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Olivia Pointurier, Delphine Moreau, Loïc Pagès, Jacques Caneill, Nathalie Colbach. Individual-based 3D modelling of root systems in heterogeneous plant canopies at the multiannual scale. Case study with a weed dynamics model. *Ecological Modelling*, 2021, 440, pp.109376. 10.1016/j.ecolmodel.2020.109376 . hal-03176760

HAL Id: hal-03176760

<https://institut-agro-dijon.hal.science/hal-03176760>

Submitted on 8 Dec 2021

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Individual-based 3D modelling of root systems in heterogeneous plant canopies at the multiannual scale. Case study with a weed dynamics model

Olivia Pointurier^a, Delphine Moreau^a, Loïc Pagès^b, Jacques Caneill^a, Nathalie Colbach^a

^aAgroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000 Dijon, France

^bUR 1115 PSH, INRAE Centre PACA, Site Agroparc, 94914 Avignon Cedex 9, France

olivia.pointurier@gmail.com

delphine.moreau@inrae.fr

loic.pages@inrae.fr

jacques.caneill@inra.fr

nathalie.colbach@inrae.fr

Corresponding author : Nathalie Colbach

INRAE, UMR1347 Agroécologie, BP 86510, 17 rue Sully, 21065, Dijon Cedex, France

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. *Ecological Modelling* 440, 109376, <https://doi.org/10.1016/j.ecolmodel.2020.109376>

Highlights

- We propose an original plant dynamics model adapted to simulate heterogeneous stands
- Root biomass ratio was a key determinant of root exploration
- It was predicted with a simple unique allometric relationship found on 30 species
- The model was evaluated with independent field data and gave satisfactory predictions
- Soil exploration depended mostly on aboveground plant morphology in simulations

Abstract

Reducing pesticide use in agriculture is essential but involves shifting towards more complex agroecosystems. Plant canopies are expected to be more heterogeneous because a more abundant weed flora is likely to remain in low-herbicide fields, and because intercropping (i.e. mixing various crop species or varieties) is a promising option to reduce chemical inputs. Simulation models are useful to understand and design complex agroecological cropping systems, but they rarely represent the root systems of plants. However, belowground processes, such as competition for soil resources or infection by root-parasitic plants, are key determinants of the structure of plant communities. The aim of our study was to develop a model that simulates heterogeneous 3D individual-based crop-weed canopies from cropping system and pedoclimate and that will ultimately be used to design agroecological cropping systems. Therefore, we (1) connected a root system model (RSCone) to a weed dynamics model (FLORSYS) in order to include both above and belowground parts of plants, (2) evaluated the prediction quality of our model, and (3) analysed the influence of species parameters on potential soil-resource uptake and root infection by parasitic plants. We used the well-known allometric relationship between root and total plant biomass to connect RSCone and FLORSYS, and we created new formalisms to model the effect of soil compaction on root growth. Our model was shown to correctly predict long-term weed dynamics in various cropping systems. From step 3), we characterized crops and weed communities that are potentially competitive for soil resources and most likely to be infected by parasitic plants, and we deduced agronomic recommendations. For example, species emerging and occupying the soil quickly were the most likely to relay broomrape infestation and control of such species should take precedence. Although we focussed on crop-weed competition, our approach can be applied to other heterogeneous canopies, for designing crop mixtures for example.

Keywords: soil resources; competition; parasitic plants; heterogeneous stands; weed management

1. Introduction

Weeds can greatly reduce yields and harvest quality, both directly, by competing with the crop for light, nutrients and water (Oerke, 2006), and indirectly, by serving as alternative hosts for pests (Norris, 2005) or increasing workload for the farmer for example (Mézière et al., 2015). Weeds are mostly controlled by herbicides, but this practice must be drastically reduced because of its detrimental side-effects on environment and human health (Novotny, 1999). Non-chemical cropping techniques, such as diversifying crop rotation or soil tillage, are efficient to control weeds provided that several are combined because their effects are partial (Liebman and Gallandt, 1997). Among them, growing mixtures of crop species is a promising weed management strategy because they are often more competitive than sole crops towards weeds (Liebman et al., 2001). As a result, reducing herbicide use is likely to make agricultural fields more heterogeneous with more diverse crop stands and possibly a more abundant residual weed flora.

Managing weeds in such heterogeneous stands requires understanding competition among plants in order to minimize the damage caused by weeds and to maximise the yield and competitiveness of crop mixtures. Light is the major source of competition between plants in agroecosystems if fertilization

provides non-limiting soil resources (Wilson, 1988a). However, as mineral fertilization must be reduced because of its environmental impact (Raun and Johnson, 1999), and as droughts become more frequent due to climate change (Turrall et al., 2011), competition for soil resources is likely to increase in agricultural fields. Soil-resource use can also be impacted by soil-borne root pests, such as root-infecting fungi (Macdonald and Gutteridge, 2012) or root parasitic plants (e.g. branched broomrape *Phelipanche ramosa* (L.) Pomel) (Parker, 2013), which moreover can be hosted by weeds (Gibot-Leclerc et al., 2003). Therefore, considering belowground competition between plants becomes crucial for designing efficient weed management strategies. As each plant is likely to be surrounded by various neighbours with different abilities to compete (different species and morphologies, at different developmental stages, different locations), understanding competition relationships in heterogeneous stands involves going down to the individual plant scale.

Given the multiple techniques to implement and the number and diversity of plants to consider, managing weeds in a context of herbicide reduction is very complex and requires adapted tools. Moreover, these tools must take into account the variability in effects depending on pedoclimatic conditions and in the long term because weed seeds persist for several years in the soil. Simulation models are useful tools to design cropping systems that manage such complexity (Bergez et al., 2010; Renton and Chauhan, 2017). Models with a 3D individual-based representation of plants are particularly adapted for heterogeneous stands because they allow to simulate the competition exerted on each plant in a field from all its neighbours (Gaudio et al., 2019; Renton, 2013; Renton and Chauhan, 2017). Mechanistic models, which are process-based, may easily be adapted to a great diversity of plant species because of their generic structure (Colbach, 2010). However, very few of such models include both above and belowground parts of plants, so they represent competition between plants only partially (Gaudio et al., 2019; Renton and Chauhan, 2017).

This is also the case of the FLORSYS model (Colbach et al., 2014; Gardarin et al., 2012; Munier-Jolain et al., 2014, 2013), for example. To our knowledge, it is to date the only mechanistic model quantifying the effects of cropping systems on the dynamics of multispecies weed floras for decades in interaction with pedoclimatic conditions (Holst et al., 2007). Therefore, this model is useful to design and evaluate sustainable weed management strategies (Colbach et al., 2017b, 2018) or crop ideotypes (Colbach et al., 2019). It simulates the competition between crops and weeds for light by representing each individual crop and weed plant in 3D in a virtual field and their shading effect on each other's growth and morphological plasticity (Colbach et al., 2014; Munier-Jolain et al., 2014, 2013). However, FLORSYS ignores plant roots and belowground processes such as uptake of soil resources or root infection by soil-borne pests. To do so, it must be connected to a root growth model with the following characteristics: (1) having a 3D individual-based representation of root systems, (2) being sufficiently simple for multiannual simulations of thousands of plants in a field, (3) being parameterized for most common crop and weed species encountered in agroecosystems and relatively easy to parameterize for new species, and (4) predicting the key state variables that drive water and nutrient uptake and infection by parasitic plants, i.e. root biomass and length density in the soil (Grenz et al., 2005; Malagoli and Le Deunff, 2014). The recently developed RSCone model is the only one in the literature meeting all required criteria (Pagès et al., 2020). RSCone is a metamodel (i.e. a simplified model derived from a pre-existing more complex model) whose structure and parameter values were derived from a root system architecture model (ArchiSimple, Pagès et al., 2014). It represents the root system of individual plants from four state variables as an envelop where root density is distributed across soil layers. RSCone is already parameterized for 35 crop and weed species, using a relatively low number of parameters (22) with a biological meaning that can be estimated from ArchiSimple simulations, thus benefitting from experience on root system architecture models and specific parameterization work of the ArchiSimple community (Bui et al., 2015; Drouet et al., 2005; Drouet and Pagès, 2003; Dunbabin et al., 2013; Faverjon et al., 2019; Moreau et al., 2017; Pagès et al., 2014; Pagès and Kervella, 2018; Pagès and Picon-Cochard, 2014).

The objectives of this study were to study the determinants of soil-resource uptake and root infection by parasitic plants by (1) connecting FLORSYS and RSCone to obtain a plant dynamics model that represents both above and belowground parts of plants in agroecosystems, (2) by evaluating the predictive power of the new FLORSYS-RSCone model by comparing simulation results to independent

field observations, (3) by identifying the key plant parameters involved in soil-resource uptake and root infection by parasitic plants from simulation results and (4) by deducing from the latter step which parameters must be measured precisely when parameterizing new species and which processes the most influence soil resources competition and parasitism. Step (3) also allowed us to deduce agronomic recommendations.

The present paper does not yet model soil-resource uptake and use or impact of root parasitic plants on host growth, which will be presented in future papers (Moreau et al., 2021; Pointurier et al., 2021).

2. Material and methods

2.1. Model structures

2.1.1. The weed dynamics model FLORSYS

FLORSYS is a mechanistic model, i.e. a model that considers processes of the life cycle of annual crops and weeds that determine their multiannual dynamics. It has been described in detail in other studies (Colbach et al., 2014; Gardarin et al., 2012; Munier-Jolain et al., 2014, 2013). We present here a quick summary of the model. The user inputs data describing the virtual field to be simulated (e.g. soil texture, latitude), weather (temperature, rainfall and radiation), cropping techniques (including crop sequence) and initial weed flora at the beginning of the simulation. From this information, FLORSYS predicts the weed seed bank and the density and biomass of weed and crop plants daily in the virtual field.

FLORSYS represents each individual, whether crop or weed plant/seed, the same way and affected by the same processes. Processes relevant for seeds in the soil are mortality, dormancy and germination which are driven respectively by seed age, season, and soil climate. Seedlings emerge provided that the seeds are sufficiently close to the soil surface and that the soil is sufficiently moist and warm, without compact soil clods blocking shoot growth. These belowground processes are represented vertically over horizontally homogeneous 1-cm-thick soil layers, down to a depth of 30 cm. Soil climate and structure are predicted by the soil submodels of STICS (Brisson et al., 2003) and DéciBlé (Chatelin et al., 2005) respectively included in FLORSYS.

