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Highlights

- Crop diversification is essential for agroecological weed management
- Mechanistic weed models are crucial to synthesize knowledge on crop diversification
- Key processes are emergence, morphology, shade response and biophysical soil memory
- FLORSYS is used to track and promote crop ideotypes and crop-diverse solutions
- Crop diversification benefits depend on production situations and cropping systems

Abstract

Crop diversification, both in time and in space, is essential for agroecological pest management. Process-based weed dynamics models are valuable tools to investigate this issue. Indeed, (1) weeds are the most harmful pest in arable crops and are essential for biodiversity, and (2) the processes driving crop-weed interactions are similar to those for crop-crop interactions in crop mixtures and crop rotations. Such models (3) synthesize existing and produce emergent knowledge on agroecological levers such as crop diversification and (4) mobilize this knowledge to cropping-system design, and (5) transfer research-based knowledge to stakeholders. The present paper illustrates these five items with the FLORSYS model. Its inputs are a detailed list of cultural operations over several years (crop succession including cover crops and crop mixtures, management techniques), together with daily weather data, soil characteristics and a regional weed species pool. FLORSYS runs at a daily time step, (1) focusing on processes leading to plant emergence and establishment of crop and weed species with different ecological requirements (essential for crops sown in different seasons and in mixtures where timing often determines the fate of a species), (2) representing and modelling the functioning of heterogeneous crop-weed canopies including diverse plant ages, morphologies and shade responses (as in crop mixtures), (3) including a carryover effect on future cropping seasons (which is essential for crop rotations), and (4) assessing weed contribution to biodiversity. Detailed biophysical model outputs allow understanding the performance of a given crop, management technique or cropping system. Together with stakeholders, detailed model outputs were aggregated into indicators of crop production as well as weed benefits and harmfulness to simplify the multicriteria comparison of cropping systems. To facilitate decision support, FLORSYS was used as a virtual farm-field network, and the resulting simulation outputs were aggregated into a faster and easier-to-use metamodel (DECIFLORSYS) using machine learning techniques. These models were used to evaluate and promote the benefits of crop diversification for agroecological weed management, by (1) identifying crop ideotypes, (2) tracking crop-diverse solutions in farm-field networks, (3) evaluating crop-diverse solutions proposed by experts and stakeholders, and (4) feeding participatory workshops with farmers. The case studies demonstrate that the benefits of crop diversification depend on the production situations and cropping systems, and thus the need for flexible rules on crop diversification and the usefulness of models such as FLORSYS to establish these rules.

Keywords. ecological intensification; mechanistic model; biological interaction; cropping system design; cover crop; intercropping; rotation; crop-weed competition; ideotype

1 Introduction

Weeds are an interesting model to investigate ecological intensification as they are the most harmful pest for crop production (Oerke, 2006), explaining why herbicides amount for a large part of sprayed pesticide (more than 40% of sold pesticides in France, Agreste, 2019). To date, the only alternative to the highly efficient herbicides is to combine a large range of partially effective techniques (Liebman and Dyck, 1993; Liebman and Gallandt, 1997) to manipulate biotic interactions (Bommarco et al., 2013). Weeds can also be beneficial, feeding fauna or protecting the soil (Blaix et al., 2018). Finally, the analysis of crop-weed interactions, which is essential for non-chemical weed control, greatly contributes to understand and manage crop diversification. The latter is a major component of ecological intensification, both in time (cover crops, crop succession) and in space (variety mixtures, intercropping, regional crop pattern) (Weisberger et al., 2019).

Rotating winter and spring crops alternates different growing seasons, deteriorating the conditions for weeds with stringent ecological requirements (e.g. autumn-emerging weeds, Chauvel et al., 2001) and allows timing specific control measures relatively to the weeds' period of susceptibility (e.g. tillage and weed germination, Cordeau et al., 2017). Similarly, diversifying crop canopies by mixing cultivars or species reduces the probability of weeds encountering suitable growing environments, mainly by increasing competition for resources and leaving fewer niches for weeds (Petit et al., 2018). The effect of habitat diversity at the landscape level also influences weed communities. The frequency and/or probability of weed species presence inside individual fields depend on adjacent semi-natural habitats and the management of neighbouring fields (Alignier and Petit, 2012), with weed floras getting increasingly similar with the proximity of the analysed fields (Alignier et al., 2013). Finally, companion crops or fallow cover crops can be introduced into a rotation to contribute to weed management, either directly by suppressing weeds by competition (Teasdale, 1996) and/or allelopathy (Sturm et al., 2018), or indirectly by favouring weed predators (Blubaugh et al., 2016).

Tailoring crop diversification to integrated pest management is particularly difficult when pest propagules survive for several years in a field as is the case for weeds (Lewis, 1973). A management decision has repercussions over several years, and benefits are often visible only in the following crop or even later. Testing the entire range of cropping systems resulting from combining crops and techniques in time and in space in experiments or farm-field networks is literally impossible, particularly when evaluating long-term effects and variability in response to weather. This is the reason why simulation models are increasingly used to evaluate and design cropping systems (Ould-Sidi and Lescourret, 2011; Dury et al., 2012; Martin et al., 2013). They are also a formidable tool to synthesize knowledge produced by different teams and disciplines, and they can be used to develop decision-support systems or to interact with farmers.

Because of the many facets of weed impacts, and their sensitivity to management techniques and biological regulations, we hypothesize that weed dynamics models are a particularly appropriate case study for investigating ecological intensification in general and crop diversification in particular. The latter is supported further by the fact that plant-plant interactions in intercropping are driven by the same processes as in a crop-weed canopy and that crops, just as weeds, have carry-over effects on the following crops in a rotation. Both crop-crop and crop-weed canopies are heterogeneous canopies where plants compete for space, light, nutrients and water (Teasdale, 1996), release allelopathic compounds that hinder competitors (Sturm et al., 2018), or harbour pests that can spread to their neighbours or successors (Gutteridge et al., 2006). Similarly to intercropping, crops and weeds could also benefit from each other, e.g. weeds could reduce nitrate leaching, protect soil from erosion or harbour pest enemies, though these aspects are rarely appreciated (Blaix et al., 2018; Moreau et al., 2020). While crop models historically mostly focused on homogeneous monospecies canopies at the annual scale (Keating and Thorburn, 2018), weed models, per force, were always at least bi-species, with a particular focus on the effects of management techniques at a multiannual scale (Colbach and Debaeke, 1998; Holst et al., 2007; Freckleton and Stephens, 2009) as weed seeds survive for several years in the soil (Lewis, 1973).

Here, we intend to illustrate that weed models are a useful basis for a modelling framework to synthesize knowledge on the functions and effects of crop diversity, to produce emergent knowledge on the functioning of the agroecosystems and for systems design, and to promote the benefits of ecological intensification, illustrating with the example of crop diversification (Figure 1). Not all weed dynamics models (Colbach and Debaeke, 1998; Holst et al., 2007; Freckleton and Stephens, 2009) are appropriate to investigate and implement crop diversification. Suitable models must be both multispecies and multiannual, they must be spatially explicit and include all management techniques, with interactions among techniques and with pedoclimatic conditions. Mechanistic models make it easier than empirical ones to synthesize knowledge on functions and effects of processes (Colbach, 2010). They make it easier to add new species, processes, knowledge, they have a larger domain of validity without reestimating parameters when switching regions, and their conclusions are more robust as knowing the cause of an effect makes it easier to predict its domain of validity. These advantages though come at a cost in terms of speed and easiness of use (Colbach, 2010). Moreover, tailoring the models' structures and outputs to stakeholders' needs is essential to ensure that models are actually used and to translate the synthesized knowledge into indicators relevant for decision making in farming (Voinov and Bousquet, 2010; Prost et al., 2012).

Here, the objective was to use an existing weed dynamics model to illustrate how such a model can be used to (1) synthesize knowledge relevant for biological interactions and agroecological management levers, using spatio-temporal crop diversification and the major concerned biological interactions as a case study, (2) evaluate and design multiperformant cropping systems based on diverse crops, and (3) conclude on the rules driving the efficacy of crop diversification for agroecological weed management. The model used as a case study was FLORSYS (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014b; Mézière et al., 2015) which is, to our knowledge, the weed dynamics model that answers most of the requirements listed above.

2 How FLORSYS models the effects of crop diversification

This section first gives a general overview of the model used as a case study, followed by sections focusing on the features and functions that are relevant for considering crop diversification and demonstrating how these were included in the FLORSYS model (Table 1). This section mostly uses previous publications to support our arguments.

2.1 General structure of FLORSYS

FLORSYS (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014b; Mézière et al., 2015) is a virtual field on which many and diverse cropping systems can be tested and evaluated, in terms of crop production, weed benefits (e.g. biodiversity) and detriments (e.g. harmfulness for production). The user enters a list of cultural operations lasting for several years, similar to the operations applied to a real field in an experimental station or a farmer's field, together with latitude, daily weather data, and soil characteristics (Figure 2). The list includes all operations (i.e. tillage, sowing, mechanical weeding, fertilisation, pesticide spraying, mowing and harvesting operations), which must be described in detail in terms of dates and options (e.g. date, density, depth, interrow, orientation, equipment, species and cultivars, seed treatments, impurity rate of the seed lot for a sowing operation) over the many years or decades that the simulation is meant to run.

These inputs influence the annual life cycle of both crop and weeds, based on a mechanistic representation of biological interactions and other biophysical processes (section 2.2) at the "grain" of the individual (plant or seed) × day. Simpler, empirical relationships are preferred for processes whose mechanistic representation would require to downscale to the cellular or molecular scale (e.g., seasonal seed dormancy is predicted from calendar date rather than abscissic acid content or phytochrome activation). For discussion on mechanistic vs empirical pest modelling, see Colbach (2010).

The thorough representation of biophysical processes produces very detailed outputs, at a daily time step and in 3D, which are essential to understand why a given technique or cropping system results in a given performance. The model thus allows testing both temporal and spatial crop diversity, by simulating diverse crop rotations (including cover crops during summer fallow and multiannual grassland) and crop mixtures (including undersown cover crops). The model is currently parameterized for 26 frequent and contrasting annual weed species and 33 cash and cover crop species (section **A.2** online).

2.2 Which processes are crucial for crop diversification

To understand and model the effects and responses of crop diversity, three key steps must be considered in the model (Table 1.B).

2.2.1 Emergence timing and establishment: the first out wins the race

Processes relative to emergence and early growth are essential to predict crop establishment in terms of timing and magnitude for species with diverse ecological requirements. This is crucial for rotations including crops sown in different seasons and, even more, for crop mixtures as the first established species often outgrows later emerging species, even if the latter are potentially more competitive. The same applies when focusing on weed dynamics as weed floras consist of species emerging in different seasons and the most harmful weed species are usually those that emerge either with or slightly earlier than the crop (Freckleton and Watkinson, 1998; Forcella et al., 2000; Fahad et al., 2015; Swanton et al., 2015). This explains why weed dynamics models are helpful to understand crop emergence in crop-diverse systems.

Initially, crop emergence models made emergence timing simply depend on temperature (Donatelli and Marchetti, 1994). Processes such as germination failure and pre-emergent seedling mortality were only considered when emergence failure in particular crop species was investigated (e.g. sugar beet, Dürr et al., 2001). FLORSYS took this generic approach a step further, by including processes relevant not only for weeds but also for crop diversification (Figure 3). For instance, cover crop seeds can be broadcast onto the soil surface where they are exposed to predation and have more trouble germinating (Gardarin et al., 2012; Cordeau et al., 2015) because of insufficient soil-seed contact (Figure 3.A and D). Moreover, genetic progress is slower for many minor crops introduced into cropping systems for diversification purposes (Meynard et al., 2018). For instance, cover crop seeds are often more dormant and smaller than major grain crops (e.g. average seed mass of FLORSYS cover crops is 20 mg, compared to 57 mg and 195 mg for cereals and grain legumes, respectively), and their seed lots can also comprise more impurities, i.e. seeds of other cultivars or species. This means less and slower germination (Figure 3.D), more seedling loss due to insufficient seed reserves (Figure 3.E) and insufficient shoot strength to grow around soil clods (Figure 3.F) as well as more seeds of other cultivars or species (whether crop or weed) introduced into the field (Figure 3.C).

2.2.2 Competition for resources: be large or be flexible

Once established, the major interaction between different plant species is competition for light and soil resources. In high-input agroecosystems of temperate climates, light is generally the resource for which crop and weed plants compete the most (Wilson and Tilman, 1993; Perry et al., 2003), and the same applies to multispecies crop canopies. FLORSYS splits competition for light into two processes. First, as in classic ecophysiological models, biomass increase is the difference between the newly produced photosynthate as a function of intercepted photosynthetic active radiation (PAR), species light use efficiency, species temperature requirements and air temperature on one hand, and, on the other hand, photosynthate loss due to respiration as a function of the existing biomass of the various plant organs (Colbach et al., 2014b). In contrast to most crop models, FLORSYS simulates these processes at the scale of each individual plant, making the intercepted light not only depend on the plant's leaf area, but also on where the plant is located in the canopy and how much light is intercepted by its neighbours (section 2.3). This level of detail is necessary to realistically represent the structure and interactions of a heterogeneous crop-weed canopy (Renton and Chauhan, 2017) and essential to allow simulating any number of species combinations in a canopy, a prerequisite to tackle crop diversification.

The other key difference with existing crop models is the inclusion of shading response (Munier-Jolain et al., 2014; Colbach et al., 2020b). FLORSYS simulates the shading response of key aboveground morphological plant variables (see examples in Table 2). This response depends on the species, and the species parameters are measured in garden-plot experiments where individual plants are grown either in unshaded conditions or under shading nets mimicking shading by neighbour plants. For each variable and each plant species at a given phenological stage, a non-linear regression is then fitted vs. shading intensity to estimate (1) the potential value in unshaded condition and (2) a parameter assessing the shading response of the variable (details in section **B.3** online). This approach allowed identifying the most plastic plant variables and the types of shading response of weeds and crop species from different botanical families (Table 2). In the studied species and varieties, the morphological characteristics that the most responded to shading are the specific leaf area (increasing leaf area for a given leaf biomass) and specific plant height (increasing plant height for a given plant biomass); generally, non-legume dicotyledenous species respond more than Poaceae, and weeds more than crops. The approach also demonstrated that there are potentially two strategies, either be large by occupying the field before neighbours cast shade and leave no space available for latecomers, or be flexible by changing one's plant shape to avoid or outgrow shade cast by early arrivals (also see section 3.3).

