



HAL
open science

Integrating plant-plant competition for nitrogen into a 3D individual-based model simulating the effects of cropping systems on weed dynamics

Delphine Moreau, Olivia Pointurier, Laurène Perthame, Nicolas Beaudoin,
Jean Villerd, Nathalie Colbach

► To cite this version:

Delphine Moreau, Olivia Pointurier, Laurène Perthame, Nicolas Beaudoin, Jean Villerd, et al.. Integrating plant-plant competition for nitrogen into a 3D individual-based model simulating the effects of cropping systems on weed dynamics. *Field Crops Research*, 2021, 268, pp.108166. 10.1016/j.fcr.2021.108166 . hal-03344431

HAL Id: hal-03344431

<https://hal.inrae.fr/hal-03344431>

Submitted on 8 Dec 2021

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

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

Integrating plant-plant competition for nitrogen into a 3D individual-based model simulating the effects of cropping systems on weed dynamics

Delphine Moreau¹, Olivia Pointurier¹, Laurène Perthame¹, Nicolas Beaudoin², Jean Villerd^{1,3}, Nathalie Colbach¹

¹ Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000 Dijon

² Agroimpact, INRAE, Laon, France

³ LAE, INRAE, Université de Lorraine, Vandoeuvre, France

Corresponding author: Delphine Moreau (delphine.moreau@inrae.fr)

INRAE, 17 rue Sully, 21065 Dijon cedex

Tel +33380693669

Fax +33380693262

<https://doi.org/10.1016/j.fcr.2021.108166>

Highlights

- We complemented a 3D mechanistic cropping-system model of crop-weed interactions
- We made it the first one to include competition for nitrogen, in addition to light
- With only a few new parameters, simulations were consistent with previous knowledge
- We illustrate the role of this model to analyze crop-weed interactions in the field
- We show its potential as a tool to design biological weed management strategies

Abstract

Promoting biological weed regulation via competition for resources requires better understanding the functioning of heterogeneous canopies in nitrogen-deficient situations. Mechanistic simulation models are powerful tools to reach this goal. Our objective was to integrate plant-plant competition for nitrogen into the preexisting FLORSYS model simulating the effects of cropping systems on weed dynamics and crop production. The formalisms were either created or inspired from other models and adapted to make them compatible with the individual-based representation of FLORSYS. Plant nitrogen uptake was simulated by confronting plant nitrogen demand (driven by shoot growth) to plant nitrogen supply (depending on root characteristics, soil-nitrogen availability and the presence of neighboring plants with roots in the same soil zone). A nitrogen stress index allowed accounting for the impact of plant nitrogen nutrition on plant photosynthesis, biomass allocation and morphology. The new formalisms consisted of only seven species-specific parameters. Despite simplifying hypotheses in formalisms, predictions were in good agreement with knowledge on canopy functioning and crop-weed interactions. We provide the first mechanistic cropping system model focusing on weeds that simulates plant-plant competition for nitrogen (in addition to competition for light). It will be useful to understand the role of nitrogen in crop-weed interactions and identify agroecological management strategies promoting weed regulation by competition.

Keywords: weed, nitrogen, competition, model, cropping system, biological regulation

1. Introduction

Weeds can greatly reduce yields and harvest quality, mainly by competing with the crops for resources (Oerke, 2006). That is the reason (together with their high efficiency) why herbicides generally play a key role for ensuring crop production in conventional cropping systems. However, reducing the use of herbicides has become necessary in view of their harmfulness for the environment and public health (www.ifen.fr). In this context, promoting biological weed regulation by shifting resource availability and use from weed to crop may provide an option for a more sustainable weed management (Petit et al., 2018). Light is generally the main resource for which crops and weeds compete in conventional cropping systems (Wilson and Tilman, 1993; Perry et al., 2003). However, the use of mineral nitrogen fertilizers should be decreased to limit their negative environmental impacts (Galloway et al., 2003; Swarbreck et al., 2019). Therefore, competition for nitrogen may play a greater role and better managing crop-weed competition for nitrogen may become crucial to maintain crop yield and quality.

To date, it remains largely unknown how to drive crop-weed competition for nitrogen in order to promote crop vs. weed growth in agricultural fields. Since the 2000s, several studies have suggested that decreasing mineral nitrogen fertilization disadvantages the growth of the weeds more than the growth of the crops and thus makes weed management easier (Ditomaso, 1995; Iqbal and Wright, 1997; Tilman et al., 1999; Van Delden et al., 2002; Blackshaw et al., 2003; Blackshaw and Brandt, 2008). However, studies supporting this hypothesis are scarce. Most of them show either that weeds become more difficult to manage when soil nitrogen availability is low (Jornsgard et al., 1996; Evans et al., 2003; Berger et al., 2007), or that crop-weed dynamics are little affected by nitrogen fertilization (Wells, 1979; Andersson and Milberg, 1998; Swanton et al., 1999). Other studies, such as Angonin et al. (1996), pointed out that the date of nitrogen application can affect crop-weed competition.

Managing crop-weed competition for nitrogen in order to promote biological weed regulation requires to consider the different components of the agroecosystem: the diversity of the management techniques affecting weed dynamics, the interactions among these techniques and with pedoclimate, the diversity of the biophysical processes affecting competition for nitrogen (e.g. soil nitrogen cycle, competition for light), the characteristics and diversity of the weed flora, and the long time-step resulting from the persistence of the weed seed bank in the soil. To cope with this complexity, using a simulation model quantifying the effects of cropping systems on weed and crop dynamics is essential. In particular, mechanistic (i.e. process-based) models are useful to synthesize existing knowledge, identify knowledge gaps, explore prospective scenarios in different contexts in the long term, and design new cropping systems (Colbach, 2010; Renton and Chauhan, 2017).

Simulating crop-weed competition requires an individual-based representation of the crop-weed community, i.e. each individual plant (either weed or crop) should be represented. Indeed, a few large weed plants within the weed community are often responsible for the majority of the weed resource capture and weed seed production (e.g. Brainard and Bellinder, 2004). Only predicting the reproducing large weed plants is not enough, as the canopy surrounding the plants will determine which weeds will become large. Moreover, the model must not only simulate weed plants but also crop plants. The earliest crop-weed interaction models simulate an average plant for each species. When compared to independent field data, model predictions were shown to be satisfactory only for monospecies cultures or when crop-weed canopies were homogeneous (i.e. uniformly distributed crop and weed plants inside the field with weed plants having emerged as a single cohort) (Debaeke et al., 1997; Deen et al., 2003). Unfortunately, crop-weed canopies show strong spatial and temporal heterogeneities. Weed distributions are known to be patchy (e.g. van Groenendael, 1988; Colbach et al., 2000; Pollnac et al., 2008; Bourgeois et al., 2012). Moreover, weed emergence occurs in one or several flushes spread over days or weeks (Forcella, 1993; Vleeshouwers and Kropff, 2000; Colbach et al., 2006) and the emergence date of weeds relative to the crop determines their success and impact on the crop (Brainard and Bellinder, 2004; Fahad et al., 2015). Finally, there are many different weed species with different effects and responses (Fried et al., 2008) and now crop mixtures become increasingly popular and/or needed to tackle the agroecological transition. Modellers increasingly agree that 3D individual-based modelling is necessary to realistically represent the structure and interactions of a heterogeneous crop-weed canopy (Renton and Chauhan, 2017; Colbach et al., 2021).

To our knowledge, COMPETE is the only individual-based mechanistic model representing crop-weed competition for nitrogen (Berger et al., 2013). However, this model focuses on only one weed and one

crop species, while the weed floras in fields generally include dozens of interacting plant species (Fried et al., 2008). Moreover, this model does not represent the effects of cropping systems on weed dynamics, which severely restricts its relevance as decision support to manage crop-weed competition. Among the existing models simulating weed dynamics (Holst et al., 2007; Renton and Chauhan, 2017), FLORSYS is, to our knowledge, the only individual-based model quantifying the effects of cropping systems (crop succession, cultural techniques in terms of tools, options and dates) on the dynamics of multispecies weed floras with a daily time-step, in interaction with pedoclimatic conditions (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014b; Munier-Jolain et al., 2014; Pointurier et al., 2021). This model is already being used to evaluate and design sustainable weed management strategies (Colbach et al., 2017; Colbach and Cordeau, 2018; Van Inghelandt et al., 2019). However, it currently only considers crop-weed competition for light, assuming that nitrogen resources are sufficient to sustain both crop and weed requirements. So, as such, this model cannot be used as a tool to manage crop-weed competition for nitrogen, especially in low inputs systems (e.g. integrated production, organic farming). To deal with this issue, the objectives of the present study were to develop new formalisms to integrate plant-plant competition for nitrogen into the preexisting FLORSYS model, and to illustrate the functioning of the new version of the model with examples of simulations. Including crop-weed competition for nitrogen into FLORSYS will provide knowledge and tools to understand and manage heterogeneous canopies in nitrogen-deficient situations and to promote the biological regulations of weeds via competition.

In this modelling paper, the Material and methods section (Section 2) presents (1) a general overview of the modeling principles in the initial FLORSYS version, (2) the general approach and key processes that we targeted when introducing plant nitrogen nutrition and competition into FLORSYS and (3) the simulation plan applied to illustrate a few model outputs. The Results section (Section 3) describes and justifies, individually for each modeled process, the formalisms that were chosen to model nitrogen competition in FLORSYS. Simulation results are also presented. Finally, the Discussion section (Section 4) analyzes the consequences of our modelling choices and discusses how the new model version could be used for designing more sustainable cropping systems in the future.

2. Material and methods

2.1. The initial FLORSYS structure

2.1.1. General overview

Details are available in section S1 of the supplementary material online as well as in previous papers (Gardarin et al., 2012; Colbach et al., 2014a; Colbach et al., 2014b; Pagès et al., 2020; Pointurier et al., 2021). To give a general overview of FLORSYS, the input variables consist of (1) a description of the simulated field (daily weather, latitude and soil characteristics); (2) all the crops and management operations in the field, with dates, tools and options; and (3) the initial weed seed bank, which is either measured on soil samples or estimated from regional flora assessments (Colbach et al., 2016). FLORSYS comprises a submodel to predict soil climate (Brisson et al. (1998) and another to predict soil structure (Chatelin et al. (2005)). The FLORSYS input variables as well as the soil state variables predicted by the two connected submodels influence the annual life cycle of annual weeds and crops, with a daily time-step.

FLORSYS predicts the multispecies crop-weed canopy in 3D, with an individual-based representation of each crop and weed plant. Crop and weed emergence is predicted as a function of soil temperature, water and structure as well as seasonal dormancy and seed depth. Crop plant location on the 3D field map depends on the sowing pattern whereas weeds are placed randomly in patches. The development and growth of each plant are predicted at a daily time-step, as a function of daily weather and cropping techniques. Plant phenology is described by successive life-stages (cotyledon stage, plantlet, vegetative, flowering onset, maturity onset, death) and depends on temperature and emergence season. At plant maturity, the newly produced weed seeds are added to the soil seed bank and crop grain seeds are harvested.

All the processes underlying plant functioning are described in FLORSYS by a series of species parameters (220 parameters). These parameters correspond to plant traits, with values depending on the species. FLORSYS parameters for all these processes are currently available for 30 arable crop species

and for 26 frequent weed species covering the main ecological niches of temperate European cropping systems (Fried et al., 2009).

In this model, all state variables are available as output variables.

2.1.2. Initial plant growth submodel

Aboveground plant part is described as a cylinder with plant leaf area distributed according to plant height. The canopy is discretized with voxels (i.e. cubic volume cells or "3D pixels"). A light microclimate submodel predicts light trickling along successive voxel layers, depending on the leaf area inside. As shown in **Figure 1**, the global plant growth of each individual plant is source-driven with the intercepted light and temperature as drivers. Shading (described by a shading index) modifies plant morphology mainly by modifying biomass allocation among compartments (e.g. leaves, stems, roots). Part of the newly produced biomass is attributed to the belowground plant part.

A root distribution submodel describes belowground plant part as a cylinder sitting on top a spilled cone with root biomass distributed in the soil profile (Pagès et al., 2020; Pointurier et al., 2021) (**Figure 2a**). This shape was chosen because it is (1) sufficiently simple for multiannual simulations of thousands of plants in a field, (2) generic (i.e. adapted for species with very different features), (3) parameterized for most common crop and weed species encountered in agroecosystems and (4) relatively easy to parameterize for new species. Biomass allocation to roots depends on total plant biomass and species parameters. In case the amount of biomass allocated to roots is lower than root requirements (determined by the root system dimensions), root biomass density within the envelope is affected (but root-system dimensions are not because insufficient resources primarily limit the emission and elongation of fine roots rather than those of primary root axes, which define the shape and size of the root-system envelope) (Pagès et al., 2020; Pointurier et al., 2021).

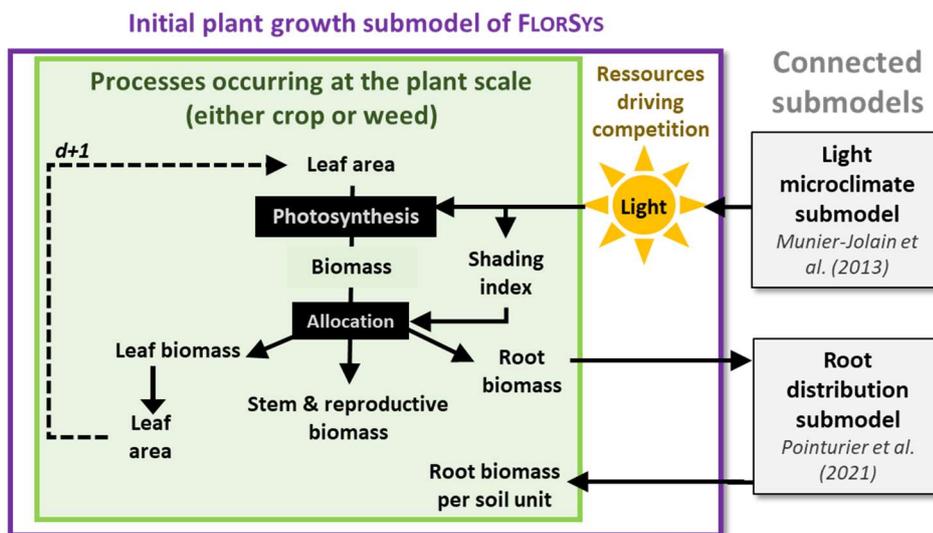


Figure 1: Overview of the initial plant growth submodel of FLORSYS integrating competition for light only. Only key variables are shown. The processes are modelled individually for each plant (either weed or crop). Dotted lines indicate how the daily time step is integrated. Key related submodels are in grey rectangles.

