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MODELLING CROPPING SYSTEM EFFECTS ON BRANCHED BROOMRAPE DYNAMICS IN INTERACTION WITH WEEDS

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ABSTRACT

Branched broomrape, *Phelipanche ramosa* (L.) Pomel, is a parasitic plant which causes important yield losses in crops, particularly in winter oilseed rape in France. In order to design efficient pest management strategies, we modelled the effects of cropping systems on branched broomrape dynamics in interaction with weeds and crops in a model called PheraSys. PheraSys functions and parameters were based on literature and on our own experiments. The model simulates the complete life-cycle of the parasite, from seed dynamics in the soil to seed production after development on the host. Interactions between the parasite and crops and weeds were characterized at the species level and at the plant scale. Based on our first results, we discussed the effects of tillage, delayed sowing and catch crops.

Keywords: *Phelipanche ramosa* (L.) Pomel, parasitic plant, model, cropping system, weed management

RÉSUMÉ

MODELISATION DES EFFETS DES SYSTEMES DE CULTURE SUR LA DYNAMIQUE DE L'OROBANCHE RAMEUSE EN INTERACTION AVEC LES ADVENTICES

L'orobanche rameuse, *Phelipanche ramosa* (L.) Pomel, est une plante parasite qui cause d'importantes pertes de rendement, particulièrement en culture de colza en France. Afin de concevoir des stratégies de gestion adaptées, nous avons modélisé l'effet des systèmes de culture sur la dynamique de l'orobanche rameuse en interaction avec les adventices et les cultures dans un modèle appelé PheraSys. Les fonctions et paramètres constituant le modèle ont été déterminés à partir de données issues de la littérature et d'expérimentations que nous avons menées. PheraSys simule le cycle de vie complet du parasite, de la dynamique de son stock semencier dans le sol à la production de semences après développement sur son hôte. Les interactions entre le parasite et les cultures et les adventices ont été caractérisées au niveau spécifique et à l'échelle de la plante. Les premiers résultats permettent de discuter des effets du travail du sol, du semis tardif et des cultures pièges.

Mots-clés : *Phelipanche ramosa* (L.) Pomel, plante parasite, modélisation, système de culture, gestion des adventices

INTRODUCTION

By competing with crops for light, water and nutrients, weeds are the major pest of cropping systems (Oerke, 2006). For several decades, weed management has mainly relied on chemical control but this intensive use of herbicides affects the environment and human health and decreased the efficiency of chemical control by selecting for resistant individuals (Heap, 2016). As a consequence, reducing the use of pesticides has become a priority for international policies and has led to the implementation of different programs such as Ecophyto in France (agriculture.gouv.fr, 2015). This reduction will probably result in a residual weed flora in fields which could feed and shelter other pests (Mézière *et al.*, 2013; Norris, 2005). Among these, branched broomrape, *Phelipanche ramosa* (L.) Pomel, is a parasitic plant which infects many crops (Parker, 2013) but also several weed species (Boulet *et al.*, 2001; Gibot-Leclerc *et al.*, 2003; Gibot-Leclerc *et al.*, 2013a). This holoparasite entirely relies on resources taken from its host to survive and reproduce and thus causes important yield losses (Heide-Jørgensen, 2013; Parker, 2013), with up to 90% in French oilseed rape (Gibot-Leclerc *et al.*, 2012). As no curative treatment is available in France in the main infected crops (ANSES, 2016), parasite management relies on a combination of preventive practices, mainly crop rotation and soil tillage (Goldwasser and Rodenburg, 2013; Rubiales *et al.*, 2009). Moreover, parasite management must include control of potential host weed species. Thus, it must include all elements that define a cropping system (Papy, 2013). Models are useful to understand, to quantify and to predict the effect of cropping systems on weed dynamics in the long term, as they are faster and cheaper for testing all the factors involved (Colbach, 2010; Colbach *et al.*, 2014). To date, no model predicts the effects of cropping systems on the dynamics of branched broomrape though several models simulate the development of other broomrape species in crops (Eizenberg *et al.*, 2005; Eizenberg *et al.*, 2012; Grenz *et al.*, 2005; López-Granados and García-Torres, 1997; Manschadi *et al.*, 2001). Among weed dynamics models, FLORSYS simulates the dynamics of multispecific weed floras in cropping systems and can be used in a large range of conditions because it takes into account the effect of climate and soil characteristics and is based on a mechanistic representation of biophysical processes. This model is increasingly used to evaluate and design sustainable weed management strategies (Colbach *et al.*, 2014). Consequently, the objectives of the present study were to develop a model of branched broomrape dynamics, called PHERASYS (for *Phelipanche ramosa* in cropping systems) based on the same principle as FLORSYS and intended to be connected to FLORSYS to account for weed-parasite interactions. The present study (1) proposed a structure for the model, (2) translated the results of our experiments into equations to represent biological processes, (3) completed missing data from the literature, and (4) identified parts of the model to improve in future. Branched broomrape consists of several pathovars i.e. genetically distinct populations with different host preferences (Brault *et al.*, 2007). Our study focussed on the pathovar predominant in oilseed rape which causes the main damages in France. When completed, the model will be used to evaluate the effects of cultural practices on parasite dynamics in interaction with weeds and pedoclimate and to design sustainable management strategies.