From emergence onwards, plant phenology is driven by temperature, with thermal time from emergence to flowering depending on the month during which plants reach the onset of vegetative stage (soon after emergence). Depending on the species and emergence season, flowering is indefinitely postponed, to account for missing vernalization. Plant growth results from the accumulation of biomass by photosynthesis after removing losses due to respiration. Biomass accumulated daily is shared among aboveground organs, i.e. leaves, stems and seeds. Photosynthesis depends on the amount of photosynthetically active radiation (PAR) intercepted by plants depending on plant morphology and shading due to neighbouring plants. To model this plant-plant interaction, each plant, whether crop or weed, is represented in three dimensions aboveground and located inside the field. Each plant is modelled as a cylinder, the dimensions of which are defined by the height and width of the plant, with leaf area distributed along plant height. Tillage and mechanical weeding operations move seeds in the soil, and kill part of germinated seeds and plants. Plants may also die from frost, herbicide applications, or ageing.

In total, 41 crop species or varieties (including both cash and cover crops) as well as 26 weed species are parameterized in FLORSYS.

2.1.2. The root-system model RSCone

The RSCone model has been described by Pagès et al (2020). From daily inputs detailing allocation of biomass to roots, soil constraint on root growth and soil temperature in each soil layer, RSCone predicts the root-system dimensions of a plant daily, together with the distribution of root biomass and root lengths (shaded lines in Table S1 in section A online). The root system is depicted in three dimensions,

as a cylinder on top of a spilled cone, inside which root density is distributed. The dimensions of the root-system envelop grow over time and are limited by soil compaction and low temperatures. Root biomass is calculated by confronting the biomass demand from roots, which is determined by the root-system dimensions, to the biomass supply given as input. Root biomass is then distributed into each soil layer within the root-system envelop, assuming a homogeneous distribution within each layer and a linear decrease with depth, from a maximal value at soil surface down to 0 at the root-system tip. Root-length density is determined by multiplying root-biomass density by the specific root length (SRL).

Twenty-one weed species and 23 crop species or varieties are parameterized in RSCone.

2.1.3. New functions and parameters to connect RSCone and FLORSYS

Integrating RSCone as a submodel of FLORSYS required connecting both models at the connecting functions described below and in Figure 1. FLORSYS runs at the field scale, representing a canopy as a collection of individual crop and weed plants, limited to their above-ground part. RSCone runs at the plant scale, only representing the below-ground part of a single plant. This was grafted here below the above-ground FLORSYS plant, making the two model connect at the scale of the individual plant, exchanging information with a daily time-step.

For now, most of the connection is one-way, i.e. FLORSYS variables are used as inputs of RSCone. Root functions such as nutrient uptake will be implemented in another paper. Here, only biomass remobilization from below to aboveground after disturbances, such as mowing or frost, are considered.

2.1.4. Phenology

RSCone and FLORSYS both run with a daily time step but they use different time units for plant age. In RSCone, plant age is given in days since germination under optimal temperature (“optimal days”). FLORSYS uses two scales, thermal time (in °C-days, with base temperature depending on species) since plant emergence, and plant stage (cotyledon, plantlet, vegetative, flowering onset, maturity onset, death) with the duration of the vegetative stage depending on the plant's emergence season. Conversions had to be done to make optimal days of RSCone compatible with thermal time in FLORSYS (see 1 in Figure 1).

2.1.5. Soil constraint on root growth

In RSCone, soil conditions can limit root-system extension in width and depth if the soil is too cold or too compacted (Pagès et al., 2020). RSCone uses soil temperature as an input, which will now be provided by FLORSYS for connecting both models.

Conversely, RSCone does not directly use soil structure variables as input, but an abstract coefficient of root-growth limitation by the soil ranging from 0 (no root growth) to 1 (no soil constraint) in each soil layer. Here, we added a function to quantify this soil constraint from soil-structure variables (see 2 in Figure 1) predicted by FLORSYS from soil texture, tillage, soil moisture and frost.

2.1.6. Allocation of biomass to roots

Allocation of biomass to roots is an input of the RSCone model and must be provided by FLORSYS. Root biomass is known to be correlated to total plant biomass (Weiner, 2004; Wilson, 1988a). Therefore, we aimed at finding a relationship to calculate biomass allocated to roots from the aboveground biomass of plants predicted by FLORSYS (see 3 in Figure 1). We collected data from different experiments described in Table 1 to investigate this relationship. We used data collected on a large range of crop and weed species, including experiments testing the effect of nitrogen and light on root growth.

The relationship between root and total plant biomass of plants was analysed as a function of the effects of species, nitrogen and light treatments with the following model using the function `lm` of R (R Core Team, 2019) and type III sum of squares (to ensure orthogonal contrasts):

$$(1) \log_{10}(\text{root biomass}) = \text{constant} + \log_{10}(\text{total plant biomass}) + \text{species} + \text{nitrogen stress index} + \text{light} + \text{two-way interactions} + \text{residuals}.$$

The nitrogen stress index was calculated as explained in Perthame et al. (2020). When plant nitrogen nutrition is optimal, the nitrogen stress index is close to zero, and nitrogen stress increases with the index value. Equation (1) was applied to the data from experiment E1 in Table 1.

In other experiments listed in Table 1, the nitrogen stress index was not calculated, and the effect of light was not tested. Only the nitrogen treatments (listed in Table 1) that we knew from previous experiments that gave near optimal plant nitrogen nutrition were kept for the analysis. The following model was fitted to the data:

$$(2) \log_{10}(\text{root biomass}) = \text{constant} + \log_{10}(\text{total plant biomass}) + \text{species} + \text{two-way interaction} + \text{residuals}.$$

As data came from various experiments, the effect of the experimental set-up was also tested:

$$(3) \log_{10}(\text{root biomass}) = \text{constant} + \log_{10}(\text{total plant biomass}) + \text{species} + \text{experiment} + \text{two-way interaction (except species} \times \text{experiment)} + \text{residuals}.$$

The interaction between species and experimental set-up could not be tested because the experiments did not have enough species in common. Models were fitted by backward selection. Note that in legume species, root biomass did not include nodule biomass since nodules only constituted a small part of belowground plant biomass under optimal nitrogen nutrition (<4%) and are not modelled in FLORSYS.

2.1.7. Remobilization from roots to aboveground biomass

When part of the aboveground plant biomass is destroyed by events such as frost or mowing, plants change their source-sink relationships, and remobilize resources from the root compartment toward the aboveground compartments (see 4 in Figure 1). Here, this was approximated by changing the biomass allocation and respiration rates (see section 3.1.3). According to preliminary simulation results (not shown), damages due to frost were overestimated. We improved the model predictions by including a snow submodel to simulate the insulating effect of snow cover that protects plants from frost damages (Jégo et al., 2014; Trnka et al., 2010) (section B1 online).

2.2. Testing the new FLORSYS-RSCone model with simulations

2.2.1. Principle

Simulations of cropping systems were performed with FLORSYS-RSCone to (1) evaluate the model by comparing simulation results to independent field observations (section 2.3.2), and (2) identify key species parameters for potential soil-resource uptake and infection by root parasitic plants (section 2.3.3). Data of ten cropping systems from the INRAE experimental station of Dijon-Époisses from 1999 to 2012 were simulated as described in Colbach et al. (2016) (section C online). They vary from herbicide-intensive to herbicide-free, with various rotations, tillage strategies and use of mechanical weeding. Initial weed seedbank (for 25 weed species) and soil characteristics given as inputs in the model were measured on soil samples taken in the fields. Weather data were obtained from the INRAE weather station (via the INRAE platform CLIMATIK in French, managed by the AgroClim laboratory of Avignon, France, <https://intranet.inrae.fr/climatik/>). Each cropping system was repeated 10 times with the same inputs to take into account the stochastic effects of FLORSYS. In total, 10 cropping systems \times 10 repetitions = 100 simulation runs were carried out, each over 13 years. The simulated field sample was 6x4m². As the evaluation of the first FLORSYS version showed the phenology submodel to badly predict flowering dates of weeds in the South of France and of some crop varieties (Colbach et al., 2016),

a corrective patch was added to keep weeds from flowering too early and to force crops to mature at harvest date.

Not all FLORSYS species have yet been parameterized in RSCone. In that case, default parameter values were calculated by averaging parameters of species from the same clade (i.e. monocotyledon or dicotyledon), as clade was shown to discriminate RSCone parameters (Pagès et al., 2020), and from the same seasonal type (i.e., winter annuals, summer annuals or perennials).

2.2.2. Model evaluation

Aboveground plant biomass, weed plant density, weed seed bank and crop yield were measured in all ten fields during the 13 years of the trial and compared to variables predicted by FLORSYS-RSCone as explained in Colbach et al. (2016). Density and aboveground biomass were measured in several quadrats per field several times a year, and weed seed bank was measured on ten soil samples every two years. As root biomass was not measured, we could not directly evaluate the prediction quality of roots in our model. Instead, we checked whether including roots improved the prediction quality of aboveground variables by FLORSYS.