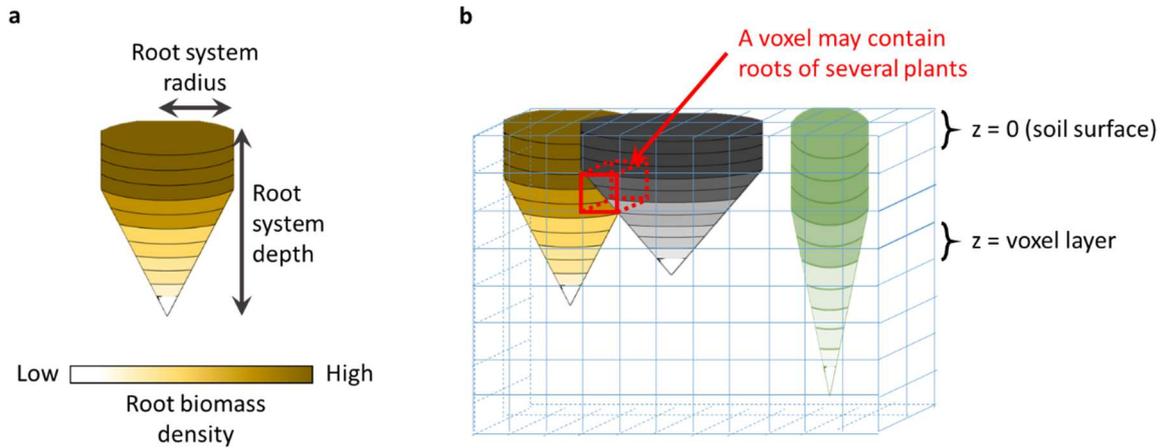


Figure 2: Representation of belowground interactions among plants in FLORSYS. (a) Each plant's root system is represented in 3D as a cylinder sitting on top a spilled cone with root biomass distributed along soil layers (Pointurier et al., 2021). (b) In the new FLORSYS version, the soil is represented in 3D and discretised in voxels. A voxel may contain roots from several neighbouring plants. Competition for nitrogen occurs at the voxel level, when the amount of nitrogen available is lower than the requirements of all the plants with roots in the voxel.

2.2. Methodology for introducing plant nitrogen nutrition and competition into FLORSYS

2.2.1. *General principles*

The following principles were used to include plant nitrogen nutrition and competition into FLORSYS: (1) using literature (from both field trials and controlled conditions) to decide which effects and processes should be included, and focusing on those relevant for comparing cropping systems in terms of weed impacts on crop production and biodiversity, (2) anchoring the new formalisms to pre-existing FLORSYS variables, (3) whenever possible, connecting existing models/submodels rather than develop new ones, (4) when introducing new formalisms into FLORSYS, inspiring them from pre-existing models, (5) preferring generic species-independent and parameter-parsimonious formalisms, and (6) using literature to fit equations and estimate parameters. Note that, as most pre-existing models are population-based models, another principle consisted in adapting their formalisms whenever necessary in order to make them compatible with the individual-based representation of FLORSYS.

2.2.2. *Overview of the targeted processes*

The introduction of plant nitrogen nutrition and competition required to introduce four key aspects into FLORSYS.

2.2.2.1. Soil-nitrogen availability

Soil-nitrogen availability is a key driver of plant nitrogen uptake (Gastal and Lemaire, 2002). However, soil-nitrogen dynamics were absent from the initial FLORSYS version. In order to introduce soil-nitrogen dynamics, we chose to connect a pre-existing model to FLORSYS rather than to add a new submodel to FLORSYS. The advantage was twofold: (1) limiting FLORSYS complexification and (2) benefiting from a model that has already been tested and evaluated.

The STICS soil submodel was used (Brisson et al., 1998) in order to predict ammonium and nitrate concentration at the elementary layer scale (1-cm high) at a daily time step. This submodel was chosen because it accounts for the cropping techniques (i.e. nitrogen fertilisation, plant-residue burial...) and the biophysical processes (i.e. net mineralisation of soil organic matter and organic residues, nitrification, ammonia volatilisation, denitrification and leaching) underlying soil-nitrogen availability at the elementary layer scale. Moreover, STICS has been tested and evaluated in a large range of arable temperate conditions (Beaudoin et al., 2008; Coucheney et al., 2015). Finally, part of the STICS soil submodel was already linked to FLORSYS to predict soil temperature and water potential (Gardarin et al., 2012).

The detail of the connexion between FLORSYS and STICS for soil-nitrogen determination is described below (see Section 3.1.7).

2.2.2.2. Plant nitrogen uptake

Plant nitrogen uptake was not predicted in the initial model version. It is known to depend on both soil-nitrogen availability and plant nitrogen requirements (Gastal and Lemaire, 2002). So, in the new nitrogen version of FLORSYS, we added the prediction of plant nitrogen uptake from the confrontation between plant nitrogen demand and soil-nitrogen supply, as for most plant nitrogen models (Spitters, 1989; Graf et al., 1990; Debaeke et al., 1997; Brisson et al., 1998; Jeuffroy and Recous, 1999).

2.2.2.3. Effect of plant nitrogen nutrition on plant growth

Plant nitrogen nutrition is known to affect plant growth rate, plant morphology and biomass allocation for example to above- vs. below-ground compartments (Chapin, 1980; Radin, 1983; Poorter et al., 1995). Biomass production (i.e. photosynthesis), allocation (to leaves, roots, stems and reproductive organs) and plant morphology were already present in the initial plant growth submodel of FLORSYS (Colbach et al., 2014a; Colbach et al., 2014b; Pointurier et al., 2021). However, their response to plant nitrogen nutrition was not predicted. The introduction of these effects in the new FLORSYS version consisted in modifying the pre-existing formalisms in order to make biomass production, allocation and plant morphology vary according to plant nitrogen nutrition level.

Note that soil-nitrogen availability may affect plant root architecture (Jeudy et al., 2016). However, this effect is mainly mediated by the effect of plant nitrogen nutrition on biomass allocation to roots (Brun et al., 2010; Moreau et al., 2017). So, in accordance with our objective to limit the complexity of our new model version, we considered that modifications of plant root architecture (i.e., the shape and size of the root system envelope and the distribution of root biomass within this envelope) in response to soil-nitrogen availability was entirely mediated by modifications of biomass allocations to roots.

2.2.2.4. 3D-soil representation

In order to make plants interact for the nitrogen resource and therefore to represent plant-plant competition for nitrogen, the FLORSYS soil was represented in 3D. This is a classical approach used in individual-based models predicting plant-plant competition for soil resources (e.g. Louarn et al., 2016). This representation was similar to that used for aboveground canopy and competition for light in FLORSYS (Section 2.1.2).

The FLORSYS soil was divided into voxels whose edge size (e.g. 10 cm) is chosen by the model user at the onset of a simulation (**Figure 2b**). Each plant's root system (represented as a cylinder on top of a spilled cone in which its root biomass is distributed) is located in this 3D soil, allowing to determine root biomass per voxel. In parallel, soil-nitrogen concentration is determined per voxel. In our model, competition for nitrogen occurs when the roots of neighbouring plants share a common voxel whose available nitrogen is insufficient to meet the demands of all these plants (**Figure 2b**). In this approach, the upscaling of nitrogen uptake from soil voxel to plant scale relies on the root system continuity taken into consideration at the individual plant level.

2.3. Simulation plan

Simulations were run using the new FLORSYS version including nitrogen competition with a twofold objective: (a) to test whether conclusions provided by simulation data were in agreement with previous knowledge, and (b) to illustrate the potentialities of the model as a tool to understand nitrogen dynamics in a complex system.

For that purpose, two series of simulation were run (**Table 1**). In accordance with objective (a), simulation series #1 aimed at determining whether modelling nitrogen-related processes at the individual plant scale in FLORSYS allowed accounting for an emergent property occurring at the canopy level, i.e. the critical nitrogen dilution curve (Greenwood et al., 1990; Justes et al., 1994). In homogeneous crop canopies, shoot nitrogen concentration progressively declines with increasing shoot biomass, even when crop nitrogen nutrition is optimal (due to a decrease in the leaf/stem ratio with plant growth and to nitrogen remobilisation from shaded to illuminated leaves of the canopy) (Gastal and Lemaire, 2002). The parameters of the nitrogen dilution curve (determined at optimal crop nitrogen

nutrition) are known to be stable across field conditions for a given species during the vegetative phase (Gastal and Lemaire, 2002). So, simulation series #1 determined whether the FLORSYS model was able to account for this dilution of nitrogen in shoot biomass at the crop canopy level.

1 **Table 1: Scenarios simulated with the nitrogen version of FLORSYS**

Series	Objective	Crop species over one cultural season	Nitrogen dose (%*)	FLORSYS version with nitrogen competition	Weed flora	Number of scenarios
#1	To determine if FLORSYS accounts for the nitrogen dilution at the canopy scale	<ul style="list-style-type: none"> • Winter wheat • Winter rape • Winter barley • Maize 	<ul style="list-style-type: none"> • 100 • 200 • 400 	yes	None	[(4 crops × 3 doses) + (1 crop × 1 dose)] × 1 FLORSYS version = 13 scenarios
		<ul style="list-style-type: none"> • Spring pea 	<ul style="list-style-type: none"> • 0 			
#2	To illustrate how FLORSYS can be used to assess the effects of nitrogen	<ul style="list-style-type: none"> • Winter wheat 	<ul style="list-style-type: none"> • 0 • 50 • 100 	yes	26 annual species, typical of Burgundy	[(1 crop × 3 doses) + (1 crop × 1 dose)] × 1 FLORSYS version + [2 crops × 1 FLORSYS version] = 6 scenarios
		<ul style="list-style-type: none"> • Spring pea 	<ul style="list-style-type: none"> • 0 			
		<ul style="list-style-type: none"> • Winter wheat • Spring pea 	Not applicable	no		

2 *In proportion to the reference situation at each fertilization date

In accordance with objective (b), simulation series #2 aimed at illustrating how the model can be used to discriminate the effects of competition for light only from those of both light and nitrogen in crop-weed interactions in the field.

Simulation series #1 lasted for one cultural season and combined two factors (**Table 1**), the crop species (wheat *Triticum aestivum*, rape *Brassica napus*, barley *Hordeum vulgare*, maize *Zea mays*, or pea *Pisum sativum*) and nitrogen fertilizer dose (except pea which was not fertilized) chosen to ensure situations without plant nitrogen stress. Simulations were run with the version of FLORSYS with nitrogen competition but without weeds in order to simulate pure-stand crop canopies.

Simulation series #2 also lasted for one cultural season and combined three factors (**Table 1**): the crop species (wheat or pea), nitrogen fertilizer dose (0%, 50% and 100%, except pea which was not fertilized) chosen to analyze the consequences of soil-nitrogen availability on crop-weed competition, and presence or absence of nitrogen competition. The latter was achieved by using either the new FLORSYS version including both light and nitrogen competition, or the previous one without nitrogen-competition formalisms.

All simulated scenarios were derived from actual cultural practices characterized in farm surveys and cropping-system trials, with typical soil and weather characteristics from the Burgundy region in France. The simulations including weeds (series #2) started with a soil weed seed bank typically found after a winter wheat (obtained by running a preliminary one-year-long simulation with winter wheat and Burgundy pedoclimate). Each scenario was repeated ten times with ten weather repetitions, each repetition consisting of years randomly chosen in the Burgundy weather database.

3. Results

3.1. Integrating plant nitrogen nutrition and competition into FLORSYS

Based on the principles described in Section 2.2, **Figure 3** (in comparison with **Figure 1**) illustrates the processes added to FLORSYS to take account of plant nitrogen nutrition and competition and how these were connected to existing functions and variables, particularly those related to light competition. The following subsections describe the functions added to (or modified in) the FLORSYS plant-growth submodel to include nitrogen nutrition and competition (**Figure 3**). The daily equations are detailed in **Appendix 1**, parameters in **Appendix 2** and variables in **Appendix 3** and **Appendix 4**.

Plant growth submodel of FLORSYS integrating N nutrition and competition

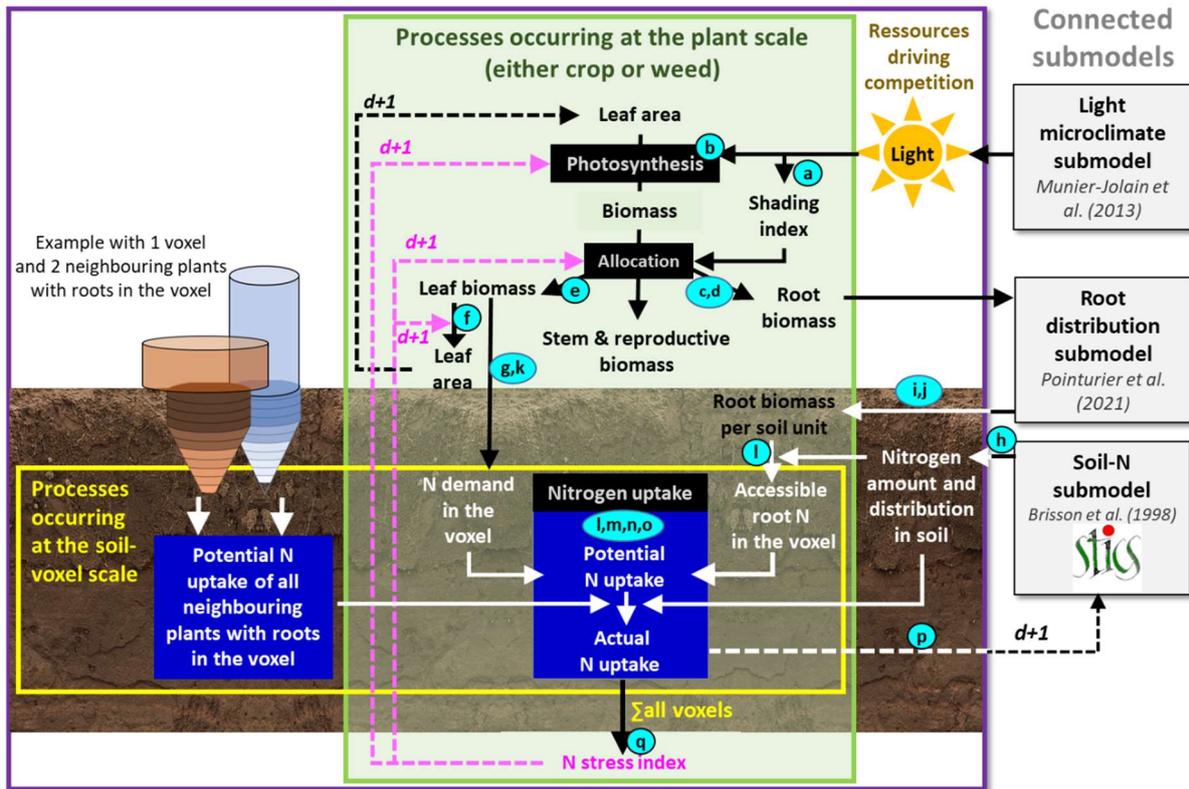


Figure 3: Overview of the new plant growth submodel of FLORSYS integrating both light and nitrogen (N) competition. Only key variables are shown. The processes are modelled individually for each plant (either weed or crop). The processes modelled at the soil-voxel level (for each voxel occupied by the plant) are in the yellow rectangle. Letters on a light blue background refer to the modelling steps of **Appendix 1**. Nitrogen nutrition variables (in white and pink) are connected to the original FLORSYS variables of the submodel (in black). Dotted lines indicate how the daily time step is integrated. Pink lines focus on the effect of plant nitrogen stress on key processes and variables. Key related submodels are in grey rectangles. Competition for nitrogen among neighboring plants occurs at the voxel level. It results from the confrontation between (1) nitrogen availability in the voxel and (2) the potential nitrogen uptake of all plants with roots in the voxel.