MATERIALS AND METHODS

1) MODEL STRUCTURE

PHERASYS structure was based on the FLORSYS structure, i.e. the dynamics of plants was modelled as a succession of life stages depending on biophysical processes. Each process was simulated with a daily time step. The model is spatially explicit inside the simulated field, for belowground processes in 1D vertical dimension, with 30 successive 1cm soil layers, for aboveground processes in 2D horizontal dimensions, detailing parasite stages on each infected crop or weed plant. PHERASYS simulates processes that determine the multi-annual parasite dynamics (Figure 1). Each day, a part of the seeds dies; non-dormant seeds can germinate only if stimulated by neighbour plant root exudates; they must attach to nearby susceptible plant roots before emerging, flowering and producing new seeds.

2) CONNEXION WITH FLORSYS

PHERASYS was connected to FLORSYS to predict the development of crops and non-parasitic weeds interacting with the parasite and to predict soil conditions (Figure 1). Soil temperature and moisture determine dormancy relief of young parasite seeds and germination progress. The root volume of stimulating plants was used to predict the number of stimulated parasite seeds and their subsequent germination and attachment to host roots. The total plant biomass and the duration of the above-ground growth time of the host plants determine the number of parasites surviving up to the end of their life cycle. The dates of emergence and flowering of stimulating plants determine the length of the germination-stimulating period and the timing of parasite fructification. Effect of tillage on parasite-seed movements in the soil was also simulated by FlorSys.

