



HAL
open science

The role of models for multicriteria evaluation and multiobjective design of cropping systems for managing weeds

Nathalie Colbach, Luc Biju-Duval, Antoine Gardarin, Sylvie Granger, Sébastien H.M. Guyot, Delphine Meziere, Nicolas Munier-Jolain, Sandrine Petit

► To cite this version:

Nathalie Colbach, Luc Biju-Duval, Antoine Gardarin, Sylvie Granger, Sébastien H.M. Guyot, et al.. The role of models for multicriteria evaluation and multiobjective design of cropping systems for managing weeds. *Weed Research*, 2014, 54 (6), pp.541 - 555. 10.1111/wre.12112 . hal-01173349

HAL Id: hal-01173349

<https://hal.science/hal-01173349>

Submitted on 30 Nov 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



The role of models for multicriteria evaluation and multiobjective design of cropping systems for managing weeds

N COLBACH*, L BIJU-DUVAL*, A GARDARIN*†, S GRANGER‡, S H M GUYOT*, D MÉZIÈRE*, N M MUNIER-JOLAIN* & S PETIT*

*INRA, UMR1347 Agroécologie, BP 86510, F-21000 Dijon France, †AgroParisTech, UMR211 Agronomie, F-78850 Thiverval-Grignon, France, and ‡AgroSup Dijon, UMR1347 Agroécologie, BP 86510, F-21000 Dijon, France

Received 6 May 2014

Revised version accepted 18 June 2014

Subject Editor: José Gonzalez-Andujar, CSIC, Spain

Summary

Weeds are both harmful for crop production and important for biodiversity, while herbicides can pollute the environment. We thus need new cropping systems optimising all cultural techniques, reconciling agricultural production, herbicide reduction and biodiversity conservation. Here, we show how to (i) develop models quantifying the effects of cropping systems on weed dynamics, (ii) integrate interactions between weeds and other organisms, (iii) predict the impact on production and biodiversity and (iv) use the model for multicriteria evaluation and multiobjective design of cropping systems. Among the existing weed dynamics models, we chose the one closest to our requirements to illustrate these different steps, that is, FLORSYS which predicts multispecific weed dynamics as a function of cultural techniques and pedoclimate. We have illustrated the development of interaction submodels with the example of a crop pathogen whose propagation is

increased when infecting grass weeds. To evaluate the weed flora impact, predicted weed densities were translated into indicators of harmfulness (crop yield loss, technical harvest problems, harvest pollution, field infestation, crop disease increase) and biodiversity (weed species richness and equitability, trophic resources for birds, insects and pollinators). Simulations were run over several years and with different weather scenarios (i) to optimise cultural techniques to control harmful weeds, (ii) to analyse the impact of changing agricultural practices (e.g. simplified tillage and rotations, no-till, temporary crops) on weed density, species and trait composition and (iii) to evaluate cropping systems for their ability to reconcile agricultural production and biodiversity, thus identifying levers for designing sustainable cropping systems.

Keywords: weed, model, cropping system, integrated weed management, biodiversity, decision aid, simulation, agroecology.

COLBACH N, BIJU-DUVAL L, GARDARIN A, GRANGER S, GUYOT SHM, MÉZIÈRE D, MUNIER-JOLAIN NM & PETIT S (2014). The role of models for multicriteria evaluation and multiobjective design of cropping systems for managing weeds. *Weed Research* **54**, 541–555.

Introduction

Weeds are among the most harmful pests, reducing crop yields, impairing the quality of crop production

and causing technical problems during harvests (e.g. Oerke, 2006). They can also host other pests such as crop pathogens (e.g. take-all disease of cereals, Gutteridge *et al.*, 2006). Consequently, farmers largely rely

on herbicides to control weeds, which are the main obstacle for switching to Integrated Pest Management (INRA, 2010). Because of the inappropriate use of herbicides, resistance to herbicides has been spreading worldwide (Powles & Yu, 2010), thus increasing management costs for farmers (Service, 2013). Moreover, herbicide use must be decreased because of recent national and European legislation (e.g. French ECO-PHYTO plan, EU directive 2009/128). In agricultural landscapes, weeds are also the main component of wild vegetation biodiversity, and they are an important trophic resource or habitat for many other biodiversity components (Marshall *et al.*, 2003; Carvalheiro *et al.*, 2011; Petit *et al.*, 2011).

Because of their dual nature, pest vs. biodiversity, weeds are a particularly interesting case study when designing innovative cropping systems relying on little or no pesticides. Weeds are greatly impacted, in terms of both abundance and functional composition, by agricultural practices (Bond & Grundy, 2001; Buhler, 2002). Indeed, since the onset of agriculture, a large part of crop management thus aimed at eliminating weeds (Mazoyer & Roudart, 1997). Conversely, more recently, some innovations were excluded because of their severe effect on biodiversity (e.g. GM crops, Freckleton *et al.*, 2003). Moreover, replacing herbicides by alternative methods can have unexpected side-effects on crop production. For instance, experimental cropping system prototypes relying less on herbicides presented a reduced crop production, not because of crop/weed competition, but because some management measures reduced the yield potential (Pardo *et al.*, 2010).

Effects of cropping practices on weeds and associated organisms are difficult to evaluate over the long-term because weed seeds can survive for several years in the soil (Gardarin *et al.*, 2010b). Moreover, a given cultural technique has variable and contradictory effects, depending on environmental conditions and other cropping system components (e.g. the efficiency of mechanical weeding depends on soil moisture during the operation, Kurstjens *et al.*, 2000). In addition, the number and diversity of cultural techniques and weed species is enormous (Lososova *et al.*, 2004; Fried *et al.*, 2008).

Thus, in past years, a multitude of indicators have been developed for evaluating cropping system effects, ranging from indicators of practices that are easy to handle but have a low explanatory potential, to predictive indicators, that is, mechanistic, process-based models which both predict and explain effects but are more difficult to use (Payraudeau & Van Der Werf, 2005). Models are essential tools to quantify and synthesise the effects of cropping practices on the

dynamics and the composition of the weed flora and the resultant harmfulness and benefits for both agricultural production and biodiversity. They are not only research tools (addressing questions such as which species traits are selected by environmental filters? Which traits are necessary to become a dominant and difficult to manage 'super' weed?) but are also essential to produce advice for stakeholders and decision-makers, ranging from farmers (Which rotation minimises harmful weeds? Which management solutions to compensate herbicide reduction?) to policy makers (Which rotation maximises ecosystem services? Does simplified tillage result in species shifts?). Methodologies have thus been developed for simulation-based cropping system design, but current crop and cropping system models often lack submodels for biotic components (weeds among them), and the evaluation and optimisation steps of these design methodologies are hindered by the multiplicity of interactions, criteria and scales to consider, particularly in the case of weeds (e.g. short-term yield loss vs. long-term seed survival, biodiversity vs. crop production) (Bergez *et al.*, 2010).

Consequently, the objective of the present paper is to illustrate how to (i) design models quantifying the effects of cropping systems on multispecific weed dynamics, (ii) integrate interactions between weeds and other organisms, (iii) translate the simulated weed flora into impacts on agricultural production and on biodiversity and (iv) use these models for multicriteria assessment and multiobjective design of cropping systems, focusing particularly on the consequences of weed flora. Among the existing weed dynamics models, the one closest to our requirements was chosen to illustrate these different steps.

Looking for a suitable model

What kind of model do we need?

To understand and predict the variability in effects observed for the different cultural techniques in a large range of situations without re-parameterisation, mechanistic models are best; these decompose the life cycle of weeds (or other organisms) into elementary processes depending on biophysical effects of cropping systems, in interaction with biological (e.g. weed stage) and environmental variables (e.g. soil structure) (Colbach *et al.*, 2005; Colbach, 2010). Indeed, it is not sufficient to quantify the average effects of techniques; farmers also need to know the probability of success of a management strategy and the risk of obtaining the opposite effect of the one they were originally aiming at.