2.2.3 The biophysical field memory: vengeance is a dish best served cold

Crops do not only interact inside a multispecies canopy, they also interact over time by changing the biophysical environment. Summer cover crops are often chosen specifically for this carryover effect (e.g. to reduce nitrate leaching, soil evapotranspiration and/or weed growth) (McCracken et al., 1994; Teasdale, 1996; Carrer et al., 2018; Gfeller et al., 2018; Sturm et al., 2018) but can also have adverse effects (e.g. reducing soil water available for cash crops in case of late termination, Munawar et al., 1990). This field memory also applies to successive crops in a rotation. FLORSYS includes the memory of physical state variables, e.g., soil structure and soil water, which will affect germination and emergence of both subsequent crops and weed communities (section 2.2.1). The effects of management techniques, plant communities and weather on the physical state variables do not need to be modelled specifically for crop and weed canopies. Generic submodels from crop models such as STICS (Brisson et al., 2003) or decision support systems such as DéciBlé (Chatelin et al., 2005) were linked to FLORSYS (Gardarin et al., 2012), demonstrating the role of mechanistic models for aggregating knowledge produced by different teams and disciplines.

The biological memory, i.e. the weed seed bank, is the main reason why weeds are so difficult to manage. Indeed, it is usually not the sole weed plant surviving in one year that damages crop production, but the hundreds or thousands of seeds it produces, which will infest later crops (Cardina et al., 1991) according to the processes described in section 2.2.1. Crops can also directly contribute to weed seed bank replenishment, via volunteers resulting from crop seeds lost before or during harvests (Gruber et al., 2008). These volunteers can compete with other crop species, resulting in yield loss (Odonovan et al., 1989), or contaminate the production of other cultivars of the same species, for instance by changing the fatty-acid composition of oilseed rape (Baux et al., 2011). The risk of a species leading to volunteers depends on seed persistence and temperature requirements (section 2.2.1). In temperate conditions, oilseed rape volunteers are thus much more common than wheat and, particularly, maize volunteers (Gruber et al., 2008).

2.3 Canopy and plant structure tailored to many contrasting species

FLORSYS consists of three spatial layers (Munier-Jolain et al., 2013; Colbach et al., 2018; Pointurier et al., 2021): (1) a generic 3D representation of plant structure, (2) a 3D location of leaf area inside the field resulting from individual plants, and (3) a spatially-explicit representation of field clusters and semi-natural habitats. This representation applies to both crop and weed species, irrespective of clade, plant growth form, plant size or shading response, as demonstrated by validation studies (section 2.5).

2.3.1 A generic plant structure

Because weed floras consist of many contrasting annual species (Fried et al., 2010), FLORSYS needed to include many contrasting annual species. The representation of individual plants had to be compatible with multiannual and multi-field simulations of thousands of plants per field. Consequently, detailed representations such as those used in functional-structural plant models (Evers et al., 2016; Gaudio et al., 2019) were too complicated for our purpose.

Instead, FLORSYS represents each plant as a combination of a cylinder (for the above-ground part of the plant) and a spilled cone (for the root system) (Figure 4.A) whose dimensions are determined daily by plant biomass and a series of state variables depending on species, plant stage and past shading exposure. For instance, the cylinder dimensions are determined by specific plant height and width (Table 2). Then, the plant variables relevant for competition processes are distributed inside the plant volume. For instance, leaf area is calculated from specific leaf area (i.e. plant leaf area per unit of leaf biomass) and leaf biomass ratio (i.e. plant leaf biomass per unit of aboveground biomass), and then distributed along layers according to median leaf area height (i.e. relative plant height below which 50% of leaf area are located) (Table 2). In total, in addition to plant above-ground biomass, eight state variables are used to determine above-ground plant morphology. These variables are derived from eight parameters describing potential morphology for a given species and stage, and five parameters describing species response to shading (section 2.2.2).

2.3.2 A voxel-based 3D representation of the canopy

At plant emergence (section 2.2.1), FLORSYS places each plant on the field map (Figure 4.B). Crop plants are usually sown in rows, and their pattern depends on the user's choices in terms of density, interrow width, sowing precision and orientation. But, they can also be sown in strips or broadcast, which can be the case for summer cover crops. Weeds are placed in aggregated patches, as this is usually the case in fields (Cardina et al., 1997; Colbach et al., 2000; Pollnac et al., 2008). Above and below-ground areas are discretized with voxels (3D pixels), including the leaf area and root density of the different plants of the field (Figure 4.C). Each day, light trickles down successive voxel layers, depending on incident radiation (PAR), leaf area, species extinction coefficients and solar angle (Figure 4.D). This representation allows calculating not only the PAR intercepted by each individual plant, but also the shade cast onto neighbour plants, thus laying the basis for plant-plant competition for light (section 2.2.2). A similar approach is currently being implemented to simulate plant:plant competition for soil resources (e.g., water, Moreau et al., 2018; nitrogen, Moreau et al., 2021; Perthame et al., submitted).

In addition to representing a large diversity of sowing pattern for single-species crops, FLORSYS's modelling approach allows simulating any kind of crop mixture, unlimited by the number of species, their characteristics, sowing patterns and dates.

2.3.3 A spatially-explicit field pattern

Crop diversification can occur not only inside each field, by mixing or alternating different crops. It is also essential to consider it at the landscape scale, which is to date rarely considered in crop models or in cropping-system design. Indeed, landscape crop patterns contribute to weed dynamics by placing favourable habitats, both in time and in space (Petit et al., 2013). This effect is larger for more mobile pests (Angelella et al., 2016) than for weeds (Petit et al., 2016). Crops can also directly interact by exchanging pollen which can affect harvest purity (Bilsborrow et al., 1998; Klein et al., 2003; Devaux et al., 2008), or indirectly by shattered crop seeds which can contribute to the establishment of feral populations in semi-natural habitats (Squire et al., 2011) and to volunteer populations in neighbour fields (Colbach, 2009). Both dispersal mechanisms make difficult or even impossible the coexistence of different production chains (Bilsborrow et al., 1998; Sausse et al., 2013).

FLORSYS allows tackling some of these questions by upscaling from the field to the field cluster, simulating several fields and semi-natural habitats in parallel and, at seed shed, dispersing weed seeds as well as shattered crop seeds from a source plot to neighbouring habitats (Colbach et al., 2018). Seed dispersal distance increases with weed plant height and decreases with seed mass; it is higher for seeds dispersed by animals and wind than for those dispersed by gravity (Thomson et al., 2011; Colbach et al., 2018). The dispersed seeds then colonize new fields and habitats or integrate existing populations, both contributing to wild plant biodiversity and damaging crops.

FLORSYS disregards seed dispersal related to human activities even though weed seeds have been reported to travel by agricultural machinery (Hodkinson and Thompson, 1997; Humston et al., 2005; Petit et al., 2012). These anthropogenic dispersal processes can lead to long dispersal events, particularly between distant fields of a given farmer. However, to date, proportions of seeds dispersed by machinery relatively to the natural dispersal fraction is only known in a few particular cases (Gao et al., 2018), which makes it difficult to include in a model.

2.4 Parameterize many contrasting species

A model aiming to understand and simulate the effects of crop diversification must necessarily include a large number of contrasting species. However, the mechanistic approach that was chosen here to simplify the continuous synthesis of knowledge (Colbach, 2010) requires an enormous amount of parameters, which hinders the addition of new species to the model. This is the reason why Gardarin et al. (Gardarin et al., 2012; Gardarin et al., 2016; Colbach et al., 2020b) developed a new methodology based on functional relationships to estimate difficult-to-measure model parameters from easily measured species traits, trait data bases and/or expert opinion (Figure 5). The approach was recently extended to crop species (Gardarin et al., 2016; Colbach et al., 2020b). It is the combination of these functional relationships with the generic representation of plants and canopies, which makes FLORSYS such a unique tool for synthesizing and using knowledge on plant species diversity in general and crop diversity in particular.

2.5 Checking virtual against actual reality

The model was evaluated with expert knowledge and independent observations in order to check modelling hypotheses, to determine the domain of validity and prediction error, and to identify missing or inadequately represented processes. Evaluation is an ongoing process, constantly acquiring new data to extend the domain of validity and rerunning simulations against previous data when new submodels are added to FLORSYS.

Historically, the first evaluation step consisted in delimiting a first domain of validity based on the model structure. This domain excluded, for instance, weed floras predominantly consisting of perennials, locations with frequent drought or nitrogen stress as these factors are not yet included in the model (Colbach et al., 2014a). The second step consisted in setting up short-term experiments in controlled conditions or well monitored field experiments (lasting 1-2 years) for evaluating key processes or functions (e.g. emergence timing and abundance, light penetration into the canopy, parameter estimation from traits) (Colbach et al., 2006; Gardarin, 2008; Munier-Jolain et al., 2013). The last step consisted in gathering data from multi-annual field trials (lasting 10 years and more) and farmers' fields (Colbach et al., 2016) to evaluate how well FLORSYS predicts weed floras (density, biomass, seed bank), crop biomass and yields over a large range of arable cropping systems and pedoclimates. Adequate data were difficult to obtain, particularly for long time series and in terms of weed observation (particularly initial weed seed bank), which sometimes made it impossible to conclude whether the model was deficient or the inputs badly estimated.

The evaluation showed that crop biomass and yields, weed seed banks, daily weed species densities and, particularly, densities averaged over the years were generally well predicted and ranked (e.g. modelling efficiency of 0.55 for crop yield, 85% of observed weed species density included inside the simulated confidence interval) 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) (see details in section A.5 online). Prediction quality was usually better at the species than at the community scale, and better at the rotation than at the daily scale. The evaluation also identified missing processes, which set off another round of modelling (e.g. competition for nitrogen and water, seed predation by carabids).

3 How FLORSYS was tailored and used to address real-world problems

This section presents different methodologies for using a model such as FLORSYS to investigate and manage ecological intensification, and illustrates them with a focus on crop diversification.

3.1 Tailor outputs to stakeholders' needs

FLORSYS's mechanistic approach makes it possible to produce detailed outputs (at a daily time step and in 3D) mimicking measurements on actual canopies and biophysical environments in experimental or farmers' fields. These outputs are essential for scientists wanting to synthesize knowledge and understand the functioning of the canopy in the virtual field.

To simplify the comparison of cropping systems (e.g., with different rotations, intercroppings and/or management plans) and to make simulations more accessible to outsiders, the detailed outputs are translated into indicators assessing crop production as well as weed impacts (i.e. benefits and detriments). FLORSYS production indicators comprise crop yield in terms of weight and energy. The latter allows comparing the production of diverse crops, to sum production over rotations and field clusters. Indicators of weed detriments describe weed harmfulness for crop production and were developed in interaction with farmers and crop advisors (Mézière et al., 2015; Colas et al., 2020), considering direct (crop yield loss and harvest pollution by weed debris) and indirect weed harmfulness for crop production (increase in weed-borne pests), technical harmfulness (harvesting problems due to weeds blocking the combine), and sociological harmfulness (field infestation as a proxy of the farmers' worry of being thought incompetent by their peers if their fields are infested with weeds even if there is no effect on yield).
Weed-benefit indicators were developed with ecologists and agronomists (Mézière et al., 2015; Colbach et al., 2020a; Moreau et al., 2020) and reflect the contribution that weeds make to biodiversity and the environment. They consider wild plant diversity (weed species richness and evenness), the role of weeds for feeding three major guilds in the agro-ecosystems (pollinators, farmland birds, carabids) and for reducing three physical farming impacts on the environment (nitrate leaching, pesticide transfer, soil erosion).

Calculating these indicators via a mechanistic model allows predicting them for any combination of crop and weed flora, once the various species are parameterized in FLORSYS. This is a fundamental difference from previous approaches in weed science, notably for estimating yield loss, which established two-by-two empirical relationships linking yield of crop x to a state variable (usually plant density) of weed y (e.g., Cousens, 1985). Such equations are next to impossible to use to assess the effects of crop diversification, as they are specific to a given crop-weed couple as well as to the location and resource availability of the field where they were established.

3.2 Move from process-based modelling to decision support

Despite these tailoring efforts, FLORSYS remains a research model in that (1) it requires numerous input variables to be assigned and parameters to be tuned, particularly when including many diverse crops, (2) it evaluates cropping-system candidates rather than actually designing these candidates, and (3) its mechanistic and individual-based approach induces a high algorithmic complexity and very slow

simulations (Colbach, 2010). In order to address these limitations, we transformed FLORSYS into a decision support system, DECIFLORSYS co-designed with future users (Colas, 2018; Colas et al., 2020) and resulting from metamodeling FLORSYS (Colas, 2018) (section **C** online for further details).
The first step consisted in building a large set of simulation results by using the research model to set up a network of several thousand virtual farm fields, including both actual systems (as in section 3.4) and systems based on random choices of techniques. The latter were essential to ensure that the domain of validity of the metamodel was not limited by current practices or experts' imagination, particularly in terms of crop diversity, rotational patterns or crop mixtures.

Then, we linked the weed impacts on crop production and biodiversity simulated by FLORSYS to cropping-system variables, as if developing an empirical model from field data. To do this, we chose two complementary machine-learning approaches, resulting into two different tools. Multivariate regression trees (Breiman et al., 1984; De'ath, 2001) provide a synthetic graphical representation ("decision tree") to identify candidate changes in cropping systems that improve their performance, through navigation among branches (see example in Figure 6). In addition, we built multivariate random forests (Breiman, 2001; Segal and Xiao, 2011), which function as black-box models ("predictor") that directly predict weed impact indicators from cropping-system variables, thus emulating FLORSYS, but with a much faster response time and easier to handle than the parent model. While the predictor is as good as FLORSYS to rank cropping systems, it cannot adequately evaluate effects that strongly interact with pedoclimatic conditions, such as the effect of tillage timing with respect to soil moisture (Colas, 2018; Colas et al., 2018; Colas et al., 2019). In terms of crop diversification, this means that rotations or intercropping strategies are correctly ranked but that the difference between the different systems might be over or underestimated.

The tools can be either generic and applicable to most of France as the example of Figure 6, or tailored to the specificities of pedoclimatic production contexts (Colas, 2018; Colas et al., 2018; Colas et al., 2019). The decision tree of Figure 6 focuses on temporal crop diversification and demonstrates the importance of the proportion of winter and spring crops in a rotation as well as the duration of crop cover. For instance, decreasing winter crops below 35% reduces both weed harmfulness for crop production and weed-based bee food offer from high to intermediate (performance profile P12 vs P11). Rotation also has an indirect effect, by changing the seasonality of cultural operations, particularly tillage. For instance, the profiles with the lowest weed impact (P3, P7) are both located within the branch starting with frequent summer tillage. But, weed impact did not only depend on seasonality or on the frequency of operations, it also varied with options, such as the tillage tool (e.g. frequent chisel ploughing to the detriment of power harrowing and residue shredding decreased weed impact in P5 vs P6) or the type of herbicides (e.g. non-systemic herbicides in P13).

3.3 Identify parameters that make a good diversification crop

This case study is a first example where simulations were run to address a real-world issue related to crop diversification. The objective was to identify which crop parameters drive crop production in weed-free and weed-infested crop stands as well as the parameters that reduce yield loss and weed reproduction (leading to yield loss in future crops). This knowledge will contribute to establish rules for choosing crops in rotations and crop mixtures and to identify ideotypes, i.e. theoretical ideal crop plants that combine all the characteristics required to reach one or several goals in a production situation (Martre et al., 2015).