3.1.1. Plant initialization

In the initial FLORSYS version, each newly emerged plant is initialized with eight variables (**Equation 1** of **Appendix 1**). For each individual plant, growth variables depend on plant species (Colbach et al., 2014a; Pointurier et al., 2021) and plants are assumed to have experienced no shading yet.

During plant establishment, seed reserves are known to fulfil plant nitrogen requirement (Fayaud et al., 2014). So, in the nitrogen version of FLORSYS, plants at emergence are also assumed to have experienced no nitrogen stress: both their above- and below-ground nitrogen contents are at optimal levels.

3.1.2. Plant photosynthesis

In the initial FLORSYS version, just after emergence, plants are still small and shading is negligible (**Equation 2**). Plant growth is driven by air temperature only (**Equation 3**), considering that light and nitrogen resources are non-limiting. Once shading starts, new plant biomass is calculated from intercepted light and temperature (**Equations 4 and 5**) and added to yesterday's total biomass from which root and aboveground biomass lost by respiration is subtracted (**Equation 6**).

Plant nitrogen stress is known to affect photosynthesis (Chapin, 1980). This phenomenon was taken into account in the nitrogen version of FLORSYS. We considered that the more nitrogen-stressed the plant is, the lower its photosynthetic efficiency is (**Equation 4**). In this model version, the nitrogen stress is

assessed for each individual plant through the calculation of a nitrogen stress index (see Section 3.1.14). The sensitivity of photosynthesis to plant nitrogen stress is known to vary with the plant species (Sinclair and Horie, 1989). This sensitivity was reflected in our model by a species-dependent parameter. This modelling approach was derived from previous models (Graf et al., 1990; Brisson et al., 1998).

3.1.3. Root biomass

In the initial FLORSYS version, the daily accumulated biomass is shared between the above- and below-ground plant parts (**Equation 7**). As described in Pointurier et al. (2021), before flowering onset, the proportion of biomass produced during the day that is allocated to roots depends on species as well as total plant biomass, according to an allometric relationship. From flowering onwards, the proportion of biomass allocated to roots decreases until it becomes nil at maturity onset.

It is known that the more stressed the plant is in terms of nitrogen, the more biomass it allocates proportionally to below- versus above-ground plant parts (Chapin, 1980; Berger et al., 2013). In the new version of the model, this phenomenon was modelled using the formalisms developed by Pointurier et al. (2021) which were developed and parameterized for a large number of crop and weed species (**Equation 7**).

3.1.4. Nitrogen remobilization from below- to above-ground plant parts

In the initial FLORSYS version, carbon remobilisation may occur from below- to above-ground plant parts, (1) in case of strong shading, (2) from flowering onset onwards (when plant respiration is supported by belowground parts only), (3) in case of mowing (affecting plant photosynthesis) (Schiltz et al., 2005; Meiss et al., 2008) or (4) when aboveground biomass is damaged by frost.

So, a feature of the nitrogen version of FLORSYS was to shift nitrogen from below- to above-ground plant parts proportionally to biomass shifts (**Equation 8**). This simplified representation assumes that all the nitrogen initially present in the remobilised biomass (even structural nitrogen) is remobilised to aboveground plant part.

3.1.5. Aboveground plant morphology

3.1.5.1. Leaf biomass ratio

In the initial FLORSYS version, the aboveground biomass is shared between leaves and other organs (including stems and reproductive organs), depending on the total plant biomass and leaf biomass ratio (ratio of leaf to aboveground biomass). The response to shading of leaf biomass ratio varies with the species (Colbach et al., 2014a; Munier-Jolain et al., 2014; Colbach et al., 2020): some increase the proportion of biomass allocated to leaves, others decrease it (this is described, respectively, by $\text{ShadeEffect} > 1$ and < 1 in **Equation 9**).

According to the literature, leaf biomass ratio also varies with nitrogen stress and this response also depends on the species (Berger et al., 2007; Freschet et al., 2015; Perthame et al., submitted-a). So, in the nitrogen version of FLORSYS, leaf biomass ratio was also made to respond to nitrogen stress with species parameters allowing to reflect species differences. We used the same principle as for shading (NstressEffect in **Equation 9**).

Plant morphological responses can be viewed as ways for plants to control their internal carbon and nitrogen ratio, in agreement with the notion of ‘balanced growth’ (Coruzzi and Bush, 2001; Grechi et al., 2007). In the nitrogen version of FLORSYS, the effect of these interactions between carbon and nitrogen were implemented as follow. If both shading and nitrogen stresses have the same effect (i.e. both stresses either increase or decrease the leaf biomass ratio), then the strongest effect is kept (**Equation 10**). If nitrogen stress and shading affect leaf biomass ratio in opposite directions, both effects are multiplied so that the effect of one stress partially cancels out the effect of the other (**Equation 10**). The combined effect of nitrogen stress and shading is then applied to the leaf biomass ratio that the plant would have had in optimal conditions (**Equation 11**), allowing to determine the leaf biomass (**Equation 12**).

3.1.5.2. Specific leaf area

In the initial FLORSYS version, specific leaf area (ratio of leaf area to leaf biomass) allows determining leaf area expansion from leaf biomass. As leaf biomass ratio, specific leaf area responds to shading with the intensity of the response depending on the species.

Specific leaf area is known to also respond to nitrogen stress with species-specificities (Poorter et al., 1995; Freschet et al., 2015; Perthame et al., submitted-a). So, this effect was introduced in the nitrogen version of the model. The principle used for leaf biomass ratio (see Section 3.1.5.1) was applied for specific leaf area in order to calculate leaf area expansion (**Equations 13-16**).

3.1.6. Plant nitrogen demand

Plant nitrogen uptake was absent from the initial FLORSYS version and was therefore introduced here, as resulting from the confrontation between plant nitrogen demand and supply in accordance with classical modelling approaches (see Section 2.2.2). In our model, plant nitrogen demand is determined by the demand of both above- and below-ground plant parts (**Equation 20**). In accordance with the experimental study of Perthame et al. (2020) on several crop and weed species, aboveground nitrogen demand is driven by plant leaf biomass with species-specificities (**Equation 17**). In accordance with other models (Strullu et al., 2014; Louarn and Faverjon, 2018) belowground nitrogen demand is determined by plant root biomass and nitrogen stress (**Equation 18**), considering that the more nitrogen-stressed a plant is, the lower is the nitrogen concentration of belowground parts, and therefore the lower is the nitrogen demand of belowground parts.

Soil-nitrogen uptake was shown to be generally negligible from the beginning of seed filling onwards. (Waldren and Flowerday, 1979; Rossato et al., 2001). Thus, plant nitrogen demand in the model is considered to be nil from this stage onwards (corresponding to the stage 'maturity onset' in FLORSYS) (**Equation 19**).

3.1.7. Nitrogen concentration in soil voxels at the beginning of the day

Plant nitrogen supply was absent from the initial model version. Inspired by other models (Soussana et al., 2012; Louarn et al., 2016), the nitrogen version of FLORSYS makes plant nitrogen supply depend on both plant root distribution in the soil (**Figure 2b**) and soil-nitrogen concentration. Soil-nitrogen concentration is provided at the beginning of each simulation day by the STICS soil submodel (Brisson et al., 1998) connected to FLORSYS. The STICS soil is divided into 1D 1-cm soil layers while the FLORSYS soil is divided into 3D voxels (**Section S2** of the Supplementary material online). To make both soil representations compatible, soil-nitrogen concentration is averaged over several 1-cm STICS layers to correspond to one FLORSYS voxel layer (e.g. ten 1-cm soil layers of STICS if the soil-voxel edge size in FLORSYS is 10 cm) (**Equation 21**). Note that the soil-nitrogen concentration at the beginning of each day is the same in all the voxels located at the same depth (i.e. on a voxel layer).

3.1.8. Root system width and root biomass per voxel at depth z

As represented in **Figure 2**, in the initial FLORSYS version, the width of the root system is determined for each plant and for each soil layer.

As, plant-plant competition for nitrogen is modelled at the voxel scale, the nitrogen version of FLORSYS determines how many voxels are occupied by the plant's roots depending on the voxel depth (Section **S3** of the Supplementary Material online; **Figure 2**; **Equations 22 and 23**). Moreover, root biomass is distributed for each plant among the voxels occupied by roots in order to determine root biomass density (i.e. root biomass per voxel) (**Equation 24**). Note that, for a given plant, root biomass density is the same for all the voxels that are on the same voxel layer.

3.1.9. Distribution of plant nitrogen demand among soil voxels

All the processes described from 3.1.9 to 3.1.14 were absent from the initial FLORSYS version and were introduced specifically in the nitrogen version of the model. Similarly to the model of Louarn and Faverjon (2018), plant nitrogen demand in the nitrogen version of FLORSYS is distributed, for each plant, among the voxels occupied by its roots (**Equation 26**). This distribution is proportional to the amount of soil-nitrogen available to the plant in each voxel, depending on the nitrogen concentration in the voxel (see Section 3.1.7) and the root nitrogen uptake capacity (**Equation 25**).

3.1.10. Plant nitrogen uptake

In accordance with Louarn and Faverjon (2018), plant nitrogen uptake is determined at the voxel level where competition may occur (**Figure 2**). For each plant, nitrogen uptake is estimated with two steps. First, the potential nitrogen uptake (i.e. nitrogen uptake in the absence of neighbouring plant) is determined for each plant. In each voxel with roots, it depends on both plant nitrogen demand and available soil nitrogen (see Section 3.1.9) (**Equation 28**). Then, actual nitrogen uptake is determined for each plant. For that purpose, for each voxel, the potential nitrogen uptake summed over all the plants with roots inside the voxel is compared to the voxel nitrogen concentration:

- If there is enough nitrogen in the voxel, all the plants meet their nitrogen requirements (**Equation 29**). The amount of nitrogen remaining in the voxel afterwards (superfluous nitrogen in **Equation 33**) may then be used to compensate insufficient nitrogen uptake in other voxels for some plants (see Section 3.1.11);
- Otherwise, within-voxel competition occurs. Nitrogen in the voxel is distributed among plants proportionally to their potential nitrogen uptake (see above) (**Equation 30-31**) in accordance with other models (Soussana et al., 2012). The amount of nitrogen missing to each plant to meet its requirements is determined (**Equation 32**). It may be partially or totally fulfilled with nitrogen remaining in other voxels explored by the plant roots (see Section 3.1.11). Note that the amount of nitrogen missing to meet plant requirements is reset at 0 at the beginning of each day (**Equation 1**).

3.1.11. Compensation for missing nitrogen

Plants were shown to adapt to the spatial heterogeneity in soil-nitrogen availability (Lainé et al., 1998). Consequently, the nitrogen version of FLORSYS allows plants to compensate for missing nitrogen. For that purpose, we consider that, if nitrogen remains in a voxel after the nitrogen uptake described above (see Section 3.1.10), plants with roots in this voxel which could not fulfil their nitrogen requirements in previous voxels, can compensate immediately by taking up more nitrogen in the voxel (**Equation 34**). This leads to a second loop in the algorithm. To be noted that compensation occurs successively, one voxel after another.

The formalisation of compensation for missing nitrogen is similar to the formalisation of plant nitrogen uptake (Section 3.1.10). First, independently for each plant in the voxel where nitrogen remains, the potential compensation is determined (**Equation 35**). Then, for all the unsatisfied plants with roots in this voxel, the actual compensation is determined (**Equation 36**). After compensation, the amount of nitrogen still missing to plants is recorded (**Equation 37**), so that it can be compensated in following voxels.

3.1.12. Nitrogen in plants after uptake

In the nitrogen version of FLORSYS, as in other models (e.g. Louarn and Faverjon, 2018), the amount of nitrogen in plants after uptake depends on both the amount of nitrogen in the plant at the preceding day and the integration over all the voxels of the amount of nitrogen taken up during the current day (**Equation 39**). The amount of nitrogen taken up is then distributed between above- and below-ground plant parts proportionally to the nitrogen demand of each plant part (**Equation 40**).

It is established that during plant establishment and early growth, seed reserves contribute to fulfil plant nitrogen requirement (Fayaud et al., 2014). To account for this process in our model, missing nitrogen is compensated when plant nitrogen uptake is lower than plant nitrogen demand, for each day from plant emergence to the end of the plantlet stage (**Equation 38**).

Experimental studies show that nitrogen uptake becomes generally negligible from the beginning of seed filling (Waldren and Flowerday, 1979; Rossato et al., 2001). To account for this effect in our model, the total amount of nitrogen in the plant remains constant from the stage ‘maturity onset’ in FLORSYS (**Equation 41**).

3.1.13. Nitrogen concentration in soil voxels and layers at the end of the day

In the nitrogen version of the model, at the end of the day, the remaining soil nitrogen concentration is averaged over all the voxels at the same depth (i.e. in a voxel layer) (**Equation 42**). The nitrogen concentration is then determined for each 1-cm soil layer to be provided to the STICS model (Section S2 of the Supplementary material online; **Equation 43**).