Variables were either analysed (1) at the species scale or (2) at the community scale, i.e. they were summed over all species. The prediction quality of the model was estimated with various complementary criteria described in Colbach et al. (2016):

The prediction bias is the mean of residuals (simulated \hat{y}_i – observed values y_i , with i in $\{1, \dots, N\}$ from different fields, years and species) and determines whether the model systematically under- or overestimated variables. It was calculated relatively to the range of variation of observations (i.e. divided by half the difference between the maximum and minimum observed values \max_{obs} and \min_{obs}):

$$Bias = \frac{\sum_i (\hat{y}_i - y_i)}{N (\max_{obs} - \min_{obs})/2}$$

The relative root square of the mean square error (RRMSEP) evaluates the relative prediction error of the model. It was calculated relatively to the standard deviation of observed values $STDEV_{obs}$ (Coucheney et al, 2015; Colbach et al, 2016), and corrected for variability in observations (i.e. variability due to measurement errors var_{obs}) and in simulations (i.e. variability due to model stochasticity var_{sim}) (Wallach, 2006):

$$RRMSEP = \frac{\sqrt{MSEP - var_{obs} - var_{sim}}}{STDEV_{obs}}$$

$$MSEP = \frac{1}{N} \sum_i (\hat{y}_i - y_i)^2$$

$var_{obs} = \frac{1}{NQ} \sum_{iq} (y_i - y_{iq})^2$ where y_{iq} is the observed variable in quadrat q for individual i (from one field \times one day \times one species) and $Q = 4$ the number of quadrats per field \times day

$var_{sim} = \frac{1}{NR} \sum_{ir} (\hat{y}_i - \hat{y}_{iq})^2$ where \hat{y}_{iq} is the simulated variable in repetition r for individual i and $R=10$ the number of repetitions per field \times day

$$STDEV_{obs} = \sqrt{\frac{1}{N} \sum (y_i - \bar{y})^2}$$
 where \bar{y} is the mean of observations

If MSEP is small or smaller than var_{obs} , and var_{sim} the difference between observed and simulated values is mostly due to, respectively observation error and/or model stochasticity.

The ability of the model to rank cropping systems and weed species correctly was calculated as the maximum between the modelling efficiency, the Pearson and the Spearman correlation coefficients between observations and predictions. Coefficients close to 1 indicate that the variables are well predicted by the model in terms of absolute values, relative values (i.e. differences between values) and ranks respectively.

The three criteria (relative bias, RRMSEP and proportion of correctly predicted observation) were calculated from data averaged over the rotation (i.e. over all simulated values or measurements per cropping system) to check the model's ability to compare cropping systems. To assess how well the model predicts outputs on a given day, the criteria were calculated from data averaged per day (i.e. averaged over quadrats, samples and repetition), except for daily weed density and biomass. For these two outputs, the proportion of correctly predicted observations was the proportion of observations inside the simulated 90%-confidence interval obtained over the 10 repetitions. This criterion was preferred over the three first evaluation criteria, because the latter are considerably deteriorated by a delay of a few days in the simulations vs the observations (or vice-versa), whereas such delays do not affect the prediction quality of the weed dynamics over the years (Colbach et al., 2016).

All the evaluation criteria were also calculated from simulations with FLORSYS before the RSCone model was connected in order to study whether the connection improved FLORSYS predictions.

2.2.3. Potential soil-resource uptake and risk of parasitism

In order to study which species parameters determine potential soil-resource uptake and risk of infection by *P. ramosa*, we analysed proxy variables (see details below) because these processes were not yet modelled in FLORSYS at the time of this study. We did not consider characteristics relative to root functioning when calculating our proxies (e.g. host status or uptake efficiency), because they are not yet included, focussing on the influence of the morphology and the photosynthetic functioning of plants on root exploration.

Root biomass summed over respectively all crop and weed plants was used as a proxy for potential soil-resource uptake by crops and weeds (Malagoli and Le Deunff, 2014). It was taken at the beginning of crop flowering, when crop root biomass is near maximal (Gregory et al., 1995) in order to get a global overview of root growth over the crop cycle. The percentage of crop root volume overlapped by root systems of weeds was also calculated at crop flowering and averaged over the field, in order to estimate crop-weed competition for soil resources.

P. ramosa is a holoparasitic (non-photosynthesizing) root-infecting plant whose seeds follow a seasonal dormancy pattern when buried in the soil, and germinate when triggered by root exudates of host plants; the parasite then attaches to roots of a host plant, grows to the detriment of that host (which usually dies without reproducing) and produces a huge number of seeds that replenish the seed bank (Parker, 2013). Here, the risk of infection by root parasitic plants such as *P. ramosa* was approximated by the cumulated root length of crops and weeds (Grenz et al., 2005) because parasitic seeds only germinate close to host roots (< 4 mm) in order to infect them quickly otherwise they die in a few days (Joel, 2013). Only crops and weeds roots in the first 30 cm of soil were considered because parasitic seeds are unlikely to be buried deeper by tillage. This proxy was calculated in autumn (end of November) and summer (end of June), when parasitic seeds are most likely to germinate (before and after dormancy respectively, Pointurier et al., 2019), as well as at crop flowering when host root exudation stops (Auger et al, 2012).

In order to analyse the relationships between species parameters and proxy variables for soil-resource uptake and parasitism, an RLQ analysis combined with a fourth-corner analysis was performed for weeds and Pearson correlations were calculated for crops as in Colbach et al (2019). The RLQ analysis was performed with the library ade4 of R (Dray and Dufour, 2007). It consisted in relating three tables (“R”, “L” and “Q”) in order to study the relationships between our proxy variables (described in table “R”, e.g. total weed root biomass for soil-resource uptake by weeds) and the species parameters (in table “Q”) while taking into account the relative contribution of each species within the weed community (given by maximum annual weed species densities in table “L”). Table L consisted of the maximum densities of weed species over the growing cycle (i.e. from sowing to harvest) for each simulated year, each cropping system and each repetition. Table Q consisted of the root parameters described in Table S2 in section A online, and the aboveground parameters described in Colbach et al (2019) were added to investigate the relative influence of the two types of parameters. The significance of the correlations obtained in the RLQ analysis was tested with a fourth-corner analysis with 999 permutations of rows and columns in table L. The latter procedure allowed to check that the correlations observed did show a relationship between proxy variables and parameters and that they were not affected by preferential

distributions of weed species depending on cropping systems or on their parameters. Results of the RLQ analysis were displayed with the package *adegraphics* of R (Siberchicot et al., 2017).

Pearson correlations between crop proxy variables and parameters were calculated with the function *rcorr* from the package *Hmisc* of R. A Principal Component Analysis (PCA) was performed on proxy variables with the function *PCA* from the library *FactoMineR* (Lê et al., 2008) and displayed using the function *fviz_pca_var* from the library *factoextra* of R. Parameters were projected as supplementary variables on the correlation circle (i.e. they were not used for calculations in the PCA) to illustrate their relationship with the proxy variables.

Proxy variables for both crops and weeds were log-transformed prior to analysis because they were skewed.

3. Results

3.1. Integration of RSCone as a root distribution submodel in FLORSYS

3.1.1. Phenology

Radicle growth and water uptake prior to seedling emergence was already included in FLORSYS in a previous work (Gardarin et al., 2012). Before emergence nitrogen uptake is negligible (Fayaud et al., 2014) and no germination stimulants for parasitic plants are exudated (Gibot-Leclerc et al., 2012). Therefore, we focused on post-emergent root-system development. We considered that the post-emergent root system starts to grow from the moment the plant emerges in FLORSYS and we readjusted the relevant RSCone timing parameters accordingly (eq. [2] in Table S1 in section A online).

We recalibrated RSCone durations, expressed in optimal days, to account for the season of emergence of the plant (eq. [3] in Table S1 in section A online). We considered that the season of emergence giving the shortest life-cycle duration in FLORSYS reflects plant development under optimal temperature and thus correspond to the RSCone durations. A plant emerging at a different season has a longer life cycle in FLORSYS and the ratio of this longer duration to the minimum duration was used to lengthen the RSCone root-stage durations. The effect of soil temperature on root-system expansion was included in the $r_{\text{Soil}_{\text{dis}}}$ variables reflecting structural and thermal constraints in the soil (see section 3.1.2).

The timing of root-system stages influences both the root-system expansion (eq. [10] and [11] taken from Pagès et al., 2020) and its root density (eq. [31] and [32] taken from Pagès et al., 2020).

3.1.2. Effect of soil limiting factors on root growth

Root-growth limitation by soil compaction was calculated from soil structure. In FLORSYS, soil structure is predicted for the top three 10-cm soil layers, as the proportion of soil clods distinguished by their degree of compaction and the process they were formed (Roger-Estrade et al., 2004). Types $b\Delta$ and $c\Delta$ are the most compact and block root growth. Contrary to $c\Delta$ clods, $b\Delta$ clods are partially fragmented so they do not completely block root growth. Stones (whose proportion in the soil is given as an input in FLORSYS) are assumed to have the same effect as $c\Delta$ clods on root growth in the top soil layers (up to 30 cm depth).

Equation [4] (in Table S1 in section A online) was based on these assumptions. Root growth is reduced proportionally to the proportion of stones, $b\Delta$ and $c\Delta$ soil clods in the soil. Only half the proportion of $b\Delta$ soil clods was considered in this equation to roughly take into account that they do not completely block root growth. This sum was divided by $1 + \text{stone proportion}$ to fit into $[0,1]$, as the clod proportions are given by FLORSYS relatively to total soil volume disregarding stones. The results is then multiplied by a 50% factor (r_{Smax}) borrowed from the STICS crop model (Brisson et al., 2003, 2002, CONTRDAMAX, 1998) which correspond to the maximal reduction the soil can exert on root growth.

The result (or rather 1-this result to get a corrective factor for root growth) was multiplied by a species parameter pen_s reflecting the species ability to penetrate the soil.

As soil structure and temperature are not predicted below 30 cm in FLORSYS, soil constraint in deeper soil layers was predicted from soil variables at 30 cm depth (eq. [5] and [7] in Table S1 in section A online).

The effects of soil compaction and temperature were then combined to get the total soil constraint growth in each layer (eq. [8] taken from Pagès et al., 2020) and applied to reduce root-system dimensions proportionally (eq. [9] to [15] taken from Pagès et al., 2020).

As soil constraint was applied to the entire root system every day in RSCone (and not only to new roots), it could happen that a sudden high soil constraint (for example compaction due to tractor wheels on a wet soil or a drop in temperature) could dramatically shrink the root system from one day to another. We added a condition to prevent such root system shrinkage (eq. [13], [14] and [15] in Table S1 in section A online) because it was unrealistic, apart in case of frost.