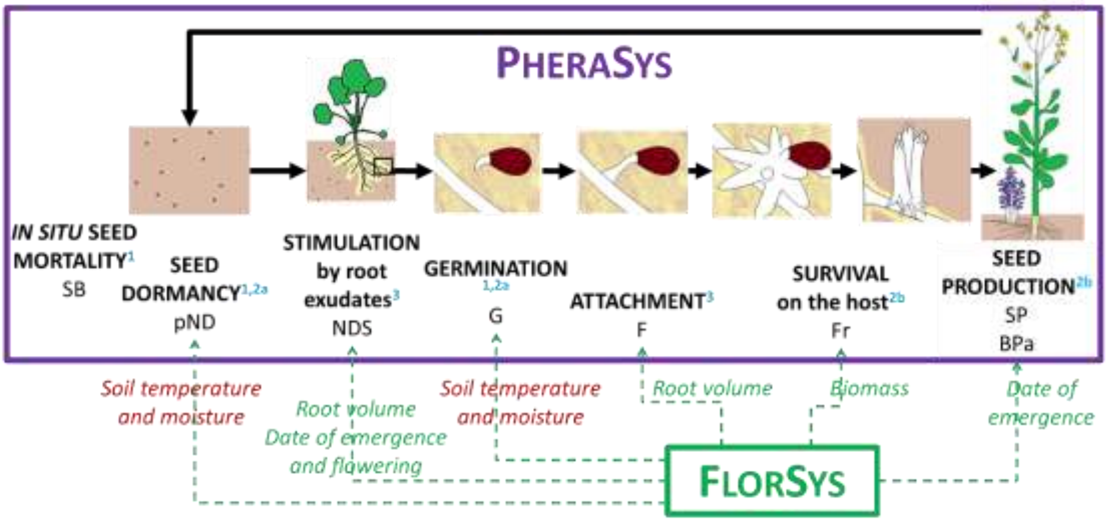

Figure 1 : Processes of branched broomrape life-cycle modelled in PheraSys (in bold). Variables (SB, pND, NDS, G, F, Fr, SP and BPa, detailed in the results section) are calculated as a function of variables describing crops, non-parasitic weeds and soil conditions predicted by FlorSys (in italics). Numbers indicate the origin of the data used: [1]own experiment still ongoing (Pointurier, 2015), [2]own data published ([2a]Gibot-Leclerc *et al.* (2004); [2b]Moreau *et al.* (2016)) and [3]other literature. (Processus du cycle de vie de l'orobanche rameuse modélisés dans PheraSys (en gras). Les variables (SB, pND, NDS, G, F, Fr, SP et BPa, détaillées dans la partie résultats) sont calculées en fonction de variables prédites par FlorSys décrivant les cultures, les adventices non parasites et les conditions du sol (en italiques). Les nombres indiquent l'origine des données utilisées : [1]expérimentation en cours (Pointurier, 2015), [2]données publiées par l'équipe ([2a]Gibot-Leclerc *et al.* (2004); [2b]Moreau *et al.* (2016)) et [3]autre littérature.)

3) DATA ORIGIN AND STATISTICAL ANALYSIS

A first, simplistic model version was built entirely from literature to identify knowledge gaps (Colbach *et al.*, 2011). Experiments were set up to study and quantify insufficiently known processes i.e. *in situ* seed mortality, seed dormancy and host-parasite trophic relationships (see [1] and [2b] on Figure 1). The new PheraSys version was inspired by the FlorSys structure and was parameterized from these experiments and from literature (see [2a] and [3] on Figure 1). It is currently being programmed while awaiting the results from the ongoing experiments.

Experimental and literature data were analysed using R (R Core Team, 2015). Linear models were fitted with the R package "lm" and non-linear models with "nls" and "nls2". The algorithm "brute-force" was used to solve cases of failed convergence. A pseudo-R^2 was calculated to estimate the predictive quality of non-linear models (UCLA: Statistical Consulting Group, 2015). Proportions of germinated seeds were analysed with a generalized linear model with a binomial error distribution and a logit transformation with the R function "glm".

RESULTS

1) *IN SITU* SEED MORTALITY

Each day, some parasite seeds die due to aging, diseases or predation. Seed mortality rate (preliminary value 0.08 seeds seeds^{-1} year^{-1}) was calculated from an ongoing seed burial experiment measuring viability of excavated seeds over time (Pointurier, 2015). As the *in situ* seed mortality rate decreased linearly over time since seed burial, annual mortality rate could be translated into a constant daily mortality rate in order to calculate the number of viable seeds in soil layer l on day d (SB_{ld} in seeds m^{-2}) using the same equation as in FlorSys (Gardarin *et al.*, 2012).

2) SEED DORMANCY

Fresh parasite seeds are dormant. To relieve dormancy, seeds require 1) a period of dry storage, followed by 2) a period of moist storage ("preconditioning"), and finally 3) a stimulation by root exudates of potential host plants. In field conditions, seed dormancy varies moreover with seasons (Murdoch and Kebreab, 2013). Dormancy was modelled as two successive phases in PHERASYS: i) dormancy relief of new seeds, as a function of soil thermal time and water potential from data from Gibot-Leclerc *et al.* (2004) ; and ii) seasonal dormancy, as a function of time since seed shed measured on the same seed burial experiment as seed mortality (Pointurier, 2015).

According to Gibot-Leclerc *et al.* (2004), soil water potential during preconditioning must exceed -2MPa to relieve dormancy. Above -2MPa, the subsequent proportion of germinated seeds only depended on the preconditioning temperature (data not shown). Thus, the proportion of non-dormant seeds among viable seeds (pND_{ld}) was modelled as a function of thermal time (base 0°C) accumulated during preconditioning ($TT_{prec\ ld}$ in °C.days) and soil water potential (Ψ_{ld} in MPa), using a Weibull equation (Figure 2). $TT_{prec\ ld}$ was calculated in each soil layer (l) each day (d) as a function of soil temperature and cardinal temperatures of preconditioning (Bradford, 2002). No seed germinates if temperature during preconditioning is too cold or too hot. In-between, the closer the preconditioning temperature is to the optimum temperature, the faster the seeds germinate once stimulated.