Figure 1 shows a proposal for organising and linking process-based models to quantify the effects of cropping systems on the benefits and harmfulness of weeds for agricultural production and biodiversity. This model association consists of four predictive components, computing (i) the effects of cropping systems on weed flora, that is, an association of several, interacting species, (ii) the effects of cropping systems on other organisms that affect both weeds and agricultural production, (iii) the interactions between weeds and these other organisms and (iv) the effects of weeds and other organisms on agricultural production and on biodiversity.

The main input is necessarily the cropping system, that is, all management variables that affect weeds and/or the other modelled organisms, either directly (e.g. herbicides kill weeds) or indirectly via environmental conditions (e.g. tractor wheels compact the soil which hinders weed emergence). Inputs must also include pedoclimatic conditions to take account of regional differences and, most importantly, to integrate interactions between cropping systems and environmental conditions (Colbach, 2010).

Models of weeds and other organisms must be multi-annual, allowing simulations over several years or even decades, to take account of long-term effects of cropping systems via long-living propagules such as the weed seedbank (Gardarin *et al.*, 2010b). The models need a daily time step because farming operations are carried out at this scale, and not at the scale of the minute or the month. Such a detailed scale is also necessary to integrate interactions with pedoclimate, for example, the efficiency of mechanical weeding depends on soil moisture during the operation (Kurstjens *et al.*, 2000). Some crop models work with an even smaller

time step (e.g. hourly, Boote *et al.*, 2013), but this is difficult to reconcile with the multiannual scale needed for weed dynamics models.

Among the existing weed-dependent organisms, we should focus on species that are strongly impacted by cropping systems (since we want to evaluate them) and that affect crop production and/or biodiversity. The first guild that springs to mind are soilborne crop pathogens because they rarely disperse from field to field (Prew, 1980) and are thus most affected by field history; in addition, they can infect weeds which thus transmit crop diseases in time and in space (Gutteridge *et al.*, 2006).

These models predict detailed variables describing crops, weeds and other organisms (e.g. daily weed density or biomass, proportion of diseased crop plants). These must be translated into indicators that reflect the consequences of weeds for agricultural production and biodiversity.

Which models fit our requirements?

Among the weed dynamics models found in literature, there is to date no model that fits the proposal of Fig. 1, though there are models that correspond to the various components. The FLORSYS model (Gardarin *et al.*, 2012; Munier-Jolain *et al.*, 2013, 2014; Colbach *et al.*, 2014a) was built by our team to answer most of our requirements, that is, mechanistic, multispecific, multiannual with a daily time step, including most cropping systems components influencing weeds, producing detailed crop and weed variables that facilitate links with other models and indicators (Holst *et al.*, 2007; Freckleton & Stephens, 2009; Colbach, 2010).

This model will be used here to illustrate (i) how to link a weed dynamics model with other models and indicators to fit the requirements of Fig. 1, and then (ii) how to use the resultant model combination to answer both scientific (e.g. Which species traits are selected in which cropping systems) and practical questions (e.g. When best to sow to reduce harmful grass weeds? Which cropping systems to minimise weed harmfulness and maximise weed-related biodiversity?).

How to predict the impact of cropping systems on weed flora?

The weed life cycle of FLORSYS

The input variables of FLORSYS are (i) the cropping system to be tested (Table 1), (ii) pedoclimate consisting of daily weather and soil characteristics (e.g. texture, organic matter content), (iii) the weed community present on the first day of the simulation, that is, the

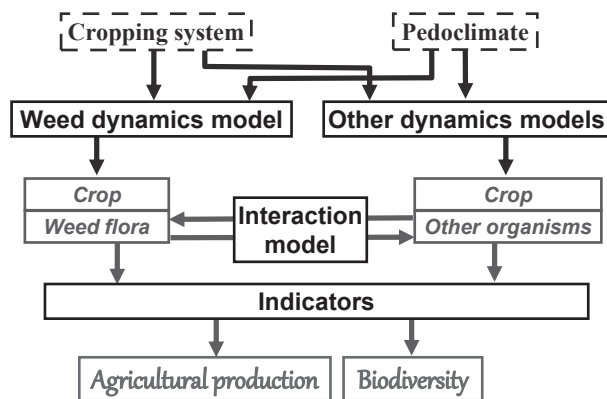


Fig. 1 Model association linking models and indicators to evaluate cropping systems and weed management strategies for their ability to reconcile agricultural production and weed-related biodiversity (Input variables, Models, Biotic components, Output variables) (Nathalie Colbach ©2014).

Table 1 Effects of cropping system on the weed life cycle (density and timing of stages) as simulated by FLORSys (Gardarin *et al.*, 2012; Munier-Jolain *et al.*, 2013, 2014; Colbach *et al.*, 2014a)

Cropping system	Intermediate effect	Effect on weeds
Tillage (including post-sowing mechanical weeding)	Fragments soil Buries and excavates seeds depending on tool, tillage depth and soil structure	Decreases mortality of germinated seeds Seed burial decreases germination and increases pre-emergent mortality due to insufficient seed reserve Seeds on soil surface germinate badly because of insufficient seed/soil contact Germinated seeds close to soil surface often die because the top soil dries faster Imbibed seeds are exposed to light if inverting tool Triggers germination flush if the soil is moist Destroys germinated seeds, seedlings and plants; adds newly produced seeds to seedbank when killing mature plants
Crop species and variety (including under sown, associated and temporary crops)	Choice of cultivation techniques Sowing season Light availability in canopy	See effects of techniques Selects weed species that are non-dormant at sowing Shading reduces photosynthesis and thus biomass accumulation and results in etiolation
Sowing date	Crop emergence date Date of last tillage	The earlier the weed seedlings emerge relative to the crop, the better they survive The later the last tillage, the more weed seeds have germinated already and are killed by tillage
Sowing density	Reduces light availability in canopy	Shading reduces photosynthesis and thus biomass accumulation and results in etiolation
Sowing pattern	Variability in light availability in canopy	Irregular sowing leads to canopy gaps where weeds grow and reproduce better
Irrigation	Increases soil moisture	Increases germination and emergence
Herbicide	Efficiency depends on active ingredient and the farmer's technical ability; it decreases with canopy density, seed depth (for root-entering herbicides) and weed stage	Foliar herbicides kill emerged plants, root-entering herbicides kill unemerged and emerged plants resulting from shallow seeds, pseudoroot herbicides kill emerging seedlings; root-entering and pseudoroot herbicides persist and act during several days. Adds newly produced seeds to seedbank when killing mature plants; these seeds germinate if soil is moist
Mowing & harvesting operations		Cut plants and reduce biomass; the older the plants at mowing and the less biomass remains, the higher mortality. Add newly produced seeds to seedbank when killing mature plants; these seeds germinate if soil is moist
Manure	Adds layer on soil surface	Improves germination of surface seeds, slightly decreases germination and emergence of buried seeds Adds seeds to soil seedbank
All traffic	Increases soil compaction via wheel traffic	Increases mortality of germinated seeds

The effect of other management techniques (e.g. nitrogen fertiliser) is not yet implemented in FLORSys.

seed density of each species. FLORSys comprises a sub-model from STICS (Brisson *et al.*, 1998) to predict soil climate and another one from DéciBlé (Chatelin *et al.*, 2005) to predict soil structure; these intermediate variables drive a large part of the pre-emergence submodel of FLORSys.

The core of FLORSys is a generic life cycle valid for all annual weed species (Fig. 2), consisting of a succession of life stages interacting with cropping system components. Shallow non-dormant weed seeds germinate

after rain or tillage in moist conditions; only seeds close to the soil surface whose roots cross moist soil layers succeed in emerging. Dormant and/or buried weed seeds germinate rarely; their disappearance is mostly due to *in situ* mortality. Crop plants emerge from sown seeds, depending on sowing depth and temperature.