3.1.3. Biomass allocation to roots

3.1.3.1. Data analysis

In experiment E1 (Table 1), root biomass was strongly correlated to total plant biomass, irrespective of species, light condition or nitrogen stress index (partial $R^2 = 63\%$ of total R^2 , $p \leq 0.02$, section D.1 online, Figure 2). The latter three factors, i.e. species, light and nitrogen stress index, as well as two-way interactions, had a significant effect ($p < 0.001$), except for the interaction between total plant biomass and nitrogen stress index. However, the effect of light was negligible (partial $R^2 = 14\%$ of total R^2 , section D.1 online) given the huge difference between shading levels (i.e., 0 vs 90%) and was removed from the model. Then, data on fescue, which had been removed from the analysis because it did not allow testing the effect of light (see Table 1), was included in the analysis. The effect of the interaction between nitrogen stress index and species was also removed because it was negligible (partial $R^2 = 0.23\%$ of total R^2), particularly compared to the primary effects of these variables and mainly due to one species (i.e. fescue, section D.2 online). Finally, the following linear model was obtained (section D.3 online):

$$(4) \log_{10}(\text{root biomass}) = a_{1s} + a_{2s} \cdot \log_{10}(\text{total plant biomass}) + a_3 \cdot (\text{nitrogen stress index}) + \text{residuals},$$

where a_{1s} , a_{2s} and a_3 are parameters described in Table S2 in section A online, with a_{1s} and a_{2s} depending on the species.

In other experiments, where the nitrogen stress index was not calculated, parameters a_{1s} and a_{2s} were determined by fitting equation (2) from section 2.2.3. A strong linear relationship was also found with this model and data ($R^2 = 0.98$, Figure 3), even though experiments with very different protocols were included in the analysis. The effect of the experiment was found significant but negligible compared to the species effect (partial $R^2 = 1$ and 7% of total R^2 respectively, $p < 0.001$, section D.4 online). As parameter a_3 did not depend on the species, the value determined with equation (4) from the E1 experiment was used for all species, even if parameters a_{1s} and a_{2s} were estimated on different experiments.

Although we only used data obtained during vegetative stages, data from other experiments showed that the relationship we found between root and total plant biomass remained valid at earlier and later stages (section D.5 online).

3.1.3.2. Formalism used to connect FLORSYS and RSCone

Model (4) was used to calculate the root biomass ratio, i.e. the ratio of the plant root biomass to its total biomass (RBR_{dsi}), depending on species and nitrogen stress index. This ratio was used to connect FLORSYS and RSCone (eq. [20] and [23] in Table S1 in section A online).

In FLORSYS, plant growth is modelled differently depending on whether the plant is surrounded by shading neighbouring plants or not. Before plants start to compete for light, i.e. at early stages (generally less than 15 days after emergence, Munier-Jolain et al., 2014), aboveground biomass accumulation is driven solely by thermal time since emergence (Colbach et al., 2014). We added an equation to calculate the amount of biomass allocated to roots in RSCone from the aboveground biomass predicted by FLORSYS and the root biomass ratio RBR_{dsi} (eq. [21] in Table S1 in section A online). We assumed that nitrogen stress was negligible (i.e. a_3 set to 0 in eq. [20] in Table S1 in section A online) because it was not observed in such young plants (Perthame et al., 2020).

When plants start to compete for light in FLORSYS, they grow by accumulating biomass from photosynthesis daily, losing some through respiration (eq. [22] in Table S1 in section A online). We used the resulting total plant biomass of the day to calculate the root biomass ratio RBR_{dsi} (eq. [23] in Table S1 in section A online) and deduced the daily amount of photosynthesized biomass to be allocated to roots (eq. [24] in Table S1 in section A online). The remaining amount of photosynthesized biomass was allocated to aboveground organs. Then, we calculated the part of biomass that was lost through respiration by roots and by aboveground organs respectively. From the beginning of flowering onward, when plants stop to allocate new biomass to roots (Gregory et al., 1995), root biomass was assumed to be remobilized for aboveground organs. The same occurred after plants lost aboveground biomass due to mowing (eq. [17] in Table S1 in section A online) or frost damage (eq. [18] in Table S1 in section A online), as long as the biomass level from before that event was not reached again (eq. [19] in Table S1 in section A online). This remobilization was modelled by charging respiration losses from both roots and aboveground organs to roots and by allocating all biomass gained by photosynthesis to aboveground organs only (eq. [25] in Table S1 in section A online).

For very small plants, because of the log-log relationship, root biomass could mathematically exceed total plant biomass (i.e. $RBR_{dsi} > 1$). To avoid this biological non-sense, we added a condition to limit RBR_{dsi} to the maximum root to total biomass ratio observed in our data (eq. [20] and [23] in Table S1 in section A online).

3.2. Simulation results

3.2.1. Crop production and multiannual species weed dynamics are well predicted by FLORSYS-RSCone

We compared simulations by FLORSYS-RSCone to independent observations from the cropping-system trial to determine the prediction quality and domain of validity of the model. This showed that weed variables were generally well predicted at the species scale (Table 2.A and B), with a small bias (7-17%), more than 50% (up to 67%) of well-ranked observations and very good predictions of daily dynamics (more than 80% of observations within the simulated confidence interval). However, predictions were less good at the community scale, particularly for seed bank and aboveground biomass (Spearman coefficients of -0.08 and 0.13, respectively), because they were generally largely overestimated (relative bias ranging from 15 to 206%, and more than 50% of daily observations lower than the simulated confidence interval). Only multiannual weed density was as well ranked at the community scale as at the species scale (Pearson coefficient of 0.65 and 0.67 respectively).

Crop variables were satisfactorily predicted (Table 2.B), with crop biomass in particular well ranked with no bias. Crop yield was less well predicted with a slight underestimation and a high prediction error. Although the model was bad at predicting yield absolute values, it correctly ranked cropping systems and years (i.e. it could predict correctly that yield in cropping system “x” on year “a” was better than in cropping system “y” on year “b” for example).

3.2.2. Modelling roots improves the predictions of FLORSYS

Comparing FLORSYS simulations carried out with or without RSCone to the independent field observations showed that integrating RSCone allowed partly to correct FLORSYS deficiencies. The additional submodel greatly improved the predictions of weed aboveground biomass (prediction error largely decreased per species by 347%) which is now better ranked (bias decreased by 70% and Spearman coefficients increased by 0.11, Table 2). The predictions of weed densities and crop production did not improve nor deteriorate overall. Weed seed bank and crop yield were slightly less well predicted (relative bias decreased by 6 and 4% respectively, and modelling efficiency by 0.09), but this was negligible compared to variations due to model stochasticity observed between two simulations (3%, 1% and 0.04 respectively, all other things being equal).

3.2.3. Crop parameters determining potential for soil-resource competition and uptake, and parasitism risk

We investigated correlations among proxy variables for potential soil-resource uptake (i.e. total crop root biomass) and parasitism risk (i.e. total crop root length) simulated by FLORSYS-RSCone to see whether the same situations (in terms of crop species, cropping systems and weather conditions) favoured the two root-dependent functions. Both proxies were strongly correlated at crop flowering (Pearson correlation coefficient = 0.85 in Table 3.A and close points on the Principal Component Analysis in section E.1 online), which is also the stage when root growth stops in FLORSYS-RSCone (section 3.1.3.2). So, though earlier resource uptake and parasitism risk might depend on different factors, the same conditions determined the final cumulative outcome.

Then, we looked at correlations between the simulated root-function proxies and the crop parameters entered into FLORSYS-RSCone to identify which species features drove root-dependent functions. These correlations were found to be very strong (absolute values of Pearson correlation coefficients of 0.3 on average, up to 0.7, major correlations in Table 3.B-H and complete results in section E.1 online), and the proxies were associated to similar species parameters (section E.1 online). But, despite investigating root-dependent functions, root parameters had less impact than parameters driving above-ground morphology and shading response (Table 3.B vs Table 4.C-H). In terms of plant structure, crops potentially able of large uptakes of soil resources and most likely to be infected by *P. ramosa* were mainly winter monocotyledons (associated to “winter_annual” and opposite to dicot species in Table 3.F), which present the longest growth duration (resulting in more biomass production, including root biomass) and emerge when *P. ramosa* seeds are non-dormant. These crops also present two other properties which are typical of winter crops, i.e. their plants are little sensitive to frost (low tFrostEarly3, tFrostMid3, tFrostLate3) and their photosynthesis does not support high temperatures (low tPhoto3). The good nitrogen-uptakers and the high parasite-exposure crops also potentially explore a large soil volume, i.e. their root systems presented a large cylinder-shaped top (high rCD). Their roots reached their maximal SRL late (high tSRLmax), thus continuously increasing their exposure to *P. ramosa* seeds per unit root length. Their plant height depended little on plant biomass (low b_HMMid and b_HMLate), resulting on homogeneously tall canopies, which intercept more light and can thus allocate more biomass to roots.

Crops likely to suffer competition for soil resources from weeds (i.e. the percentage of crop root volume overlapped by root systems of weeds) tended to have the same species characteristics (section E.1 online) as good nitrogen uptakers. Indeed, any feature that increases the root biomass and volume (the proxy for nitrogen uptake) also increases the probability of its overlapping with weed roots. But correlations between the crop-weed competition proxy and crop parameters were very weak (absolute values of Pearson correlation coefficients ≤ 0.3 , section E.1 online) as the crop-weed root overlap also depended on weed characteristics.

Different parameters drove risk of parasitism at different dates, with opposite effects possible (arrows perpendicular or in opposite directions on the PCA in section E.1 online). The strongest correlations with species parameters were found at dormancy induction of *P. ramosa* seeds in autumn (significant coefficients of 0.4 on average compared to 0.3 at the other dates, section E.1 online). The crops most

likely to be infected then were characterized by early robust establishment adapted to autumn conditions, good light interception and fast root-system growth. In detail, they were dicotyledons (Table 3), which emerge better than monocotyledons, particularly in compacted soil. They had an epigeal germination requiring relatively wet conditions (high baseWP), which are typical of autumn, and their photosynthesis was sensitive to high temperatures (low tPhoto4), which is typical of winter crops. They also grew quickly after emergence (high RGR).