3.3.1 Monitor a virtual farm-field network

FLORSYS was used to run virtual experiments in seven French and Spanish regions, with 272 cropping systems collected from farm surveys, farm-field networks and crop advisors, and varying in terms of crop rotations, herbicide use and tillage intensity (Colbach and Cordeau, 2018; Colbach et al., 2019). Two series of simulations were run. The first started with a regional weed flora pool from the cropping system's region of origin and predicted actual yield in weed-infested crop stands; the second was run without any weeds to estimate potential yield in weed-free crop stands. The comparison of the yields from the two series allowed calculating weed-caused yield loss. In each series, each cropping system was simulated over 30 years to include long-term effects, and repeated with 10 weather series to assess interactions with weather. Here, simulations worked with past weather data recorded by weather stations but future scenarios predicted by climate models (Xu et al., 2012; Boulard et al., 2017) can also be used. The simulated outputs in terms of crop grain yield, weed-caused yield loss, weed seed production (as a proxy for future yield loss) and weed-based trophic resources for domestic bees (as one example of weed benefits) were analysed as if they were measurements from actual farmers' fields.

3.3.2 The winner depends on the goal

The crop features that increase potential yield are different from those that reduce yield loss or weed seed production (i.e., yield loss in future crops). This is a frequently reported antagonism (Sardana et al., 2017), which makes the breeding of crop varieties that are both productive and competitive against weeds more difficult. So, in addition to the advice of Figure 6 on, e.g., the balance between winter and spring crops, Table 3 gives further pointers to which crops to combine in a rotation.
When weed pressure is low, thanks to efficient management techniques, a crop or variety maximizing potential yield (i.e., yield in the absence of weeds) can be used. In the virtual farm-field network, potential yield increased with decreasing base temperature and, particularly, base water potential which ensure early emergence and better emergence success in spring and summer (Table 3). Other features ensuring high yield in weed-free conditions were leaves concentrated toward the top of plants (high RLH), vertically rather than laterally growing plants (low WM) with small thick leaves (low SLA), resulting in taller plants per unit biomass that shade less and/or cover less ground. Another feature was a weak shading response (low mu_HM, mu_RLH, mu_SLA) resulting in homogenous canopies as plants grew irrespective of their neighbours.

However, when a weed-tolerant crop was needed in the rotation, the required species profile differed. The crops with the lowest yield loss were wide, shading and flexible, i.e. they grew laterally in unshaded conditions (high WM), had thinner larger leaves, particularly from flowering onwards (high SLA) and etiolated when shaded by neighbour plants, with taller plants (high mu_HM) and even thinner larger leaves (high mu_SLA). If the objective is to limit infestation of future crops that might be more weed-sensitive or present fewer management options, that yet another profile is needed. Crops that photosynthesized well at lower temperatures and invested in plant width rather than height (low HM) reduced weed seed production the most.

3.3.3 Which ideotypes for crop diversification

The present case study demonstrated that ideotypes aiming to maximise yield potential are not the same as those that efficiently compete with weeds for light. As illustrated in the previous section, Table 3 can be a guide to choose crops in a rotation depending on whether the year's focus should be on production to boost the current income, or on weed suppression to safeguard the next year's productivity. When extrapolated to crop mixtures, the trade-off between yield potential and weed suppression could mean that crop species with a high yield potential can be mixed and grown together without hindering each other in terms of light use. It certainly means that crop species must be mixed together to efficiently occupy more ground and leave no niches for weeds. While this has already been demonstrated experimentally (Verret et al., 2017), our model-based approach allows us to identify the most relevant processes and species parameters or traits. This is essential to determine in which situations rules for combining traits and species are valid and to extrapolate to a larger range of contrasting crop and weed species. This approach will also be a key tool to investigate which crop trait mixtures answer to different performance goals.

3.3.4 Crop parameters alone do not assure success

Yield potential mostly depended on crop choice (partial R^2 of 0.46, compared to 0.06 for cropping system (other than crop and variety choice) in the analysis of Table 3, section **D.1.2.3** online). But, the opposite was true for weed impacts and control, they were mostly driven by management (e.g. partial R^2 of 0.42 for cropping system vs 0.08 for crop species for weed seed production). Choosing optimal crop parameters was not enough to ensure weed suppression, crop management also had to be adapted. This means that crop diversification is doubly efficient because it not only diversifies crop species and varieties, it also diversifies management practices as these strongly depend on the crops.

3.4 Track crop-diverse solutions

The previous simulation study showed that though crop parameters mostly drive potential crop production, they only determine a small part of performance in terms of actual production and, particularly, weed impacts. Here, we present three different approaches of using models such as FLORSYS to demonstrate how to combine crop species in time and in space and how to identify appropriate management practices to reach different goals, mainly to reconcile reduced herbicide use with reduced yield loss due to weeds and improved weed contribution to biodiversity.

3.4.1 Track high-performance farmers' practices in virtual farm-field networks

The same approach as in section 3.3 can be used to set up a virtual farm-field network to track innovations among farmers' practices (Colbach and Cordeau, 2018). The main difference lies in the analysis of the simulated data: instead of linking species parameters to cropping system performance, the idea is to determine which combinations of crops and techniques allow reaching performance goals. Classification and regression trees as those used to build DECIFLORSYS (section 3.2) are useful, but instead of classifying cropping systems according to their performance, the trees were used to specifically track those systems that reach these performances goals, here to minimise both yield loss and herbicide use intensity. The other difference lies in the source of analysed cropping systems. Here, we explored cropping systems that existed in reality and are thus feasible from a socio-economic point of view.

This analysis demonstrated the importance of crop diversity for reconciling low yield loss and low herbicide use (Table 4). Three "winning" types of strategies could be identified among the investigated farmers' cropping systems, which differed in terms of rotation, tillage strategy etc. Strategy S1 consisted of maize monocultures, relying heavily on herbicides as well as mechanical weeding to limit yield loss. Strategy S2 was based on rotations that were diverse in time (lasting for at least 4 years) and in space (with crop mixtures or cover crops during summer fallow), combining both spring and winter crops. Crops were either long-lasting winter crops (e.g. oilseed rape), or shorter winter and spring crops preceded by cover crops. This diversity, combined with frequent tillage, particularly in summer, and occasional mouldboard ploughing allowed reducing herbicide intensity. Strategy S3 went even further in terms of crop diversification in the rotations, reducing winter crop frequency even more and adding temporary grassland to the mix. Annual crop cover was shorter (which also meant fewer fallow cover crops), leaving more time for superficial tillage as well as more mouldboard ploughing. No minimum herbicide or mechanical weeding was required.

This case study demonstrated not only how a weed dynamics model can be used to investigate the effects of crop diversity in cropping systems on crop production and weed impacts, but also the key role of crop diversity for managing weeds, particularly when aiming to reconcile multiple goals.

3.4.2 **Ex ante** *evaluation of innovations proposed by experts and policies*

The FLORSYS model can also be used to evaluate prospective cropping systems that are designed by experts or stakeholders (section 3.5) or expected to result from policy changes (
Table 5,
Table 6.C and D). The simulation plan is the same as for the previous studies (i.e. over several decades, repetitions with several weather series, see section 3.3.1). What changes are the origin of the inputs and, to a lesser degree, the methods for analysing the simulated data.

FLORSYS can complement cropping system trials, both to evaluate prototypes imagined by experts to identify the best candidates to test in fields, and to extrapolate systems that are implemented in trials. In

the latter case, long-term simulations allow assessing the carryover effect of crop rotations (section 2.2.3) faster and longer than in fields, the weather repetitions allow increasing the genericity of the results, particularly when they are associated with different initial weed floras or pedoclimate, and the multiple simulation outputs allow assessing weed functions that are difficult or impossible to monitor in fields. The example of
Table 5, for instance, shows that the system with the highest yield used nearly no herbicides (IWM ~0 herbicides) but presented a high crop diversity in terms of species and cultivar richness, sowing seasons (including both winter and spring crops) and cover crops. A high species/cultivar number and cover-crop frequency was though not enough to ensure production if it were not accompanied by tillage and alternating sowing seasons (IWM simplified). This is consistent with results from a meta-analysis on crop diversification effects (Weisberger et al., 2019). Moreover, crop diversity did not ensure weed benefits, as demonstrated by the low weed-based bee-food offer in the IWM ~0 herbicides system.

The necessity of looking at weed impacts over time even when focusing on annual practices is demonstrated by another study that investigated the effects of wheat sowing strategies on weed infestation at a 10-year scale (Colbach et al., 2014b). Techniques simply changing the sowing pattern (e.g. density, interrow width, row orientation) only had an immediate effect at the annual scale. But increasing crop diversity during one single year had repercussions during several years, both positive (associating wheat with faba bean reduced yield loss for up to 10 years) and negative (introducing a cover crop before wheat increased weed infestation in later crops because it left no time for false seed bed techniques).

FLORSYS also allows assessing larger spatial scales, for instance to assess annual crop diversity in a field cluster or the effect of introducing semi-natural habitats (section 2.3.3). Case studies demonstrated that spatial diversity can compensate for uniformity in individual fields. For instance, including permanent grass strips in a field cluster solely cultivated by maize monoculture in Aquitaine (South-Western France) increased weed-based biodiversity more than shifting the whole cluster to a diverse rotation including one legume and one winter crop, and this without adverse effect on crop production (Colbach et al., 2018). Most importantly, FLORSYS can assess prospective scenarios such as those resulting from planned policy changes, allowing policy makers to check whether goals are actually reached (e.g. do permanent grass strips promote biodiversity?) and that there are no unexpected side-effects (e.g. do new cultivars adversely affect biodiversity?).

3.4.3 Optimize rotations with an algorithmic approach

In the previous approach, the tested cropping systems were designed by experts. While there is often no match for experts when it comes to optimizing a given management technique in a given location considering short-term effects, they simply cannot juggle with all the relevant techniques, particularly when considering multiple criteria in the long-term. So, the tested systems are often limited by the expertise and the imagination of the experts. An alternative is to assess randomly constructed cropping systems, as during the development of the decision support system (section 3.2). However, the number of candidate systems is so huge that the search for the optimal system is difficult.

To overcome this problem, models can be combined with optimization algorithms to identify a series of solutions answering to a set of constraints and objectives (Press et al., 2007; Venter, 2010). This approach can tailor both crop trait combinations and crop rotations to stakeholders' needs, using an iterative loop: (1) determine the optimization objectives (e.g. maximize both yield and weed-based bee food offer), (2) change inputs (either crop parameters or cropping system components), using an optimization algorithm, and simulate the resulting scenario with FLORSYS, (3) compare the simulated performance with the fixed objectives to check whether the change in inputs led to an improved performance, (4) return to step 2 and continue until objectives are achieved.

The different optimization algorithms (genetic algorithm, Goldberg, 1989; Firefly algorithm, Yang and He, 2013) differ in the way they change the inputs to move towards the goal. When antagonist objectives are considered (e.g. maximizing both yield and biodiversity), a Pareto front is constructed, which is a set of "Pareto-optimal" solutions (Craven, 1986): for each point of the Pareto front, it is impossible to increase one indicator without deteriorating at least another indicator. Once the set of solutions has been obtained, the stakeholders can choose a compromise according to their constraints.

The example of Figure 7 aims to identify three-year rotations that reconcile production with weed-based bee-food offer in one production situation and focusing on cereal-based rotations. Here, cereal monocultures maximised yield to the detriment of biodiversity (bottom right of Figure 7) whereas legume-based rotations tended to improve biodiversity (top left). The rotations with the highest number of different crop species were found toward the center of the figure, i.e. they presented both medium biodiversity and medium production. This study also demonstrated that a given rotation can result in a very different performance, depending on crop management. For instance, mouldboard ploughing increased production to the detriment of biodiversity in some rotations (WWB, wheat/wheat/barley) whereas the opposite occurred in other cases (OWB: oilseed rape/wheat/barley).

3.5 Implicate stakeholders in crop diversification

3.5.1 The limits of research

The present case studies illustrate part of the enormous amount of knowledge already produced by scientists on crop diversification in the particular case of weed management, and methodologies on how to produce knowledge and management rules for particular production situations and goals. However, innovations proposed by scientists are often disregarded by farmers because they are incompatible with farming constraints (Meynard et al., 2018) or with farmers' risk perception and management (Wilson et al., 2008). Crop advisors can also be reticent to promote the necessary changes (Pasquier and Angevin, 2017). In this context, models are invaluable teaching tools to propagate knowledge and promote innovations via training sessions, participatory workshops and role-playing games (Martin et al., 2011; Hossard et al., 2013; Meylan et al., 2013; Sausse et al., 2013). This is particularly true of easy-to-use models (like the one developed in section 3.2), which allow stakeholders to directly and immediately see the consequences of changes in their practices in their particular production situation.

3.5.2 Participatory workshops including stakeholders

We combined cropping-system prototyping and model simulations to make use of the knowledge synthesized by FLORSYS and DECIFLORSYS (Van Inghelandt, 2018; Van Inghelandt et al., 2019). Workshops were run with farmers, using facilitation methods (e.g. board games) to foster interaction among famers during the prototyping (Lefèvre et al., 2014; Berthet et al., 2016). We split workshops into several steps. First, the general context was determined by identifying the farmers' constraints and objectives, among which possible and acceptable diversification crops, and a reference cropping system (in this case, an oilseed rape – cereal rotation heavily infested by autumnal grass weeds) which served as a baseline to evaluate the future prototypes. Then, crop-diverse prototypes were designed by several farmer groups, using the facilitation tool MISSION ECOPHYT'EAU® (composed of a game board and cards, http://www.agriculture-durable.org/ressources/mission-ecophyteau/), the DECIFLORSYS decision trees (see example of Figure 6) and ranking tables to stimulate discussions and the proposal of prototypes. These were immediately assessed with the DECIFLORSYS predictor, leading in turn to alternative proposals. During a recess of several days, the prototypes were simulated with the FLORSYS research model to fine-tune management techniques in terms of dates and options and to identify the biophysical reasons for the simulated performance. These simulation results were presented to the farmers during the final workshop day, and based on the participants' reaction, a further round of prototypes was proposed and tested with the DECIFLORSYS predictor.

3.5.3 Going beyond local prototypes

In addition to the prototypes and their performance as predicted by our tools, the simulation-based workshops contributed to evacuate some misconceptions that farmers had, in particular on the role of crop diversity and its effect on weed dynamics (Table 7). Among the major lessons of the workshops for farmers were the need to evaluate rotations at a multiannual scale, to consider the effect of weather on the success of management techniques. The latter was achieved by repeating cropping systems with different weather series, which allows running frequency analyses to determine the probability of success of a cropping practice (e.g., the probability that delayed winter wheat sowing reduces the emergence of autumnal grass weeds in the crop, Colbach et al., 2014a) or to link this probability to weather variables (e.g., delaying the first tillage operation until at least 50 mm rainfall post-harvest optimises false seed bed effects , Colbach and Mézière, 2013). The major conclusion of workshops for the research team was the farmers' need for biophysical explanations of cropping system performance, which the DECIFLORSYS decision support system cannot provide.