Pre-emergent processes are simulated for an average m² of the simulated field. After emergence, weed and crop plants are placed on a field subsample (e.g.

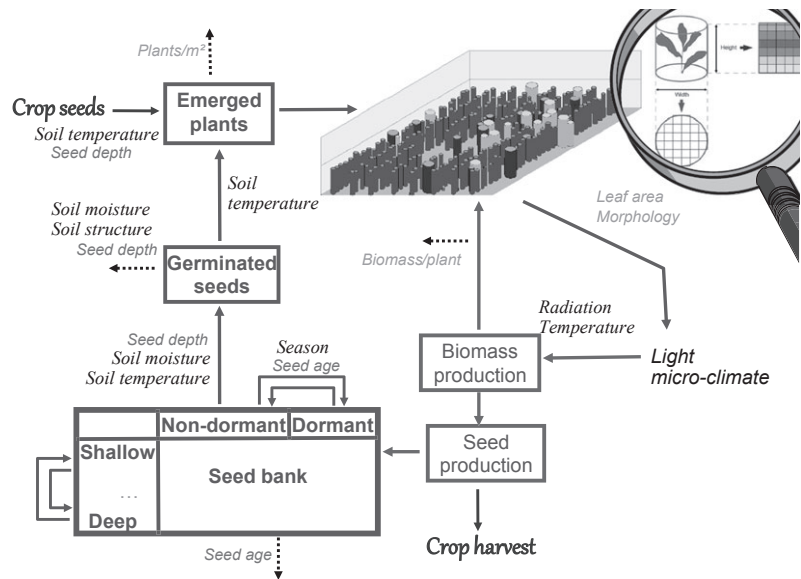


Fig. 2 Crop and weed life-cycle simulated by FLORSYS (Gardarin *et al.*, 2012; Munier-Jolain *et al.*, 2013, 2014; Colbach *et al.*, 2014a). Life-stages linked by functions (←) depending on cultural techniques, Plant variables, Seed variables and Pedoclimatic conditions, with mortality processes (←•••) (Nathalie Colbach ©2014).

8 × 4 m²), the crop plants according to their sowing pattern (e.g. row-sown or broadcasted) listed in the input variables, the weeds in patches. The above-ground part of plants is represented by a cylinder, with height, diameter and leaf distribution depending on the species, plant stage and past shading conditions, which can lead to etiolation. Each day, light availability is calculated in each point of this 3D-canopy, resulting in biomass accumulation and subsequent plant-cylinder growth. At weed maturity, seed production is calculated as a function of biomass and the seeds added to the soil seedbank. Crop seeds are exported during harvest and are used to calculate crop yield.

The effect of cropping systems on weeds

The relationships between the life stages depend on environmental variables and management techniques (Table 1). For instance, tillage buries and excavates seeds, it breaks dormancy and triggers germination, but it also uproots seedlings and plants and covers them with soil. All these effects vary with the tillage tool and depth, tractor speed, soil moisture, as well as weed species and stages. This principle, that is, breaking the impact of a technique into individual effects that interact with environmental conditions and weed variables, was used for all cultural techniques.

Parameterising weed species with functional relationships

The detailed life cycle and the biophysical representation of the cropping system effects require a large

number of parameters to describe the behaviour of each species in FLORSYS. Consequently, we developed a method based on functional relationships, where model parameters are estimated from species traits or, in some cases, from expert knowledge. For instance, the thicker the seed coat, the lower the seed mortality rate in the soil and the higher the seed dormancy level (Gardarin *et al.*, 2012; see details in Table S1). To date, all pre-emergent process parameters (seed mortality, dormancy, germination, pre-emergent growth) can be estimated from seed traits (mass, shape, area, coat thickness, lipid content), taxa (dicotyledonous vs. monocotyledonous) and usual emergence period in the field (Gardarin *et al.*, 2010a,b,c, 2011; Gardarin & Colbach, in press).

Model ‘validation’

The model complexity complicates the evaluation with independent field observations (‘validation’). Different approaches must be combined in such a case. First, the potential domain of validity should be determined from the model structure (Table 2.1). For instance, FLORSYS was developed for arable, annual crops in temperate climates. Drought-sensitive species might thus be overestimated when simulating un-irrigated fields in drier regions, because the model does not integrate crop/weed competition for water, even though it considers some water-dependent processes (e.g. germination driven by soil water potential, pre-emergent weed seedling mortality due to drought; Gardarin *et al.*, 2012).

Table 2 Domain of validity and evaluation ('validation') of FLORSys

Process	What is correctly predicted	Limits of domain of validity	Reference
1. Analysis of model structure			
Reproduction	16 annual weed species	Disregards perennials and infrequent annuals	Model structure
Water availability	Temperate climates, irrigated fields	Overestimates drought-sensitive species in unirrigated fields in dry regions?	Hypothesis
Competition for nitrogen	Well-fertilised fields	Underestimates oligotrophic species in nitrogen-poor conditions?	Hypothesis
Phenology	Fields at Burgundy latitude	Bad prediction of flowering dates of day-length-sensitive species?	Hypothesis
2. Validation of submodels			
Emergence flush after seed shed or burial	Timing, ranking of situations, magnitude of emergence density, including for species whose parameters were estimated with functional relationships	Emergence is overestimated if seedling loss due to disease	Gardarin (2008)
Light interception in heterogeneous canopies	Incident photosynthetically active radiation, ranking of situations	PARi is badly predicted on cloudy days in dense and homogenous canopies in winter	Munier-Jolain <i>et al.</i> (2013)
Weed species abundance	Ranking of species and regions	The modelled species are overestimated to the detriment of perennials and infrequent annuals	Colbach <i>et al.</i> (2014b)
Potential crop yield	Magnitude	Plant loss is overestimated if sudden frost with snow	Colbach <i>et al.</i> (2014a)
Soil seedbank*	Ranking of situations, magnitude of densities	Surface seed density is overestimated in long-term no-till	Colbach <i>et al.</i> (2006)
3. Validation of complete model			
Weed density over the years	To be done		

*Evaluation for one grass weed species only, *Alopecurus myosuroides* Huds.

In a second step, individual model components should be evaluated by comparing predictions to independent observations (Table 2.2), usually by setting up specific experiments. For instance, Gardarin (2008) sowed weed seeds of different species at different depths, soil moistures and temperatures and monitored emergence and final seed survival, showing that FLORSys correctly predicted the timing and magnitude of emergence, including for species whose parameters were estimated from functional relationships, except when rot killed seedlings.

Finally, the complete model must also be tested in a large range of cultural and pedoclimatic conditions, a step that is currently underway for FLORSys. Because of the multiplicity of input variables and the multianual model scale, it is unconceivable that sufficient specific validation experiments could be set up, but also difficult to find existing trials and surveys that recorded the necessary data.

How to integrate biotic interactions

Principle

We illustrated the integration of biotic interactions with the soilborne crop pathogen *Gaumannomyces graminis* vs. *tritici* causing take-all disease in straw cereals and important yield losses (up to 50%, Schoeny *et al.*, 2001). This fungus mostly depends on the cropping system (Ennaïfar *et al.*, 2007) and can infect several grass weeds (Gutteridge *et al.*, 2006). Simple models already existed in the literature predicting (i) disease incidence from past crops, crop management variables and weather variables (Ennaïfar *et al.*, 2007) and (ii) the resultant crop yield loss from disease incidence and nitrogen fertiliser (Schoeny *et al.*, 2001).

After linking these two equations to FLORSys, two additional submodels were developed (Mézière *et al.*, 2013) quantifying: (i) the increase in crop disease due to diseased grass weeds in the current as well as in

previous crops, by adding the density of grass weeds (weighted by the disease susceptibility of their species) to the density of disease-susceptible crop plants in the above-described disease equation, and (ii) the decrease in seed production of diseased grass weeds by applying the crop yield loss equation weighted by the weed species susceptibility. This model combination was named TAKEALLSYS.