3.1.14. *Plant nitrogen stress index*

Plants can experience nitrogen stress in field conditions (e.g. Berry et al., 2002). In order to quantify the degree of fulfilment of plant nitrogen requirement, the nitrogen version of FLORSYS calculates a nitrogen stress index each day for each plant. This approach is similar to the approach developed in several models simulating the effects of nitrogen uptake on plant growth (Graf et al., 1990; Debaeke et al., 1997; Brisson et al., 1998; Louarn and Faverjon, 2018). In FLORSYS, the nitrogen stress index is based on the amount of aboveground nitrogen per unit leaf biomass (Perthame et al., 2020) (**Equation 44**). It takes values close to 0 for plants with an optimal nitrogen nutrition to sustain growth. It increases with the intensity of nitrogen stress (up to 1) and negative values point to nitrogen excess.

In FLORSYS, the nitrogen-stress-index value is used the following day to modulate plant photosynthesis, biomass allocation to above- vs. below-ground plant parts, and aboveground plant morphology (Sections 3.1.2, 3.1.3 and 3.1.5) (**Figure 3**). This allows to reflect, for example, that both photosynthesis and biomass allocation to the aboveground (vs. belowground) part decrease with increasing plant nitrogen stress (Brouwer, 1962; Chapin, 1980). Note that from the beginning of seed filling (corresponding to ‘maturity onset’ in FLORSYS), i.e. when plant nitrogen uptake stops (see Section 3.1.6), the value of plant nitrogen stress index remains constant until the end of plant cycle (**Equation 45**). This is the end of the daily nitrogen loop.

3.2. The particular case of legume species

Legume species present two main specificities that must be considered when modelling crop nitrogen competition with weeds: (1) these species are able to symbiotically fix atmospheric dinitrogen, and (2) their competitive ability with non-legume species for nitrogen is generally low (Corre-Hellou et al., 2006; Corre-Hellou et al., 2007). In the nitrogen version of FLORSYS, the ability of legume species to symbiotically fix atmospheric dinitrogen is indirectly taken into account, considering that nitrogen-fixing legume plants always fulfil their nitrogen requirement, whatever the amount of mineral nitrogen they take up (**Equation 39**). Legume plants are considered to be able to fix dinitrogen (**Equation 27**) after a time lag which is necessary to establish an effective symbiosis with *Rhizobium* bacteria, as shown by Moreau et al. (2008).

The lower competitiveness of nitrogen-fixing legume plants for nitrogen is taken into consideration when within-voxel competition for nitrogen occurs. In this situation, nitrogen-fixing legume plants can take up mineral nitrogen only if nitrogen remains in the voxel after uptake by the other plants (**Equations 29-31**). Moreover, nitrogen-fixing legume plants cannot compensate for missing nitrogen (see Section 3.1.11).

3.3. Occasional processes

Two main processes affecting plant and soil nitrogen may occur occasionally (**Appendix 5**).

3.3.1. *Plant nitrogen loss*

Outside the nitrogen loop, occasional events (e.g. frost, strong shading or mowing) may occur, resulting in plant biomass loss. In this case, in the nitrogen version of FLORSYS, the amount of nitrogen of the affected (above- and/or below-ground) compartment is reduced proportionally to biomass loss (**Equation 46**).

3.3.2. *Crop nitrogen return to soil*

Some cultural operations may cause crop biomass and therefore nitrogen return to soil. These operations are mowing (including shredding), harvest, tillage (except rolling), mechanical weeding and herbicide application (if the herbicide spectrum includes the current crop). So, in the nitrogen version of FLORSYS, the biomass returning to soil (**Equation 47**) is converted into nitrogen and carbon using parameters of the STICS model (the carbon to nitrogen ratio of the residues determines the decomposition dynamics) (Brisson et al., 1998).

3.4. Integrating the effects of pedoclimate and management practices

The pedoclimatic inputs relevant for FLORSYS to simulate plant nitrogen nutrition and for the linked STICS soil submodel to predict soil-nitrogen availability are soil texture and structure, organic soil nitrogen concentration, daily temperature, ETP, precipitation, radiation.... The main cropping system components relevant for plant-plant competition for nitrogen in FLORSYS not only include nitrogen fertilisation techniques (date, dose, type of fertilizer) but also any technique influencing soil state variables (e.g., water availability) as well as crop and weed emergence and growth.

3.5. Parameterizing a range of crop and weed species

Eight new parameters need to be estimated to run the nitrogen submodel of FLORSYS (in red bold in **Appendix 2**). Seven of them are species-dependent (i.e. all of them except rN which is a non-specific parameter accounting for the effect of plant nitrogen stress on biomass allocation to roots) (Pointurier et al., 2021). The species-dependent parameters were estimated from data available in the literature or from specific experiments (see the references in **Appendix 2** and Section **S4** of the Supplementary material online). At present, they were estimated only for a limited number (seven) of weed and crop species (Section **S5** of the Supplementary material online). Rules based on species similarity were established to estimate parameter values for species for which no experimental data could be found (e.g. species A behaves like species B for process X).

3.6. Output variables

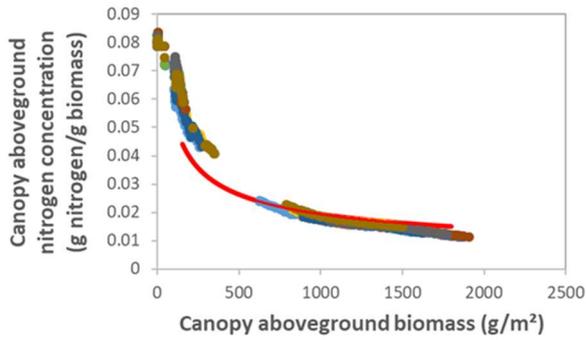
The main output variables of the plant growth submodel are plant densities and biomass (discriminating roots, seeds and remaining) per day, m² and species (Colbach et al., 2014b; Pointurier, 2019). With the nitrogen integration into FLORSYS, the new output variables are (1) for each day of a simulation, the amount of nitrogen per soil layer and (2) for each day of a simulation and each plant species (either crop or weed), the amount of nitrogen and the nitrogen stress index. If needed, variables can also be accessed for each individual plant.

3.7. Examples of simulation

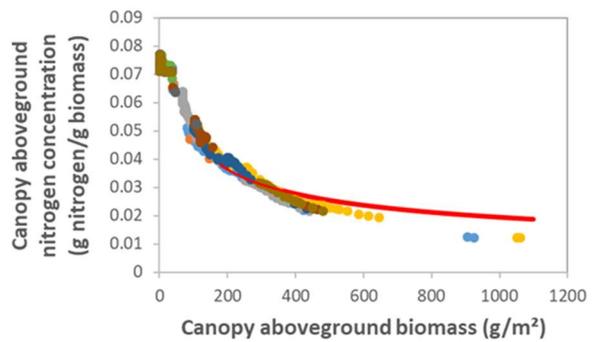
3.7.1. *Does FLORSYS account for nitrogen dilution in biomass at the canopy level (simulation series#1)?*

For each simulated crop species, shoot nitrogen concentration decreased progressively with increasing shoot canopy biomass during the vegetative growth when crop nitrogen stress was close to nil (**Figure 4**). For wheat, barley and, to a lesser degree pea, the relationship between shoot nitrogen concentration and biomass was similar for the ten weather repetitions and the simulated curves were close to the dilution curves referenced in the literature (Justes et al., 1994; Ney et al., 1997; Zhao, 2014). For maize and rape, the differences among weather repetitions and the deviations to the published dilution curves were greater.

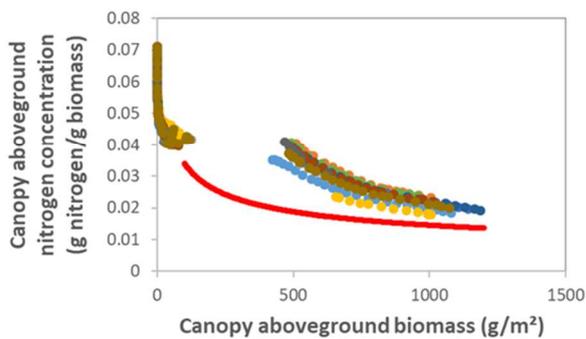
(a) Wheat



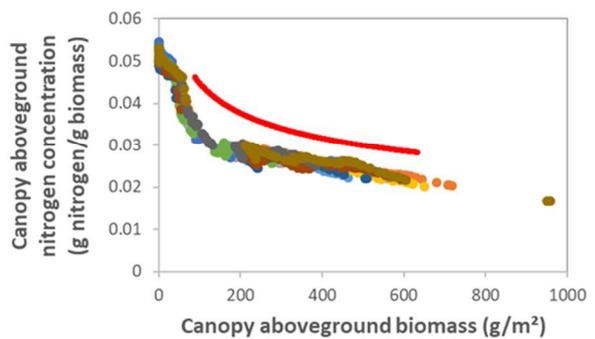
(b) Barley



(c) Maize



(d) Rape



(e) Pea

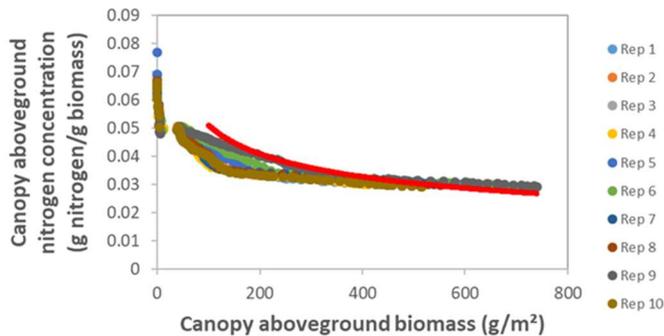


Figure 4: Simulated dilution of nitrogen in aboveground biomass at optimal plant nitrogen nutrition during vegetative stages for five crop species. For each crop species, the ten weather repetitions are shown. Only data until flowering stage and without nitrogen stress ($-0.1 < N_{\text{stress}} < 0.1$) are included. The red curves show the official nitrogen dilution curves (from Justes et al. (1994) for wheat, Zhao (2014) for barley, Plénet and Lemaire (1999) for maize, Colnenne et al. (1998) for rape and Ney et al. (1997) for pea).

3.7.2. Can FLORSYS be used to discriminate the effects of competition for light only versus competition for both light and nitrogen (simulation series#2)?

For wheat and pea, the dynamics crop and total weed biomass were compared using two FLORSYS versions, without vs. with competition for nitrogen (competition for light was integrated in both versions).

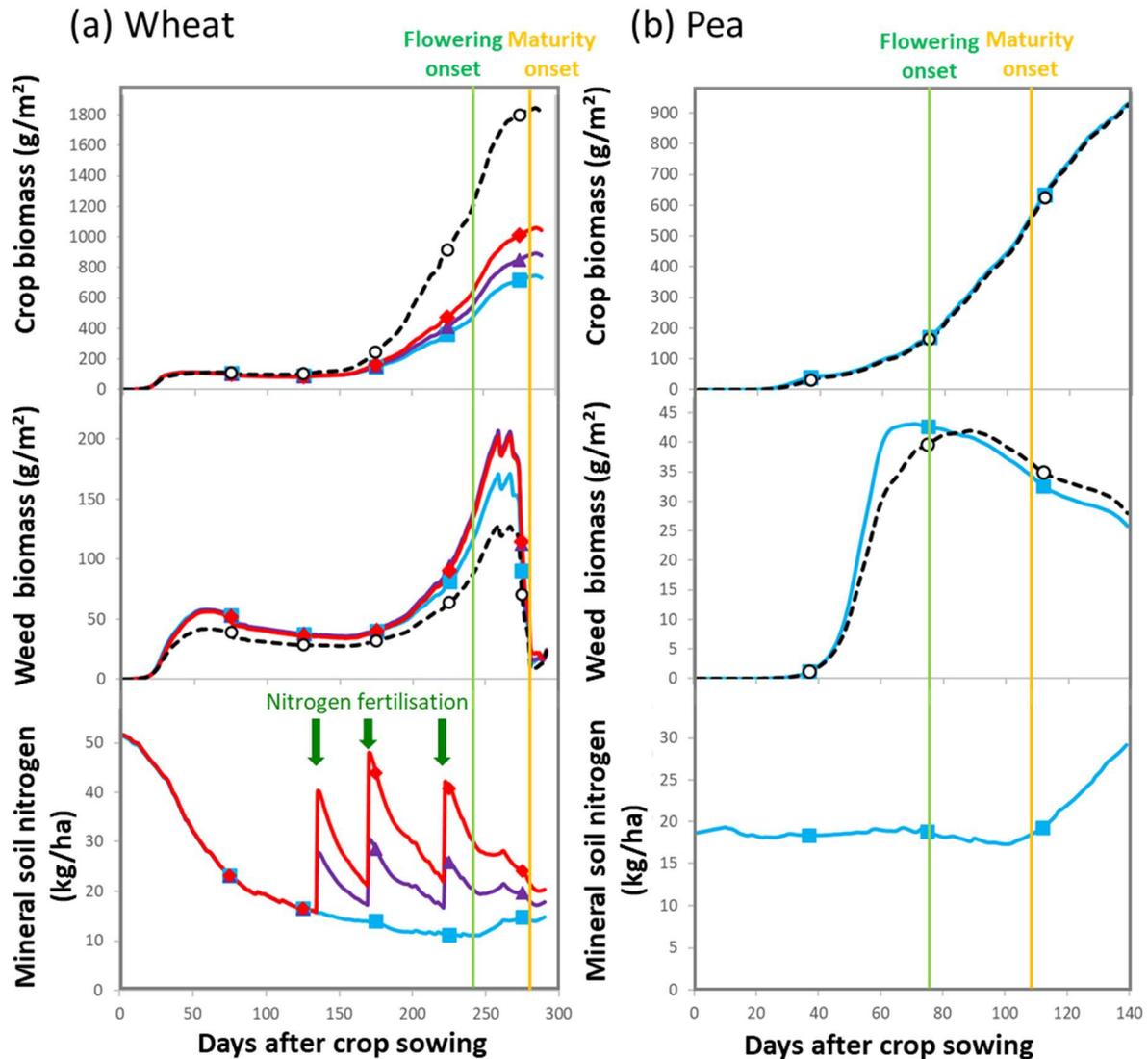


Figure 5: Simulation of crop biomass, weed biomass and soil-mineral nitrogen under different levels of nitrogen competition during (a) wheat and (b) pea growing seasons. Black dashed lines for simulation data with only light competition (initial version of the model without the nitrogen competition submodel). The other lines for simulation data with both light and nitrogen competition (new version with the nitrogen competition submodel): blue for no nitrogen fertilization, purple for 50% of the reference nitrogen dose, and red for 100% of the reference nitrogen dose. Values are averages over 10 weather repetitions.