4 Strengths and limits of using mechanistic weed dynamics models to address ecological intensification

As illustrated in Figure 1, models such as FLORSYS and the associated simulation methodology cover the key steps to investigate and promote the benefits of ecological intensification, as demonstrated here with crop diversification. The case studies demonstrated that, generally, (1) crop diversification inside fields and in landscapes is essential to regulate crop pests such as weeds with few or no herbicides, (2) while a judicious choice of crop traits is essential, it is useless without a well-reasoned cropping system, (3) many conclusions in terms of crop diversification only have a local validity (Table 6), which proves the need for flexible rules and the usefulness of models such as FLORSYS and optimization algorithms to establish these rules.

But, all the advantages of model-based approaches are subject to the model's prediction quality. Checking the model's predictions against independent field observations is even more crucial for a mechanistic model aggregating data and models from different scales, teams and disciplines, to make sure that the new entity produces consistent results. When we did that for FLORSYS (section 2.5), it pointed to a major drawback of complex mechanistic models, i.e. the difficulty to find adequate data for evaluating the model and its many submodels.

The possibility of continuous evolution allowed by mechanistic model structures is crucial, particularly in a context of input reduction and climate change. Even without considering the many other pests and organisms implicated in ecological intensification, many plant-plant interactions are still disregarded in FLORSYS. Including perennial weeds will be essential to assess no-till systems (Armengot et al., 2016), plant-plant competition for water (Moreau et al., 2018) must be considered to assess drought-resistant crops in rotations and mixtures, and plant-microbe interactions may affect competitive relationships among plants, e.g. for nitrogen (Moreau et al., 2019). Allelopathy is another avenue that is often proposed for biological regulations of weeds (Sturm et al., 2018) but as yet, there is no evidence that it is actually relevant for weed control in field conditions where it is very difficult to discriminate from competition effects. Furthermore, even though the FLORSYS plant structure concept was initially based on a tree model (Chave, 1999), the model will not be adequate to tackle agroforestry systems (Malézieux et al., 2009) without major changes as the spatio-temporal "grain" and shape of trees is too different from that of weeds.

Mechanistic models such as FLORSYS are efficient in predicting the effect of cropping systems on the agroecosystem functioning but ecological intensification must be beyond biophysical processes (Figure 1). Though section 3 illustrates how we bridged the gap between biophysical and decision processes, we never went beyond the cropping system scale. But, including novel crops into rotation often means a major upheaval for the farmers who must learn to manage the new crop and have to find a buyer for its production, which can be a major obstacle to diversifying rotations (Meynard et al., 2018). Methodologies based on FLORSYS-like models can only partially contribute to lifting such lock-ins, by amplifying the diversity in conventional crops, using different varieties, intercropping, or management techniques promoting biological weed regulation. But, fundamentally, such socio-technical lock-ins can only be tackled by designing agrifood systems, including production chains and advice (Meynard et al., 2017).

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6 References

Agreste, 2019. Données de vente des produits phytopharmaceutiques 2016-2017. Agreste Chiffres et Données Agriculture, p. 12. https://agreste.agriculture.gouv.fr/agreste-web/download/publication/publie/Chd1905/cd2019-5bsva.pdf

Alignier, A., Petit, S., 2012. Factors shaping the spatial variation of weed communities across a landscape mosaic. Weed Res. 52, 402–410. 10.1111/j.1365-3180.2012.00934.x

Alignier, A., Ricci, B., Biju-Duval, L., Petit, S., 2013. Identifying the relevant spatial and temporal scales in plant species occurrence models: the case of arable weeds in landscape mosaic of crops. Ecological Complexity 15, 17-25.

Angelella, G.M., Holland, J.D., Kaplan, I., 2016. Landscape composition is more important than local management for crop virus-insect vector interactions. Agriculture Ecosystems & Environment 233, 253-261. https://doi.org/10.1016/j.agee.2016.09.019

Armengot, L., Blanco-Moreno, J.M., Bàrberi, P., Bocci, G., Carlesi, S., Aendekerk, R., Berner, A., Celette, F., Grosse, M., Huiting, H., Kranzler, A., Luik, A., Mäder, P., Peigné, J., Stoll, E., Delfosse, P., Sukkel, W., Surböck, A., Westaway, S., Sans, F.X., 2016. Tillage as a driver of change in weed communities: a functional perspective. Agric. Ecosyst. Environ. 222, 276-285. https://doi.org/10.1016/j.agee.2016.02.021

Baux, A., Colbach, N., Pellet, D., 2011. Crop management for optimal low-linolenic rapeseed oil production - Field experiments and modelling. Eur. J. Agron. 35, 144-153.

Berthet, E.T.A., Barnaud, C., Girard, N., Labatut, J., Martin, G., 2016. How to Foster Agroecological Innovations? A Comparison of Participatory Design Methods. Journal of Environmental Planning and Management 59, 280–301.

Bilsborrow, P.E., Evans, E.J., Bowman, J., Bland, B.F., 1998. Contamination of edible double-low oilseed rape crops via pollen transfer from high erucic cultivars. J Sci Food Agr 76, 17-22.

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

Blubaugh, C.K., Hagler, J.R., Machtley, S.A., Kaplan, I., 2016. Cover crops increase foraging activity of omnivorous predators in seed patches and facilitate weed biological control. Agriculture Ecosystems & Environment 231, 264-270. https://doi.org/10.1016/j.agee.2016.06.045

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. Trends in Ecology & Evolution 28, 230-238. 10.1016/j.tree.2012.10.012

Boulard, D., Castel, T., Camberlin, P., Sergent, A.-S., Asse, D., Bréda, N., Badeau, V., Rossi, A., Pohl, B., 2017. Bias correction of dynamically downscaled precipitation to compute soil water deficit for explaining year-to-year variation of tree growth over northeastern France. Agricultural and Forest Meteorology 232, 247-264. https://doi.org/10.1016/j.agrformet.2016.08.021

Breiman, L., 2001. Random Forests. Machine Learning 45, 5-32.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and regression trees. Chapman and Hall (Wadswoth, Inc.), New York, USA.

Brisson, N., Gary, C., Justes, E., Roche, R., Mary, B., Ripoche, D., Zimmer, D., Sierra, J., Bertuzzi, P., Burger, P., Bussiere, F., Cabidoche, Y.M., Cellier, P., Debaeke, P., Gaudillere, J.P., Henault, C., Maraux, F., Seguin, B., Sinoquet, H., 2003. An overview of the crop model STICS. Eur. J. Agron. 18, 309-332.

Bürger, J., Granger, S., Guyot, S.H.M., Messéan, A., Colbach, N., 2015. Simulation study of the impact of changed cropping practices in conventional and GM maize on weeds and associated biodiversity. Agricultural Systems 137, 51-63. https://doi.org/10.1016/j.agsy.2015.03.009

Cardina, J., Johnson, G.A., Sparrow, D.H., 1997. The nature and consequence of weed spatial distribution. Weed Sci. 45, 364-373.

Cardina, J., Regnier, E., Harrison, K., 1991. Long-term tillage effects of seed banks in three Ohio soils. Weed Science. 39, 186-194.

Carrer, D., Pique, G., Ferlicoq, M., Ceamanos, X., Ceschia, E., 2018. What is the potential of cropland albedo management in the fight against global warming? A case study based on the use of cover crops. Environ. Res. Lett. 13. https://doi.org/10.1088/1748-9326/aab650

Chatelin, M.H., Aubry, C., Poussin, J.C., Meynard, J.M., Masse, J., Verjux, N., Gate, P., Le Bris, X., 2005. DéciBlé, a software package for wheat crop management simulation. Agricultural Systems 83, 77-99.

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

Chave, J., 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. Ecol. Modelling 124, 233-254.

Colas, F., 2018. Co-développement d'un modèle d'aide à la décision pour la gestion intégrée de la flore adventice. Métamodélisation et analyse de sensibilité d'un modèle mécaniste complexe (FLORSYS) des effets des systèmes de culture sur les services et disservices écosystémiques de la flore adventice. Univ. Bourgogne Franche-Comté, Dijon, France, p. 334.

Colas, F., Cordeau, S., Granger, S., Jeuffroy, M.-H., Pointurier, O., Queyrel, W., Rodriguez, A., Villerd, J., Colbach, N., 2020. Co-development of a decision support system for integrated weed management: contribution from future users. Eur. J. Agron. 114, 126010. https://doi.org/10.1016/j.eja.2020.126010

Colas, F., Queyrel, W., Van Inghelandt, B., Villerd, J., Colbach, N., 2018. Un OAD pour la gestion agroécologie que adventices. De FlorSys à FLO², ou comment passer d'un modèle de recherche, complet mais compliqué à utiliser, á un outil d'aide à la décision fonctionnel. Phytoma 719, 14-18.

Colas, F., Villerd, J., Colbach, N., 2019. Simplification d'un modèle complexe pour le développement d'un modèle d'aide à la décision pour la gestion agroécologique de la flore adventice. Végéphyl – 24e conférence du COLUMA - Journées Internationales sur la Lutte Contre Les Mauvaises Herbes, Orléans, France.

Colbach, N., 2009. How to model and simulate the effects of cropping systems on population dynamics and gene flow at the landscape level. Example of oilseed rape volunteers and their role for co-existence of GM and non-GM crops. Environmental Sciences & Pollution Research 16, 348–360.

Colbach, N., 2010. Modelling cropping system effects on crop pest dynamics: how to compromise between process analysis and decision aid. Plant Sci. 179, 1-13.

Colbach, N., 2018. How to extrapolate cropping system trials with the FLORSYS simulation model. Report for IWMPRAISE milestone. INRA, Dijon, France, p. 11.

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

Colbach, N., Biju-Duval, L., Gardarin, A., Granger, S., Guyot, S.H.M., Mézière, D., Munier-Jolain, N.M., Petit, S., 2014a. The role of models for multicriteria evaluation and multiobjective design of cropping systems for managing weeds. Weed Res. 54, 541–555. https://doi.org/10.1111/wre.12112

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

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

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

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

Colbach, N., Cordeau, S., Garrido, A., Granger, S., Laughlin, D., Ricci, B., Thomson, F., Messéan, A., 2018. Landsharing vs landsparing: How to reconcile crop production and biodiversity? A simulation study focusing on weed impacts. Agric. Ecosyst. Environ. 251, 203-217. https://doi.org/10.1016/j.agee.2017.09.005

Colbach, N., Darmency, H., Fernier, A., Granger, S., Le Corre, V., Messéan, A., 2017a. Simulating changes in cropping practices in conventional and glyphosate-resistant maize. II. Effect on weed impacts on crop production and biodiversity. Environmental Science and Pollution Research 24, 13121-13135. https://doi.org/10.1007/s11356-017-8591-7

Colbach, N., Debaeke, P., 1998. Integrating crop management and crop rotation effects into models of weed population dynamics: a review. Weed Sci. 46, 717-728.
Colbach, N., Fernier, A., Le Corre, V., Messéan, A., Darmency, H., 2017b. Simulating changes in cropping practices in conventional and glyphosate-resistant maize. I. Effects on weeds. Environmental Science and Pollution Research 24, 11582-11600. https://doi.org/10.1007/s11356-017-8591-7
Colbach, N., Forcella, F., Johnson, G.A., 2000. Temporal trends in spatial variability of weed populations in continuous no-till soybean. Weed Sci. 48, 366-377.
Colbach, N., Gardarin, A., Moreau, D., 2019. The response of weed and crop species to shading: which parameters explain weed impacts on crop production? Field Crops Research 238, 45-55. https://doi.org/10.1016/j.fcr.2019.04.008
Colbach, N., Mézière, D., 2013. Using a sensitivity analysis of a weed dynamics model to develop sustainable cropping systems. I Annual interactions between crop management techniques and biophysical field state variables. Journal of Agricultural Science, Cambridge 151, 229-245. https://doi.org/10.1017/S0021859612000159
Colbach, N., Moreau, D., Dugué, F., Gardarin, A., Strbik, F., Munier-Jolain, N., 2020b. The response of weed and crop species to shading. How to predict their morphology and plasticity from species traits and ecological indexes? Eur. J. Agron. 121, 126158. https://doi.org/10.1016/j.eja.2020.126158
Cordeau, S., Guillemin, J.P., Reibel, C., Chauvel, B., 2015. Weed species differ in their ability to emerge in no-till systems that include cover crops. Annals of Applied Biology 166, 444-455. https://doi.org/10.1111/aab.12195
Cordeau, S., Smith, R.G., Gallandt, E.R., Brown, B., Salon, P., DiTommaso, A., Ryan, M.R., 2017. Timing of tillage as a driver of weed communities. Weed Sci. 65, 504-514. https://doi.org/10.1017/wsc.2017.26
Cousens, R., 1985. A simple model relating yield loss to weed density. Ann. appl. Biol. 107, 239-252.
Craven, B.D., 1986. Theory of Multiobjective Optimization (Yoshikazu Sawaragi, Hirotaka Nakayama and Tetsuzo Tanino). SIAM Review 28, 584-586. https://doi.org/10.1137/1028177
De'ath, G., 2001. Multivariate regression trees: A new technique for modeling species-environment relationships. Ecology 83, 1105-1117. https://doi.org/10.2307/3071917
Devaux, C., Klein, E.K., Lavigne, C., Sausse, C., Messéan, A., 2008. Environmental and landscape effects on cross-pollination rates observed at long-distance among French oilseed rape (*Brassica napus*) commercial fields. Journal of Applied Ecology 45, 803-812.
Donatelli, M., Marchetti, R., 1994. A multi-crop submodel to predict emergence time: model definition and preliminary testing. 3rd ESA Congress, Abano-Padova, Italy, pp. 350-351.
Doré, T., Makowski, D., Malézieux, E., Munier-Jolain, N., Tchamitchian, M., Tittonell, P., 2011. Facing up to the paradigm of ecological intensification in agronomy: Revisiting methods, concepts and knowledge. Eur. J. Agron. 34, 197-210. 10.1016/j.eja.2011.02.006
Dürr, C., Aubertot, J.N., Richard, G., Dubrulle, P., Duval, Y., Boiffin, J., 2001. SIMPLE: A model for SIMulation of PLant Emergence predicting the effects of soil tillage and sowing operations. Soil Science Society of America Journal 65, 414-423.
Dury, J., Schaller, N., Garcia, F., Reynaud, A., Bergez, J.E., 2012. Models to support cropping plan and crop rotation decisions. A review. Agron. Sustain. Dev. 32, 567-580. 10.1007/s13593-011-0037-x
Evers, J.B., van der Werf, W., Stomph, T.J., Bastiaans, L., Anten, N.P.R., 2016. Understanding and optimizing species mixtures using functional-structural plant modelling. Journal of Experimental Botany 70, 2381-2388. https://doi.org/10.1093/jxb/ery288
Fahad, S., Hussain, S., Chauhan, B.S., Saud, S., Wu, C., Hassan, S., Tanveer, M., Jan, A., Huang, J., 2015. Weed growth and crop yield loss in wheat as influenced by row spacing and weed emergence times. Crop Protection 71, 101-108. https://doi.org/10.1016/j.cropro.2015.02.005
Forcella, F., Benech-Arnold, R.L., Sanchez, R., Ghersa, C.M., 2000. Modeling seedling emergence. Field Crops Research 67, 123-139.
Freckleton, R.P., Stephens, P.A., 2009. Predictive models of weed population dynamics. Weed Res. 49, 225-232.
Freckleton, R.P., Watkinson, A.R., 1998. Predicting the determinants of weed abundance: a model for the population dynamics of Chenopodium album in sugar beet. Journal of Applied Ecology 35, 904-920.
Fried, G., Petit, S., Reboud, X., 2010. A specialist-generalist classification of the arable flora and its response to changes in agricultural practices. BMC ecology 10, 20.
Gao, P., Zhang, Z., Sun, G., Yu, H., Qiang, S., 2018. The within-field and between-field dispersal of weedy rice by combine harvesters. Agron. Sustain. Dev. 38, 55. https://doi.org/10.1007/s13593-018-0518-2
Gardarin, A., 2008. Modélisation des effets des systèmes de culture sur la levée des adventices à partir de relations fonctionnelles utilisant les traits des espèces. Université de Bourgogne, Dijon, France, p. 280.
Gardarin, A., Coste, F., Wagner, M.-H., Dürr, C., 2016. How do seed and seedling traits influence germination and emergence parameters in crop species? A comparative analysis. Seed Science Research 26, 317-331. https://doi.org/10.1017/s0960258516000210

Gardarin, A., Dürr, C., Colbach, N., 2010. Effects of seed depth and soil structure on the emergence of weeds with contrasted seed traits. Weed Res. 50, 91-101.