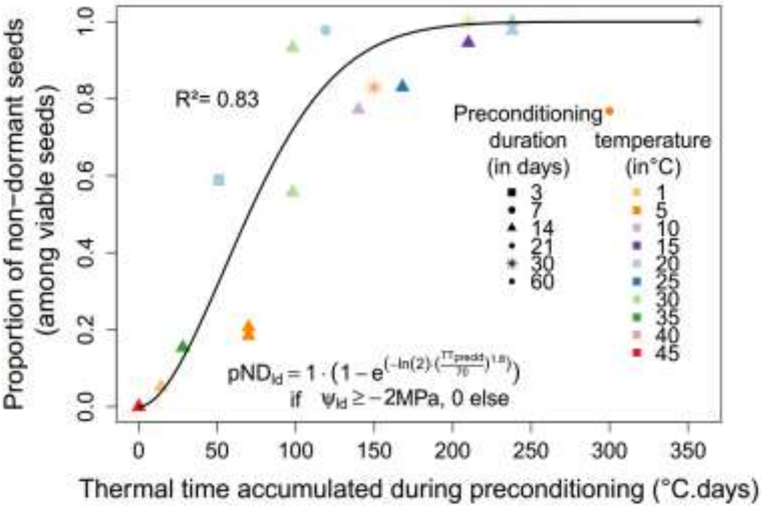

Figure 2 : Dormancy relief of branched broomrape seeds as a function of thermal time accumulated during preconditioning. Based on data from Gibot-Leclerc *et al.* (2004). (Perte de dormance des semences d'orobanche rameuse en fonction du temps thermique accumulé pendant le préconditionnement. D'après les données de Gibot-Leclerc *et al.* (2004).)

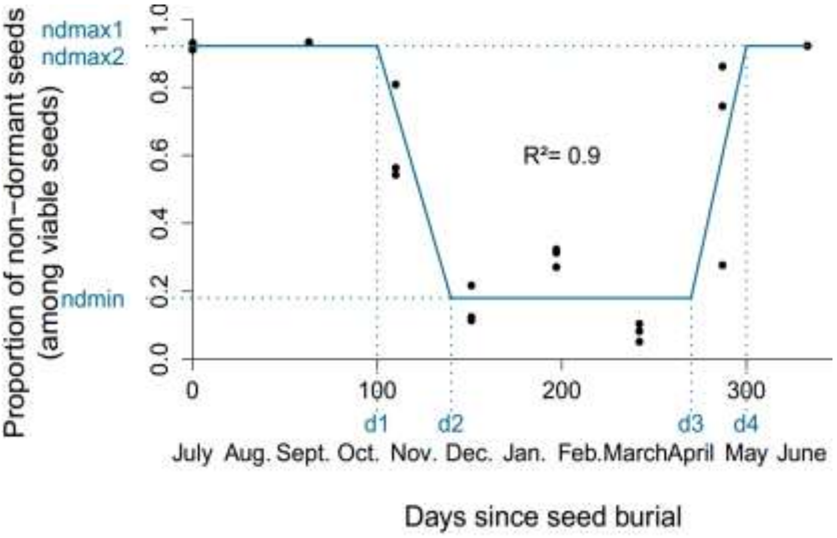

Figure 3 : Seasonal dormancy of branched broomrape seeds as a function of time since seed burial. d1, d2, d3, d4, ndmax1, ndmax2 and ndmin are detailed in the text below. Based on Pointurier (2015). (Dormance saisonnière des semences d'orobanche rameuse en fonction du temps depuis enfouissement. d1, d2, d3, d4, ndmax1, ndmax2 et ndmin sont explicités dans le texte ci-dessous. D'après Pointurier (2015).)

