
L8	Maximum plant height			Smaller	Taller		Similar	Smaller	
L9	Plant height homogeneity		reproduction	Better			Worse		
L10	Plant width homogeneity		vegetative	Better		Better	Worse		
L11	Plant width per biomass		vegetative	Narrower			Large		
L12			reproduction	Wider	**Wider**	Wider	Narrower	Similar	
L13	%biomass allocated to leaves		emergence	Less	**Less**	**Less**	More	Similar	
L14			reproduction	**More**	**More**	**More**	Similar	Similar	
L15	Leaf area distribution along plant height		emergence	Lower	Higher	Higher	Higher	Lower	
L16			vegetative	Higher	Higher	Higher	Lower	Lower	
L17	Shading response	Plant height per biomass	emergence	Smaller	Taller	Smaller	Taller	Smaller	
L18		Plant width per biomass	reproduction	Wider	Narrower	Narrower	Narrower	Wider	Narrower
L19		% biomass allocated to leaves	vegetative	More		More	Less		
L20			reproduction	More	Less	**Less**	Less	More	
L21		Leaf area per leaf biomass	reproduction	Smaller		Smaller	Larger		
L22		Leaf area distribution along plant height	vegetative	Higher	Lower		Lower	Higher	
L23			reproduction	Lower	**Lower**	Lower	Higher	Higher	
L24	Root-system width (maximum)			Similar			Wider		
L25	Root biomass distribution			Shallow	Deeper		Deeper	Shallow	
L26	Root growth in compacted soil			Better	Worse		Worse	Better	
L27	Frost sensitivity		reproduction	Similar			Lower		
L28	Photosynthesis in warm conditions			Worse	Better	Better	Similar	Worse	
L29	Pea varieties answering to the rules								
L30	Actual varieties			Isard	DCG0449	DCG0449		Isard	DCG0449 Isard
L31	Virtual varieties						4	4	4

(*continued on next page*)

Table 6 (*continued*)

B. Combinations of beneficial WHEAT characteristics *(italics show parameters that do no vary among existing varieties)*			**Ideotype characteristics compared to existing varieties**					
			Additive designs		**Substitutive designs**		**Incomplete designs**	
			IdWheatAdd	*IdWheatAdd2*	*IdWheatSub*	*IdWheatSub2*	*IdWheatInc*	*IdWheatInc2*
L1	*Emergence of shallow seeds*		Faster	Faster	Faster	Faster		Faster
L2	Maximum pre-emergent shoot length					Smaller		
L3	*Seedling mortality in broadcast seeds*		Less					Less
L4	Post-emergent growth			Slower				
L5	Leaf area at emergence					Larger		
L6	Maximum plant width		Wider	Wider		Wider		
L7	Plant height per biomass	repro-	Smaller		Taller			Taller
L8	Leaf area distribution vs plant height	duction	Lower	Higher				
L9	Biomass allocation to roots		More					More
L10	Root-system growth			Faster				Similar
L11	Root biomass distribution		Similar	Similar				
L12	*Light conversion efficiency*			Worse				Worse
L13	*Photosynthesis efficiency in cool conditions*			Worse		Similar		Worse
L14	Frost sensitivity	emergence	Better	Better				Better
L15	Frost sensitivity	reproduction				Worse		Worse
L16	Wheat varieties answering to the rules							
L17	Actual varieties						Caphorn	
L18	Virtual varieties		E F	D	C E G	E	A B C E G	E

[§] Pea ideotypes *IdPeaAdd* and *IdPeaAdd2* are identical respectively to pea ideotypes *IdPeaCo2* and *IdPeaCo* co-selected with wheat, regardless of intercropping design. Pea ideotype *IdPeaAdd2* is also identical to the generalist pea ideotype *IdPeaYield2*, which is the opposite of *IdPeaYield* of Table 4.

i.e., the impact on a given indicator (e.g., weed tolerance of pea in intercrop) was either always positive or negative, regardless of varieties or other techniques.