In wheat, nitrogen competition strongly affected crop and total weed growth (**Figure 5a**). On average, including nitrogen competition (in addition to competition for light) in FLORSYS reduced wheat biomass by 42 to 60 % just before harvest (depending on the nitrogen fertilization dose). At the peak of weed biomass (corresponding to 259 days after sowing), nitrogen competition increased total weed biomass by 48 to 60 %. However, the inclusion of nitrogen competition increased weed biomass (in absolute value) much less than it decreased wheat biomass, suggesting that wheat plants were nitrogen-limited not only because of weed competition. Indeed, plant nitrogen stress values higher than 1 (between 0.23 and 0.31 depending on the nitrogen fertilization regime; data not shown) showed that the wheat crop was nitrogen-stressed in all the simulations. This nitrogen stress probably results from interactions among soil characteristics, climate and nitrogen fertilization and indicates that the 100% nitrogen fertilizer rate is too low for targeting the potential yield in the simulated situation.

When running FLORSYS including nitrogen competition, increasing nitrogen dose promoted wheat growth, while weed growth was not significantly modified (**Figure 6**). Thus, competition for nitrogen globally promoted weed at the expense of wheat growth, and the more the nitrogen dose increased, the more wheat vs. weed growth was promoted. The contribution of each weed species to total weed biomass varied little with nitrogen fertilizer dose when including nitrogen competition in simulations (data not shown). Differences with situations disregarding nitrogen competition were minor (**Figure 7a**): the dominating species were the same, only their proportion varied slightly.

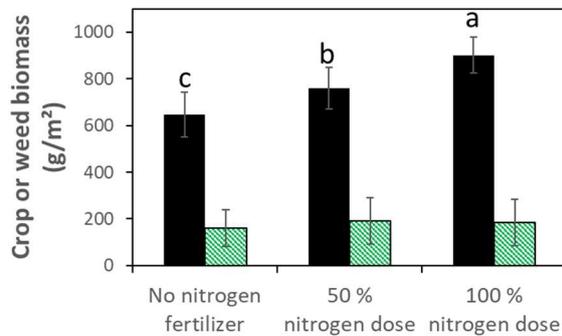


Figure 6: Response of wheat and weed biomass to nitrogen dose at the date of the peak of weed biomass (259 days after sowing). Black bars show wheat biomass and green bars show total weed biomass. The three nitrogen treatments are shown: no nitrogen fertilization, 50% and 100% of the reference nitrogen dose. Values are mean and standard deviation over the 10 weather repetitions. Different letters among nitrogen treatments for wheat biomass indicate significant differences (lsd test after anova; $P < 0.001$). The nitrogen dose did not significantly affect total weed biomass ($P > 0.05$).

Including nitrogen competition in simulations did not affect pea growth. Weed growth was slightly modified (**Figure 5b**): the peak of biomass was earlier (17 days) and slightly higher (+ 3 %) with nitrogen competition. Weed flora composition was globally not affected (**Figure 7b**).

These simulations also allowed checking that the mineral soil nitrogen dynamics were correctly simulated. In wheat, soil nitrogen decreased continuously from crop emergence onwards as crop and weed plants took up nitrogen (**Figure 5a**). Each time the crop was fertilized, soil nitrogen peaked and then decreased again until the next fertilizing operation, with noticeable differences according to the fertilizer dose. Conversely, in pea, soil nitrogen remained stable until 107 days after sowing (**Figure 5b**): during this phase, pea nitrogen nutrition mainly relied on mineralized soil nitrogen and nitrogen fixation (beginning 36 days after sowing). After 107 days after sowing, corresponding to the onset of pea seed filling, mineral soil nitrogen increased as pea nitrogen demand was nil and organic soil nitrogen was mineralized (**Equation 19 in Appendix 1**).

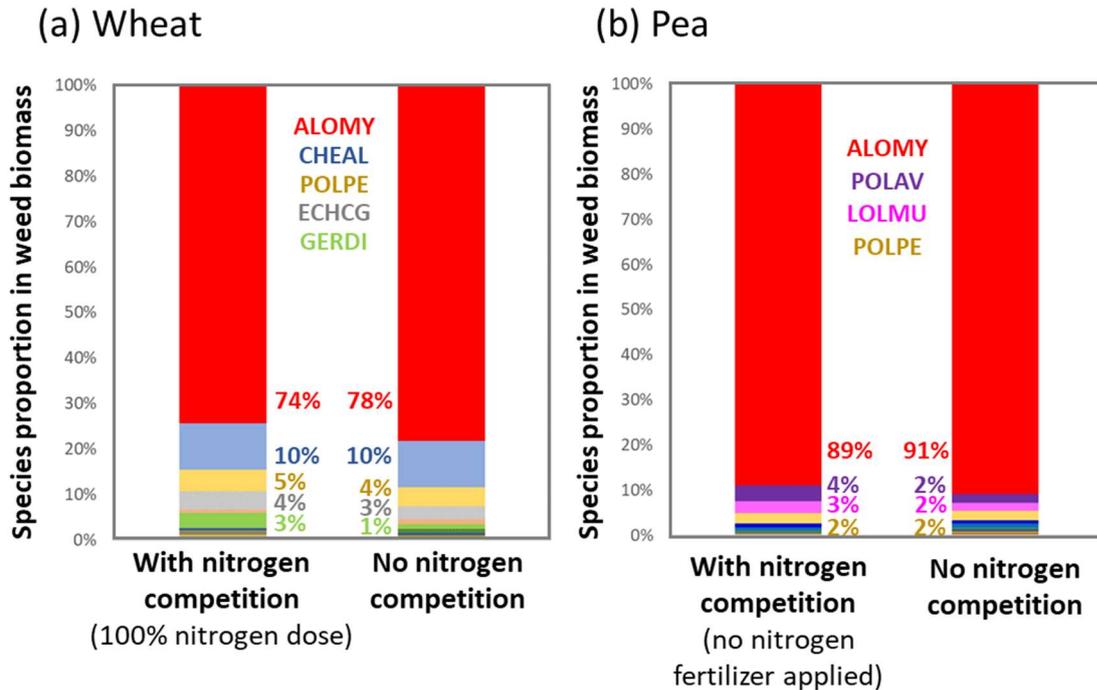


Figure 7: Simulation of weed flora composition in (a) wheat and (b) pea. Weed species proportion is compared at 265 and 85 days after sowing for wheat and pea, respectively. Values are averages over 10 weather repetitions. Weed species are named by their EPPO code: ALOMY for *Alopecurus myosuroides*, CHEAL for *Chenopodium album*, POLPE for *Persicaria maculosa*, ECHCG for *Echinochloa crus-galli*, GERDI for *Geranium dissectum*, POLAV for *Polygonum aviculare* and LOLMU for *Lolium multiflorum*.

4. Discussion

4.1. The first mechanistic cropping system model focusing on weeds that simulates plant-plant competition for nitrogen

Until now, weed simulation models mostly focused on competition for light, reflecting their origin in countries where light is a major limiting resource (Renton and Chauhan, 2017). In this study, the introduction of nitrogen into FLORSYS makes it the first process-based model able to simulate the effects of cropping systems on weed dynamics by accounting for the role of plant-plant competition for nitrogen, in addition to competition for light (which was already integrated). The introduction of nitrogen into FLORSYS benefited from formalisms previously published, either in individual-based models (Soussana et al., 2012; Berger et al., 2013; Louarn and Faverjon, 2018) or in models using the canopy as a unit of representation (Spitters, 1989; Graf et al., 1990; Debaeke et al., 1997; Brisson et al., 1998; Jeuffroy and Recous, 1999). In the second case, formalisms were downscaled to be valid at the individual plant level. In addition, new representations of plant nitrogen uptake were proposed in our modelling approach. This is the case of the compensation (see Section 3.1.11): if nitrogen uptake in one soil voxel is insufficient to fulfil plant nitrogen requirements in this voxel, we proposed that it could be compensated by increasing nitrogen uptake in other voxels. This original representation, which we did not find in other previous models in the literature, allowed reflecting the plant adaptation to the spatial heterogeneity in soil-nitrogen availability. Given the genericity of the equations we developed, such a representation should be easily transferable to other models simulating plant-plant competition for nitrogen (e.g. for ley pastures, which are usually multispecies including legumes).

The connection of the nitrogen-related functions of the soil submodel of STICS (Brisson et al., 1998) to this new FLORSYS version provided a simple way to integrate soil-nitrogen availability in our model. Indeed, without adding new equations related to soil-nitrogen dynamics directly to FLORSYS, this approach allowed to integrate soil-nitrogen dynamics and many underlying mechanisms which are

simulated by STICS (i.e. net mineralisation of soil organic matter and organic residues, nitrification, ammonia volatilisation, denitrification and leaching).

When modelling nitrogen competition in FLORSYS, one concern was to minimize the number of new parameters to facilitate parameterizing the many crop and weed species needed to simulate agroecological cropping systems (Malezieux et al., 2009). So, in spite of the many new processes that we integrated into FLORSYS to account for plant nitrogen nutrition, only seven new species-dependent parameters were introduced (in addition to a species-independent one).

4.2. Several simplifying assumptions in accordance with the domain of use of FLORSYS

Some processes related to plant functioning were neglected. For example, the spatial distribution of roots for a given plant was assumed symmetric (radial symmetry), neglecting the ability of plant roots to proliferate in soil patches with higher nutrient content (Ferrieri et al., 2017; Izzo et al., 2019). Another example is the effect of nitrogen on phenology. But, even though this occurs, it is not systematic and both anticipated or delayed phenology (e.g. flowering date) were reported, depending on plant species and environments (Wang and Tang, 2019; Luo et al., 2020).

Other processes were represented very roughly, e.g. the ability of legume plants to fix atmospheric nitrogen. It was important to include legume crop species in the model, as they are essential for future sustainable cropping systems. One major simplifying assumption in our model was that nitrogen-fixing legume plants always fulfil their nitrogen requirements. A few field studies reported suboptimal nitrogen nutrition in legumes (Guinet et al., 2018). This simplification may result in overestimated legume growth in simulations. However, the impact of this simplification may be limited as situations of nitrogen limitation in legumes in real-field conditions may be infrequent (Guinet et al., 2018), and crop nitrogen limitation does not necessarily result in crop yield reduction (Ravier et al., 2017).

Species parameterization was approximate for some processes. For instance, the negative effect of plant nitrogen stress on photosynthetic efficiency was assumed to be proportional and identical for all species. Even though this is not entirely true (Sinclair and Horie, 1989; Grindlay, 1997), this is a classic hypothesis in modelling approaches (Brisson et al., 1998). A sensitivity analysis to this model parameter will be useful to analyze the consequences on key output variables.

Other simplifications concern the spatial representation of soil nitrogen dynamics. We used the 1D STICS soil model (across successive soil layers) to predict soil-nitrogen concentration even though FLORSYS works with a 3D root distribution. Our approach indirectly assumes that horizontal nitrogen transfers occur very rapidly (i.e. daily) within a soil voxel layer, from zones with low soil-nitrogen uptake to zones with high soil-nitrogen uptake. This approach also assumes that the spatial variability of nitrogen uptake between plants, due to the the spatial variability of the dynamics of their root lateral expansion, largely exceeds the impact of lateral variability of mineral nitrogen, which was not provided by the soil-nitrogen submodel of STICS. This probable unrealistic representation of soil nitrogen dynamics may affect plant-plant competition for nitrogen and therefore plant nitrogen stress, particularly in situations with low plant densities, patchy weed distributions and/or canopy gaps. A perspective in the midterm could be to use another soil submodel with a 3D representation (e.g. Louarn et al., 2016). This could be useful to quantify the effects of nitrogen positioning (e.g. sowing row vs. inter-row) on crop-weed interactions. In this case, it will be sufficient to change the soil submodel connected to FLORSYS. The FLORSYS formalisms reflecting plant nitrogen uptake will be kept the same.

All these simplifying assumptions are acceptable considering that FLORSYS is used as a cropping system model primarily devoted to the analysis of the cumulative multiannual effects of cropping systems. A high precision in the predictions at the plant scale is not the main objective, provided that the ranking of cropping systems according to their performances related to weed regulation is correct within the domain of validity of the model (Colbach et al., 2016; Pointurier et al., 2021). Moreover, adding even more details to the simulated processes not only increases the risk of errors but also the duration of the simulation. Indeed, each process is simulated daily over several years or decades, for each individual crop and weed plant (up to several thousand per m² when a field is highly infested by weeds) and for each above- and below-ground voxel (up to several thousand per m² field). Parsimony is thus required when new submodels are developed (Renton and Chauhan, 2017). This parsimony principle was respected here by (1) using a 3D representation only for plant-based processes (and not for horizontal nitrogen transfers), (2) using a simplified generic root-system representation that applies to all crop and

weed species, (3) using the same nitrogen-related formalism that again apply to all crop and weed species, which allowed to (4) add only seven new species-specific parameters. Despite these restrictions, the first (albeit limited) model evaluation shows the model to produce realistic results (see the following section).

4.3. Predictions regarding nitrogen dilution in crop canopies are consistent with literature

Despite simplifications, our simulations with the nitrogen version of FLORSYS were consistent with previous knowledge, notably the dilution of shoot nitrogen with increasing shoot biomass at the crop canopy level. Yet, this well-known phenomenon observed in the field (Gastal and Lemaire, 2002) was not integrated as such in FLORSYS equations. Thus, our approach for modelling (1) the processes underlying carbon and nitrogen nutrition at the individual plant level and (2) plant-plant interactions (via light and nitrogen availability) were robust enough to account for this emergent property at the canopy level. Interestingly, the less well predicted species were either only roughly parameterized (maize), pointing to the model sensitivity to nitrogen parameters, or highly plastic in response to shading (rape; Munier-Jolain et al., 2014), in accordance with the important effect of interactions between carbon and nitrogen nutrition on the nitrogen dilution curve (Gastal and Lemaire, 2002). However, it will be necessary to go further in model evaluation. The next step will consist in evaluating the new model version with independent field data including weeds.