Consequences for bioagressor management

A simulation study with the FLORSYS-TAKEALLSYS association of a large range of cropping systems and two pedoclimates showed that the pathogen had no significant effect on the multiannual dynamics of grass weeds such as *Alopecurus myosuroides* Huds. (black-grass) and cannot be used for biological control. Moreover, the disease-related crop yield loss did not notably increase in integrated weed management scenarios, which do thus not result in a new pest problem. Finally, this yield loss can greatly increase in cropping systems that do not control *A.myosuroides*, particularly in untilled fields (Mézière *et al.*, 2013).

How to estimate direct and indirect benefits and harmfulness of weeds?

Principle

Daily weed variables (weed seedbank, plant densities, biomass...) predicted by FLORSYS were translated into indicators that reflect the consequences of weeds for agricultural production and biodiversity and allow the assessment and rank the performance of cropping systems. Indicators are considered here as '(i) an informative function, that is, to supply simplified information about a complex system (e.g. an agrosystem), or an unmeasurable criteria (e.g. biodiversity, sustainability) (...); (ii) a decision aid function to help to achieve the initial objectives, for example, the sustainability of a farming system' (Bockstaller & Girardin, 2003).

First, five harmfulness indicators were developed to take account of the criteria most frequently listed by farmers via an Internet survey (Mézière *et al.*, 2015): (i) crop yield loss, (ii) harvest pollution by weed seeds, stems and leaves, (iii) harvesting problems due to green weed biomass blocking the combine and (iv) field infestation represented by weed biomass averaged over cropping seasons. A fifth indicator was added: (v) the increase in crop disease in the presence of weeds predicted by TAKEALLSYS.

The indicators for weed contribution to biodiversity were developed in collaboration with ecologists (Mézière *et al.*, 2015). Two of them reflect the weed

contribution to vegetation biodiversity: (i) species richness, that is, the number of weed species present during the cropping seasons and (ii) Pielou's index for species equitability, that is, the dominance of the weed flora by one or a few species. The other three indicators appraise weeds as a trophic resource for other organisms in the agro-ecosystems, considering the seasons of activity and food shortage: (iii) the number of weed seeds weighted by the species contribution to farmland bird diet and present on soil surface in autumn and winter (Wilson *et al.*, 1999; Marshall *et al.*, 2003), (iv) lipid-rich seeds on soil surface in summer to feed insects such as carabids (A Trichard, pers. comm) (Trichard *et al.*, in preparation) and (v) weed flowers weighted by the species contribution to feed domestic bees in spring and summer (Bockstaller *et al.*, 2012).

Antagonisms and synergies between harmfulness and biodiversity

A large range of contrasting cropping systems were identified by farm surveys in two regions, simulated with FLORSYS over several years and repeated with different weather series (Mézière *et al.*, 2015). Antagonisms and synergies between weed-related harmfulness and biodiversity were identified by determining correlations between the indicator values, showing that weed harmfulness generally increased with increasing weed-related biodiversity (i.e. positive correlation coefficient values in Table 3). These correlations were though weak (i.e. low correlation values), and others were negative, showing that increased biodiversity could occur with decreased harmfulness (e.g. trophic resource for insects vs. yield loss or field infestation). Consequently, there are cropping systems that may reconcile agricultural production and biodiversity.

How to use the model for evaluating and designing cropping systems?

In this section, FLORSYS and its companion model and indicators were used to illustrate how models can be used to optimise cultural techniques and cropping systems for managing weeds, to reconcile agricultural production and biodiversity.

Optimising cultural techniques

Models such as FLORSYS can be used to optimise individual cultural techniques to minimise harmful weeds. Simulations showed that management strategies must be tested with different weather scenarios. Indeed, a given option can reduce weed infestation on average

Table 3 Antagonisms and synergies between weed harmfulness and contribution to biodiversity. Spearman correlations between annual values of indicators simulated with the FLORSys model association in 26 cropping systems identified by farm surveys in Burgundy and Poitou-Charentes. Each system was simulated over 30 years and repeated 20 times with randomly chosen weather scenarios from its original region (Mézière *et al.*, 2015)

Biodiversity indicators	Harmfulness indicators				
	Crop yield loss*	Harvest pollution†	Harvesting problems‡	Field infestation§	Additional crop disease¶
Species richness**	0.24	0.10	0.10	0.20	ns
Species equitability††	0.08	0.18	0.11	0.14	-0.06
Trophic resource for					
Birds‡‡	ns	ns	ns	0.09	-0.13
Insects (carabids)§§	-0.13	0.22	0.20	-0.13	ns
Pollinators (domestic bees)¶¶	ns	0.16	0.13	ns	ns

ns, not significantly different from zero at $P = 0.05$.

*Relative yield difference between weed-infested and weed-free fields.

†Weed seeds and plant debris in crop harvest.

‡Green weed biomass above cutting height.

§Average weed biomass in crop.

¶Relative crop disease incidence in weed-infested vs. weed-free fields.

**Number of weed species in crop.

††Pielou's index.

‡‡Preferred weed seeds on soil surface in autumn and winter.

§§Lipid-rich seeds on soil surface in summer.

¶¶Preferred weed flowers in spring and summer.

(e.g. delayed sowing), but only be efficient in certain settings (e.g. delay after 31 October) and weather years (e.g. 57–64% of years according to regions); it can even result in the opposite of the initial objective (e.g. delaying sowing from 3 October to 10 October increased weed emergence by 10% in 7–14% of the weather scenarios) (Table 4).

Moreover, a management option can be efficient in the short term (e.g. a summer catch crop decreases weed-related yield loss in the following winter wheat, first year of Fig. 3), but disastrous in the long term (e.g. the summer catch crop limits opportunities for false seedbed techniques, thus leaving more weed seeds to emerge in subsequent crops, years 2, 4 and 6 of

Fig. 3). More generally, inadequate management in 1 year (e.g. no herbicides during the first year of Fig. 3) can impact weed dynamics and crop production for several years (the yield loss took several years to decrease in Fig. 3 despite herbicides being applied during years 2–10). Management scenarios must thus always be evaluated over several years.

Changing cultural techniques modifies the density and composition of the weed flora

Simulations were carried out in three French regions to study the impact of modified agricultural practices on weed floras. Typical current regional cropping sys-

Table 4 Effect of delaying wheat sowing date on blackgrass emergence (*Alopecurus myosuroides* Huds.) after sowing simulated with the monospecific prototype of FLORSys. Frequency analysis with 10 weather repetitions from Northern France and Burgundy (based on Colbach *et al.*, 2005)

Delay sowing date		Northern France		Burgundy	
		% Years where weed emergence		% Years where weed emergence	
From	To	Decreased by $\geq 10\%$	Increased by $\geq 10\%$	Decreased by $\geq 10\%$	Increased by $\geq 10\%$
3 October	10 October	7	7	14	14
10 October	17 October	7	0	0	7
17 October	24 October	7	7	0	7
24 October	31 October	14	7	50	0
31 October	7 November	57	0	64	0
7 November	14 November	50	0	71	0

Frequency analysis with 10 weather repetitions from Northern France and Burgundy (based on Colbach *et al.*, 2005).