4. Discussion

4.1. What is new?

In the present paper, we adapted to intercropping the approach developed by Colbach et al. (2022) on sole-crop pea. This approach combined detailed experimental measurements characterizing varieties from a previous study (Colbach et al., 2020b) with a simulation study to test actual and virtual varieties in virtual field networks, in order to identify ideotypes of varieties and cropping systems for agroecological weed management in the particular case of pea–wheat intercropping. We already discussed the model's prediction quality and the novelty of this approach as well as their advantages and limits in our previous paper (Colbach et al., 2020b), in terms of variability of investigated situations, use of parameters reflecting intrinsic plant properties that vary little with the environment (instead of working with integrative environmental-dependent traits), and lower risk of confusion effects. In contrast to previous studies (even simulation studies), the present and our previous work (Colbach et al., 2020b) also took into account root parameters.

The present study is one of very rare studies analysing pea varieties in terms of weed competitiveness in intercrops (Gronle et al., 2015). Though intercrops are being studied by many teams, investigations of pea varieties in intercrops are rare. Most intercrop studies focus on nitrogen use of legume–cereal intercrops (Hauggaard-Nielsen and Jensen, 2001; Hauggaard-Nielsen et al., 2009; Bedoussac and Justes, 2010a) or look at economic performance and environmental impacts (Pelzer et al., 2012). Variety studies often focused on species synergy and how to maximise yield potential (Kammoun et al., 2021). These were mostly field experiments (Annicchiarico et al., 2021), often with cereals other than soft wheat (Hauggaard-Nielsen and Jensen, 2001; Kammoun et al., 2021) or simulation studies with functional-structural plant models (Barillot et al., 2012, 2014b). The latter describe plant morphology much more in detail than FLORSYS to the detriment of management practices or emergence dynamics (Gaudio et al., 2019).

4.2. Are the results consistent with previous studies?

Despite using soil and weather data from a single location, our simulations show the same general tendencies (direction and magnitude) as those reported in published field trials (from five countries, among which several locations in France and Denmark) and meta-analyses (covering all continents except Australia). For instance, the reduction in pea yield when switching from sole crop to intercrop in our simulations (28%-81%, average = 55%) is within the range observed in previous field studies (see details in section E.3.2 online): 50% (Bedoussac and Justes, 2010b), 50% (Kammoun et al., 2021), 30–65% (Ghaley et al., 2005), 50–75% (Naudin et al., 2010), 30% (Moutier et al., 2022), 78–84% (Annicchiarico et al., 2021), 36% (Hauggaard-Nielsen and Jensen, 2001). This pea yield reduction was larger than the reduction in wheat yield in intercrop vs sole wheat (20%-50%, average 30%), which is consistent with field reports on wheat outcompeting pea (Annicchiarico et al., 2021). Just as in field reports (Corre-Hellou et al., 2011; Gu et al., 2021), wheat was more competitive than pea in the simulations, intercrops reduced weed biomass, and they did this more compared to sole pea (the weaker crop) than to sole wheat (the stronger crop). Field experiments also confirmed that the choice of pea variety in the intercrop influenced the intercrop performance to a larger degree than the choice of cereal variety (Hauggaard-Nielsen and Jensen, 2001). As wheat is already more competitive than pea, there seems to be less room for improvement in wheat than in pea varieties. Our simulations also showed that management of intercrops and other crops in the rotation was more influential than varieties. However, field experiments rarely investigate management, other than comparing additive vs substitutive designs, which we did here as well, but in interaction with many other factors and over a larger range of sowing densities.

Few past studies included some of our pea varieties. Among these, Kammoun et al. (2021) reported pea yields in intercrops of the same

Table 7
The key intercrop management techniques driving yield, weed tolerance and weed suppression in pea-wheat intercrop. The most influential techniques per indicator were selected based on relative variable importance predictor (VIP) summed over indicators in classification and regression trees. Probabilities ≥ 0.90 in green (an increase in technique values results in an increased indicator value) and red (an increase in technique values results in a decreased indicator value). Empty cells indicate that the techniques had no significant effect on the indicator, or cumulated VIP < 0.01 or probability of stable effect < 0.90. For complete results, see section F.5 online.