4.4. A tool to assess nitrogen competition effects

FLORSYS provides a powerful tool to decipher, quantify and understand processes that are intrinsically linked to other processes and therefore difficult to measure under real field conditions. This is the case of competition for nitrogen that is intrinsically linked to competition for light. In our study, comparing simulations run with the nitrogen FLORSYS version and the original one (i.e. with competition for light only) allowed illustrating how our model can be used to quantify the importance of nitrogen competition in crop-weed interactions. In our simulation example with a pea crop, these interactions were only slightly affected by nitrogen competition. This finding is in line with the specificities of pea nitrogen nutrition relying on symbiotic nitrogen fixation (Voisin et al., 2002). Conversely, in our simulations with a wheat crop, nitrogen competition strongly affected both crop and weed growth, and overall competition for nitrogen promoted weed vs. crop growth. Previous studies suggested complex interactions between the relative nitrophily of competing species and soil-nitrogen availability to explain the outcome of competition (Moreau et al., 2013; Moreau et al., 2014). To our knowledge, this nitrophily hypothesis has not been tested yet, and future virtual experiments with the new FLORSYS version will be useful to test it (after model evaluation). Further multiannual simulations will also be needed to identify the key management techniques (e.g. related to nitrogen fertilization or to crop species/variety choice via their parameter values) and options (e.g. the best nitrogen fertilization dose and/or date, the best crop variety) to combine, according to the pedoclimatic and floristic context and the cropping system. Further simulations (including sensitivity analyses) will also be needed to identify the key plant parameters explaining crop- and weed-differential responses to nitrogen fertilization (Perthame et al., submitted-b). Such simulation-based approaches were proven to be relevant to better understand the determinants of competition and to design management guidelines for farmers and technical advisors (Colbach et al., 2017; Colbach et al., 2019; Colbach et al., 2021).

4.5. A tool to give insights in the study of ecological intensification

Ecological intensification aims at driving ecological functions and associated ecosystem services in order to sustain crop production while reducing negative environmental impacts (Bommarco et al., 2013). In the case of weed management, driving crop-weed competition is viewed as an important component in order to promote biological weed regulation while reducing herbicide use and the associated negative impacts (Liebman et al., 2016; Renton and Chauhan, 2017; Sardana et al., 2017). Further research is still needed to determine how to drive competition in order to promote crop growth at the expense of weed growth. For that purpose, mechanistic crop-weed competition models, such as FLORSYS, and the associated simulation methodology can help to investigate the benefits of ecological intensification (Colbach et al., 2019; Colbach et al., 2021). Especially, the analysis of crop-weed competition for both light and nitrogen, as provided by the new FLORSYS version, will be helpful to

better understand the role of multivariety or multispecies cash crop canopies, such as ley pastures, cereal-legume associations, companion crops or fallow cover crops in low nitrogen-input systems (Corre-Hellou et al., 2011; Fletcher et al., 2016; Gaudio et al., 2019; Martin et al., 2020). Moreover, crop-crop interactions in intercropping are driven by the same processes as in a crop-weed canopy. So, beyond this specific challenge of biological weed regulation, the new FLORSYS version should also be helpful to better understand multispecies canopies as an option to drive ecological functions in low nitrogen-input systems (plant-plant competition, niche complementarity). Finally, FLORSYS is helpful to transfer knowledge on ecological intensification to stakeholders, via virtual experiments or by further synthesizing this knowledge in decision-support systems (Colbach et al., 2021). Such tools do not only help individual farmers to design or fine-tune cropping systems, they also facilitate dialog and creativity in workshops.

5. Conclusions

By complementing the preexisting FLORSYS model, this study provides the first mechanistic cropping system model focusing on weeds that simulates plant-plant competition for nitrogen (in addition to competition for light). In spite of the many processes that we integrated into the model, only seven new species-dependent parameters were introduced (in addition to a species-independent one). Our simulations were consistent with previous knowledge, notably the dilution of shoot nitrogen with increasing shoot biomass at the crop canopy level. Examples of simulations also showed the potential of the new FLORSYS version to better understand the role of nitrogen competition in crop-weed interactions, and to determine how to drive competition in order to penalize weed growth. After parameterizing more crop and weed species, the next steps will (1) evaluate the new model version with independent field data, following Colbach et al. (2016), and (2) perform a sensitivity analysis to identify the key nitrogen fertilization options and crop parameters to combine to promote biological weed regulation by competition in agroecological cropping systems.

6. Acknowledgments

This work was supported by INRAE, the research programme ‘Assessing and reducing environmental risks from plant protection products’ funded by the French Ministries in charge of Ecology and Agriculture, CoSAC project (ANR-15-CE18-0007), the Casdar RAID project funded by the French Ministry in charge of Agriculture and Food (Ministère de l’Agriculture et de l’Alimentation, avec la contribution financière du compte d’affectation spéciale ‘Développement agricole et rural’) and the European Union’s Horizon 2020 Research and innovation programme under grant agreement N. 7272171 (ReMIX project).

7. References

- Andersson, T.N., Milberg, P., 1998. Weed flora and the relative importance of site, crop, crop rotation, and nitrogen. *Weed Sci* 46, 30-38.
- Angonin, C., Caussanel, J.P., Meynard, J.M., 1996. Competition between winter wheat and *Veronica hederifolia*: Influence of weed density and the amount and timing of nitrogen application. *Weed Res* 36, 175-187.
- Beaudoin, N., Launay, M., Sauboua, E., Ponsardin, G., Mary, B., 2008. Evaluation of the soil crop model STICS over 8 years against the “on farm” database of Bruyères catchment. *Eur J Agron* 29, 46-57.
- Berger, A., McDonald, A., Riha, S., 2007. Does soil nitrogen affect early competitive traits of annual weeds in comparison with maize? *Weed Res* 47, 509-516.
- Berger, A.G., McDonald, A.J., Riha, S.J., 2013. Simulating Root Development and Soil Resource Acquisition in Dynamic Models of Crop-Weed Competition. In: Timlin, D., Ahuja, L.R. (Eds.), *Enhancing Understanding and Quantification of Soil-Root Growth Interactions*, Vol 4. Amer Soc Agronomy, Madison, pp. 229-244.
- Berry, P.M., Sylvester-Bradley, R., Philipps, L., Hatch, D.J., Cuttle, S.P., Rayns, F.W., Gosling, P., 2002. Is the productivity of organic farms restricted by the supply of available nitrogen? *Soil Use and Management* 18, 248-255.
- Blackshaw, R.E., Brandt, R.N., 2008. Nitrogen fertilizer rate effects on weed competitiveness is species dependent. *Weed Sci* 56, 743-747.

Blackshaw, R.E., Brandt, R.N., Janzen, H.H., Entz, T., Grant, C.A., Derksen, D.A., 2003. Differential response of weed species to added nitrogen. *Weed Sci* 51, 532-539.

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230-238.

Bourgeois, A., Gaba, S., Munier-Jolain, N., Borgy, B., Monestiez, P., Soubeyrand, S., 2012. Inferring weed spatial distribution from multi-type data. *Ecol Modell* 226, 92-98.

Brainard, D.C., Bellinder, R.R., 2004. Assessing variability in fecundity of *Amaranthus powellii* using a simulation model. *Weed Res* 44, 203-217.

Brisson, N., Mary, B., Ripoche, D., Jeuffroy, M.H., Ruget, F., Nicoullaud, B., Gate, P., Devienne-Barret, F., Antonioletti, R., Durr, C., 1998. STICS: a generic model for the simulation of crops and their water and nitrogen balances. I. Theory and parameterization applied to wheat and corn. *Agronomie* 18, 311-346.

Brouwer, R., 1962. Nutritive influences on the distribution of dry matter in the plant. 10, 399-408.

Brun, F., Richard-Molard, C., Pages, L., Chelle, M., Ney, B., 2010. To what extent may changes in the root system architecture of *Arabidopsis thaliana* grown under contrasted homogenous nitrogen regimes be explained by changes in carbon supply? A modelling approach. *J. Exp. Bot.* 61, 2157-2169.

Chapin, F.S., 1980. The Mineral Nutrition of Wild Plants. *Annual Review of Ecology and Systematics* 11, 233-260.

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

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

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

Colbach, N., Biju-Duval, L., Gardarin, A., Granger, S., Guyot, S., Mézière, D., Munier-Jolain, N., Petit, S., 2014a. The role of models for multicriteria evaluation and multiobjective design of cropping systems for managing weeds. *Weed Res* 54, 541-555.

Colbach, N., Bockstaller, C., Colas, F., Gibot-Leclerc, S., Moreau, D., Pointurier, O., Villerd, J., 2017. Assessing broomrape risk due to weeds in cropping systems with an indicator linked to a simulation model. *Ecol Indic* 82, 280-292.

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

Colbach, N., Colas, F., Cordeau, S., Maillot, T., Queyrel, W., Villerd, J., Moreau, D., 2021. The FLORSYS crop-weed canopy model, a tool to investigate and promote agroecological weed management. *Field Crops Research* 261, 108006.

Colbach, N., Collard, A., Guyot, S.H.M., Meziere, D., Munier-Jolain, N., 2014b. Assessing innovative sowing patterns for integrated weed management with a 3D crop:weed competition model. *Eur J Agron* 53, 74-89.

Colbach, N., Cordeau, S., 2018. Reduced herbicide use does not increase crop yield loss if it is compensated by alternative preventive and curative measures. *Eur J Agron* 94, 67-78.

Colbach, N., Forcella, F., Johnson, G., 2000. Temporal trends in spatial variability of weed populations in 3 continuous no-till soybean. *Weed Sci.* 48.

Colbach, N., Gardarin, A., Moreau, D., 2019. The response of weed and crop species to shading: Which parameters explain weed impacts on crop production? *Field Crops Research* 238, 45-55.

Colbach, N., Moreau, D., Dugué, F., Gardarin, A., Strbik, F., Munier-Jolain, N., 2020. The response of weed and crop species to shading. How to predict their morphology and plasticity from species traits and ecological indexes? *Eur J Agron* 121, 126158.

Colnenne, C., Meynard, J., Reau, R., Justes, E., Merrien, A., 1998. Determination of a critical nitrogen dilution curve for winter oilseed rape. *Ann Bot* 81, 311-317.

Corre-Hellou, G., Brisson, N., Launay, M., Fustec, J., Crozat, Y., 2007. Effect of root depth penetration on soil nitrogen competitive interactions and dry matter production in pea–barley intercrops given different soil nitrogen supplies. *Field Crops Research* 103, 76-85.

Corre-Hellou, G., Dibet, A., Hauggaard-Nielsen, H., Crozat, Y., Gooding, M., Ambus, P., Dahlmann, C., von Fragstein, P., Pristeri, A., Monti, M., Jensen, E.S., 2011. The competitive ability of pea-barley intercrops against weeds and the interactions with crop productivity and soil N availability. *Field Crops Research* 122, 264-272.

Corre-Hellou, G., Fustec, J., Crozat, Y., 2006. Interspecific competition for soil N and its interaction with N₂ fixation, leaf expansion and crop growth in pea–barley intercrops. *Plant and Soil* 282, 195-208.

Coruzzi, G., Bush, D.R., 2001. Nitrogen and Carbon Nutrient and Metabolite Signaling in Plants. *Plant Physiology* 125, 61-64.

Coucheney, E., Buis, S., Launay, M., Constantin, J., Mary, B., García de Cortázar-Atauri, I., Ripoché, D., Beaudoin, N., Ruget, F., Andrianarisoa, K.S., Le Bas, C., Justes, E., Léonard, J., 2015. Accuracy, robustness and behavior of the STICS soil–crop model for plant, water and nitrogen outputs: Evaluation over a wide range of agro-environmental conditions in France. *Environmental Modelling & Software* 64, 177-190.

Debaeke, P., Caussanel, J.P., Kiniry, J.R., Kafiz, B., Mondragon, G., 1997. Modelling crop:weed interactions in wheat with ALMANAC. *Weed Res* 37, 325-341.

Ditomaso, J.M., 1995. Approaches for improving crop competitiveness through the manipulation of fertilization strategies. *Weed Sci* 43, 491-497.

Evans, S.P., Knezevic, S.Z., Lindquist, J.L., Shapiro, C.A., Blankenship, E.E., 2003. Nitrogen application influences the critical period for weed control in corn. *Weed Sci* 51, 408-417.

Fahad, S., Hussain, S., Chauhan, B.S., Saud, S., Wu, C., Hassan, S., Tanveer, M., Jan, A., Huang, J., 2015. Weed growth and crop yield loss in wheat as influenced by row spacing and weed emergence times. *Crop Protection* 71, 101-108.

Fayaud, B., Coste, F., Corre-Hellou, G., Gardarin, A., Dürr, C., 2014. Modelling early growth under different sowing conditions: A tool to predict variations in intercrop early stages. *Eur J Agron* 52, 180-190.

Ferrieri, A.P., Machado, R.A.R., Arce, C.C.M., Kessler, D., Baldwin, I.T., Erb, M., 2017. Localized micronutrient patches induce lateral root foraging and chemotropism in *Nicotiana attenuata*. *J. Integr. Plant Biol.* 59, 759-771.

Fletcher, A.L., Kirkegaard, J.A., Peoples, M.B., Robertson, M.J., Whish, J., Swan, A.D., 2016. Prospects to utilise intercrops and crop variety mixtures in mechanised, rain-fed, temperate cropping systems. *Crop Pasture Sci.* 67, 1252-1267.

Forcella, F., 1993. Seedling Emergence Model for Velvetleaf. *Agron J* 85, 929-933.

Freschet, G.T., Swart, E.M., Cornelissen, J.H.C., 2015. Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction. *New Phytologist* 206, 1247-1260.

Fried, G., Chauvel, B., Reboud, X., 2009. A functional analysis of large-scale temporal shifts from 1970 to 2000 in weed assemblages of sunflower crops in France. *Journal of Vegetation Science* 20, 49-58.

Fried, G., Norton, L.R., Reboud, X., 2008. Environmental and management factors determining weed species composition and diversity in France. *Agric Ecosyst Environ* 128, 68-76.

Galloway, J.N., Aber, J.D., Erisman, J.W., Seitzinger, S.P., Howarth, R.W., Cowling, E.B., Cosby, B.J., 2003. The Nitrogen Cascade. *BioScience* 53, 341-356.

Gardarin, A., Dürr, C., Colbach, N., 2012. Modeling the dynamics and emergence of a multispecies weed seed bank with species traits. *Ecol Modell* 240, 123-138.

Gastal, F., Lemaire, G., 2002. N uptake and distribution in crops: an agronomical and ecophysiological perspective. *J. Exp. Bot.* 53, 789-799.

Gaudio, N., Escobar-Gutiérrez, A.J., Casadebaig, P., Evers, J.B., Gérard, F., Louarn, G., Colbach, N., Munz, S., Launay, M., Marrou, H., Barillot, R., Hinsinger, P., Bergez, J.-E., Combes, D., Durand, J.-L., Frak, E., Pagès, L., Pradal, C., Saint-Jean, S., Van Der Werf, W., Justes, E., 2019. Current knowledge and future research opportunities for modeling annual crop mixtures. A review. *Agron Sustain Dev* 39, 20.

Graf, B., Gutierrez, A.P., Rakotobe, O., Zahner, P., Delucchi, V., 1990. A simulation model for the dynamics of rice growth and development: Part II—The competition with weeds for nitrogen and light. *Agricultural Systems* 32, 367-392.