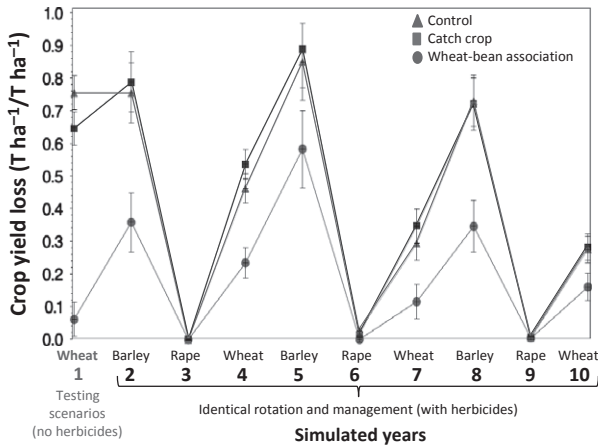


Fig. 3 Long-term effect of cultural techniques on weed-induced crop yield loss (mean and standard-error of 10 weather repetitions) simulated with FLORSYS. Effect of summer fallow (control, triangles), catch crop (squares) and association with field bean in separate rows (circles) on yield loss of a herbicide-free winter wheat and on yield of the nine subsequent, herbicide-sprayed crops in Burgundy (based on Colbach *et al.*, 2014a) (Nathalie Colbach ©2014).

tems as well as possible prospective systems were identified via farm surveys (Colbach *et al.*, 2009; Mézière *et al.*, 2015), the Biovigilance-Flore database which monitors cropping systems and weed floras in France (Fried *et al.*, 2008) and expert opinion. These systems were simulated with FLORSYS, showing the disastrous effect on weed control of simplified rotations and tillage, direct sowing or earlier sowing (Colbach *et al.*, 2014b). More interestingly, by applying ecological analytical methodologies (i.e. RLQ analyses) to the simulated weed flora, these simulations allowed the understanding of which species traits were selected in the different cropping systems. For instance, increasing

mouldboard ploughing frequency selected species with thick-coated seeds with low lipid content (Fig. 4). Indeed, thick seed coats increase the persistence of buried seeds (Gardarin *et al.*, 2010b; Gardarin & Colbach, in press). Seeds can thus survive for several years after burial by ploughing and are still viable when another ploughing carries them back to soil surface after a few years where they can germinate and emerge. Conversely, in unploughed or untilled fields, seeds that germinate early and fast after triggering by rain or tillage (which also present a high lipid content, Gardarin *et al.*, 2011) might be at an advantage because they can avoid predation, which is high on the soil surface (Cromar *et al.*, 1999).

These practice-trait correlations can be used to predict the behaviour of weed species other than those used in the simulation study (Fig. 5); for instance, based on its seed coat thickness and seed lipid content, a species such as *Polygonum lapathifolia* (L.) Gray (POLLA in Fig. 5) should be more adapted to frequent ploughing than *Papaver rhoeas* L. (PAPRH), an assumption verified in field observations (e.g. mouldboard ploughing decreased *P. rhoeas* densities, Cirujeda *et al.*, 2003).

How to reconcile agricultural production and weed-related biodiversity

The analysis of weed harmfulness and weed-related biodiversity concluded that there are cropping systems that reconcile crop production and biodiversity. To identify these systems, a typology of cropping systems was built based on their performance, that is, their values for the ten harmfulness and biodiversity indicators. Ten profiles were identified (Fig. 6), the most

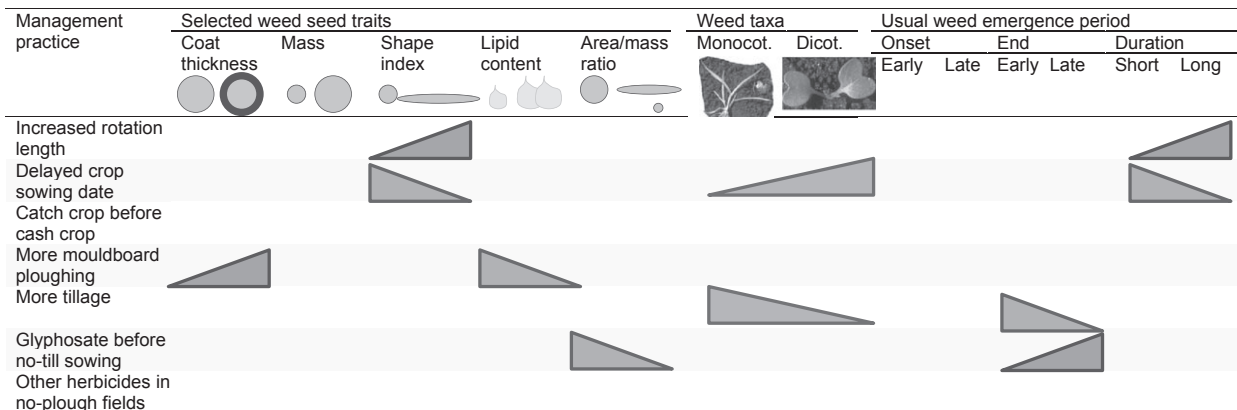


Fig. 4 Weed seed traits selected by modified agricultural practices. Pearson correlations determined by RLQ analyses applied to weed flora simulated with FLORSYS in 30 cropping systems in three regions (Burgundy, Poitou-Charentes, Aquitaine). Red and green triangles show negative and positive correlations, blue triangles effects of qualitative variables (based on Colbach *et al.*, 2014b) (Nathalie Colbach ©2014).

13653180, 2014, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/weve.12112 by Cochrane France, Wiley Online Library on [30/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

interesting being profile 5, which maximises biodiversity (the profile's pie chart comprises a lot of green) and minimises weed harmfulness (little blue or pink in the pie). Only one management pathway leads to this profile, that is, cropping systems with less than one tillage operation per year averaged over the rotation, usually no-till systems. Consequently, direct drilling does not necessarily reduce agricultural production, as suggested by the important increase in weed densities seen in the previous section, particularly when accompanied by cultural measures to compensate the absent tillage. Other profiles (e.g. profile 2) can be reached by several management pathways. Multiple pathways are particularly interesting, as farmers can choose the option best adapted to their objectives and constraints.

Discussion

Models: going beyond 'reality'

Models are considered here as a simplified representation of a system, to understand and take decisions and to paraphrase a famous modellers' maxim, 'they are all wrong but some are useful' (Box & Draper, 1986). So, when and how are models such as FLORSYS useful and what can they do that experiments, field surveys or expert opinion cannot?

Here, FLORSYS was used as a virtual field where numerous and diverse cultural techniques were monitored in detail over the long term, which is essential to produce robust advice. Additional combinations of cropping system variables must still be simulated to check the decision trees of the previous section and to improve them by integrating additional cultural

techniques. The faster the model, the more and the longer systems can be tested. For instance, the faster, monospecific FLORSYS version was used to test 100 000 cropping systems over 20 years (Colbach *et al.*, 2013).

FLORSYS produces quantitative predictions. In the example of section '*Optimising cultural techniques*', FLORSYS not only predicted that later sowing would reduce weed emergence (which experts are able to do as well), but also how much (which field trials could also do, but only for a few situations) and determined probabilities of success and risk of failure necessary for farmers to take their decisions (which only a huge network of field surveys could do and only for a few cultural practices). The long-term simulation scale is also essential for weeds, because management options can be useful over the short term, but disastrous over the long-term as illustrated in section '*Optimising cultural techniques*'. Long-term field trials do exist (Moss *et al.*, 2004; Chikowo *et al.*, 2009), but they usually only test a few systems and do not have any true replication, in contrast to model-based approaches (Parysow & Gertner, 1997).