Intercrop management technique	Unit	Simulated variation		Potential yield		Weedy yield or weed tolerance		Weed suppression	Total VIP	Reasons for effect (based on the analysis of simulated state variables)
		Min	Max	P	W	P	W			
Tillage										
Superficial tillage	operations per year	0	10			+			0.02	Reduces weed seed bank by triggering germination during summer fallow ("false seed bed"), kills weed plants before sowing
Tillage after 1 Nov	operations per year	0	10				+		0.03	More weed destruction and late sowing (see sowing date)
Time from last tillage to crop sowing	days	0	147			–	–	–	0.23	Leaves more time for weeds to reinfest the field after the last tillage operation cleaned out all weeds
Crop residue shredding operations	operations per year	0	4			+	+		0.04	Destroys weeds during summer fallow
Sowing										
Sowing date		01 Oct	30 Nov				+		0.07	Leaves more time for false seed bed techniques; shortens the time during which weeds can grow inside the crop
Proportion of pea rows in intercrop	rows/ rows	0.20	0.80		–				0.02	Pea plants occupy more space in field and leave less for companion wheat
Interrow width	cm	4	52		–	–	–		0.15	More competition between crop plants inside a given row, more light missed by crops
Crop species are sown in separate rows	yes (1) or no (0)	0	1	+	–				0.03	Pea suffers more from interspecies competition but wheat plants suffer more from intraspecies competition
Total sowing density vs sole crop density	seeds·m²/ seeds·m²	0.06	4.89	+	+				0.03	More pea and wheat plants in field, intercepting more light and leaving less space and resources for weeds
Pea sowing density vs pure pea	seeds·m²/ seeds·m²	0.03	3.23	+	+			+	0.05	More pea plants and leaf area to produce pea biomass and shade weeds (but not on wheat)
Wheat sowing density vs pure wheat	seeds·m²/ seeds·m²	0.02	2.50	–	+	+			0.07	More wheat plants and leaf area to produce wheat biomass and shade weeds and companion pea
Other										
Multi-entry herbicides	number per year	0	4			+	+		0.01	Destroys weed plants (and more efficiently than herbicides entering only via either leaves, roots or meristem)
Anti-monocot herbicides	number per year	0	4				+		0.01	Fewer monocot weeds survive and compete with the crop
Anti-dicot herbicides	number per year	0	4				+		0.01	Fewer dicot weeds survive and compete with the crop
Mechanically weeded field area	m² / m²	0.00	1.00					+	0.02	More weeds are destroyed
Harvest date		06 Jun	15 Aug	+	+	+	+	–	0.76	Leaves more time for crop biomass accumulation BUT leaves more time for weeds to grow and reproduce

order of magnitude as ours though some of our varieties had either lower or higher yields. Kammoun et al. (2021) also found a negative correlation between intercrop pea yield and intercrop wheat yield (–1.6 t pea yield/ha per additional t wheat yield, section E.2 online) as well as a positive correlation between intercrop pea yield and sole-crop pea yield ($y = 0.558x - 0.432$, $R^2 = 0.23$, section E.1 online) similar to ours. The latter correlation, which means that varieties are ranked similarly in sole crops and intercrops in terms of performance, has been observed in other field trials (Annicchiarico et al., 2021) and is consistent with the low variability of pea morphogenesis between sole crops and intercrops reported elsewhere (Barillot et al., 2014a).

The studies on pea traits relevant for a high pea yield in intercrops and/or a high intercrop yield identify traits similar to ours (Table 8). Our simulations not only confirmed literature results from single locations and/or years over many contrasting cropping systems, weed floras and weather years. Thanks to the mechanistic nature of FLORSYS, synthetic traits could also be decomposed into variety-specific environment-independent parameters. Moreover, our study discriminated yield potential, weed tolerance and weed suppression, whereas the reports in Table 8 disregarded weeds.

The few literature studies investigating weed suppression in pea-cereal intercrops reported conclusions similar to ours, e.g., that leafy varieties are more weed-suppressive and that shading (or high light interception) was essential (Poggio, 2005; Gronle et al., 2015). But the use of numerous species-intrinsic process-close parameters (e.g., sensitivity of height biomass ratio to shading) rather than integrative environment-dependent traits (e.g., plant height) allowed further conclusions. For instance, it was not so much plant height in unshaded conditions that determined weed tolerance or suppression but rather how much leaf area there was and where it was located when plants were shaded (by weeds or companion crops) as shown by the shading response of height biomass ratio, leaf biomass allocation rate and toward leaf-area shift. Moreover, field studies can usually only investigate one or a few parameters, which are chosen based on expert opinion. Such an approach can overestimate the impact of easily measured aboveground traits and miss hard-to-measure belowground processes (as root-system width or distribution identified here). It cannot investigate parameter combinations whose key role was demonstrated here for pea in intercrops, as was done previously for sole pea (Colbach et al., 2022) and cereals (Andrew et al., 2015).