Grechi, I., Vivin, P., Hilbert, G., Milin, S., Robert, T., Gaudillère, J.P., 2007. Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. *Environmental and Experimental Botany* 59, 139-149.

Greenwood, D.J., Lemaire, G., Gosse, G., Cruz, P., Draycott, A., Neeteson, J.J., 1990. Decline in Percentage N of C3 and C4 Crops with Increasing Plant Mass. *Ann Bot* 66, 425-436.

Grindlay, D.J.C., 1997. Towards an explanation of crop nitrogen demand based on the optimization of leaf nitrogen per unit leaf area. *J. Agric. Sci.* 128, 377-396.

Guinet, M., Nicolardot, B., Revellin, C., Durey, V., Carlsson, G., Voisin, A.-S., 2018. Comparative effect of inorganic N on plant growth and N₂ fixation of ten legume crops: towards a better understanding of the differential response among species. *Plant and Soil* 432, 207-227.

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

Iqbal, J., Wright, D., 1997. Effects of nitrogen supply on competition between wheat and three annual weed species. *Weed Res* 37, 391-400.

Izzo, L.G., Romano, L.E., De Pascale, S., Mele, G., Gargiulo, L., Aronne, G., 2019. Chemotropic vs Hydrotropic Stimuli for Root Growth Orientation in Microgravity. *Frontiers in Plant Science* 10.

Jeudy, C., Adrian, M., Baussard, C., Bernard, C., Bernaud, E., Bourion, V., Busset, H., Cabrera-Bosquet, L., Cointault, F., Han, S.M., Lamboeuf, M., Moreau, D., Pivato, B., Prudent, M., Trouvelot, S., Truong, H.N., Vernoud, V., Voisin, A.S., Wipf, D., Salon, C., 2016. RhizoTubes as a new tool for high throughput imaging of plant root development and architecture: test, comparison with pot grown plants and validation. *Plant Methods* 12.

Jeuffroy, M.-H., Recous, S., 1999. Azodyn: a simple model simulating the date of nitrogen deficiency for decision support in wheat fertilization. *Eur J Agron* 10, 129-144.

Jornsgard, B., Rasmussen, K., Hill, J., Christiansen, J.L., 1996. Influence of nitrogen on competition between cereals and their natural weed populations. *Weed Res* 36, 461-470.

Justes, E., Mary, B., Meynard, J.-M., Machet, J.-M., Thelier-Huché, L., 1994. Determination of a critical nitrogen dilution curve for winter wheat crops. *Ann Bot* 74, 397-407.

Lainé, P., Ourry, A., Boucaud, J., Salette, J., 1998. Effects of a localized supply of nitrate on NO₃-uptake rate and growth of roots in *Lolium multiflorum* Lam. *Plant and Soil* 202, 61-67.

Liebman, M., Baraibar, B., Buckley, Y., Childs, D., Christensen, S., Cousens, R., Eizenberg, H., Heijting, S., Loddo, D., Merotto Jr, A., 2016. Ecologically sustainable weed management: How do we get from proof-of-concept to adoption? *Ecol. Appl.* 26, 1352-1369.

Louarn, G., Faverjon, L., 2018. A generic individual-based model to simulate morphogenesis, C-N acquisition and population dynamics in contrasting forage legumes. *Ann Bot* 121, 875-896.

Louarn, G., Faverjon, L., Migault, V., Escobar-Gutiérrez, A., Didier, C., 2016. Assessment of '3DS', a soil module for individual-based models of plant communities.

Luo, L., Zhang, Y., Xu, G., 2020. How does nitrogen shape plant architecture? *J. Exp. Bot.*

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

Martin, G., Durand, J.-L., Duru, M., Gastal, F., Julier, B., Litrico, I., Louarn, G., Médiène, S., Moreau, D., Valantin-Morison, M., Novak, S., Parnaudeau, V., Paschalidou, F., Vertès, F., Voisin, A.-S., Cellier, P., Jeuffroy, M.-H., 2020. Role of ley pastures in tomorrow's cropping systems. A review. *Agron Sustain Dev* 40, 17.

Meiss, H., Munier-Jolain, N., Henriot, F., Caneill, J., 2008. Effects of biomass, age and functional traits on regrowth of arable weeds after cutting. *Journal of Plant Diseases and Protection* 21, 493-499.

Moreau, D., Abiven, F., Busset, H., Matejicek, A., Pagès, L., 2017. Effects of species and soil-nitrogen availability on root system architecture traits. Study on a set of weed and crop species. *Annals of Applied Biology* 171, 103-116.

Moreau, D., Busset, H., Matejicek, A., Munier-Jolain, N., 2014. The ecophysiological determinants of nitrophily in annual weed species. *Weed Res* 54, 335-346.

Moreau, D., Milard, G., Munier-Jolain, N., 2013. A plant nitrophily index based on plant leaf area response to soil nitrogen availability. *Agron Sustain Dev* 33, 809-815.

Moreau, D., Voisin, A.-S., Salon, C., Munier-Jolain, N., 2008. The model symbiotic association between *Medicago truncatula* cv. Jemalong and *Rhizobium meliloti* strain 2011 leads to N-stressed plants when symbiotic N₂ fixation is the main N source for plant growth. *J. Exp. Bot.* 59, 3509-3522.

Munier-Jolain, N.M., Collard, A., Busset, H., Guyot, S.H., Colbach, N., 2014. Investigating and modelling the morphological plasticity of weeds. *Field Crops Research* 155, 90-98.

Munier-Jolain, N.M., Guyot, S.H.M., Colbach, N., 2013. A 3D model for light interception in heterogeneous crop:weed canopies: Model structure and evaluation. *Ecol Modell* 250, 101-110.

Ney, B., Doré, T., Sagan, M., 1997. Grain legumes. Diagnosis of the nitrogen status in crops. Springer, pp. 107-117.

Oerke, E.C., 2006. Crop losses to pests. *J. Agric. Sci.* 144, 31-43.

Pagès, L., Pointurier, O., Moreau, D., Voisin, A.-S., Colbach, N., 2020. Metamodelling a 3D architectural root-system model to provide a simple model based on key processes and species functional groups. *Plant and Soil* 448, 231-251.

Perry, L.G., Neuhauser, C., Galatowitsch, S.M., 2003. Founder control and coexistence in a simple model of asymmetric competition for light. *Journal of Theoretical Biology* 222, 425-436.

Perthame, L., Colbach, N., Brunel-Muguet, S., Busset, H., Lilley, J.M., Matejcek, A., Moreau, D., 2020. Quantifying the nitrogen demand of individual plants in heterogeneous canopies: a case study with crop and weed species. *Eur J Agron* 119.

Perthame, L., Colbach, N., Busset, H., Matejcek, A., Moreau, D., submitted-a. Morphological response of weed and crop species to nitrogen stress in interaction with shading. *Weed Res.*

Perthame, L., Moreau, D., Maillot, T., Colbach, N., submitted-b. Can modulations of nitrogen fertilization techniques and crop traits help to promote biological weed regulation by competition? *Field Crops Research*.

Petit, S., Cordeau, S., Chauvel, B., Bohan, D., Guillemain, J.-P., Steinberg, C., 2018. Biodiversity-based options for arable weed management. A review. *Agron Sustain Dev* 38, 48.

Plénet, D., Lemaire, G., 1999. Relationships between dynamics of nitrogen uptake and dry matter accumulation in maize crops. Determination of critical N concentration. *Plant and Soil* 216, 65-82.

Pointurier, O., 2019. Modélisation des effets des systèmes de culture sur la dynamique de la plante parasite orobanche rameuse en interaction avec les adventices. PhD Thesis. Université Bourgogne Franche-Comté, Dijon, France, p. 156.

Pointurier, O., Moreau, D., Pagès, L., Caneill, J., Colbach, N., 2021. Individual-based 3D modelling of root systems in heterogeneous plant canopies at the multiannual scale. Case study with a weed dynamics model. *Ecol Modell* 440.

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

Poorter, H., Vandevijver, C., Boot, R.G.A., Lambers, H., 1995. Growth and carbon economy of a fast-growing and a slow-growing grass species as dependent on nitrate supply. *Plant and Soil* 171, 217-227.

Radin, J.W., 1983. Control of plant growth by nitrogen: differences between cereals and broadleaf species. *Plant, Cell & Environment* 6, 65-68.

Ravier, C., Meynard, J.-M., Cohan, J.-P., Gate, P., Jeuffroy, M.-H., 2017. Early nitrogen deficiencies favor high yield, grain protein content and N use efficiency in wheat. *Eur J Agron* 89, 16-24.

Renton, M., Chauhan, B.S., 2017. Modelling crop-weed competition: Why, what, how and what lies ahead? *Crop Protection* 95, 101-108.

Rossato, L., Laine, P., Ourry, A., 2001. Nitrogen storage and remobilization in *Brassica napus* L. during the growth cycle: nitrogen fluxes within the plant and changes in soluble protein patterns. *J. Exp. Bot.* 52, 1655-1663.

Sardana, V., Mahajan, G., Jabran, K., Chauhan, B.S., 2017. Role of competition in managing weeds: An introduction to the special issue. *Crop Protection* 95, 1-7.

Schiltz, S., Munier-Jolain, N., Jeudy, C., Burstin, J., Salon, C., 2005. Dynamics of exogenous nitrogen partitioning and nitrogen remobilization from vegetative organs in pea revealed by ¹⁵N in vivo labeling throughout seed filling. *Plant Physiology* 137, 1463-1473.

Sinclair, T.R., Horie, T., 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: a review. *Crop Science* 29, 90-98.

Soussana, J.-F., Maire, V., Gross, N., Bachelet, B., Pagès, L., Martin, R., Hill, D., Wirth, C., 2012. Gemini: A grassland model simulating the role of plant traits for community dynamics and ecosystem functioning. Parameterization and evaluation. *Ecol Modell* 231, 134-145.

Spitters, C., 1989. Weeds: population dynamics, germination and competition. In: Rabbinge, R., Ward, S., van Laar, H. (Eds.), *Simulation and systems management in crop protection. Simulation monographs.* Pudoc, Wageningen, pp. 182-216.

Strullu, L., Beaudoin, N., de Cortázar Aauri, I.G., Mary, B., 2014. Simulation of Biomass and Nitrogen Dynamics in Perennial Organs and Shoots of *Miscanthus* × *Giganteus* Using the STICS Model. *BioEnergy Research* 7, 1253-1269.

Swanton, C.J., Anil, S., Robert, C.R., Bonnie, R.B.-C., Knezevic, S.Z., 1999. Effect of Tillage Systems, N, and Cover Crop on the Composition of Weed Flora. *Weed Sci* 47, 454-461.

Swarbreck, S.M., Wang, M., Wang, Y., Kindred, D., Sylvester-Bradley, R., Shi, W., Varinderpal, S., Bentley, A.R., Griffiths, H., 2019. A Roadmap for Lowering Crop Nitrogen Requirement. *Trends in Plant Science* 24, 892-904.

Tilman, E.A., Tilman, D., Crawley, M.J., Johnston, A.E., 1999. Biological weed control via nutrient competition: Potassium limitation of dandelions. *Ecol. Appl.* 9, 103-111.

Van Delden, A., Lotz, L.A.P., Bastiaans, L., Franke, A.C., Smid, H.G., Groeneveld, R.M.W., Kropff, M.J., 2002. The influence of nitrogen supply on the ability of wheat and potato to suppress *Stellaria media* growth and reproduction. *Weed Res* 42, 429-445.

van Groenendael, J.M., 1988. Patchy distribution of weeds and some implications for modelling population dynamics: a short literature review. *Weed Res* 28, 437-441.

Van Inghelandt, B., Queyrel, W., Colas, F., Guyot, B., Colbach, N., 2019. Combiner prototypage et modèles en ateliers de co-conception de systèmes de culture pour une gestion durable des adventices : apports méthodologiques et perspectives. Séminaire final du projet de recherche ANR CoSAC-Gestion des adventices dans un contexte de changement, Paris, France, pp. 39-41.

Vleeshouwers, L.M., Kropff, M.J., 2000. Modelling field emergence patterns in arable weeds. *New Phytologist* 148, 445-457.

Voisin, A.S., Salon, C., Munier-Jolain, N.G., Ney, B., 2002. Quantitative effects of soil nitrate, growth potential and phenology on symbiotic nitrogen fixation of pea (*Pisum sativum* L.). *Plant and Soil* 243, 31-42.

Waldren, R.P., Flowerday, A.D., 1979. Growth Stages and Distribution of Dry Matter, N, P, and K in Winter Wheat1. *Agron J* 71, 391-397.

Wang, C., Tang, Y.J., 2019. Responses of plant phenology to nitrogen addition: a meta-analysis. *Oikos* 128, 1243-1253.

Wells, G., 1979. Annual weed competition in wheat crops: the effect of weed density and applied nitrogen. *Weed Res* 19, 185-191.

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

Zhao, B., 2014. Determining of a critical dilution curve for plant nitrogen concentration in winter barley. *Field Crops Research* 160, 64-72.

8. Appendix

Appendix 1: Equations of the daily processes of the nitrogen version of FLORSYS

Equations with d: day in days, l: soil layer in cm (with l=0 at soil surface), (x,y,z): coordinates in number of voxels (with z counting from soil surface downward), s: species, i: individual plant, c: cohort (all plants of the same species emerging the same day), stage \in {cotyledon, plantlet, vegetative, flowering, maturity onset, full maturity}. **Parameters are in blue (bold)** while state variables are in black. Grey cells show equations that are used in the nitrogen version of FLORSYS without modifications.