Moreover, the crops the most likely to be infected had large, quickly growing root systems (high Emax, rD and a2), thus increasing the probability of encountering *P. ramosa* seeds, although they allocated a low proportion of biomass to their roots (low aa1). Their plants were wide per unit biomass (high WMMid and WMLate), which increases soil coverage and, thus, light interception and root biomass production. From flowering onwards, the high-risk crops allocated a larger proportion of their biomass to leaves (high LBRLate, again improving light interception), which were located lower on the plant (low RLHLate). The high-risk crops were also those that etiolated most when shaded by neighbour plants, succeeding in maintaining light interception and biomass production: they increased their plant height per unit biomass (high mu_HMEarly), allocated more biomass to stems (low mu_LBREarly, mu_LBRMid and mu_LBRLate), compensating with thinner larger leaves (high mu_SLAEarly and mu_SLAMid) which were shifted toward the plant top (high mu_RLHEarly and mu_RLHLate).

At dormancy release of *P. ramosa* seeds in summer, no strong correlations between proxy for parasitism and parameters could be identified (Table 3). At that time, plant morphology is the cumulated result not only of species parameters, but also of pedoclimatic conditions and cropping techniques, which vary over the years, the weather repetitions and the cropping systems.

3.2.4. Weed parameters determining potential for soil-resource competition and uptake, and parasitism risk

In contrast to crops, simulated root-function proxies in weeds were positively correlated from early stages onwards (Table 4.A), indicating that the same factors already drove root-dependent functions much earlier in the season than for crops. The correlations were again the largest in weeds at crop flowering (Pearson correlation coefficients = 0.85), confirming that the same factors determined the final outcome in both root-dependent functions.

Correlations between simulated proxies and model parameters were weaker for (multispecies) weeds than for (pure-stand) crops (absolute values of correlation coefficients <0.2, Table 4.B-E, compared to up to 0.7 in Table 3). Moreover, in contrast to crops, although the root-function proxies were highly correlated in weeds, they were not associated to the same species parameters, indicating that other factors (cropping system and/or weather) were more determinant. Only a predominantly low shade response after emergence within the weed community (low mu_SLAEarly) increased both proxies. Risk of weed infection by *P. ramosa* at crop flowering was moreover associated with weed species with more leaf area at their top (high RLHEarly) and a low relative growth rate after emergence (low RGR). The multispecies nature of the weed community made it much more difficult to understand the reasons for these correlations, such as the low RGR or the low mu_SLAEarly which are detrimental to biomass production. But, in a multispecies community, reducing one species type leaves niches for other species types that are driven by a combination of parameters (which are not captured by the present analysis method) rather than a single easy-to-identify parameter.

In contrast to crops, no opposite effects were observed between weed parameters driving proxies for parasitism at different dates (arrows in the same direction on the RLQ axes in section E.2 online). Most key parameters were the same at crop flowering and at dormancy release of *P. ramosa* seeds (low RGR and high mu_SLAEarly at both dates). The proxy at the latter date was moreover associated with weed species with a low base temperature for germination and growth (low baseT), which allow an earlier and faster root-system growth.

The proxy for early weed infection (in autumn at dormancy induction) was correlated to several other weed species parameters (Table 4.B-E). There were six above-ground parameters (compared to only four root parameters), indicating that root-dependent functions depend at least as much on light interception than on root architecture. Weed infection was linked to weed species that allocated more biomass aboveground than to roots (low root biomass ratio a_2), that placed their large initial leaf area (high LA0 and SLAearly) above other plants thanks to a large allocation of biomass to stems (low leaf biomass ratio LBREarly) and a top distribution of the leaf area on the plant (RLHEarly). High-risk weed plants responded less to shade in terms of plant width and leaf area after emergence (low $\mu_{WMEarly}$ and $\mu_{SLAEarly}$). For these species, having fine roots (high srl_{max}) increased the risk to encounter parasitic seeds more than exploring a large volume of soil (as illustrated by low E_{max} and rE). All these parameters were found to have a similar but much lower influence on the proxies for soil-resource uptake and parasitism in summer (correlation coefficients twice lower or not significant, section E.2 online).

The proxy for competition exerted by weeds over crops for soil resources was the best correlated to two parameters of aboveground morphology (last column of Table 4.B-E). As for the proxy for soil-resource uptake, weed floras including many species with a low relative growth rate (high RGR) after emergence exerted potentially more competition towards crops. Competition was also increased by weeds that increased biomass allocation to leaves when shaded after emergence (high $\mu_{LBREarly}$).

4. Discussion

4.1. What is new in our modelling approach?

By connecting two existing models, RSCone and FLORSYS, we developed the first plant dynamics model for heterogeneous multispecies canopies that (1) takes into account both aboveground and root compartments, so that it could ultimately integrate competition between plants for all resources (light, water and nutrients), (2) for as many as 56 species of crops and weeds interacting in a field (3) for several years (4) under the influence of cropping techniques and pedoclimate (Gaudio et al., 2019). The major originality of our model is the individual-based representation of plants in the competition submodel, which makes it adapted for simulating heterogeneous stands. For example, Gemini is another model which predicts the multiannual dynamics of multispecies plant stands under the influence of management techniques and pedoclimate (Soussana et al., 2012). But, it simulates competition between populations of plants made of clones of the same species and distributed homogeneously. Therefore, contrary to our model, Gemini is not able to simulate competition between plants in agroecosystems where weed distribution is often patchy (Rew and Cousens, 2001).

Connecting RSCone and FLORSYS required developing additional formalisms. The allometric relationship we used to calculate the proportion of plant biomass allocated to roots is well known (Weiner, 2004; Wilson, 1988b) but was never parameterized for so many species with a unique formalism. We also improved it in order to take into account that plants allocate more biomass to roots under nitrogen deficiency. Other additional formalisms were more original because they had to link different approaches chosen by the respective teams that developed FLORSYS and RSCone. For example, we combined agronomical knowledge on soil structure synthesized in FLORSYS to knowledge on the developmental biology of roots from RSCone, in order to predict the effect of soil compaction on root growth. Generally, this effect is estimated empirically from measures of penetrometer resistance (Bengough et al., 2011; Colombi et al., 2018) or bulk density (Brisson et al., 2003). We used a more mechanistic approach that allowed, for example, to simulate that roots grow more easily in a compact soil that has been fragmented by tillage than in a continuously compact soil (Tardieu, 1994). However, this approach did not allow us to model shrinkage cracks, whereas they allow roots to attain resources below compact soil layers (Hasegawa and Sato, 1987). Modelling shrinkage cracks would require a very fine-scale representation of the soil (Sánchez et al., 2014) which is not compatible with our modelling purposes at the field scale.

Our work shows that simulation models are useful to synthesize current knowledge from different approaches and disciplines. However, linking such different approaches required to make some assumptions for which no quantitative measurements were available (e.g. we assumed that only half the proportion of $b\Delta$ contributed to block root growth). Fortunately, our simulations showed that, in the context we tested (i.e. a few cropping systems and a local pedoclimate and weed flora of Burgundy), parameters from our additional formalisms had only a limited influence on the model outputs, except for parameters from the allometric relationship, so our assumptions seem acceptable. Moreover, the model was shown to correctly predict the daily and multiannual weed dynamics as well as crop production. The evaluation step comparing simulations to independent observations constitutes another original aspect of our work because it is rarely done for models, particularly for weed dynamics models (Holst et al., 2007). Including the root submodel improved the overall prediction quality of FLORSYS, and this even without detailed root system architecture or functions simulating soil-resource uptake and use, because there was less overestimation in terms of biomass as suspected by Colbach et al (2016).

Therefore, when parameterizing new species, only parameters of the allometric relationship need to be measured precisely in priority. Given the genericity of the allometric relationship and the low influence of other formalisms we developed, our approach could easily be adapted for connecting other models, benefitting from parameters already acquired in our study for 30 species of crops and weeds for the allometric relationship. However, further simulations with a large diversity of cropping systems and pedoclimatic and floristic contexts must be run first to define in which conditions our formalisms and conclusions apply.

4.2. What are the parameters involved in potential uptake of soil resources and root parasitism risk?

Species parameters were more correlated to proxies for uptake of soil resources and root parasitism for crops than for weeds. For the latter, proxy variables were the result of a community of interacting species and parameters rather than of individual species or parameters. Therefore, links between proxy variables and parameters were less obvious for weeds and could even seem counter intuitive. For example, weed communities most likely to be infected by *P. ramosa* in autumn, i.e. communities with the largest cumulated root length, consisted mostly of species that did not invest much in roots and that explored the soil only at short distance. Instead, they invested in strategically placed leaf area after emergence (above neighbours) to occupy space as fast as possible and shade their neighbours rather than be shaded (as illustrated by their low shading response). Indeed, occupying the field area as quickly as possible is crucial for a plant to survive and grow within a community (Colbach et al., 2019; Liebman and Gallandt, 1997), particularly if soil resources are assumed to be mostly non-limiting as in the present case. In terms of belowground exploration, the fine scale seemed most important for parasitism of weeds because root length density was the key parameter (as demonstrated by the specific root length parameter) rather than root-system volume (depending on root-system lateral extension). This is consistent with literature reporting that large specific root length is a crucial trait for belowground exploration because it allows to explore greater soil volumes per unit of biomass invested in roots (Ma et al., 2018).

In contrast to weeds, in terms of morphology and photosynthetic functioning, the crops most likely to be infected in autumn were large both above and belowground and very plastic in response to shade all along their life-cycle. Therefore, it is likely that for crops, which are deliberately sown and promoted by farming practices to the detriment of weeds, exerting a strong competition once established is at least as important as being able to establish quickly.

In summer, key parameters for parasitism risk and potential soil-resource uptake were different and more difficult to interpret. For example, for crops, they were characteristics of winter cereals. It is difficult to tell whether these characteristics did promote parasitism risk and potential uptake or whether this reflected the way we estimated missing parameters, i.e. by averaging parameters by clade and seasonal type.

Generally, root parameters were less influential than aboveground parameters in our simulations. This is not surprising considering that the FLORSYS-RSCone function was one way here, with RSCone root variables driven by FLORSYS state variables. But, the feedback from RSCone to FLORSYS, i.e. root-dependent functions are not modelled yet, except for remobilization. Uptake of soil resources and *P. ramosa* infection have a retroactive effect on plant growth (respectively beneficial and detrimental) (Barker et al., 1996; Lins et al., 2007; Weiner, 2004), which could amplify the influence of root parameters. To complete the two-way connection between RSCone and FLORSYS, we recently included these key root-dependent functions, i.e. plant-plant competition for nitrogen (Moreau et al, 2021) and *P. ramosa* infection (Pointurier et al, 2021) and their effects on plant growth and morphology into FLORSYS. However, even after implementing such root functions in the model, aboveground parameters could still be more influential than root parameters because soil-resource uptake (Berger et al., 2013) and the number of broomrapes supported by their hosts (Grenz et al., 2008) are driven by the aboveground parts of plants.