In our seed-burial experiment, the proportion of non-dormant seeds followed a seasonal dormancy pattern (Figure 3). Seasonal dormancy was lowest after seed rain, during the months when oilseed rape is usually sown; it increased during early autumn and was highest during winter and early spring. Dormancy relief started in summer and seeds were again little dormant during summer. A broken-sticks model adapted from the one used in FLORSYS (Gardarin *et al.*, 2012) was fitted to the data (Figure 3). d1, d2, d3 and d4 are the dates of dormancy induction onset, induction end, release onset and release end respectively; ndmax1, ndmin and ndmax2 the proportion of germinated seeds before dormancy induction, during dormancy and after dormancy release respectively.

3) STIMULATION OF GERMINATION

After preconditioning, germination is triggered by root exudates of plants. The ability of species to stimulate germination was compiled from the literature (see Colbach *et al.* (submitted)). The percentages of induced germination were used to calculate the relative species ability to stimulate parasite germination compared to a positive control. This method allowed us to compile data from different experiments (Figure 4).

Parasite seeds must be close to the stimulating root to be able to perceive germination stimulants (Goldwasser and Yoder, 2001). This was taken into account in PHERASYS by calculating a “stimulating zone” as the soil volume located at less than 36 mm from the roots of stimulating plant p of species h. As root exudates are mainly released at root tips (Dennis *et al.*, 2010), parasite seeds were only stimulated by the “new” stimulating zone each day, i.e. the stimulating zone on the present day minus the one from the day before. As host plants stimulate parasite germination up to flowering (Auger *et al.*, 2012), the number of stimulated seeds among non-dormant seeds (NDS_{ld}) was calculated each day d from emergence to flowering of each stimulating plant.

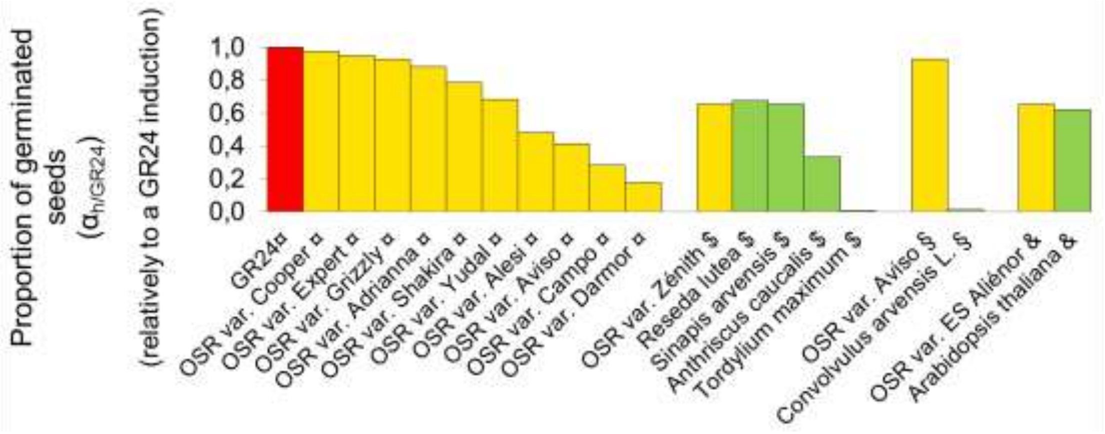

Figure 4: Ability of plants (crops and weeds) to stimulate branched broomrape germination relatively to reference (i.e. synthetic stimulation molecule GR24). OSR var.: oilseed rape variety. Based on data from ¤Gauthier *et al.* (2012), $Gibot-Leclerc *et al.* (2003), §Gibot-Leclerc *et al.* (2013a) and &Auger *et al.* (2012). (Capacité de plantes (cultures et adventices) à stimuler la germination des semences d’orobanche rameuse par rapport à la référence (le stimulant de synthèse GR24). OSR var.: variété de colza. D’après les données de ¤Gauthier *et al.* (2012), $Gibot-Leclerc *et al.* (2003), §Gibot-Leclerc *et al.* (2013a) et &Auger *et al.* (2012).)

4) GERMINATION PROGRESS

Once stimulated, seeds start to germinate and the wetter and the warmer the soil layer is, the faster seeds germinate (Pointurier, 2015), using the same principle as Gardarin *et al.* (2011). In addition, too hot or too cold temperatures (above or below threshold values) shut down germination. When the soil is too dry (i.e. below base water potential), germination stops and new root exudates are necessary to trigger germination again. Cardinal temperatures and base water potential of germination were taken from Gibot-Leclerc *et al.* (2004).