Despite the use of a great number of parameters, the generic 3D representation of plants in FLORSYS required simplifications that led to ignoring some species-specific processes such as lodging in pea. Fortunately, intercropping pea with cereals prevents lodging (Podgórska-Lesiak and Sobkowicz, 2013) and missing this process was therefore not a major issue for the present study. Other species-specific processes are not ignored but included implicitly in the plant representation as is the case for tillering in wheat. Analogies can therefore be

Table 8
Consistency of literature reports with simulation results in terms of pea-variety traits and parameters relevant for pea yield in pea-cereal intercrops. For detailed list of FLORSYS parameters and their meaning, see Table 4 and section F.3 online.

Literature reports (details in section E.3.1 online)		Our simulation study	
Traits increasing yield	Reference	Corresponding effects in FLORSYS	Corresponding FLORSYS parameters
Leafiness	(Barillot et al., 2012)	High leaf biomass ratio	LBR mu_LBR
Any that increase light interception (e.g., a high leaf area index at early stages or tall plants)…	(Barillot et al., 2014b; Annicchiarico et al., 2021)	Strong shading response increasing biomass allocation rate to leaves, plant width & height per biomass, leaf area height	mu_HBR mu_WBR mu_LBR mu_RLH mu_SLA
…particularly at early stages and/or when shaded	(Hauggaard-Nielsen and Jensen, 2001)		
Determinate growth which comes with a smaller root system and a greater proportion of vegetative growth before flowering	(Hauggaard-Nielsen and Jensen, 2001)	Limited root system	RBR Emax rateDepth
Heavy seeds	(Annicchiarico et al., 2021)	Better emergence and post-emergence ground-cover	gamma r50 LA0 RGR
High winter survival		Better frost tolerance	tFrost
Late maturing plants		Later harvesting	

found to check the consistencies of results: the need for a good tillering ability (Andrew et al., 2015; van der Meulen and Chauhan, 2017) is for instance consistent with the need for wider wheat plants identified in Table 6.

4.3. Implications for farmers and crop breeders

The present study as well as literature (Annicchiarico et al., 2021; Kammoun et al., 2021) showed that pea yields in pea–cereal intercrops and pea sole crops are correlated, which should make it easier to breed and choose pea varieties for intercropping. This will be more complicated for competitiveness against weeds as pea performance in intercrops was less correlated to sole-crop pea performance for competitiveness than for yield. Actually, intercrop management (as well as rotation and management of other crops) was shown to be the key driver of weed tolerance and, particularly, weed suppression whereas the choice of pea variety was crucial for yield potential. What makes the choice of the best pea variety more difficult, is that high-yielding varieties were not necessarily competitive against weeds here, in line with literature (Sardana et al., 2017). However, our simulations showed that there was no definite trade-off, indicating that that the yield potential vs. weed competition trade-off is not inevitable in pea, as shown already in cereals (Andrew et al., 2015).

Moreover, although pea-variety yields in intercrops were strongly correlated to pea-variety yields in sole pea in our simulations, there were variety outliers that performed better in intercrops than expected from their sole-crop performance. These outliers point to traits pertinent for improving pea performance in intercrops. In addition, the yield correlations as well as the two generalist ideotypes identified across all simulations disregarded genotype × environment interactions, which can be large (Vasileva and Kosev, 2021). Indeed, when crop management and the intercropped wheat variety were accounted for, more productive (and sometimes highly contrasting) pea ideotypes were identified, with similar performances. The resulting Table 6 could be used for decision support, for breeders on which traits to select for, and for farmers to adapt pea-variety choice to intercrop management, and vice-versa.

The ideotyping of Table 6 targeting different goals and contexts allowed several practical conclusions:

- similar intercrop yields can be obtained with different species yield proportions,
- the choice of the pea variety is more important than that of the wheat variety (though this needs to be confirmed with a larger range of wheat varieties), and a high pea yield in weedy intercrops needs to combine a high-potential pea variety with a weed-suppressive wheat variety and weed-preventive management,
- pea ideotypes depend on the intercropping design and on the intercropped wheat ideotype, but those selected for additive designs are also those that work best in average over all designs and/or intercropped wheat varieties.