Some weed dynamics models developed in the past (Holst *et al.*, 2007; Freckleton & Stephens, 2009; Colbach, 2010) can tackle the multiplicity and multiannuality aspects of cropping system simulations and are often faster than the more complex FLORSYS. However, the latter is probably the one model closest to a virtual field, allowing the experimenter to 'measure' a large number of weed, crop or soil variables that are often impossible to monitor in the field. This makes the produced results and advice more robust, because understanding the causes of an effect makes it easier to judge their domain of validity. This detailed output

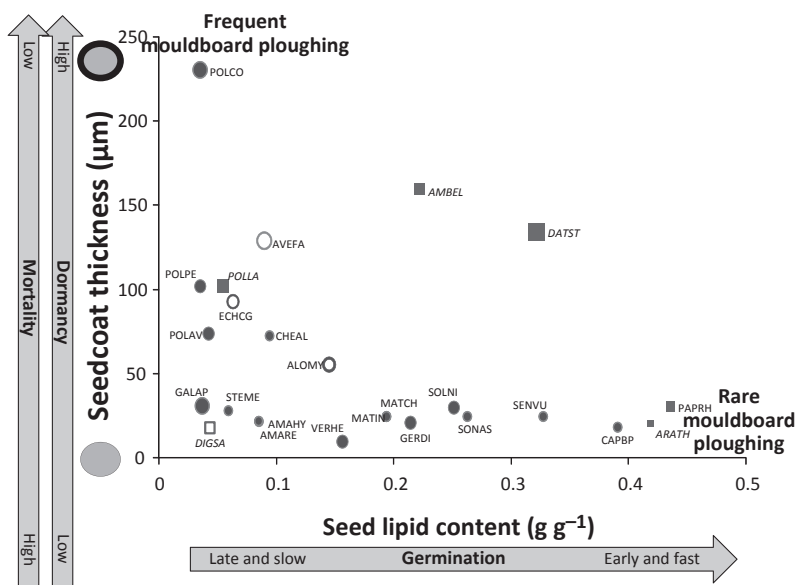


Fig. 5 Predicting the adaptation to mouldboard ploughing frequency from two seed traits for unstudied species (□) based on the correlations between agricultural practices and seed traits estimated with RLQ analyses of 16 weed species (●) simulated with FLORSYS (based on Colbach *et al.*, 2014b). The larger the symbols, the heavier the seeds; open symbols show monocotyledons. Seed mortality decreases and seed dormancy increases with increasing seed coat thickness (Gardarin *et al.*, 2010b; Gardarin & Colbach, in press); seeds with a high lipid content germinate earlier and faster (Gardarin *et al.*, 2011). Species are identified with EPPO codes (Nathalie Colbach ©2014).

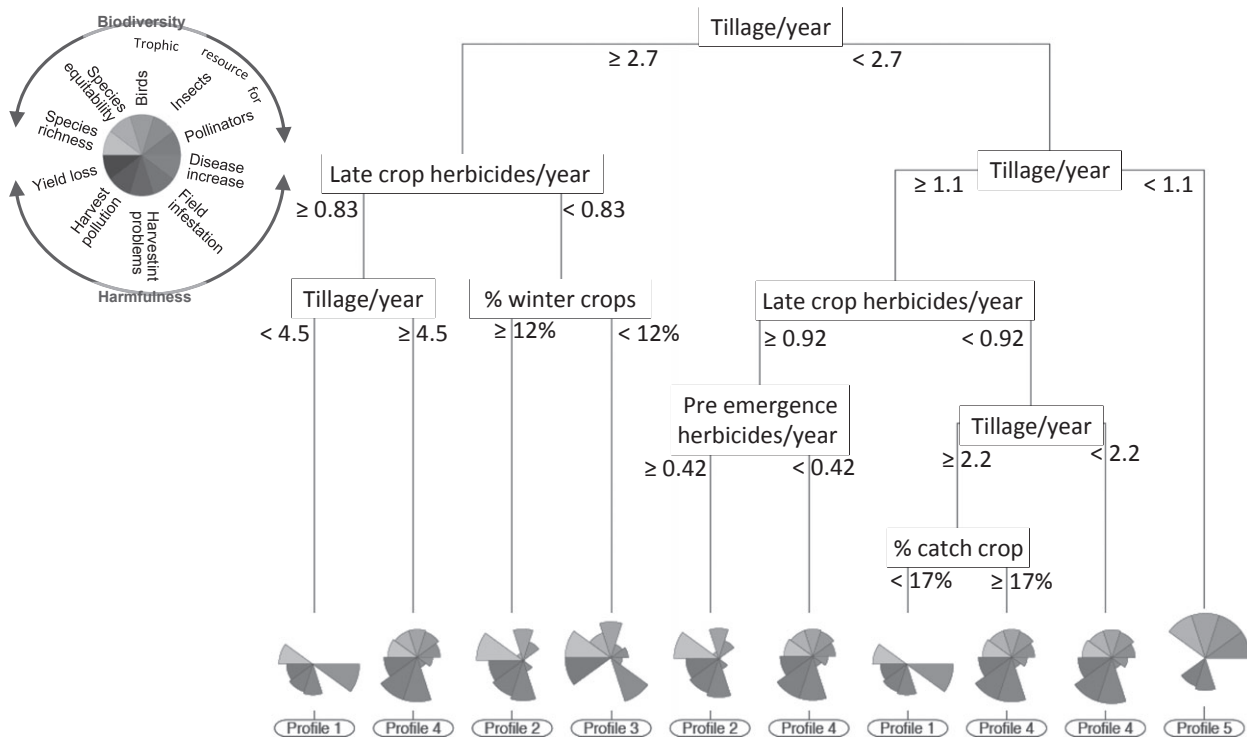


Fig. 6 Cropping system typology (with principal component analysis followed by clustering) based on weed harmfulness and weed-related biodiversity performances simulated with FLORSys. Identification of management strategies to reach the different performance profiles (with regression trees from PCA co-ordinates) (based on Mézière, 2013) (Delphine Mézière ©2013).

also made possible the connection of a series of diverse and very precise indicators to assess the impact of weeds on crop production and biodiversity, drawing on weed variables that are difficult to access in fields (e.g. weed seeds on soil surface) and at a scale impossible to achieve in surveys (e.g. daily or weekly).

Some of the trait-based conclusions of section ‘*Changing cultural techniques...*’ (e.g. ploughing selects thick-coated seeds because of their better persistence) could be drawn from expert knowledge, but a weed dynamics model is necessary to take account of all traits (e.g. ploughing possibly also selects large-seeded species, as these germinate and emerge better when buried, Gardarin *et al.*, 2010a) and life-cycle processes, leading to trade-offs (e.g. produce many small seeds with low survival probability vs. few heavy seeds with a higher survival, Moles & Westoby, 2006). Such analyses could also be carried out on data collected in field surveys for which the RLQ method of section ‘*Changing cultural techniques...*’ was initially applied (Fried *et al.*, 2012). Simulations replace and enlarge the survey data and, in the particular case of mechanistic models based on functional traits, they can go much further in understanding plant response to combinations of management techniques and their effects on crop production and biodiversity components (Qué-tier *et al.*, 2007).

Modelling as a dynamic and iterative process

Modelling does not result in an optimal product finished once and for all. Rather, a model is a dynamic product resulting from an iterative process, where the product is alternatively evaluated to determine where it is wrong and where useful, and improved to take account of new knowledge and user requirement. Once a workable version of a model is finished and running, model evaluation (‘validation’) is essential to confirm the modelling choices, to determine the model’s domain of validity and prediction error and to identify model parts that need to be improved. This step is unfortunately still comparatively rare for weed dynamics models (Holst *et al.*, 2007). Here, we showed that though the FLORSys model association already encompasses a large range of processes and produces logical results, it neglects several processes that are crucial for cropping system design, for example, crop/weed competition for water or nitrogen (Iqbal & Wright, 1997). Similarly, only a small number of biological interactions are integrated here (plant/plant and plant/fungus), though others could potentially regulate weeds (e.g. weed seed predation by insects, Trichard *et al.*, 2013) and be used in agroecological management practices. The robustness of some trait/parameter relationships also needs checking, particularly when no

functional assumption exists to explain the relationship, for example, the earlier and faster germination of lipid-rich seeds (Gardarin *et al.*, 2011) whose correlation may be contingent of the analysed species dataset.

The range of indicators for evaluating cropping systems can also evolve. They are crucial for optimising cropping systems (see section ‘*Which methods and tools for optimising cropping systems*’) and need thus to be extended to answer the requirements of the model end-users, by including for instance additional organisms (e.g. wild bees and other pollinators) or environmental processes (e.g. land cover for reducing erosion or nitrate leaching, herbicide use and toxicity).