It is noteworthy that our proxies quantify potential parasitism and soil-resource uptake, but disregard major aspects involved such as nitrogen uptake efficiency of plants (Aziz et al., 2017) or host status (Qasem and Foy, 2007), which we are currently implementing in the model.

4.3. Agronomic implications

As potential soil-resource uptake was strongly correlated to the risk of parasitism in the simulations, it will often be difficult to both improve crop nutrition and reduce *P. ramosa* infection in situations where the latter is an issue. However, it is possible, because the crops with the highest potential uptake were cereals, which generally do not host *P. ramosa* (Parker, 2013). Some species of cereals could even contribute to control *P. ramosa* by depleting the parasite seed bank because they are false-hosts (e.g. oat, *Avena sativa*, Fernández-Aparicio et al., 2009), i.e. they stimulate *P. ramosa* germination but do not support its development (Goldwasser and Rodenburg, 2013). In the case of cover crops, the correlation between increased soil-resource uptake and increased *P. ramosa* infection is actually an opportunity to reduce both nitrate leaching and *P. ramosa* seed banks. Indeed, the principle of “*P. ramosa* catch crops” is to promote *P. ramosa* infection on host crops to reduce the parasite seed bank and destroy the infected crops before *P. ramosa* reproduction (Goldwasser and Rodenburg, 2013).

Our approach allows identifying ideotypes of crops, 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), here greater soil exploration abilities. For example, breeding less vigorous varieties which would be less likely to encounter *P. ramosa* seeds would be a solution for host crops such as oilseed rape for which no parasite resistance has yet been found (Fernández-Aparicio et al., 2016). However, such varieties would be less competitive for soil resources against non-parasitic weeds, and their benefits would depend on whether parasitic or non-parasitic weeds were the main limiting factor.

Identifying ideotypes is also interesting for designing crop mixtures. For example, we showed that mixing winter cereals with dicotyledons, which take up potentially fewer soil resources according to our simulations, is relevant under limited water and nutrient supply. Another option is to mix species that explore complementary niches (for example one taking up superficially and the other one more in depth) (Postma and Lynch, 2012). Our approach could be adapted to identify such mixtures.

The trade-off between soil-resource uptake and *P. ramosa* control is interesting for weed management. It means that strategies targeting resource-hungry weed species (e.g. deep banding fertilization that limits nutrient uptake by weeds to the advantage of crops, Blackshaw et al., 2004) also control weeds that favour *P. ramosa* infection. The latter could though be achieved by different management strategies as we showed that interactions between different species with different parameters are very important within the weed community. For example, limiting broomrape infestation via weeds could be achieved either by directly controlling massively infected weed species, as generally advised (www.terresinovia.fr/-/en-savoir-plus-sur-l-orobanche-rameuse), or by tolerating non-host weeds that compete with the latter (Colbach et al., 2017a). Simulating a large number of cropping systems with our

model could help to better understand the link between cropping techniques and proxies, and to identify different efficient strategies, including complex ones relying on interactions between weed species.

5. Conclusion

By connecting a root model to a weed dynamics model, we developed one of the rare plant dynamics model adapted to take into account competition for all resources (light, water and nutrients) in multispecies heterogeneous stands. We focused on weed dynamics in agroecosystems, but our approach is sufficiently generic to be adapted to crop models aiming at designing crop mixtures for example. We also propose a method to identify major plant characteristics involved in competition between crops and weeds for soil resources, which could be adapted for designing crops mixtures.

We used proxies for competition for soil resources and for parasitism of crops and weeds, and the results will help to implement the actual processes in FLORSYS. This will ultimately make FLORSYS a powerful tool for designing agroecological cropping systems. It will allow testing complex strategies that modulate competitive relationships between crops, weeds and broomrape, via, e.g., sowing dates and patterns or fertilization.

6. Acknowledgements

This project is supported by INRAE, the French project CoSAC (ANR-14-CE18-0007), the research programme “Assessing and reducing environmental risks from plant protection products” funded by the French Ministries in charge of Ecology and Agriculture, and by the University of Rostock (Crop Health Department, Faculty of Agricultural and Environmental Sciences). We are very grateful to Antoine Gardarin, Maé Guinet, Laurène Perthame and Anne-Sophie Voisin for providing data for our analysis.

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8. Illustrations

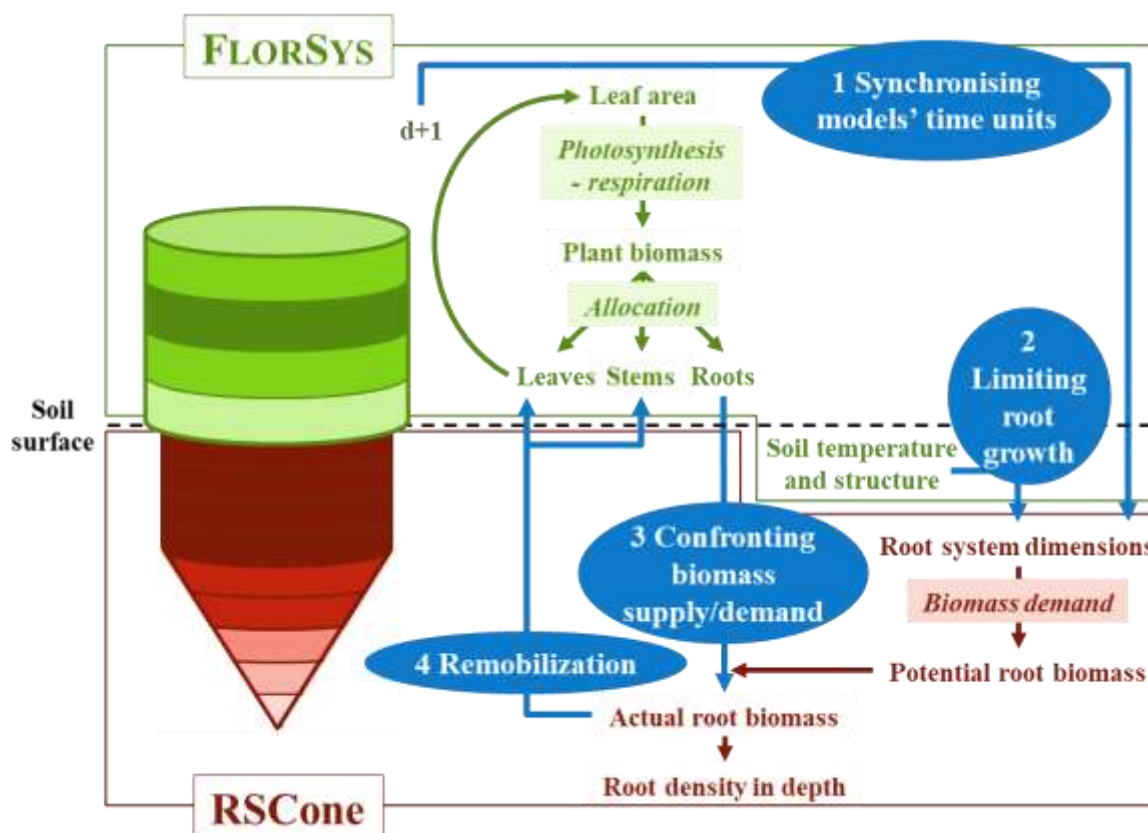


Figure 1: Overview of the variables linking FLORSYS (Colbach et al., 2014; Gardarin et al., 2012; Munier-Jolain et al., 2014, 2013), which predicts aboveground plant growth, soil structure and climate, to RSCone (Pagès et al., 2020), which predicts root growth. Variables (in bold) and processes (in italics in boxes) from FLORSYS are in green and those from RSCone in brown. Blue arrows show variables used to connect both models, with connecting functions added in the present paper in blue ellipses. Cylinder and cone shapes show how FLORSYS and RSCone represent the aboveground and root parts of plants in three dimensions, with vertical distributions of leaf area and roots respectively within homogeneous horizontal layers. The crop-weed canopy is represented in 3D, consisting of individual crop and weed plants; connections between FLORSYS and RSCone run daily at the scale of each individual plant; competition for resources occurs when neighbouring plants overlap or cast shade.

Table 1: Data used for parameterizing the relationship between root and total plant biomass for several crop and weed species at vegetative stage.