Gardarin, A., Dürr, C., Colbach, N., 2012. Modeling the dynamics and emergence of a multispecies weed seed bank with species traits. Ecol. Modelling 240, 123-138. http://dx.doi.org/10.1016/j.ecolmodel.2012.05.004

Gaudio, N., Escobar-Gutierrez, A.J., Casadebaig, P., Evers, J.B., Gérard, F., Louarn, G., Colbach, N., Munz, S., Launay, M., Marrou, H., Barillot, R., Hinsinger, P., Bergez, J.-E., Combes, D., Durand, J.-L., Frak, E., Pagès, L., Pradal, C., Saint-Jean, S., Werf, W.V.D., Justes, E., 2019. Modeling mixed annual crops: current knowledge and future research avenues. A review. Agron. Sustain. Dev. 39, 20. https://doi.org/10.1007/s13593-019-0562-6

Gfeller, A., Herrera, J.M., Tschuy, F., Wirth, J., 2018. Explanations for *Amaranthus retroflexus* growth suppression by cover crops. Crop Protection 104, 11-20. https://doi.org/10.1016/j.cropro.2017.10.006

Goldberg, D.E., 1989. Genetic algorithms in search, optimization and machine learning. Addison-Wesley Longman Publishing Co., Inc., Boston, MA, USA.

Gruber, S., Colbach, N., Barbottin, A., Pekrun, C., 2008. Gene escape and postharvest approaches for minimising it. CAB reviews 3, No. 015, 017 pp.

Gutteridge, R.J., Jenkyn, J.F., Bateman, G.L., 2006. Effects of different cultivated or weed grasses, grown as pure stands or in combination with wheat, on take-all and its suppression in subsequent wheat crops. Plant Pathology 55, 696-704. 10.1111/j.1365-3059.2006.01405.x

Hodkinson, D.J., Thompson, K., 1997. Plant dispersal: the role of man. Journal of Applied Ecology 34, 1484-1496. 10.2307/2405264

Holst, N., Rasmussen, I.A., Bastiaans, L., 2007. Field weed population dynamics: a review of model approaches and applications. Weed Res. 47, 1-14.

Hossard, L., Jeuffroy, M.H., Pelzer, E., Pinochet, X., Souchere, V., 2013. A participatory approach to design spatial scenarios of cropping systems and assess their effects on phoma stem canker management at a regional scale. Environmental Modelling & Software 48, 17-26. 10.1016/j.envsoft.2013.05.014

Humston, R., Mortensen, D.A., Bjørnstad, O.N., 2005. Anthropogenic forcing on the spatial dynamics of an agricultural weed: the case of the common sunflower. Journal of Applied Ecology 42, 863-872. 10.1111/j.1365-2664.2005.01066.x

Keating, B.A., Thorburn, P.J., 2018. Modelling crops and cropping systems—Evolving purpose, practice and prospects. Eur. J. Agron. 100, 163-176. https://doi.org/10.1016/j.eja.2018.04.007

Klein, E.K., Lavigne, C., Foueillassar, X., Gouyon, P.H., Laredo, C., 2003. Corn pollen dispersal: Quasi-mechanistic models and field experiments. Ecological monographs 73, 131-150.

Lefèvre, V., Capitaine, M., Peigné, J., Roger-Estrade, J., 2014. Farmers and agronomists design new biological agricultural practices for organic cropping systems in France. Agron. Sustain. Dev. 34, 623-632. https://doi.org/10.1007/s13593-013-0177-2

Lewis, J., 1973. Longevity of crop and weed seeds: survival after 20 years in soil. Weed Res. 13, 179-191.

Liebman, M., Dyck, E., 1993. Crop rotation and intercropping strategies for weed management. Ecological applications 3, 92-122.

Liebman, M., Gallandt, E.R., 1997. Many Little Hammers: Ecological Management of Crop-Weed Interactions. In: Jackson, L.E. (Ed.), Ecology in Agriculture. Academic Press, San Diego, CA, pp. 291-343.

Maillot, T., Mion, M., Vioix, J.-B., Colbach, N., 2019. Conception de systèmes de cultures par algorithmes d'optimisation. In: Colbach, N., Angevin, F., Bockstaller, C., Chauvel, B., Denieul, C., Moreau, D., Omon, B., Pellet, D., Rodriguez, A., Trannoy, L., Volan, S., Vuillemin, F. (Eds.), Gestion des adventices dans un contexte de changement - Séminaire CoSAC Paris, France, pp. 32-35.

Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., de Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: concepts, tools and models. A review. Agron. Sustain. Dev. 29, 43-62.

Martin, G., Felten, B., Duru, M., 2011. Forage rummy: A game to support the participatory design of adapted livestock systems. Environmental Modelling and Software 26, 1442–1453.

Martin, G., Martin-Clouaire, R., Duru, M., 2013. Farming system design to feed the changing world. A review. Agron. Sustain. Dev. 33, 131-149. https://doi.org/10.1007/s13593-011-0075-4

Martre, P., Quilot-Turion, B., Luquet, D., Memmah, M., Chenu, K., Debaeke, P., 2015. Model-assisted phenotyping and ideotype design. Academic Press Ltd-Elsevier Science Ltd, London.

McCracken, D.V., Smith, M.S., Grove, J.H., Blevins, R.L., MacKown, C.T., 1994. Nitrate leaching as influenced by cover cropping and nitrogen source. Soil Science Society of America Journal 58, 1476-1483.

Meylan, L., Merot, A., Gary, C., Rapidel, B., 2013. Combining a typology and a conceptual model of cropping system to explore the diversity of relationships between ecosystem services: The case of erosion control in coffee-based agroforestry systems in Costa Rica. Agricultural Systems 118, 52-64.

Meynard, J.-M., Jeuffroy, M.-H., Le Bail, M., Lefèvre, A., Magrini, M.-B., Michon, C., 2017. Designing coupled innovations for the sustainability transition of agrifood systems. Agricultural Systems 157, 330-339. https://doi.org/10.1016/j.agsy.2016.08.002

Meynard, J.M., Charrier, F., Fares, M., Le Bail, M., Magrini, M.B., Charlier, A., Messean, A., 2018. Socio-technical lock-in hinders crop diversification in France. Agron. Sustain. Dev. 38, 13. https://doi.org/10.1007/s13593-018-0535-1

Mézière, D., Petit, S., Granger, S., Biju-Duval, L., Colbach, N., 2015. Developing a set of simulation-based indicators to assess harmfulness and contribution to biodiversity of weed communities in cropping systems. Ecological Indicators 48, 157-170. http://dx.doi.org/10.1016/j.ecolind.2014.07.028

Moreau, D., Bardgett, R.D., Finlay, R.D., Jones, D.L., Philippot, L., 2019. A plant perspective on nitrogen cycling in the rhizosphere. Functional Ecology 33, 540-552. https://doi.org/10.1111/1365-2435.13303

Moreau, D., Busset, H., Matejicek, A., Colbach, N., 2018. Response of weed species to water stress: quantification and formalisation in a model of crop-weed interactions. Proceedings XVe ESA, Geneva, Switzerland, p. 19.

Moreau, D., Pointurier, O., Nicolardot, B., Villerd, J., Colbach, N., 2020. In which cropping systems can residual weeds reduce nitrate leaching and soil erosion? Eur. J. Agron. 119, 126158. https://doi.org/10.1016/j.eja.2020.126015

Moreau, D., Pointurier, O., Perthame, L., Beaudoin, N., Villerd, J., Colbach, N., 2021. Integrating plant-plant competition for nitrogen into a 3D individual-based model simulating the effects of cropping systems on weed dynamics. Field Crops Research 268, 108166. https://doi.org/10.1016/j.fcr.2021.108166

Munawar, A., Blevins, R.L., Frye, W.W., Saul, M.R., 1990. Tillage and cover crop management for soil-water conservation. Agronomy Journal 82, 773-777. 10.2134/agronj1990.00021962008200040024x

Munier-Jolain, N.M., Collard, A., Busset, H., Guyot, S.H.M., Colbach, N., 2014. Investigating and modelling the morphological plasticity of weeds in multi-specific canopies. Field Crops Research 155, 90-98. http://dx.doi.org/10.1016/j.fcr.2013.09.018

Munier-Jolain, N.M., Guyot, S.H.M., Colbach, N., 2013. A 3D model for light interception in heterogeneous crop:weed canopies. Model structure and evaluation. Ecol. Modelling 250, 101-110. http://dx.doi.org/10.1016/j.ecolmodel.2012.10.023

Odonovan, J.T., Kirkland, K.J., Sharma, A.K., 1989. Canola yield and profitability as influenced by volunteer wheat infestations. Canadian Journal of Plant Science 69, 1235-1244. 10.4141/cjps89-145

Oerke, E.-C., 2006. Crop losses to pests. Journal of Agricultural Science 144, 31-43 10.1017/S0021859605005708

Ould-Sidi, M.M., Lescourret, F., 2011. Model-based design of integrated production systems: a review. Agron. Sustain. Dev. 31, 571-588. 10.1007/s13593-011-0002-8

Pasquier, C., Angevin, F., 2017. Freins et leviers à la réduction de l'usage d'herbicides en grande culture. In: Colbach, N., Moreau, D., Angevin, F., Rodriguez, A., Volan, S., Vuillemin, F. (Eds.), Gestion des adventices dans un contexte de changement : Connaissances, méthodes et outils pour l'élaboration de stratégies innovantes, Séminaire de restitution à mi-parcours du projet de recherche ANR CoSAC, Paris, France, pp. 67-69.

Perry, L.G., Neuhauser, C., Galatowitsch, S.M., 2003. Founder control and coexistence in a simple model of asymmetric competition for light. Journal of Theoretical Biology 222, 425-436. https://doi.org/10.1016/S0022-5193(03)00055-9

Perthame, L., Colbach, N., Brunel-Muguet, S., Busset, H., Lilley, J.M., Moreau, D., submitted. How to quantify the nitrogen demand of individual plants in heterogeneous canopies? Case study with crop-weed canopies. Annals of Botany.

Perthame, L., Petit, S., Colbach, N., 2018. Cropping systems for driving biological regulation of weeds. A simulation study of seed predation by carabids. Proceedings XVe ESA, Geneva, Switzerland, p. 154.

Petit, S., Alignier, A., Colbach, N., Joannon, A., Le Coeur, D., Thenail, C., 2012. Weed dispersal by farming at various spatial scale. A review. Agron. Sustain. Dev. DOI 10.1007/s13593-012-0095-8.

Petit, S., Alignier, A., Colbach, N., Joannon, A., Le Coeur, D., Thenail, C., 2013. Weed dispersal by farming at various spatial scale. A review. Agron. Sustain. Dev. 33, 205-217. https://doi.org/10.1007/s13593-012-0095-8

Petit, S., Cordeau, S., Chauvel, B., Bohan, D., Guillemin, J.-P., Steinberg, C., 2018. Biodiversity-based options for arable weed management. A review. Agron. Sustain. Dev. 38. https://doi.org/10.1007/s13593-018-0525-3

Petit, S., Gaba, S., Grison, A.-L., Meiss, H., Simmoneau, B., Munier-Jolain, N., Bretagnolle, V., 2016. Landscape scale management affects weed richness but not weed abundance in winter wheat fields. Agric. Ecosyst. Environ. 223, 41-47. http://dx.doi.org/10.1016/j.agee.2016.02.031

Pointurier, O., Moreau, D., Pagès, L., Caneill, J., Colbach, N., 2021. Individual-based 3D modelling of root systems in heterogeneous plant canopies at the multiannual scale. Case study with a weed dynamics model. Ecol. Modelling 440, 109376. https://doi.org/10.1016/j.ecolmodel.2020.109376

Pollnac, F.W., Rew, L.J., Maxwell, B.D., Menalled, F.D., 2008. Spatial patterns, species richness and cover in weed communities of organic and conventional no-tillage spring wheat systems. Weed Res. 48, 398-407.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 2007. Numerical Recipes: The Art of Scientific Computing, 3rd ed. Cambridge University Press, New York, NY, USA.

Prost, L., Cerf, M., Jeuffroy, M.H., 2012. Lack of consideration for end-users during the design of agronomic models. A review. Agron. Sustain. Dev. 32, 581-594.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Renton, M., Chauhan, B.S., 2017. Modelling crop-weed competition: Why, what, how and what lies ahead? Crop Protection 95, 101-108. https://doi.org/10.1016/j.cropro.2016.09.003

Sardana, V., Mahajan, G., Jabran, K., Chauhan, B.S., 2017. Role of competition in managing weeds: An introduction to the special issue. Crop Protection 95, 1-7. https://doi.org/10.1016/j.cropro.2016.09.011

Sausse, C., Le Bail, M., Lecroart, B., Remy, B., Messean, A., 2013. How to manage the coexistence between genetically modified and conventional crops in grain and oilseed collection areas? Elaboration of scenarios using role playing games. Land Use Pol. 30, 719-729. https://doi.org/10.1016/j.landusepol.2012.05.018

Segal, M., Xiao, Y., 2011. Multivariate random forests. Wiley Interdisc. Rew.: Data Mining and Knowledge Discovery 1, 80-87. 10.1002/widm.12

Squire, G., Breckling, B., Dietz Pfeilstetter, A., Jorgensen, R., Lecomte, J., Pivard, S., Reuter, H., Young, M., 2011. Status of feral oilseed rape in Europe: its minor role as a GM impurity and its potential as a reservoir of transgene persistence. Environmental Science and Pollution Research 18, 111-115. 10.1007/s11356-010-0376-1

Sturm, D.J., Peteinatos, G., Gerhards, R., 2018. Contribution of allelopathic effects to the overall weed suppression by different cover crops. Weed Res. 58, 331-337. https://doi.org/10.1111/wre.12316

Swanton, C.J., Nkoa, R., Blackshaw, R.E., 2015. Experimental methods for crop–weed competition studies. Weed Sci. 63, 2-11.