Model development thus is an interactive loop, successively improving the model to take account of new knowledge and user requirements. Such a progressive expansion is certainly necessary, but the danger is to produce an obese monster too slow and too difficult to operate, particularly for non-modellers, with the additional danger of amplifying prediction error resulting from the enormous amount of required input variables and parameters. Metamodelling is a possible solution, where the mechanistic model is used to run a huge number of virtual experiments whose results are then used to build a simpler and faster empirical model for decision aid (Colbach, 2010), using a principle similar to that of the decision trees of Fig. 6.

Which methods and tools for optimising cropping systems

Like FLORSYS, most crop and cropping system models are much too complex to be usable for directly designing and optimising cropping systems as a function of a set of objectives and constraints. Simulation-based cropping system design therefore combines generating a large number of candidate systems with evaluation methods to select the best solutions. GSEC loops consisting of generation, simulation, evaluation, comparison and choice of systems are considered best to find the optimal systems (Bergez *et al.*, 2010). Here, we propose to adapt this iterative loop (Fig. 7) where cropping systems candidates are proposed by stakeholders (ranging from farmers to regulators), from expert opinion and, particularly, from judiciously combining management variables identified in the decision trees such as the one presented in Fig. 6. These systems are then simulated with the FLORSYS model association, which predicts the harmfulness and biodiversity performance which is judged by stakeholders, thus discriminating acceptable cropping systems to be communicated to farmers from unacceptable cropping systems which need to be improved. The knowledge synthesised in the decision trees and the

knowledge produced by the practice-trait correlations of Fig. 4 can both be used to improve those cropping systems rejected by stakeholders at the previous step.

This iterative loop leaves open a huge field of methodological development and many methods are available for each step (Bergez *et al.*, 2010). Here, we propose to start the loop with a relatively small number of candidate situations, which must be compensated later when the cropping systems deemed unsatisfactory by the multicriteria evaluation are improved, using optimisation rules. Simulation-based optimisation is a huge field in operational research, also implicating artificial intelligence-based techniques, which we will not attempt to broach here. These methods are essential to reduce the number of explored situations and to avoid missing interesting candidates. Lately, there has been a shift to more participatory methods, involving end-users to ensure that the resulting cropping system innovations are indeed feasible and adopted by farmers (Hossard *et al.*, 2013), which has often not been the case in the past (Vanloqueren & Baret, 2008).

Conclusion

Models are the result of an iterative and complementary loop between experiments, field surveys and expert opinion on one hand, formalisation of knowledge and simulations on the other hand. Because of their synthetic and quantitative nature, models can go much

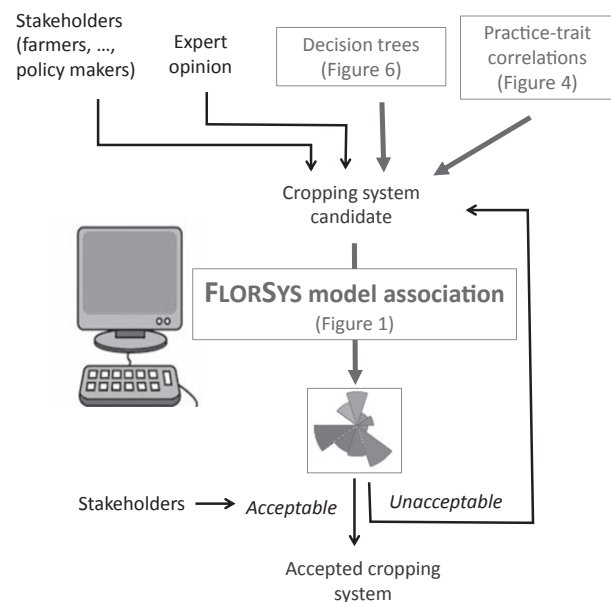


Fig. 7 Contribution of the FLORSYS model association and the present simulation results to designing weed management strategies for reconciling agricultural production and weed-related biodiversity (Nathalie Colbach ©2014).

further in terms of multicriteria evaluation and multi-objective design of cropping systems. This is particularly true when aiming at reconciling potentially antagonistic objectives like agricultural production, biodiversity conservation and low pesticide use.

Acknowledgements

The present work was financed by INRA, ANR SYSTERRA ADVHERB (ANR-08-STRA-02) and the research programme 'Assessing and reducing environmental risks from plant protection products' driven by the French Ministry of Ecology (APR 2011- Ecophyto 2018 'Change agricultural practices to preserve ecosystemic services').

References

- BERGEZ JE, COLBACH N, CRESPO O *et al.* (2010) Designing crop management systems by simulation. *European Journal of Agronomy* **32**, 3–9.
- BOCKSTALLER C & GIRARDIN P (2003) How to validate environmental indicators. *Agricultural Systems* **76**, 639–653.
- BOCKSTALLER C, RICOU C, SCHNELLER C *et al.* (2012) Assessing the pollination value of field margin flora by means of a predictive indicator. In: *12th ESA Congress*, Helsinki, Finland.
- BOND W & GRUNDY AC (2001) Non-chemical weed management in organic farming systems. *Weed Research* **41**, 383–405.
- BOOTE KJ, JONES JW, WHITE JW, ASSENG S & LIZASO JI (2013) Putting mechanisms into crop production models. *Plant, Cell & Environment* **36**, 1658–1672.
- BOX GEP & DRAPER NR (1986) *Empirical Model-Building and Response Surface*. John Wiley & Sons, New York, NY, USA.
- BRISSON N, MARY B, RIPOCHE D *et al.* (1998) STICS: a generic model for the simulation of crops and their water and nitrogen balances. I. Theory and parameterization applied to wheat and corn. *Agronomie* **18**, 311–346.
- BUHLER DD (2002) Challenges and opportunities for integrated weed management. *Weed Science* **50**, 273–280.
- CARVALHEIRO L, VELDTMAN R, SHENKUTE G *et al.* (2011) Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters* **14**, 251–259.
- CHATELIN MH, AUBRY C, POUSSIN JC *et al.* (2005) DéciBlé, a software package for wheat crop management simulation. *Agricultural Systems* **83**, 77–99.
- CHIKOWO R, FALOYA V, PETIT S & MUNIER-JOLAIN N (2009) Integrated Weed Management systems allow reduced reliance on herbicides and long term weed control. *Agriculture, Ecosystems and Environment* **132**, 237–242.
- CIRUJEDA A, RECASENS J & TABERNER A (2003) Effect of ploughing and harrowing on a herbicide resistant corn poppy (*Papaver rhoeas*) population. *Biological Agriculture & Horticulture* **21**, 231–246.
- COLBACH N (2010) Modelling cropping system effects on crop pest dynamics: how to compromise between process analysis and decision aid. *Plant Science* **179**, 1–13.
- COLBACH N, DÜRR C, ROGER-ESTRADE J & CANEILL J (2005) How to model the effects of farming practices on weed emergence. *Weed Research* **45**, 2–17.
- 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. *European Journal of Agronomy* **24**, 113–128.
- COLBACH N, GRANGER S & MUNIER-JOLAIN NM (2009) Using weed dynamics models for evaluating and developing integrated cropping systems. In: *XIIIème Colloque international sur la biologie des mauvaises herbes*, 195–205, Dijon, France.
- COLBACH N, GRANGER S & MÉZIÈRE D (2013) Using a sensitivity analysis of a weed dynamics model to develop sustainable cropping systems. II. Long-term effect of past crops and management techniques on weed infestation. *Journal of Agricultural Science* **151**, 247–267.
- COLBACH N, COLLARD A, GUYOT SHM, MÉZIÈRE D & MUNIER-JOLAIN NM (2014a) Assessing innovative sowing patterns for integrated weed management with a 3D crop: weed competition model. *European Journal of Agronomy* **53**, 74–89.
- COLBACH N, GRANGER S, GUYOT SHM & MÉZIÈRE D (2014b) A trait-based approach to explain weed species response to agricultural practices in a simulation study with a cropping system model. *Agriculture, Ecosystems & Environment* **183**, 197–204.
- CROMAR HE, MURPHY SD & SWANTON CJ (1999) Influence of tillage and crop residue on postdispersal predation of weed seeds. *Weed Science* **47**, 184–194.
- ENNAÏFAR S, MAKOWSKI D, MEYNARD JM & LUCAS P (2007) Evaluation of models to predict take-all incidence in winter wheat as a function of cropping practices, soil, and climate. *European Journal of Plant Pathology* **118**, 127–143.
- FRECKLETON RP & STEPHENS PA (2009) Predictive models of weed population dynamics. *Weed Research* **49**, 225–232.
- FRECKLETON RP, SUTHERLAND WJ & WATKINSON AR (2003) Deciding the future of GM crops in Europe. *Science* **302**, 994–996.
- FRIED G, NORTON LR & REBOUD X (2008) Environmental and management factors determining weed species composition and diversity in France. *Agriculture, Ecosystems & Environment* **128**, 68–76.
- FRIED G, KAZAKOU E & GABA S (2012) Trajectories of weed communities explained by traits associated with species' response to management practices. *Agriculture, Ecosystems & Environment* **158**, 147–155.
- 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*. PhD thesis, Université de Bourgogne, Dijon, France.
- GARDARIN A & COLBACH N (in press) How much of seed dormancy in weeds can be explained by seed traits? *Weed Research* **55**.