5) PARASITE ATTACHMENT

Germinated seeds produce a radicle which grows towards the host root to attach and establish vascular connections to take up water and nutrients from the host (Joel, 2013). The ability of species to allow branched broomrape attachment was compiled from the literature (see Colbach *et al.* (submitted)). Radicle elongation is limited to 4 mm (Gibot-Leclerc *et al.*, 2012), so only germinated parasite seeds within a 4mm “attachment zone” around host roots could attach in the model.

6) PARASITE SURVIVAL ON HOST

Only a few attached parasite shoots will survive on the host until their maturity (Moreau *et al.*, 2016). We assumed that a host can support only a limited number of mature parasites depending on the biomass it allocates to them. Indeed, the total number of emerged parasites per host plant (γ_{ph}) increases with increasing host biomass at rosette stage ($BHProsette_{ph}$ in g, see Figure 5). Small hosts did not support the development of any emerged parasite, meaning that a minimum host biomass (BHP_{min}, in g) is required to allow further parasite development.

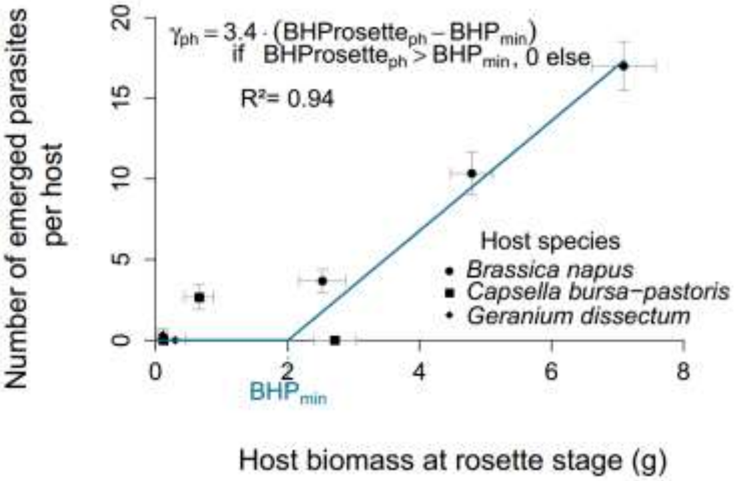

Figure 5 : Number of emerged branched broomrape per host plant as a function of host biomass at rosette stage. Based on data from Moreau *et al.* (2016). (Nombre d'orobanches rameuses émergées par plante hôte en fonction de la biomasse de l'hôte au stade rosette. D'après les données de Moreau *et al.* (2016).)

As parasites compete with each other for host resources (Moreau *et al.*, 2016), we also assumed that the number of parasites surviving on host p until seed production (Fr_{ph}) increases up to a maximum with increasing total number of attached parasites the day of seed production ($Ftot_{ph}$). We adapted a density-dependent relationship used to simulate intra-specific competition between oilseed rape seedlings for emergence (Colbach *et al.*, 2001).

7) PARASITE SEED PRODUCTION

At the end of its life cycle, the parasite produce seeds which are released and replenish the soil seedbank. The number of seeds produced by all parasite shoots of host plant p (SP_{ph} in seeds m^{-2}) increases with increasing above-ground parasite biomass, using the same log-log equation as in FlorSys. The ratio of parasite seed biomass vs. above-ground parasite biomass is currently being measured following a protocol adapted from Lutman *et al* (2011). Above-ground biomass of each parasite shoot of a given host plant on the day of parasite fructification (BPa_{ph} in g) is predicted from the number of emerged parasite shoots that compete for resources on the same host (Fr_{ph}) (Moreau *et al.*, 2016). Branched broomrape seed production on oilseed rape occurs around 3000°C.days (base 0°C) or 1700°C days (base 5°C) after host emergence whatever the year, the host emergence date or the experimental conditions (fields or greenhouse) (Gibot-Leclerc, 2004). As the parasite life-cycle duration does not depend on host life cycle duration (Gibot-Leclerc *et al.*, 2013b), fructification date is assumed to be 3000°C.days after host emergence whatever the host species in the model.