Teasdale, J.R., 1996. Contribution of cover crops to weed management in sustainable agricultural systems. Journal of Production Agriculture 9, 475-479.

Thomson, F.J., Moles, A.T., Auld, T.D., Kingsford, R.T., 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. Journal of Ecology 99, 1299-1307. 10.1111/j.1365-2745.2011.01867.x

Van Inghelandt, B., 2018. Comment combiner prototypage et modèles en ateliers de co-conception de systèmes de culture pour atteindre une gestion agroécologique des adventices? AgroParisTech, Paris, France, p. 55.

Van Inghelandt, B., Queyrel, W., Cavan, N., Colas, F., Guyot, B., Colbach, N., 2019. Combiner expertise et modèles en ateliers de co-conception de systèmes de culture pour une gestion durable des adventices : apports méthodologiques et perspectives. In: Colbach, N., Angevin, F., Bockstaller, C., Chauvel, B., Denieul, C., Moreau, D., Omon, B., Pellet, D., Rodriguez, A., Trannoy, L., Volan, S., Vuillemin, F. (Eds.), Gestion des adventices dans un contexte de changement - Séminaire CoSAC Paris, France, pp. 39-41.

Venter, G., 2010. Review of Optimization Techniques. In: Blockley, R., Shyy, W. (Eds.), Encyclopedia of Aerospace Engineering. John Wiley & Sons Ltd, Chichester, UK.

Verret, V., Gardarin, A., Pelzer, E., Médiène, S., Makowski, D., Valantin-Morison, M., 2017. Can legume companion plants control weeds without decreasing crop yield? A meta-analysis. Field Crops Research 204, 158-168. https://doi.org/10.1016/j.fcr.2017.01.010

Voinov, A., Bousquet, F., 2010. Modelling with stakeholders. Environmental Modelling & Software 25, 1268-1281. https://doi.org/10.1016/j.envsoft.2010.03.007.

Weisberger, D., Nichols, V., Liebman, M., 2019. Does diversifying crop rotations suppress weeds? A meta-analysis. PLOS ONE 14, e0219847. https://doi.org/10.1371/journal.pone.0219847

Wilson, R.S., Tucker, M.A., Hooker, N.H., LeJeune, J.T., Doohan, D., 2008. Perceptions and beliefs about weed management: perspectives of Ohio grain and produce farmers. Weed Technology 22, 339-350. https://doi.org/10.1614/WT-07-143.1

Wilson, S.D., Tilman, D., 1993. Plant competition and resource availability in response to disturbance and fertilization. Ecology 74, 599-611.

Xu, Y., Castel, T., Richard, Y., Cuccia, C., Bois, B., 2012. Burgundy regional climate change and its potential impact on grapevines. Climate Dynamisc 39, 1613-1626.

Yang, X.-S., He, X., 2013. Firefly algorithm: recent advances and applications. International Journal of Swarm Intelligence 1, 36-50. https://doi.org/10.1504/IJSI.2013.055801

7 Illustrations

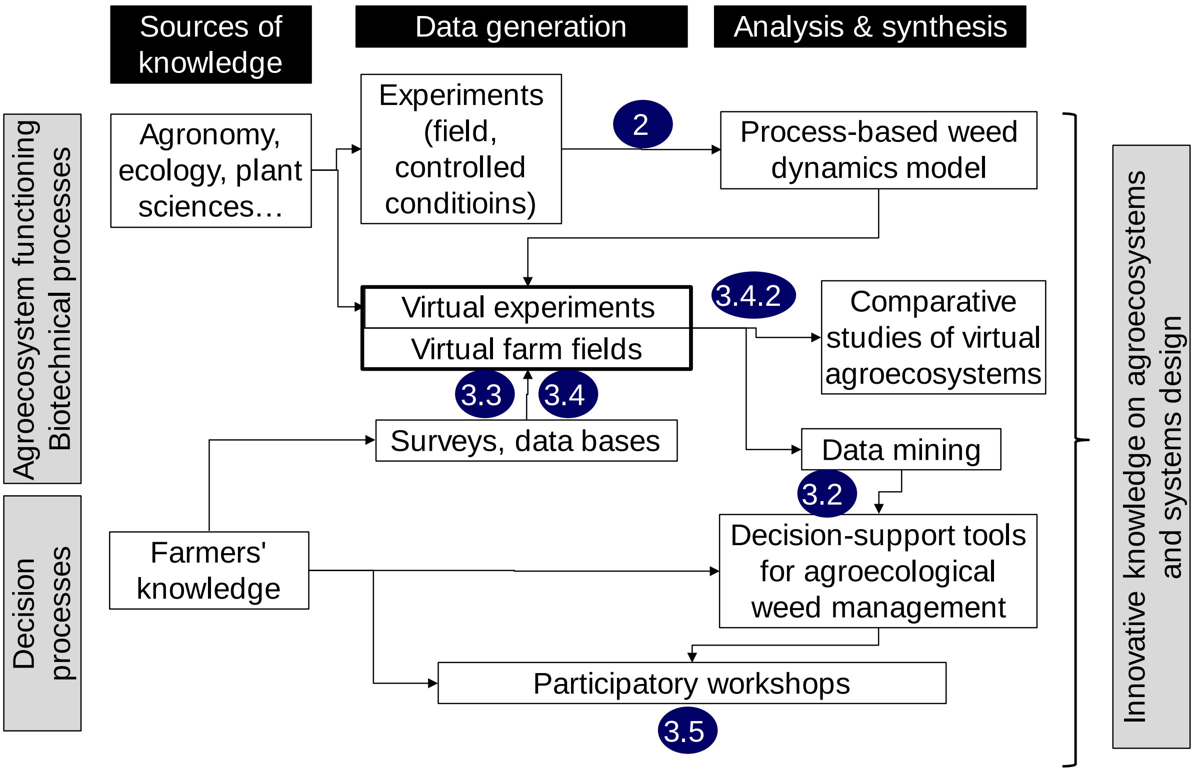


Figure 1. Avenues of research explored with the help of a weed dynamics model to investigate ecological intensification (adapted from Doré et al., 2011). Numbers refer to the sections of the present paper

Table 1. Key issues to model crop diversification and main solutions to address these in a weed dynamics model such as FLORSYS

What should be modelled/simulated	How does FLORSYS tackle this	Section
A. Model structure		
All cultural techniques	Inputs include detailed multiannual lists of operations	2.1
Large domain of validity, Variability due to pedoclimate	Mechanistic structure including the key processes for temperate arable farming and whose parameters do not change with location. Effects of cultural techniques are decomposed into individual processes which depend on soil & plant state variables, plant processes depend on weather and soil state variables	2.1
Multispecies	Generic plant structure, species parameters can be estimated from easily accessible species traits	2.3.1
Facilitate the addition of new species	Species parameters can be estimated from easily accessible species traits	2.4
Crop patterns in landscapes	Spatially-explicit field clusters including semi-natural habitats, with weed dispersal among fields/habitats	2.3.3
B. Key processes		
Emergence in different seasons (rotation), difference in timing in crop mixtures	Seasonal dormancy determines seed readiness to germinate, base temperature and water potential determine timing and germination speed, seed size determines ability to emerge in compact soil or when deeply buried	2.2.1
Plant-plant interactions in heterogeneous canopies	3D individual-based canopy with generic plant structure, overlapping leaf distribution determines light absorption and shading, overlapping root systems determine competition for soil resources, plant growth and morphology result from resource uptake and response to stresses (shading, nitrogen deficiency)	2.2.2, 2.3.2
Multiannual carry over effect in rotations	Weed seed bank with dormancy and mortality processes, crop volunteers arising from lost crop seeds, soil water and nitrogen dynamics	2.2.3
C. Model outputs		
Tailor to stake-holders' needs	Detailed outputs for diagnosis of cropping-system performance, translate detailed outputs into indicators of crop production and weed impacts	3.1
Support farmers	Metamodel FLORSYS in decision trees to redesign cropping systems and random forests to rapidly evaluate their multi-performance	3.2

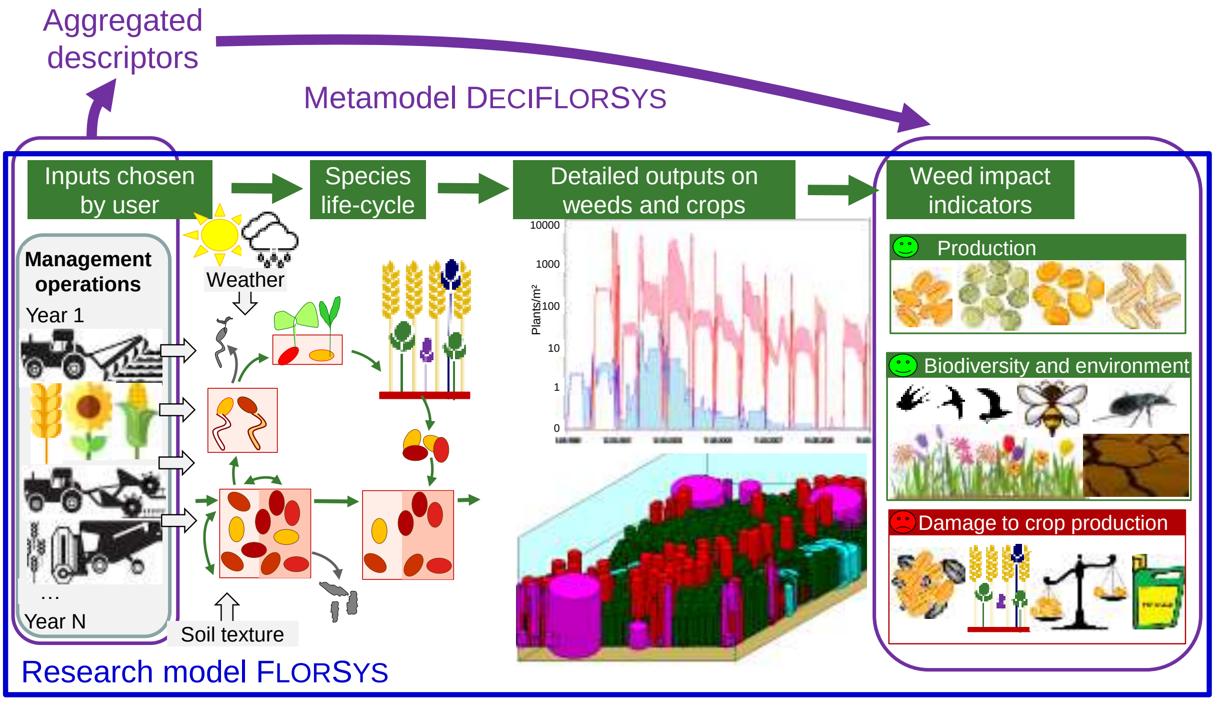


Figure 2. General representation of the (1) research model FLORSYS (blue rectangle) which simulates crop growth and weed dynamics from a detailed description of cropping system, weather and soil inputs based on a mechanistic representation of biophysical processes at a daily time step and in 3D, and then aggregates these data into indicators of weed benefits and detriments (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014b; Mézière et al., 2015), and the (2) metamodel DECIFLORSYS (purple boxes and arrows) which directly estimates weed impacts from aggregated cropping system inputs based on machine learning (Colas, 2018; Colas et al., 2020) (Nathalie Colbach © 2018).

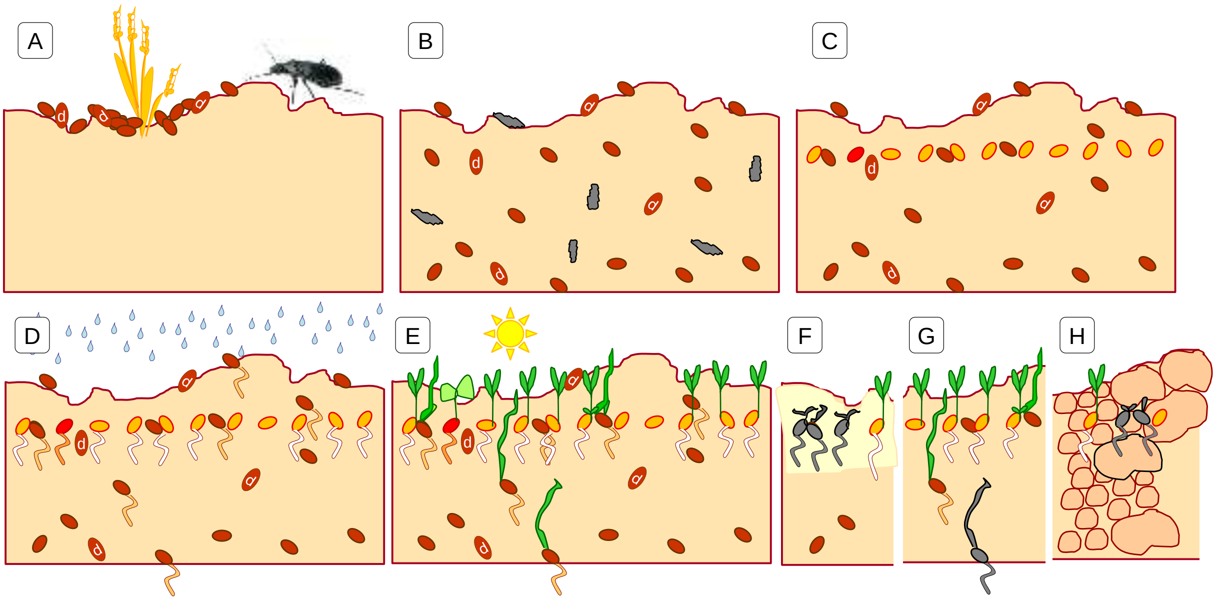
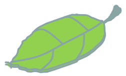
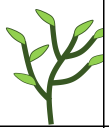
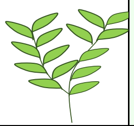
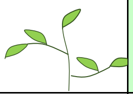
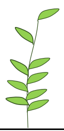


Figure 3. Processes leading to plant emergence and establishment as summarized in FLORSYS (Gardarin et al., 2012; Colbach et al., 2014b; Perthame et al., 2018). Once weed plants mature, weed seeds (d=dormant) are shed onto soil surface where they can be eaten by predators (A). Tillage operations and, to a lesser degree, weather and fauna bury seeds at different depths, depending on the tool, its options and soil structure, and seeds die (dark grey) over time due to age, diseases etc (B). Crop seeds are sown, usually close to soil surface, and sometimes comprising unwanted seeds (in red, from other cultivars, crop or weed species) (C). Once the soil is moist and warm enough for the species, non-dormant seeds germinate but deeply buried seeds and those on soil surface germinate badly, the latter because they have trouble absorbing water due to insufficient soil-seed contact, the former because of insufficient O_2, excessive CO_2 or soil weight (D). Shoots grow toward soil surface, from the reserves inside the seed; once outside the soil, photosynthesis kicks in (E). Seedlings die without emerging if the soil dries after germination and the root is too short to reach deeper moisture layers (F), if the seed is buried too deeply and the seed reserve are insufficient to reach the soil surface (G), or if soil clods block shoot growth (H). (Nathalie Colbach 2018 ©)