- GARDARIN A, DÜRR C & COLBACH N (2010a) Effects of seed depth and soil structure on the emergence of weeds with contrasted seed traits. *Weed Research* **50**, 91–101.
- GARDARIN A, DÜRR C, MANNINO MR, BUSSET H & COLBACH N (2010b) Seed mortality in the soil is related to the seed coat thickness. *Seed Science Research* **20**, 243–256.
- GARDARIN A, GUILLEMIN JP, MUNIER-JOLAIN NM & COLBACH N (2010c) Estimation of key parameters for weed population dynamics models: base temperature and base water potential for germination. *European Journal of Agronomy* **32**, 162–168.
- GARDARIN A, DÜRR C & COLBACH N (2011) Prediction of germination rates of weed species: relationships between germination parameters and species traits. *Ecological Modelling* **222**, 626–636.
- GARDARIN A, DÜRR C & COLBACH N (2012) Modeling the dynamics and emergence of a multispecies weed seed bank with species traits. *Ecological Modelling* **240**, 123–138.
- GUTTERIDGE RJ, JENKYN JF & BATEMAN GL (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.
- HOLST N, RASMUSSEN IA & BASTIAANS L (2007) Field weed population dynamics: a review of model approaches and applications. *Weed Research* **47**, 1–14.
- HOSSARD L, JEUFFROY MH, 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.
- INRA (2010) Ecophyto R&D. Quelles voies pour réduire l'usage des pesticides. Available at: <http://institut.inra.fr/Missions/Eclairer-les-decisions/Etudes/Toutes-les-actualites/Ecophyto-R-D> (last accessed 7 August 2014).
- IQBAL J & WRIGHT D (1997) Effects of nitrogen supply on competition between wheat and three annual weed species. *Weed Research* **37**, 391–400.
- KURSTJENS DAG, PERDOK UD & GOENSE D (2000) Selective uprooting by weed harrowing on sandy soils. *Weed Research* **40**, 431–447.
- LOSOSOVA Z, CHYTRY M, CIMALOVA S *et al.* (2004) Weed vegetation of arable land in Central Europe: gradients of diversity and species composition. *Journal of Vegetation Science* **15**, 415–422.
- MARSHALL EJP, BROWN VK, BOATMAN ND *et al.* (2003) The role of weeds in supporting biological diversity within crop fields. *Weed Research* **43**, 77–89.
- MAZOYER M & ROUDART L (1997) *Histoire des agricultures du monde. Du néolithique à la crise contemporaine*. Éditions du Seuil, Paris, France.
- MÉZIÈRE D (2013) *Compromis biodiversité - nuisibilité des communautés adventices dans les systèmes de culture. Développement d'une méthode de diagnostic combinant simulations et indicateurs*. PhD thesis, Université de Bourgogne, Dijon, France.
- MÉZIÈRE D, LUCAS P, GRANGER S & COLBACH N (2013) Does integrated weed management affect the risk of crop diseases? A simulation case study with a grass weed and a soil-borne cereal disease *European Journal of Agronomy* **47**, 33–43.
- 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.
- MOLES AT & WESTOBY M (2006) Seed size and plant strategy across the whole life cycle. *Oikos* **113**, 91–105.
- MOSS SR, STORKEY J, CUSSANS JW, PERRYMAN SAM & HEWITT MV (2004) The Broadbalk long-term experiment at Rothamsted: what has it told us about weeds? *Weed Science* **52**, 864–873.
- MUNIER-JOLAIN NM, GUYOT SHM & COLBACH N (2013) A 3D model for light interception in heterogeneous crop: weed canopies. Model structure and evaluation. *Ecological Modelling* **250**, 101–110.
- MUNIER-JOLAIN NM, COLLARD A, BUSSET H, GUYOT SHM & COLBACH N (2014) Modelling the morphological plasticity of weeds in multi-specific canopies. *Field Crops Research* **155**, 90–98.
- OERKE E (2006) Crop losses to pests. *Journal of Agricultural Science* **144**, 31–43.
- PARDO G, RIRAVOLOLONA M & MUNIER-JOLAIN NM (2010) Using a farming system model to evaluate cropping system prototypes: are labour constraints and economic performances hampering the adoption of Integrated Weed Management? *European Journal of Agronomy*, **33**, 24, 32.
- PARYSOW P & GERTNER G (1997) Virtual experimentation: conceptual models and hypothesis testing of ecological scenarios. *Ecological Modelling* **98**, 59–71.
- PAYRAUDEAU S & VAN DER WERF HMG (2005) Environmental impact assessment for a farming region: a review of methods. *Agriculture, Ecosystems and Environment* **107**, 1–19.
- PETIT S, BOURSALT A, LE GUILLOUX M, MUNIER-JOLAIN N & REBOUD X (2011) Weeds in agricultural landscapes. A review. *Agronomy for Sustainable Development* **31**, 309–317.
- POWLES SB & YU Q (2010) Evolution in action: plants resistant to herbicides. In: *Annual Review of Plant Biology*, Vol. 61 (eds S MERCHANT, WR BRIGGS & D ORT), 317–347. Annual Reviews, Palo Alto, CA, USA.
- PREW RD (1980) Studies on the spread of *Gaeumannomyces graminis* var. *tritici* in wheat. I. Autonomous spread. *The Annals of Applied Biology* **94**, 391–396.
- QUÉTIÈRE F, LAVOREL S, THUILIER W & DAVIES I (2007) Plant-trait-based modeling assessment of ecosystem-service sensitivity to land-use change. *Ecological Applications* **17**, 2377–2386.
- SCHOENY A, JEUFFROY MH & LUCAS P (2001) Influence of take-all epidemics on yield formation of winter wheat. *Phytopathology* **91**, 694–701.
- SERVICE RF (2013) What happens when weed killers stop killing? *Science* **341**, 1329.
- TRICHARD A, ALIGNIER A, BIJU-DUVAL L & PETIT S (2013) The relative effects of local management and landscape context on weed seed predation and carabid functional groups. *Basic and Applied Ecology* **14**, 235–245.

VANLOQUEREN G & BARET PV (2008) Why are ecological, low-input, multi-resistant wheat cultivars slow to develop commercially? A Belgian agricultural “lock-in” case study *Ecological Economics* **66**, 436–446.

WILSON JD, MORRIS AJ, ARROYO BE, CLARK SC & BRADBURY RB (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous

birds in northern Europe in relation to agricultural change. *Agriculture Ecosystems & Environment* **75**, 13–30.

Supporting Information

Additional supporting information may be found in the online version of this article at the publisher’s web-site.