DISCUSSION

1) INNOVATIONS AND CONSISTENCY OF PHERASYS WITH THE LITERATURE

PheraSys goes much further than previous models of broomrape dynamics (Eizenberg *et al.*, 2005; Eizenberg *et al.*, 2012; Grenz *et al.*, 2005; López-Granados and García-Torres, 1997; Manschadi *et al.*, 2001) because it includes seasonal seed dormancy and interactions between the parasite and a multi-specific flora. Interactions with several species of crops and weeds were characterized at the individual plant level by predicting the number of parasite germinations and attachments as a function of host root volume and the number of mature parasite shoots as a function of host plant biomass. These interactions also depend on specific characteristics of plants, i.e. their ability to stimulate parasite germination and to allow parasite attachment. The new formalisms that we proposed for modelling parasite survival on host plants are consistent with the literature. For instance, we assumed that the number of parasites infecting a host is limited by the amount of biomass that the host allocates to parasites as was also observed for *Orobanche minor* on red clover (Eizenberg *et al.*, 2005). Other formalisms used here were inspired from literature and improved with new knowledge. For example, the calculation of a "stimulating zone" was inspired from Grenz *et al.* (2005). We added a dynamic and more realistic approach by restricting this volume to root tips. Dormancy of other broomrape species has also already been modelled as a function of duration and temperature of preconditioning above a minimum threshold (Kebreab and Murdoch, 1999). We added maximum and optimal temperatures to this approach to take into account that high temperatures slow down dormancy relief, and we included the effect of water potential during preconditioning. Kebreab and Murdoch (1999) simulated two independent successive phases of dormancy, dormancy relief followed by dormancy induction, as we did. While both depended on temperature and duration of preconditioning in their model, we chose to model the second phase as the first part of a seasonal cycle of dormancy depending on time since seed shed. Finally, several formalisms we used were adapted from FLORSYS with minor modifications, namely *in situ* seed mortality, seasonal dormancy, germination progress and seed production. This highlights that some processes are quite similar for both parasitic and non-parasitic plants.

2) AGRONOMIC IMPLICATIONS

Table I: Effects of cultural practices on branched broomrape dynamics in PHERASYS. (Effets des pratiques agricoles sur la dynamique de l'orobanche rameuse dans PHERASYS.)

Practice	Effect on parasite in PHERASYS	Formalism in PHERASYS
Soil tillage	Tillage moves seeds in the soil, which influences the proximity of parasite seeds to stimulating/attaching roots and so influences the number of germinations/attachments.	Seed movements in the soil = f(tool, depth of tillage, soil structure) (predicted by FLORSYS) Stimulated/attached seeds = f(volume of stimulating/attaching roots)
Crop species and variety	Crop species promote parasite infestation if they stimulate germinations and/or allow parasite attachment. Parasites produce more seeds on large hosts. Host crops dying or destroyed before parasite reproduction are used as trap crops.	Stimulated/attached seeds = f(specific ability to stimulate germination/allow attachment) Parasites producing seeds = f(host biomass) Parasites die before the end of their life-cycle if the host dies
Sowing date	Delayed sowing shifts the crop cycle towards the period of parasite seed dormancy and thus reduces in-crop parasite germinations. The more parasite emergence is delayed, the less time there is to damage the crop and to reproduce.	Germinated seeds = f(non-dormant seeds) Period of stimulation of germination = between emergence and flowering of stimulating crops
Weed management	Indirect effects via the non-parasitic weed flora (see crop species and variety).	Non-parasitic weed flora = f(cropping systems) (predicted by FLORSYS)
Sowing density	High sowing densities increase the likelihood that a parasite seed encounters a stimulating/host root and that it germinates/attaches.	Germinated/attached seeds = f(volume of stimulating/host roots)
Fertilization	Indirect effect by influencing host biomass which determines the number of germinations, attachments and parasites producing seeds.	Plant biomass = f(fertilization) (to be included in FLORSYS) Stimulated/attached seeds = f(volume of stimulating/host roots) Parasites producing seeds = f(host biomass)