4.4. From theory to practice: what remains to be done?

A few limitations of our approach as well as possible solutions were already discussed in our previous work on sole-crop pea (Colbach et al., 2022), e.g., simulating more soil and weather types, using optimisation algorithms to track better ideotypes, "packaging" results into ergonomic tools for easier decision support, linking the difficult-to-measure FLORSYS parameters to features that can be measured routinely in field trials by breeders etc.

Two further issues particularly apply to intercropping. The present study produced novel results on pea ideotypes for weed competitiveness in pea–cereal intercrops, focusing on the main resource for which crops and weeds compete in conventional, temperate, arable cropping systems, i.e., light (Wilson and Tilman, 1993; Perry et al., 2003; Colbach et al., 2023). This limitation is acceptable insofar as over-yielding by intercrops is mostly attributed to a more efficient use of light by their canopies in time and in space (Malézieux et al., 2009; Bedoussac and Justes, 2010a). However, legume–cereal intercrops are often grown to reduce mineral fertilization, particularly in organic systems. The same study thus needs to be repeated including crop–crop–weed competition for nitrogen as lack of mineral nitrogen differently affects plant growth and morphology according to the species (Perthame et al., 2022). Because of climate change, competition for water may also become a key issue (Laurent et al., 2023) and in both cases, the role of root parameters will probably change and increase. Conversely, allelopathy could contribute to biological weed regulation even if field-based evidence that allelopathic crops affect weeds is scarce (Mahé et al., 2022) and allelopathic wheat varieties could affect their companion legume.

The other point was the small number of varieties, particularly for wheat, that were used as a basis for the virtual varieties and the resulting smaller variability among (actual and virtual) wheat varieties than among pea varieties (2.3.1). This meant that the probability of missing winning varieties or parameter combinations was greater for wheat than for pea. It might also explain (at least partially) why pea varieties were more influential than wheat varieties in terms of yield and weed competitiveness, even though field reports supported the stronger influence of pea vs wheat varieties (Hauggaard-Nielsen and Jensen, 2001). But, considering the high cost of parameterizing species and varieties in FLORSYS, the present study was a first necessary sensitivity analysis to determine the parameters that must be estimated the most precisely. Among these were some parameters that had been estimated as average

values for the species, without discriminating varieties. This knowledge will help to determine which parameters must be estimated more precisely in the future, to simplify parameterization protocols and to facilitate the addition of further varieties to investigate pea–wheat ideotype combination more in detail in the future.

Finally, the identification of relevant traits to be selected for weed tolerance and/or suppressiveness opens the way to (i) large scale screenings of germplasm collections in order to identify accessions presenting such traits; and (ii) to genetic studies in order to identify useful markers/genes for selecting those traits.

5. Conclusion

The present study tracked the most influential pea-variety parameters and their combinations to maximise pea production and biological weed regulation in pea–wheat intercrops depending on the objective, the intercropped wheat variety and intercropping design, using simulations with a multiannual multispecies crop-weed model. These parameters are variety-inherent traits, which do not vary with the environment. These are pointers for breeders and farmers to breed and choose pea varieties for biological weed control in pea-wheat intercrops. The study showed that breeding weed-competitive pea varieties for intercrops is more complicated than for sole pea because pea performance in intercrops is less correlated to sole-crop pea performance for competitiveness than for yield. Intercrop management (as well as rotation and management of other crops) was shown to be the key driver of weed tolerance and weed suppression whereas the choice of pea variety was crucial for yield potential. The present methodology can be applied to identify ideotypes for weed management in other crops or even crop mixtures. Further research is needed to resolve the trade-off between pea parameters that promote potential yield and those driving weed suppression and to link model parameters to variables routinely measured during crop breeding.

CRediT authorship contribution statement

Nathalie Colbach: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Judith Burstin:** Writing – review & editing, Visualization, Methodology. **Delphine Moreau:** Writing – review & editing, Visualization, Methodology, Funding acquisition, Conceptualization.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2026.128313.

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