Table 2. Typology of shading responses identified in 25 weed species and 30 crop species and varieties from garden-plot experiments, using FLORSYS parameters driving plant-plant competition for light (based on Colbach et al., 2020b)

		Morphology resulting from parameter values		Average relative variation when shading increases from 0 to 75%[§]					
				Crops			Weeds		
Plant state variable	Unit	Low	High	Cereal (8)[#]	Legume (17)	Other (5)[$]	Poaceae (6)	Dicots (19)[&]	Reason for response to shading
Specific Leaf Area SLA (plant leaf area vs plant leaf biomass)	cm²/g			1.38	1.31	1.73	1.46	1.52	Increase light interception area with thinner larger leaves
Leaf biomass ratio LBR (plant leaf biomass vs total plant above-ground biomass)	g/g			1.05	0.97	0.86	1.10	1.00	Either increase light interception area by increasing leaf biomass to the detriment of stem biomass, or increase stem biomass to increase stem length and reach the light
Specific (allometric) plant height HM (height per unit above-ground biomass)	cm/g			1.39	1.23	1.49	1.71	1.41	Reach the light by increasing plant height
Specific (allometric) plant width WM (width per unit above-ground biomass)	cm/g			1.16	1.20	1.20	1.21	1.29	Avoid shade cast by neighbour by growing laterally
Median relative leaf height (relative plant height below which 50% of leaf area are located)	cm/cm			1.04	1.00	0.98	1.04	1.00	Reach the light by moving leaf area toward the top

[§] For a given plant on day d, each plant variable V_{pd} is calculated as $V_{pd} = \mathbf{V0}ss\ e^{\mu\_V_{ss} \cdot SI_{pd}}$ where $\mathbf{V0}_{ss}$ is the potential value of the variable in unshaded conditions, $\boldsymbol{\mu\_V}_{ss}$ is the species shading response at the given stage, and SI_{pd} is the cumulated shading intensity since plant emergence. SI_{pd} is 1-incident light for plant p on day relative to incident light above the canopy, weighted by the number of days since emergence (details in section **B.3.1** online); in experiments, it is measured as the incident light in sunny conditions vs below a shading net (Munier-Jolain et al., 2014); in simulations, it is predicted from the voxelized 3D light submodel (Figure 4). The values of these columns are $\boldsymbol{\mu\_V}_{mean} \cdot 0.75$, using values averaged over all species and stages, for crops and weeds, respectively.

[#] Number between brackets are number of species.

[$] *Brassicaceae, Asteraceae, Boraginaceae*

[&] *Amaranthaceae, Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Cucurbitaceae, Euphorbiaceae, Geraniaceae, Malvaceae, Plantaginaceae, Polygonaceae, Rubiaceae, Solanaceae*

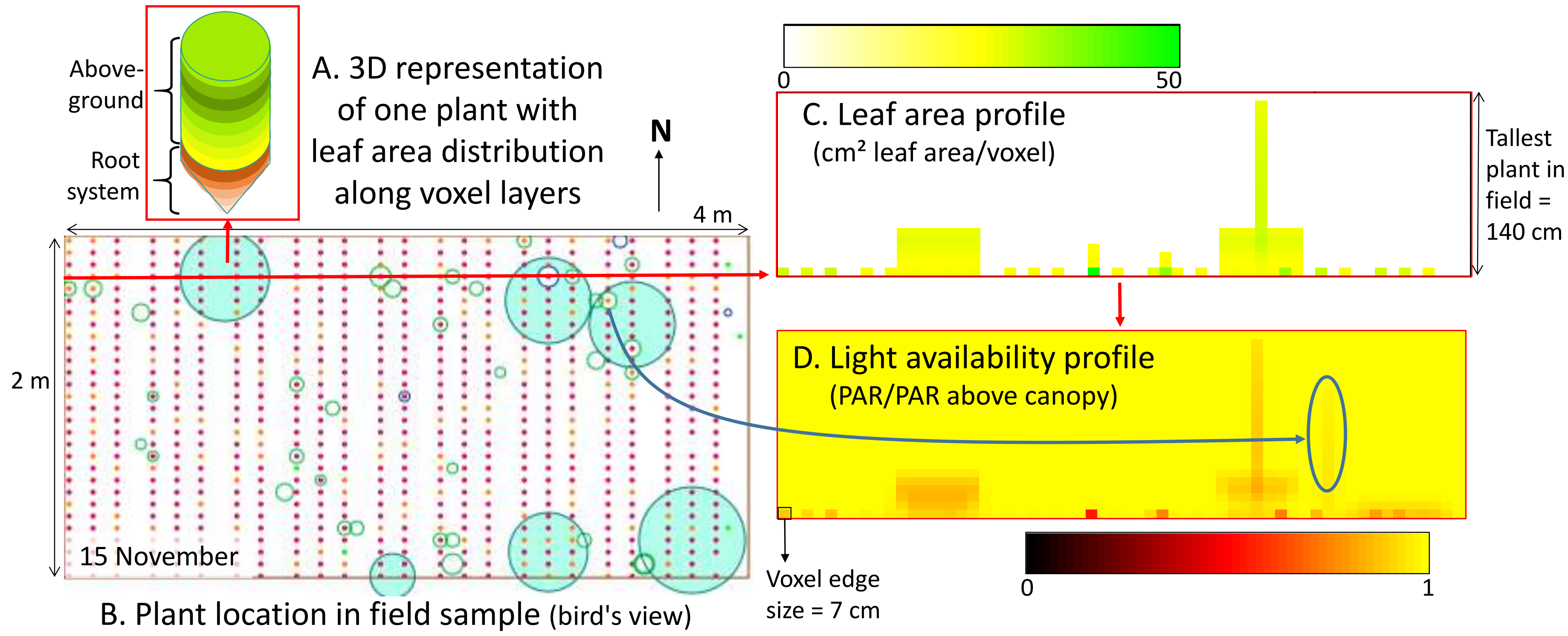


Figure 4. Illustration of a wheat (●)-field bean (●) mixture a few days after emergence, sown into the surviving plants of a broadcast cover crop mixture (*Phacelia tanacetifolia* ○, *Helianthus annuus* ○, *Guizotia abyssinica* ○, *Trifolium alexandrinum* ○, *Sorghum bicolor* ○) simulated with FLORSYS (Munier-Jolain et al., 2013; Colbach et al., 2018; Pointurier et al.). Each plant is represented as a cylinder above a cone (A) and placed on a field sample (B). The canopy is represented in 3D, locating leaf area in voxels (C). Each day, light trickles down successive voxel layers vertically and laterally, depending on incident PAR, leaf area and solar angle which varies with latitude, season and hour (D). The area with lower light availability marked with a blue ellipse on Figure D is the result of shade cast by a tall plant (linked to the ellipse by the blue arrow) located south of the transect marked by the red line on Figure B (Nathalie Colbach 2018 ©)

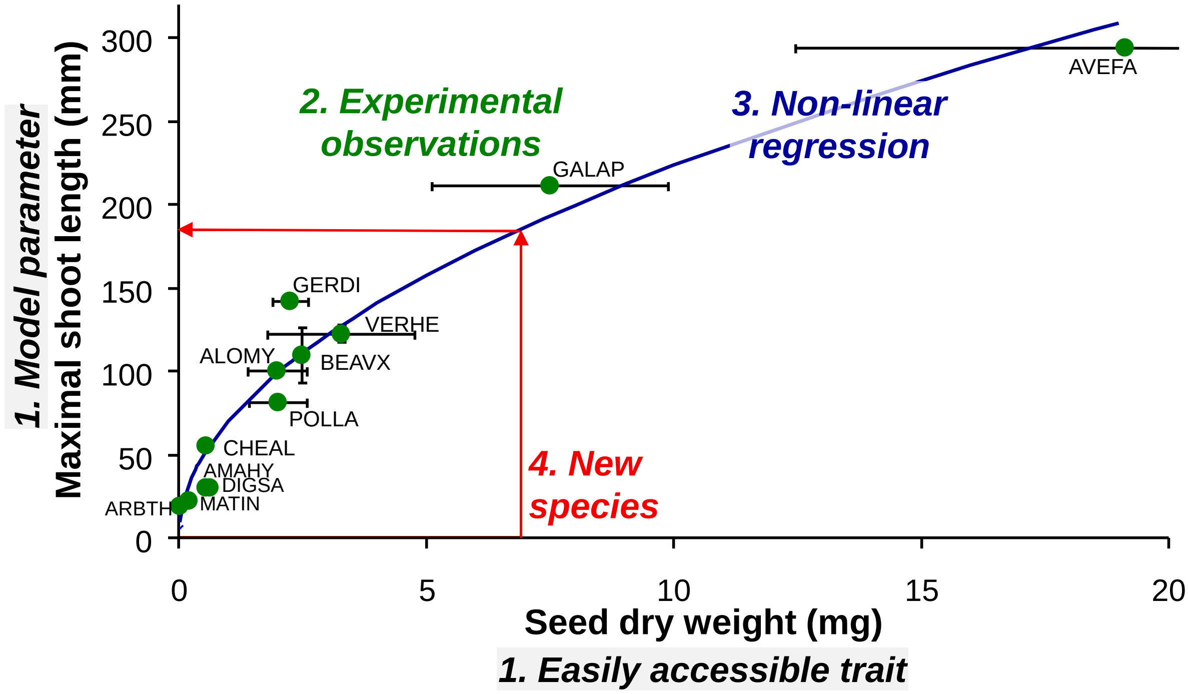


Figure 5. Principle of functional relationships for estimating model parameters from easily accessible traits and other characteristics, illustrated with an example of the maximal shoot length (hypocotyl or epicotyl with first leaf, depending on the species) during pre-emergent growth in darkness in the soil (Gardarin et al., 2010). (1) For each model parameter, identify one or several easily available traits (or other characteristics) that have a biological link with the model parameter. (2) Identify a range of species that are potentially contrasting in terms of parameter and trait values and measure parameter and trait values experimentally. (3) Fit a predictive function (which can depend on several traits) to the data and introduce it into the model. (4) To add a new species to the model, measure the trait and let the model estimate the parameter. Abbreviations refer to EPPO codes for species (https://gd.eppo.int/) (Nathalie Colbach © 2018)

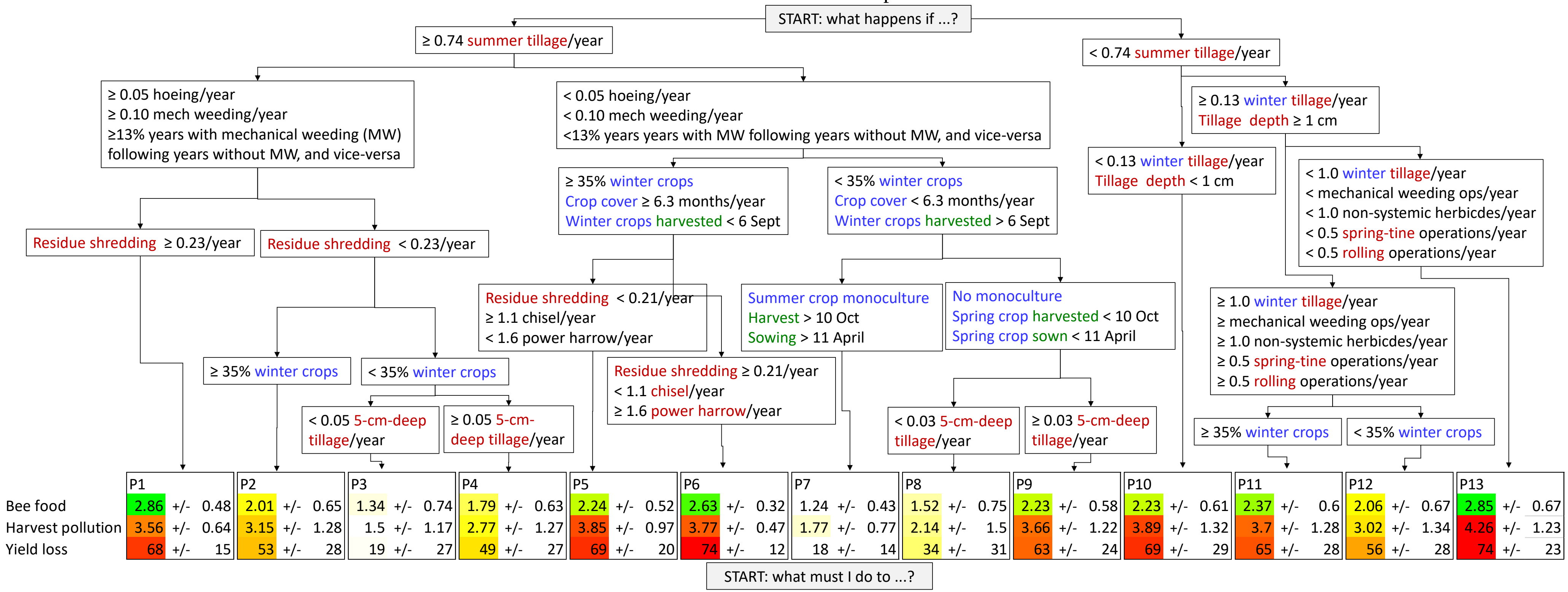


Figure 6: Decision tree for crop diversification, identifying cropping system rules for reaching a series of 13 weed impact profiles based on a multivariate regression tree linking weed impact indicators simulated by FLORSYS to combinations of cropping system variables (blue: rotation, green: sowing/harvest, brown: tillage, black: weed control), based on 4350 cropping systems resulting from a random combination of cultural techniques from 20 French regions. Indicator values were rescaled to [0,1], averaged over 30 years and 10 weather repetitions, and coloured from white (minimum) to green (maximum) for biodiversity, from white to red (maximum) for harmfulness to crop production. Uncoloured cells show standard-error including weather effects and variability among systems in a branch. Cross-validation error of the tree was 0.106. The tree can be read top-down to get an idea of the performance of a proposed combination of management practices, or bottom-up to identify the practices corresponding to a target performance (based on data and methods from Colas, 2018; Colas et al., 2020) (Floriane Colas © 2019)

Table 3. The main crop parameters driving potential production and weed impact. Pearson correlation coefficients between parameters and annual potential production as well weed impacts simulated with FLORSYS on 272 cropping systems × 30 years × 10 weather repetitions. Only correlations exceeding 0.35 were kept; blank cells and missing parameters point to lower correlations. Only years with annual grain production were kept for the analysis (based on data and methods from Colbach et al., 2019)