Exp.	Species tested (crops in bold, weeds in plain font)	Light treatment	Nitrogen treatment (mM of nitrates in the nutrient solution)	Growth medium (in greenhouse)	Sampling stages (time since sowing)	Reference
E1	Wheat (<i>Triticum aestivum</i>) cv Caphorn, fescue (<i>Schedonorus arundinaceus</i>) cv Soni (without light limitation), Lucerne (<i>Medicago sativa</i>) cv Agathe NF¹, <i>Alopecurus myosuroides</i>, oilseed rape (<i>Brassica napus</i>) cv Kadore, <i>Geranium molle</i>	100% (no shading) and -90% ³	0.2 to 14 mM	Expanded clay and attapulgate	Vegetative (37-125 DAS ²)	(Perthame et al., submitted)
E2	Wheat (<i>Triticum aestivum</i>) cv Caphorn, <i>Galium aparine</i>, <i>Polygonum aviculare</i>	100% (no shading)	10 and 14 mM	Expanded clay and attapulgate	Vegetative (55-151 DAS ²)	(Perthame et al., submitted)
		-60%	5 and 10 mM			
E3	<i>Abutilon theophrasti</i> , <i>Alopecurus myosuroides</i> , <i>Amaranthus hybridus</i>	100% (no shading)	10.5 mM	Expanded clay and attapulgate	Vegetative (25-94 DAS ²)	(Moreau et al., 2018)
E4	Chickpea (<i>Cicer arietinum</i>) cv Twist, common bean (<i>Phaseolus vulgaris</i>) cv Flavert, common vetch (<i>Vicia sativa</i>) cv Candy, faba bean (<i>Vicia faba</i>) cv Espresso, fenugreek (<i>Trigonella foenum-graecum</i>) cv Fenu-fix, lentil (<i>Lens culinaris</i>) cv Anicia, lupine (<i>Lupinus albus</i>) cv Feodora, Narbonne vetch (<i>Vicia narbonensis</i>) cv Clara, pea (<i>Pisum sativum</i>) cv Kayanne, soybean (<i>Glycine max</i>) cv Sultana	100% (no shading)	2.5 mM	Hydroponics	Vegetative (6-24 DAS ²)	(Guinet, 2019; Seneze J., 2018)
E5		100% (no shading)	14 mM	Rhizotrons (=transparent tubes inner coated with a membrane and filled with expanded clay and attapulgate, where roots grew between the tube wall and the membrane)	Vegetative (27 DAS ²)	
E6	Pea (<i>Pisum sativum</i>) genotypes Amino, Austin, Cameor, Cuzco 1, Isard, Kayanne, L1073, Livioletta, Nepal A and Pi186093	100% (no shading)	14 mM	Hydroponics	Vegetative (7-28 DAS ²)	
E7	Pea (<i>Pisum sativum</i>) genotypes Kayanne and Pi186093	100% (no shading)		Expanded clay and attapulgate	Vegetative (14-28 DAS ²)	
E8	<i>Alopecurus myosuroides</i> , wheat (<i>Triticum aestivum</i>) cv Caphorn, <i>Bromus hordeaceus</i>, <i>Cyanus segetum</i>, oilseed rape (<i>Brassica napus</i>) cv Kadore, <i>Echinochloa crus-galli</i>, <i>Geranium molle</i>, <i>Tripleurospermum inodorum</i>, pea (<i>Pisum</i>	100% (no shading)	10.5 mM	Expanded clay and attapulgate	Vegetative (14-56 DAS ²)	(Moreau et al., 2017)

Exp.	Species tested (crops in bold, weeds in plain font)	Light treatment	Nitrogen treatment (mM of nitrates in the nutrient solution)	Growth medium (in greenhouse)	Sampling stages (time since sowing)	Reference
	<i>sativum</i>) cv Kayanne , <i>Teucrium botrys</i> , <i>Microthlaspi perfoliatum</i> , <i>Vulpia myuros</i>					
E9	<i>Alopecurus myosuroides</i> , <i>Brachypodium distachyon</i> , <i>Bromus hordeaceus</i> , oilseed rape (<i>Brassica napus</i>) cv Kadore , <i>Cyanus segetum</i> , <i>Echinochloa crus-galli</i> , <i>Geranium molle</i> , <i>Tripleurospermum inodorum</i> , strong-spined medick (<i>Medicago truncatula</i>) , <i>Teucrium botrys</i> , <i>Microthlaspi perfoliatum</i> , wheat (<i>Triticum aestivum</i>) cv Caphorn , <i>Vulpia myuros</i>	100% (no shading)	14 mM	Silty clay loam soil	Vegetative (56 and 77 DAS ²)	(Moreau et al., 2015)
E10	<i>Vulpia myuros</i> , <i>Teucrium botrys</i> , <i>Microthlaspi perfoliatum</i> , <i>Bromus hordeaceus</i> , <i>Geranium molle</i> , <i>Alopecurus myosuroides</i> , <i>Cyanus segetum</i> , <i>Echinochloa crus-galli</i> , <i>Tripleurospermum inodorum</i> , <i>Persicaria lapathifolia</i> , oilseed rape (<i>Brassica napus</i>) cv Kadore , wheat (<i>Triticum aestivum</i>) cv Caphorn	100% (no shading)	10.5 mM	Expanded clay and attapulgite	Vegetative (34-64 DAS ²)	(Moreau et al., 2014, 2013)

¹NF for 'Non-Fixing', ²DAS for days after sowing, ³no data for fescue under 90% shading

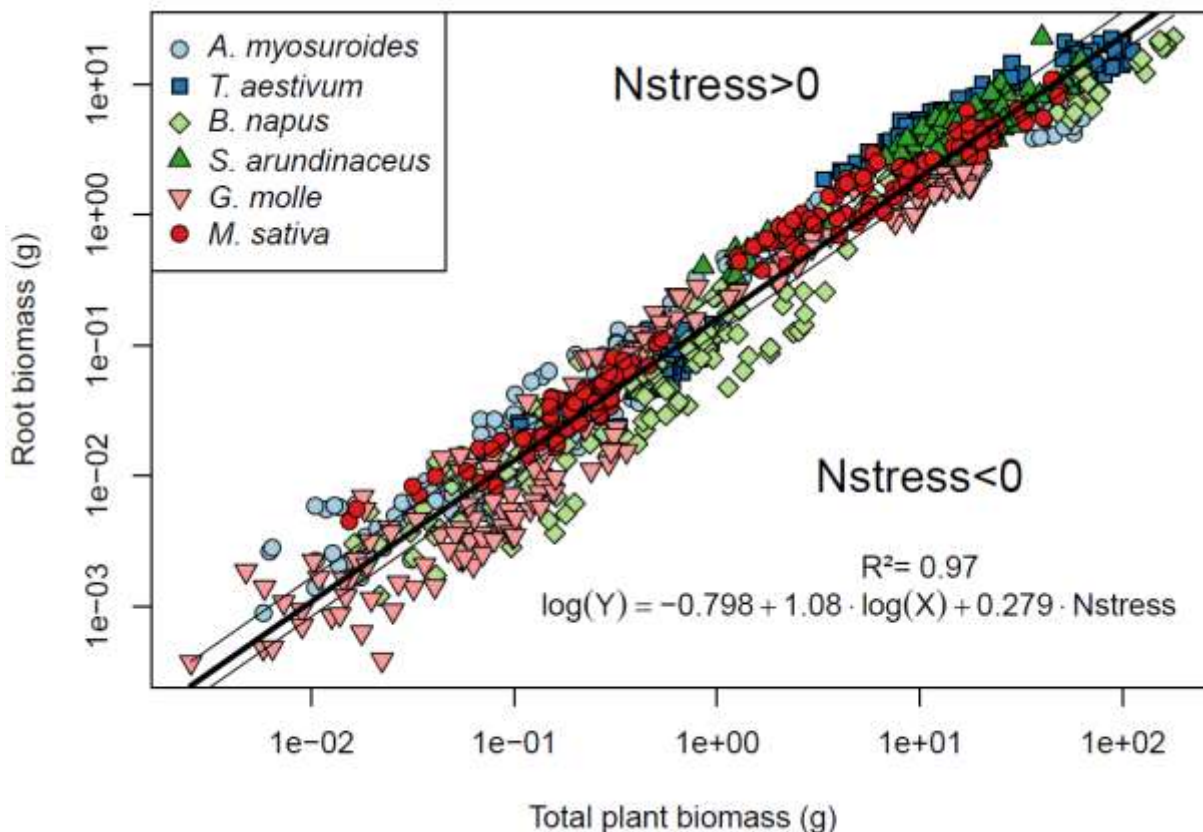


Figure 2: Root biomass as a function of total plant biomass and nitrogen stress index for six species of crops and weeds under different shading and nitrogen stress conditions during the vegetative stage (data from experiment E1 in Table 1). Each data point represents a plant, each coloured symbol a species. For illustrative purposes, a simplified regression was fitted here, disregarding the species effect. The lines show the root vs the total plant biomass for optimal nitrogen nutrition (no nitrogen stress, thick line), supra-optimal (nitrogen stress <0, thin line, 5% quantile of stress values) and sub-optimal (nitrogen stress >0, thin line, 95% quantile of stress values). In FLORSYS, the intercept and slope of this regression depend on the species.

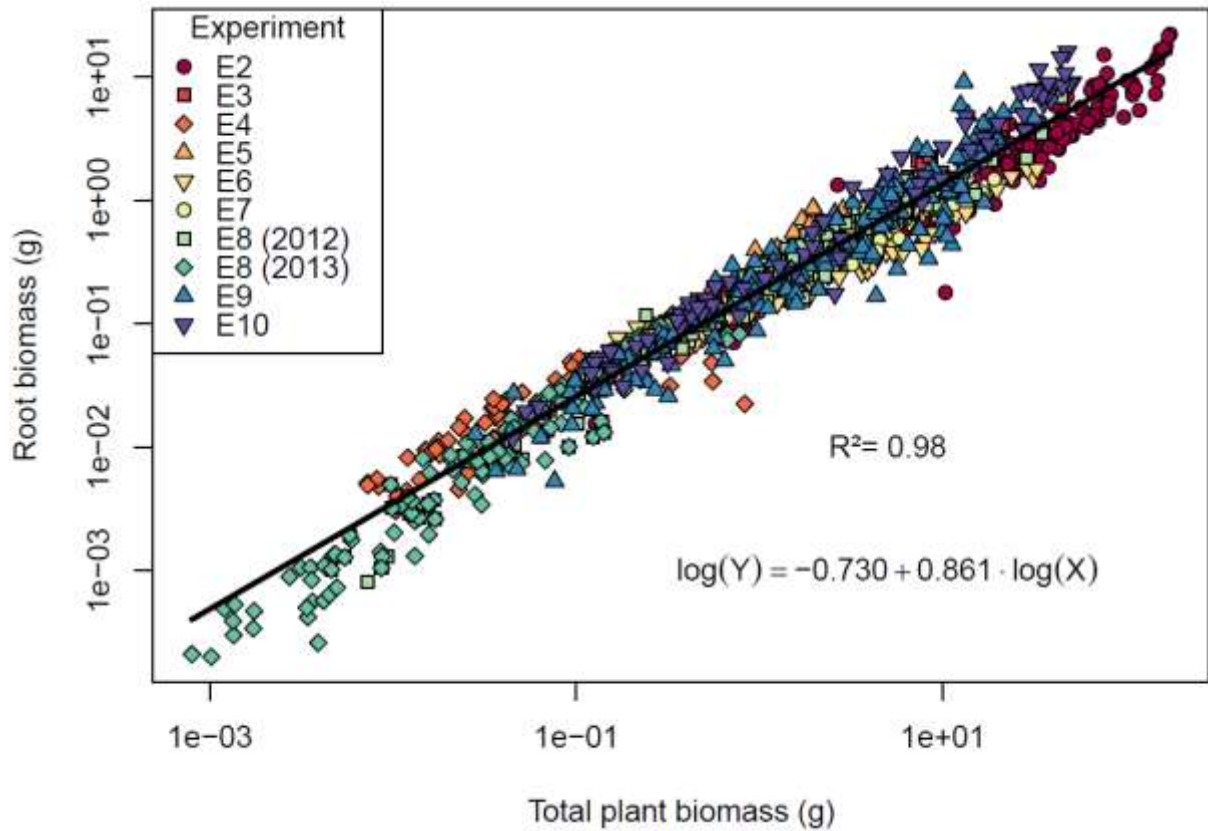


Figure 3: Root biomass as a function of total plant biomass for 28 species of crops (with 10 varieties of pea) and weeds. Data from several experiments were used (details in Table 1), each coloured symbol representing an experiment. Each data point represents a plant. For illustrative purposes, a simplified regression was fitted here, disregarding the species effect (thick line). In FLORSYS, the intercept and slope of this regression depend on the species.