The different processes modelled in PHERASYS allowed to integrate the effect of several cultural practices (Table I). Reduced tillage prevents germination of broomrape seeds if it leaves the seeds close to soil surface and thus far from stimulating roots (Rubiales *et al.*, 2009). Conversely, burying parasite by deep tillage and counting on natural mortality to deplete the seedbank is not an efficient option because the mortality rate of deeply buried seeds is very low according to our field experiment (Pointurier, 2015). Delaying crop sowing toward parasite seed dormancy is more promising to reduce parasite infection (Gibot-Leclerc, 2004), though yield potential can decrease in late-sown crops (Mendham *et al.*, 1981). These recommendations need to be confirmed and completed once our two-year seed burial experiment is finished.

Characterizing the interactions of the parasite with several species of crops and weeds improves the optimization of crop rotation and weed management. For example, host plants can be used as catch plants if they are destroyed before parasites produce seeds (Goldwasser and Rodenburg, 2013). We assumed that the parasite life-cycle duration is constant (in thermal time since host emergence) whatever the host. That means that species with a short life cycle would die before parasites could reproduce. For example, *Capsella bursa-pastoris* and *Geranium dissectum* are weeds that could be tolerated to play this role, provided that our assumption is true and that they do not allow secondary attachments on host crops or otherwise increase infection of host crops (Gibot-Leclerc *et al.*, 2013a). Our assumption is supported by Manschadi *et al.* (2001) who showed that the timing of *O. crenata* stages is constant (in thermal time since host emergence) and does not depend on host phenology. Moreover, we showed that the larger the host biomass is, the more parasites develop on the host. Again, short-living weed species tend to have a lower biomass and could be tolerated.

The management improvements we advised above are based on individual effects of cultural practices but we did not explain how to combine these practices to design efficient pest management strategies. Once the software programming is finished, PHERASYS will allow to test the effect of combinations of practices on parasite dynamics. It could be used as a decision support system to design efficient cropping systems to manage branched broomrape. The efficiency of decision support systems has been recognized (agriculture.gouv.fr, 2015) and the team is currently working on the development of a decision support system from FLORSYS (Colas *et al.*, 2016; Colbach *et al.*, 2016).

3) PERSPECTIVES

As suggested above, processes modelled in PHERASYS are quite generic. The same model structure could be used for other pathovars of branched broomrape, albeit with different parameter values. Indeed, our ongoing seed burial experiments suggest big differences in seed mortality and seasonal dormancy between pathovars. Pathovars are also morphologically distinct (e.g. seed weight), with different life cycle durations (Gibot-Leclerc *et al.*, 2013b). Similarly, PHERASYS could be parameterized for other broomrape species, accounting, for example, for different sensitivities to temperature and moisture conditions during preconditioning (Kebreab and Murdoch, 1999; Song *et al.*, 2005).

Here, we focused on modelling host plant effect on parasite dynamics. We are currently working on the inverse aspect, i.e. the reduction of host biomass caused by the parasite (Moreau *et al.*, 2016), in order to predict the yield of infected crops. Other cultural practices must be included in PHERASYS such as biofumigation. Biofumigation consists in suppressing soil-borne pathogens by using biocidal compounds derived from *Brassica* plants grown in the fields or incorporated in the soil (Kirkegaard and Sarwar, 1998). The most interesting candidate is 2-phenylethyl isothiocyanate which is the major germination stimulant of branched broomrape produced by oilseed rape (Auger *et al.*, 2012). This side-effect of biofumigation could be used during fallow or non-host crops to stimulate suicidal parasite germinations.

CONCLUSION

PHERASYS is to date the first model which simulates the effect of cropping systems on branched broomrape dynamics. This approach is fundamental to develop efficient pest management programs. PHERASYS identifies potential management improvements by providing a better knowledge about hitherto badly known below-ground processes (e.g. *in situ* seed dormancy) and host-parasite relationships, particularly with weeds. It suggests that delayed crop sowing and catch crops could be efficient pest control measures. Our team is now working on another original approach to integrate the effect of parasitism on host growth and development into PHERASYS. This would allow to predict yield of infected crops, a key criterion for farmers to evaluate cropping systems. Finally, as every model, PHERASYS must be validated and recommendations derived from the model should be assessed, considering the limits of the model.

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