Crop parameter	Unit	Potential grain yield (T/ha)	Grain yield loss (T/T)	Weed seed production (seeds/m²)
Habitat requirements				
Base temperature	°C	-0.43		
Base water potential	MPa	-0.82		
Minimum & optimum temperature for photosynthesis	°C			0.36
Potential plant morphology (unshaded conditions)				
Specific leaf area SLA, before reproduction	cm²/g	-0.49		
Specific leaf area SLA, flowering-maturity	cm²/g	-0.80	-0.45	
Specific plant height HM, after emergence	cm/g			0.35
Specific plant width WM, during vegetative phase & reproduction	cm/g	-0.82	-0.44	
Leaf biomass ratio LBR, flowering- maturity	g/g	-0.77		
Relative median leaf area height RLH, during reproduction	m²/m²	0.77		
Maximum plant height	cm	-0.57		
Maximum plant width	cm	-0.51		
Response to shading				
Ability to increase HM, after emergence	No unit	-0.82	-0.36	
Ability to increase HM, during reproduction	No unit	-0.73		
Ability to increase relative leaf area height RLH, after emergence	No unit	-0.57		
Ability to increase SLA, before reproduction	No unit	-0.78	-0.37	

Table 4. Typology of surveyed farmers' cropping systems established based on their simulated performance in terms of reduced weed harmfulness and herbicide use intensity. Main management practices of the three best strategies identified with classification and regression trees (Breiman et al., 1984; rpart() function of R Core Team, 2016) among 272 existing cropping systems collected in 7 regions from France and Spain and simulated with FLORSYS over 30 years and with 10 weather repetitions. Empty cells indicate that there was the systems of a strategy type had nothing in common for this technique (based on data and methods from Colbach and Cordeau, 2018)

	Strategy	S1	S2	S3
	Simulated yield loss	< 10%	< 20%	< 20%
		and	and	and
	Surveyed herbicide use intensity (TFI)	< 0.8	< 0.8	< 1.2
	Simulated risk of failure[$]	0%	0%	0%
Rotation	% winter crops	0%	25-75%	15%-64%
	% spring crops	100% (maize)	25-75%	> 36%
	% temporary grassland	0%	< 20%	> 20%
	Number of crops & cultivars	1	> 4	
	Duration of crop cover (/year)	< 6 months	> 8.3 months	< 8 months
Tillage	Superficial tillage/year	< 3.4	> 3.4	> 3.4
	In summer /year (April-Sept)	< 2.4	> 2.4	> 2
	1st tillage (since harvest)	> 24 days	< 24 days	
	Ploughing frequency	< 1 year /2	< 1 year/2	
	Ploughing frequency Oct-March		> 1 year/ 5	> 1 year /3
Herbicides	1st herbicide (since sowing)	< 5 months	< 5 months	
	Dosage (% full dose)	31-58%	<58%	
	Products per year	1.3-3	1.3-2.1	
	Variable among years	No	Yes	
	% Systemic	> 82%	< 82%	< 83%
	Root-entering	< 12%	< 12%	
Mechanical	Operations per year	0.25-1.6	0.25-1.6	
weeding	Variable among years	Yes	Yes	

[$] Failure = yield loss > 40% or TFI > 1.6 in average over rotation

Table 5. Weed impact on biodiversity and crop production on a cropping system trial extrapolated over time and tested with different weather series. Weed-impact indicator values simulated with FLORSYS and averaged over 30 years and 10 weather repetitions. In each column, cells were coloured from green (the best performance) to red (the worst performance) for crop diversity, weed benefits and crop production, and vice-versa for weed detriments. Numbers of a given column followed by the same letter were not significantly different at p=0.05 (least significant difference test) (based on data from Colbach et al., 2016; Colbach, 2018)

Cropping system[§]	Crop diversity over 12 years			Herbi-cide use (TFI)	Yield (MJ/ha)		Weed impact			
	Number of species and cultivars	% winter crops	% years with cover crops				Yield loss (%)		Bee food (no unit)	
Reference	4	100%	8%	1.6	63563	C	50.9	D	2.30	B
IWM simplified	18	77%	39%	1.7	51067	ED	58.4	C	2.42	B
IWM intermediate	10	63%	8%	0.8	54443	D	55.3	DC	2.74	A
IWM complete	8	55%	0%	0.7	67402	BC	40.9	FE	2.05	DC
IWM ~0 herbicides	12	63%	16%	0.1	69077	BC	50.5	D	2.10	C

[§] IWM (integrated weed management) scenarios were simplified (no plough, little tillage, no mechanical weeding, herbicides), intermediate (plough, tillage, no mechanical weeding, herbicides), complete (plough, tillage, mechanical weeding, herbicides), ~0 herbicides (plough, tillage, mechanical weeding, no herbicides)

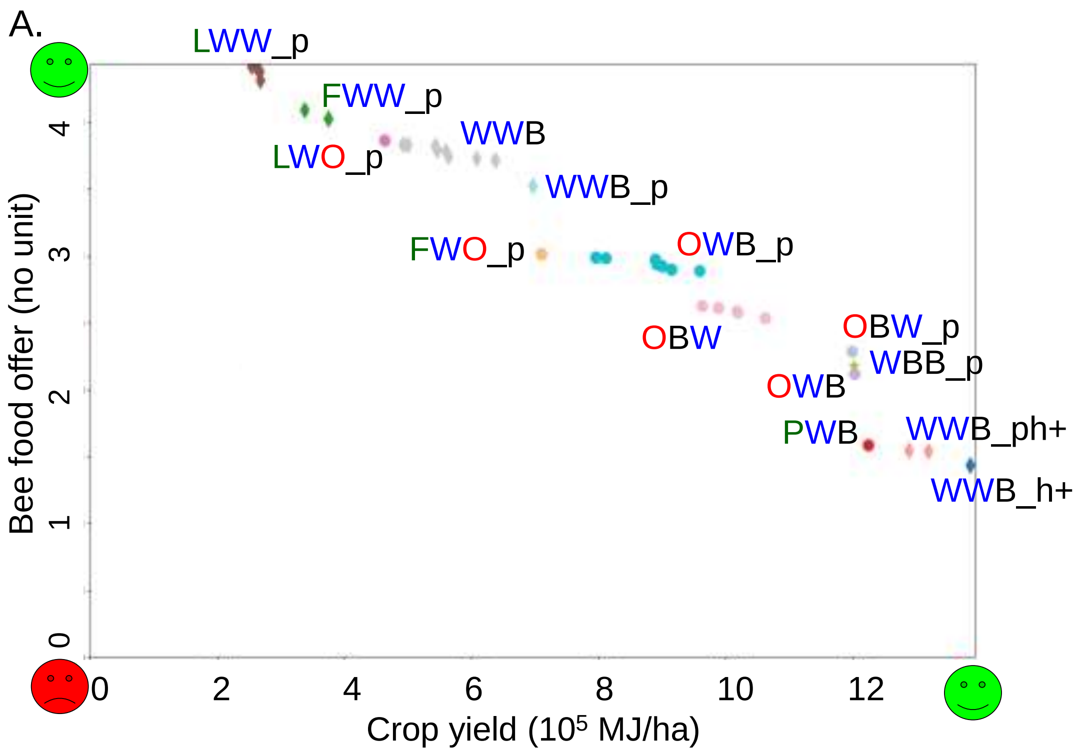
Table 6. Case studies using FLORSYS to investigate different issues relative to crop diversity, with key conclusions.

Topic: evaluate the effect of…	Method: compare cropping-system scenarios		Key conclusions	Reference
	Based on	Differing in terms of …		
A. Identify multiperformant ideotypes				
Crop and cultivar traits	Existing crops and farmers' practices	Crop and cultivar traits, production situation, farming system, crop diversity, management practices	Ideotypes aiming to maximise yield potential are not the same that efficiently compete with weeds for light	Table 3
B. Track crop-diverse solutions in farming practices				
Farmers' herbicide use intensity	Existing farmers' practices	Production situation, farming system, crop diversity, all management practices	There are contrasting crop-diverse strategies that reconcile reduced herbicide use with low weed-caused yield loss	Table 4
C. Ex ante evaluation of innovations proposed by experts				
Integrated weed management	Cropping system trial	Crop diversity, intensity of tillage, mechanical weeding and herbicides (Burgundy, basic rotation of oilseed rape and winter cereals)	Crop diversification (different crops/cultivars, alternating sowing seasons, cover crops) can compensate for reduced herbicide use but does not guarantee weed benefits	Table 5
Wheat sowing patterns	Experts	Cover crop, interrow width, sowing date, sowing density, mix with field bean (Burgundy, oilseed rape - winter cereals rotation)	Crop mixture during one single year reduces yield loss for up to 10 years; cover crops can increase weed infestation in later years if they hinder false seed bed techniques	(Colbach et al., 2014b)
Prototypes	Farmers	Crop diversity, tillage, mechanical weeding (Champagne crayeuse, oilseed rape - cereals rotation)	Crop diversification reduces weed-borne yield loss, rotations including multiannual crops perform better than those with crop mixtures	(Van Inghelandt, 2018)
Annual crop diversity	Experts	Annual crop diversity in a field cluster (South-West France, maize-based rotations)	Crop diversity increases weed benefits for biodiversity and weed harmfulness for production	(Colbach et al., 2018)
D. *Ex ante* evaluation of innovations resulting from actual or potential policy changes				
New maize cultivar submitted to regulatory body	Agricultural statistics, crop advisors	Crop diversity, maize cultivars, changes in management practices accompanying the new cultivars (South-West France, maize-based rotations)	Simplified rotations and simplified tillage increase weed impacts, cover crops reduce them	(Bürger et al., 2015; Colbach et al., 2017a; Colbach et al., 2017b)
Permanent grass strips required by farming policy	Experts	Crop diversity and permanent grass strips in field cluster (South-West France, maize-based rotations)	10% grass strips can compensate for monocultures and are better than diverse rotations to reconcile production and biodiversity	(Colbach et al., 2018)
E. Algorithm-based optimization to meet contrasting objectives				
3-year cereal-based rotation	Algorithm	Rotation and management strategy (Burgundy, cereal-based rotations)	Wheat monocultures maximise production to the detriment of biodiversity, the most diverse rotations result in medium production and medium biodiversity	Figure 7

Simulation plans consisted of running each cropping system over 10-30 years, and repeating it with 10 weather series. Weed-caused yield loss was the relative difference in grain yield in simulations with vs without weeds.

Table 7. Contribution of weed dynamics models to promote crop diversification. Case study of participatory workshops from Champagne region using the FLORSYS research model and the DECIFLORSYS decision-support system to make integrated weed management strategies benefit from crop diversification (based on data from Van Inghelandt, 2018)

Model	Use in workshops	Farmers' reaction	Take-home message for farmers
Decision tree, ranking table (DECIFLORSYS)	Ranking of cropping system components, discriminating various effects related to each technique	Surprised at low rank of crop choice variables	Crop effects consist of direct effects related to competition and indirect effects due associated management techniques, which are often more influential
Random-forest predictor (DECIFLORSYS)	Instantaneous evaluation of prototypes, with two distinct farmers' groups	Tested variants of initially proposed prototypes, "played" with different, even unusual, crops	Contrasting diversification solutions (e.g. cash crop mixtures vs multiannual crops) can be proposed for a same problem, depending on the participants' risk adversity
FLORSYS	Impact of diversified rotations on weed flora composition and long-term dynamics	Interested in long-term evaluation, surprised by weed shifts in diversified rotations	Crop diversification results in weed shifts, not in weed extinction; include new crops to anticipate and avoid the advent of problematic weeds; solutions are farm-specific
FLORSYS	Assess performance of individual crops in rotation	Surprised at bad performance of alternative crops (e.g. legumes)	Need to evaluate performance at rotation scale as diversification crops can have lower yields but their carryover effect can improve the performance of later crops because of reduced weed seed production
FLORSYS	Assess effect of including cover crops	Surprised at bad performance of the following cash crops	Weather hazards can jeopardize cover-crop establishment whose success needs monitoring and adapted tactical decisions; cover crops can increase long-term weed infestation if they hinder false seed bed techniques
FLORSYS	Fine-tune systems in terms of crop succession and management techniques (precise dates and options) and understand reasons of performance		The new crop rotation must be accompanied with consistent management practices, notably tillage dates with respect to soil moisture to optimise false seed bed techniques



B. Cropping system[§]	Rotation: Species (number)	Legumes (%)	Cereals (%)	Fallow management[$]: Residue shredding	Plough	Superficial tillage[&]	Roll	Glyphosate	Herbicides on cash crops[&]	Mechanical weeding
LWW_p	2	33	66	1 year/3	1 year/3	1/year	2 years/3	None	1.33/year	None
FWW_p	2	33	66	1 year/3	1 year/3	1.33/year	2 years/3	None	1.33/year	3 year/3
LWO_p	3	33	33	1 year/3	1 year/3	1.33/year	3 years/3	1 year/3	1.33/year	None
WWB	2	0	100	None	None	1.67/year	1 year/3	1 year/3	2.66/year	None
WBB_p	2	0	100	None	1 year/3	4.33/year	None	2 years/3	2.66/year	2 year/3
FWO_p	3	33	33	1 year/3	1 year/3	2.66/year	2 years/3	None	1.67/year	3 year/3
OWB_p	3	0	66	None	1 year/3	4/year	1 year/3	1 year/3	2.33/year	2 year/3
OBW	3	0	66	None	None	3/year	1 year/3	1 year/3	3/year	None
OBW_p	3	0	66	None	1 year/3	4.33/year	1 year/3	2 years/3	2.33/year	2 year/3
WWB_p	2	0	100	1 year/3	1 year/3	2/year	1 year/3	1 year/3	2.66/year	None
OWB	3	0	66	None	None	2/year	None	1 year/3	3/year	None
PWB	3	33	66	None	None	3.66/year	None	2 years/3	2.66/year	None
WWB_ph+	2	0	100	None	1 year/3	3.66/year	2 years/3	3 years/3	3.33/year	None
WWB_h+	2	0	100	None	None	3.66/year	None	1 year/3	3.33/year	None

[§] W=winter wheat, B=winter barley, T=triticale, O=oilseed rape, L=lucerne, P=peas, F=faba bean; h+ indicates a high intensity of herbicide use; p indicates the use of mouldboard ploughing. [$] None of the seletected systems included cover crops. [&] Number of operations averaged over rotation

Figure 7: Cropping systems based on a 3-year rotation aiming to reconcile crop production with weed-based bee-food offer (based on data and methods from Maillot et al., 2019).

A. Pareto front built with a genetic algorithm from a data base of management strategies (consisting of crops and the associated management techniques) from Burgundy comprising wheat, barley, triticale, oilseed rape, lucerne, pea, faba bean, maize, soybean, sorghum, sugar beet and sunflower. Each data point is one cropping system. When running the genetic algorithm, the same system may be tested several times and a given system can occur several times in the figure, with a variation in results resulting from stochastic processes in FLORSYS.

B. Synthetic description of the optimal cropping systems ranked according to increasing crop production.