Table 2: RSCone-FLORSYS ability to rank cropping systems and weed species (in case variables were analysed at the species scale). Crop and weed variables are given per species or at the community scale (summed over all simulated species). Values in italics shows variations compared to simulations without RSCone.

A. Daily weed dynamics

Variable	Species scale	Daily dynamics ^x					
		Correct		Over-estimated	Under-estimated		
Weed biomass (aboveground) (g m ⁻²)	Community	0.24	<i>0.01</i>	0.68	<i>-0.01</i>	0.08	<i>0.00</i>
	Per species	0.79	<i>-0.01</i>	0.14	<i>0.01</i>	0.07	<i>0.00</i>
Weed plant density (plants m ⁻²)	Community	0.34	<i>-0.01</i>	0.55	<i>0.02</i>	0.11	<i>-0.02</i>
	Per species	0.86	<i>0.00</i>	0.10	<i>0.00</i>	0.04	<i>0.00</i>

^x Proportion of observations inside the simulated confidence interval. Colours: from red (0) to green (1) for the first column, from green (0) to red (1) for the two other columns. Colours for values in italics: from green (improvement in prediction quality when connecting RSCone to FLORSYS) to red (deterioration in prediction quality).

B. Annual and multiannual crop and weed variables

Variable	Species scale	Relative bias (%) [§]		Relative prediction error (%) [§]		Proportion of correctly predicted observations		
						Proportion ^{&}	In terms of [#]	
Crop yield (t ha ⁻¹)	Per species	-8%	4%	110%	4%	0.42	-0.09	Absolute values
Crop biomass (g m ⁻²)	Per species	-2%	0%	~0	0%	0.59	0.03	Rank
Weed seed bank (seeds m ⁻²)	Community	15%	6%	~0	0%	-0.08	0.01	Rank
	Per species	7%	0%	74%	-3%	0.51	0.02	Rank
Multiannual weed biomass (aboveground) (g m ⁻²)	Community	206%	-70%	~0	0%	0.13	0.11	Rank
	Per species	17%	-5%	~0	-347%	0.55	-0.04	Rank
Multiannual weed plant density (plants m ⁻²)	Community	154%	1%	228%	-6%	0.65	0.11	Relative values
	Per species	17%	-1%	148%	-3%	0.67	0.01	Rank

[§] Relatively to the range of variation of observations $\frac{1}{2}[\max-\min \text{ observed values}]$. Colours: from green (0%) to red (150%), grey (too much variability in observations to conclude).

[§] Corrected for variability in observations and in simulations, relatively to the standard deviation of observations. Colours: red (bad, > 120%), yellow (satisfactory, 60-90%), light green (good, 30-60%), green (very good, < 30%) and grey (too much variability in observations to conclude), with thresholds based on Colbach et al (2016).

[&] Maximum of the modelling efficiency, the Pearson and the Spearman correlation coefficients. Colours: from red (0) to green (1).

[#] Cells were coloured from yellow for the worst case (model only ranks situations correctly) to green (model also predicts absolute values correctly).

Table 3: Pearson correlations between parameters and proxy variables for soil-resource uptake, competition for soil resources and *Phelipanche ramosa* infection in crops. Correlations between proxy variables are in blue. Correlations between parameters and a high potential uptake, competitiveness for soil resources and a low risk of parasitism are in green, opposite correlations are in red. The darker the colour, the stronger the correlation. Only significant correlations $\geq |0.50|$ are presented. The complete table can be found in section E.1 online. Some parameters were calculated at different stages: after emergence in young seedlings (“Early”), during vegetative stage (“Mid”) and from flowering onwards (“Late”).

Parameter/proxy		Proxy for				
		Parasitism at			Soil-resource uptake	Competition with weeds for soil resources
		dormancy induction (autumn)	dormancy release (summer)	crop flowering		
					at crop flowering	
A. Proxies						
Parasitism at	dormancy induction of parasitic seeds					
	dormancy release of parasitic seeds					
	crop flowering				0.851	
Soil-resource uptake	at crop flowering			0.851		
Competition for soil resources						
B. Root parameters						
Timing of maximum SRL (tSRLmax , days under optimal temperature)					0.520	
Maximum root-system extent (E_{max} , cm)		0.550				
Speed at which root-system depth increases (rD , cm per day under optimal temperature)		0.504				
Ratio of speed at which depth of cylinder-shaped part of root system increase vs speed of total root-system depth increase (rCD , cm per day under optimal temperature)					0.635	
Root biomass when total plant biomass is near 0 (aa1 , g·g ⁻¹)		-0.610				
Slope of allometric relationship of root vs total plant biomass (a2 , no unit)		0.647				
C. Parameters for early growth						
Relative growth rate (RGR , cm ² ·cm ⁻² ·°Cday ⁻¹)		0.563				
Epigeal preemergent growth (1=epigeal, 0=hypogaeal)		0.622				
Base water potential for germination (baseWP , Mpa)		0.661				
D. Parameters for potential aboveground morphology in unshaded conditions						
Leaf biomass ratio (leaf biomass vs. aboveground biomass, LBR , g·g ⁻¹)	Late	0.696				
Impact of biomass on plant height (the larger the parameter, the more height increases with biomass, b_{HM} , no unit)	Mid				-0.530	
	Late				-0.590	
Specific plant width (width per unit of aboveground biomass, WM , cm·g ⁻¹)	Mid	0.686				
	Late	0.665				
Median relative leaf height (relative plant height below which 50% leaf area are located, RLH , cm·cm ⁻¹)	Late	-0.688				
E. Parameters for response to shading						
Increase of specific leaf area under shading (mu_{SLA} , no unit)	Early	0.600				
	Mid	0.535				
Increase of leaf biomass ratio under shading (mu_{LBR} , no unit)	Early	-0.635				
	Mid	-0.556				
	Late	-0.597				
Increase of specific plant height under shading (mu_{HM} , no unit)	Early	0.575				
Distribution of leaf area towards the top of the plant under shading (mu_{RLH} , no unit)	Early	0.636				
	Late	0.541				
F. Taxonomy						
Dicot species		0.520			-0.516	
G. Life-cycle parameters						
Seasonal type: winter annual				0.514	0.516	
H. Parameters for sensitivity to temperatures						
Temperature above which photosynthesis starts to decrease (tPhoto3 , °C)				-0.554		
Maximum temperature for photosynthesis (tPhoto4 , °C)		-0.532				
Temperature below which all plants die due to frost (tFrost3 , °C)	Early			-0.532		
	Mid			-0.533		
	Late			-0.509	-0.504	

Table 4: Correlations between parameters and proxy variables for soil-resource uptake, competition for soil resources and *Phelipanche ramosa* infection in weeds. Correlations between proxies are Pearson correlations (in blue), and correlations between proxies and parameters are results from the fourth-corner analysis (in red and green). Correlations between parameters and a high potential uptake, competitiveness for soil resources and risk of parasitism are in red, opposite correlations are in green. The darker the colour, the stronger the correlation. Only significant correlations $>|0.10|$ are presented. The complete table can be found in section E.2 online. Some parameters were calculated at different stages: after emergence in young seedlings (“Early”), during vegetative stage (“Mid”) and from flowering onwards (“Late”).

Parameter/proxy		Proxy for				
		Parasitism at			Soil-resource uptake	Competition with crops for soil resources
		dormancy induction (autumn)	dormancy release (summer)	crop flowering		
		At crop flowering				
A. Proxies						
Parasitism at	dormancy induction of parasitic seeds		0.355	0.343	0.370	0.284
	dormancy release of parasitic seeds	0.355		0.865	0.783	0.518
	crop flowering	0.343	0.865		0.847	0.471
Soil-resource uptake	at crop flowering	0.370	0.783	0.847		0.480
Competition for soilresources		0.284	0.518	0.471	0.480	
B. Root parameters						
Maximum root-system extent (E_{max} , cm)			-0.116			
Speed at which root-system extent increases (rE , cm per day under optimal temperature)			-0.121			
Maximum SRL (srl_{max} , cm·g ⁻¹)			0.112			
Slope of allometric relationship of root vs total plant biomass (a₂ , no unit)			-0.106			
C. Parameters for early growth						
Relative growth rate (RGR , cm ² ·cm ⁻² ·°Cday ⁻¹)			-0.139	-0.105		-0.129
Leaf area at emergence (LA₀ , cm ²)			0.101			
Base temperature for germination (baseT , °C)			-0.115			
D. Parameters for potential aboveground morphology in unshaded conditions						
Specific leaf area (total leaf area vs. total leaf biomass, SLA , cm ² ·g ⁻¹)	Early		0.104			
Leaf biomass ratio (leaf biomass vs. aboveground biomass, LBR , g·g ⁻¹)	Early		-0.118			
Median relative leaf height (relative plant height below which 50% leaf area are located, RLH , cm·cm ⁻¹)	Early		0.116		0.118	
E. Parameters for response to shading						
Increase of specific leaf area under shading (mu_{SLA} , no unit)	Early		-0.124	-0.160	-0.149	-0.118
Increase of leaf biomass ratio under shading (mu_{LBR} , no unit)	Early					0.120
Increase of specific plant width under shading (mu_{WM} , no unit)	Early		-0.103			