Process	#	When	Equation	Parameters and variables (for details, see Appendix 2 and Appendix 3)
Initialisation	1	$\forall s, \forall c, \forall i$ If d=emergence	$SI_{dsi} = 0$ $TBM_{dsi} = f(\text{species})$ (Colbach et al., 2014b) $LBM_{dsi} = f(\text{species})$ (Colbach et al., 2014b) $RBM_{dsi} = f(\text{species})$ (Colbach et al., 2014b) $Nstress_{dsi} = 0$ $Naboveground_{dsi} = LBM_{dsi} \cdot \mathbf{cNreq_s}$ $Nbelowground_{dsi} = RBM_{dsi} \cdot \mathbf{cRootN_s}$ $Nplant_{dsi} = Naboveground_{dsi} + Nbelowground_{dsi}$	<ul style="list-style-type: none"> • SI_{dsi} = Cumulated shading since emergence • TBM_{dsi} = Total plant biomass • LBM_{dsi} = Plant leaf biomass • RBM_{dsi} = Plant root biomass • $Nstress_{dsi}$ = Plant nitrogen stress index • $Naboveground_{dsi}$ = Amount of nitrogen in the plant aboveground part • $\mathbf{cNreq_s}$ = Optimal amount of nitrogen in the vegetative aboveground part of the plant per unit of leaf biomass • $Nbelowground_{dsi}$ = Amount of nitrogen in the belowground plant part • $\mathbf{cRootN_s}$ = Response rate of root nitrogen concentration to nitrogen stress • $Nplant_{dsi}$ = Total amount of nitrogen in plant
		$\forall s, \forall c, \forall i, \forall d$	$missingN_{dsi} = 0$	<ul style="list-style-type: none"> • $missingN_{dsi}$ = Amount of nitrogen missing to the plant to meet its nitrogen requirement
(a) Shading (Munier-Jolain et al., 2013; Munier-Jolain et al., 2014)	2	$\forall d, \forall s, \forall c, \forall i$	$SI_{dsi} = f(\text{plant aboveground morphology, aboveground morphology of neighbour plants})$	
(b) Photosynthesis (Munier-Jolain et al.,	3	$\forall d, \forall s, \forall c, \forall i$ If $SI_{dsi} < 0.05$	$\Delta TBM_{dsi} = f(LA_{d-1si}, \text{temperature}_d, \text{species})$	<ul style="list-style-type: none"> • ΔTBM_{dsi} = Daily accumulated total biomass

2013; Colbach et al., 2014b)				<ul style="list-style-type: none"> • LA_{dsi} = Plant leaf area • $temperature_d$ = Mean air temperature
	4	$\forall d, \forall s, \forall c, \forall i$ If $SI_{dsi} \geq 0.05$	If $N_{stress_{d-1s}} \in [0,1]$ Then $\epsilon b_{dsi} = (1 - N_{stress_{d-1s}}) \cdot cN\epsilon b_s \cdot \epsilon b_{totmax_s}$ else $\epsilon b_{dsi} = \epsilon b_{totmax_s}$	<ul style="list-style-type: none"> • ϵb_{dsi} = Radiation use efficiency • $cN\epsilon b_s$ = Response rate of maximal radiation use efficiency to nitrogen stress • ϵb_{totmax_s} = Maximal radiation use efficiency
	5		$\Delta TBM_{dsi} = \epsilon b_{dsi} \cdot PAR_{dsi} \cdot f_1(temperature_d) - f_2(temperature_d, TBM_{d-1s})$	<ul style="list-style-type: none"> • PAR_{dsi} = Intercepted radiation
	6		$TBM_{dsi} = TBM_{d-1s} + \Delta TBM_{dsi} - \Delta RBM_{resp_{dsi}} - \Delta ABM_{resp_{dsi}}$	<ul style="list-style-type: none"> • $\Delta RBM_{resp_{dsi}}$ = Aboveground biomass lost by respiration • $\Delta ABM_{resp_{dsi}}$ = Root biomass lost by respiration
(c) Root biomass allocation (Pointurier et al., 2021)	7	$\forall d, \forall s, \forall c, \forall i$	<p>If $TBM_{dsi} \leq 0.0001$ g/plant, Then $RBR_{dsi} = 0$</p> <p>Else if $stage_{sc} \in [cotyledon, vegetative]$ then $RBR_{dsi} = \frac{r1_s \cdot (TBM_{dsi} - 0.0001)^{r2_s} \cdot 10^{rN \cdot N_{stress_{d-1s}}}}{TBM_{dsi}}$</p> <p>else if $stage_{sc} = flowering$, then $RBR_{dsi} = \frac{r1_s \cdot (TBM_{dsi} - 0.0001)^{r2_s} \cdot 10^{rN \cdot N_{stress_{d-1s}}}}{TBM_{dsi}} \cdot PropTTflo_{dsi}$</p> <p>else if $stage_{sc} = maturity$ onset then $RBR_{dsi} = 0$</p> <p>If $RBR_{dsi} > 0.567$ then $RBR_{dsi} = 0.567$ If $RBR_{dsi} < 0$ then $RBR_{dsi} = 0$</p> <p>$RBM_{dsi} = RBM_{d-1s} + RBR_{dsi} \cdot \Delta TBM_{dsi}$</p>	<ul style="list-style-type: none"> • RBR_{dsi} = Proportion of root biomass in total plant biomass • $r1_s$ and $r2_s$ = Parameters to predict root biomass from total biomass • rN = Parameter reflecting the effect of nitrogen stress on biomass allocation to roots • $PropTTflo_{dsi}$ = Proportion of elapsed thermal time from beginning to end of flowering
(d) Nitrogen remobilization from below- to above-ground parts	8	$\forall d, \forall s, \forall c, \forall i$ If $RBM_{dsi} < RBM_{d-1s}$	$N_{belowground_temp_{dsi}} = N_{belowground_{d-1s}} - N_{belowground_{d-1s}} \cdot \frac{(RBM_{d-1s} - RBM_{dsi})}{RBM_{d-1s}}$ $N_{aboveground_temp_{dsi}} = N_{aboveground_{d-1s}} + N_{belowground_{d-1s}} \cdot \frac{(RBM_{d-1s} - RBM_{dsi})}{RBM_{d-1s}}$	<ul style="list-style-type: none"> • $N_{belowground_temp_{dsi}}$ = Amount of nitrogen in the belowground part after remobilisation to aboveground part • $N_{aboveground_temp_{dsi}}$ = Amount of nitrogen in the aboveground part after remobilisation from belowground part

(e) Leaf biomass allocation (Munier-Jolain et al., 2014; Perthame et al., submitted-a)	9	$\forall d, \forall s, \forall c, \forall i$	If $N_{stress_{d-1s_i}} \in [0,1]$ Then $N_{stressEffectLBR_{d_{si}}} = \exp(LBR_mu_{Ns, x} \cdot N_{stress_{d_{si}}})$ Else $N_{stressEffectLBR_{d_{si}}} = 1$ $ShadeEffectLBR_{d_{si}} = \exp(LBR_mu_{s, x} \cdot SI_{d_{si}})$	<ul style="list-style-type: none"> $N_{stressEffectLBR_{d_{si}}}$ = Effect of nitrogen stress on leaf to aboveground biomass ratio LBR_mu_{Ns} = Response parameter of the ‘leaf to aboveground biomass ratio’ to nitrogen stress $ShadeEffectLBR_{d_{si}}$ = Effect of shading on leaf to aboveground biomass ratio $LBR_mu_{s, x}$ = Response parameter of the ‘leaf to aboveground biomass ratio’ to shading for species s at stage x
	10		If $N_{stressEffectLBR_{d_{si}}} \geq 1$ and $ShadeEffectLBR_{d_{si}} \geq 1$ Then $effectLBR_{d_{si}} = \max(N_{stressEffectLBR_{d_{si}}}, ShadeEffectLBR_{d_{si}})$ Else if $N_{stressEffectLBR_{d_{si}}} \leq 1$ and $ShadeEffectLBR_{d_{si}} \leq 1$ Then $effectLBR_{d_{si}} = \min(N_{stressEffectLBR_{d_{si}}}, ShadeEffectLBR_{d_{si}})$ Else $effectLBR_{d_{si}} = N_{stressEffectLBR_{d_{si}}} \cdot ShadeEffectLBR_{d_{si}}$	<ul style="list-style-type: none"> $effectLBR_{d_{si}}$ = Global effect of shading and nitrogen stress on leaf to aboveground biomass ratio
	11		$LBR_{d_{si}} = LBR0_s \cdot effectLBR_{d_{si}}$	<ul style="list-style-type: none"> $LBR_{d_{si}}$ = Leaf to aboveground biomass ratio $LBR0_s$ = Leaf to aboveground biomass ratio in optimal conditions
	12		$LBM_{d_{si}} = LBM_{d-1s_i} + LBR_{d_{si}} \cdot [\Delta TBM_{d_{si}} - (\Delta TBM_{d_{si}} \cdot RBR_{d_{si}})]$	
(f) Leaf area expansion (Munier-Jolain et al., 2014; Perthame et al., submitted-a)	13	$\forall d, \forall s, \forall c, \forall i$	If $N_{stress_{d-1s_i}} \in [0,1]$ Then $N_{stressEffectSLA_{d_{si}}} = \exp(SLA_mu_{Ns} \cdot N_{stress_{d_{si}}})$ Else $N_{stressEffectSLA_{d_{si}}} = 1$ $ShadeEffectSLA_{d_{si}} = \exp(SLA_mu_s \cdot SI_{d_{si}})$	<ul style="list-style-type: none"> $N_{stressEffectSLA_{d_{si}}}$ = Effect of nitrogen stress on specific leaf area SLA_mu_{Ns} = Response parameter of specific leaf area to nitrogen stress $ShadeEffectSLA_{d_{si}}$ = Effect of shade on specific leaf area SLA_mu_s = Response parameter of specific leaf area to nitrogen stress
	14		If $N_{stressEffectSLA_{d_{si}}} \geq 1$ and $ShadeEffectSLA_{d_{si}} \geq 1$ Then $effectSLA_{d_{si}} = \max(N_{stressEffectSLA_{d_{si}}}, ShadeEffectSLA_{d_{si}})$ Else if $N_{stressEffectSLA_{d_{si}}} \leq 1$ and $ShadeEffectSLA_{d_{si}} \leq 1$ Then $effectSLA_{d_{si}} = \min(N_{stressEffectSLA_{d_{si}}}, ShadeEffectSLA_{d_{si}})$ Else $effectSLA_{d_{si}} = N_{stressEffectSLA_{d_{si}}} \cdot ShadeEffectSLA_{d_{si}}$	<ul style="list-style-type: none"> $effectSLA_{d_{si}}$ = Global effect of shading and nitrogen stress on specific leaf area
	15		$SLA_{d_{si}} = SLA0_s \cdot effectSLA_{d_{si}}$	<ul style="list-style-type: none"> $SLA_{d_{si}}$ = Specific leaf area

				<ul style="list-style-type: none"> • SLA₀, = Specific leaf area in optimal conditions
	16		$LA_{dsi} = SLA_{dsi} \cdot LBM_{dsi}$	
(g) Plant nitrogen demand (Perthame et al., 2020)	17	$\forall s, \forall c, \forall i, \forall d$ If $stage_{sc} < maturity$ onset	$AG_Ndem_{dsi} = LBM_{dsi} \cdot cNreq_s - Naboveground_{d-1si}$ If $AG_Ndem_{dsi} < 0, AG_Ndem_{dsi} = 0$	<ul style="list-style-type: none"> • AG_Ndem_{dsi} = Aboveground nitrogen demand
	18		$BG_Ndem_{dsi} = RBM_{dsi} \cdot cRootN_s \cdot \min(1, 1 - Nstress_{d-1si}) - Nbelowground_d$ $1si$ If $BG_Ndem_{dsi} < 0, BG_Ndem_{dsi} = 0$	<ul style="list-style-type: none"> • BG_Ndem_{dsi} = Belowground nitrogen demand
	19	$\forall s, \forall c, \forall i, \forall d$ If $stage_{sc} \geq maturity$ onset	$AG_Ndem_{dsi} = 0$ $BG_Ndem_{dsi} = 0$	
	20	$\forall s, \forall c, \forall i, \forall d$	$Ndem_{dsi} = AG_Ndem_{dsi} + BG_Ndem_{dsi}$	<ul style="list-style-type: none"> • $Ndem_{dsi}$ = Plant nitrogen demand
(h) Nitrogen concentration in soil voxels at the beginning of the day	21	$\forall d$ $\forall z \in [1, D_{dsc}]$	$VoxNconcBeg_{dz} = \left(\sum_{l=z*vox}^{(z+1)*vox-1} SoilNconcBeg_{dl} \cdot 10^{-5} \cdot vox^2 \right)$	<ul style="list-style-type: none"> • D_{dsc} = Depth of the root system of plants of cohort c • $VoxNconcBeg_{dz}$ = Voxel-nitrogen concentration at the beginning of the day • $SoilNconcBeg_{dl}$ = Soil-nitrogen concentration per soil layer at the beginning of the day • vox = Soil voxel width
(i) Root system extension in voxel layer z (Pagès et al., 2020)	22	$\forall d, \forall s, \forall c, \forall i$ $\forall z$	$E_{dsiz} = \sum_{l=z*vox}^{(z+1)*vox-1} E_{dsil} / vox$	<ul style="list-style-type: none"> • E_{dsiz} = Root system lateral radius (in number of voxels) in voxel layer z • E_{dsil} = Root system lateral radius (in cm) in soil layer l
	23	$\forall d, \forall s, \forall c, \forall i$ $\forall z$	$nbVox_{dsiz}$ = number of voxels whose center is inside a circle of radius E_{dsiz} (Section S3 of the supplementary material online)	<ul style="list-style-type: none"> • $nbVox_{dsiz}$ = Number of voxels whose center is inside a circle of radius E_{dsiz}
(j) Distribution of root biomass density with depth (Pagès et al., 2020)	24	$\forall d, \forall s, \forall c, \forall i$	$RBD_{dsiz} = \left(\sum_{l=z*vox}^{(z+1)*vox-1} RBD_{dsil} \cdot vox^3 \right) / vox$	<ul style="list-style-type: none"> • RBD_{dsiz} = Root biomass density (g/voxel) in a voxel in voxel layer z • RBD_{dsil} = Root biomass density (g/cm³) in soil layer l
(k) Distribution of plant nitrogen demand among soil voxels	25	$\forall d, \forall s, \forall c, \forall i$ $\forall z \in [1, D_{dsc}]$	$Navailable_{dsiz} = \min(VoxNconcBeg_{dz}, RBD_{dsiz} \cdot SNUmax_s)$	<ul style="list-style-type: none"> • $Navailable_{dsiz}$ = Nitrogen available in a voxel at layer z • SNUmax_s = Maximum specific nitrogen uptake

	26		<p>If $\sum_{z=1}^{D_{dsc}} \text{Navailable}_{dsiz} \cdot \text{nbVox}_{dscz} > 0$ then $\text{Ndem}_{dsiz} =$ $\text{Ndem}_{dsi} \cdot \text{Navailable}_{dsiz} / (\sum_{z=1}^{D_{dsc}} \text{Navailable}_{dsiz} \cdot \text{nbVox}_{dscz})$ Else $\text{Ndem}_{dsiz} = 0$</p>	<ul style="list-style-type: none"> • Ndem_{dsiz} = Plant nitrogen demand in a voxel 	
(l) N₂-fixating plants	27	$\forall d, \forall s, \forall c, \forall i$	<p>If $\text{legume}_s = \text{YES}$ and $\text{DD}_d > \text{Dminfix}_s$ Then $\text{fixN2}_{dsi} = \text{yes}$ Else $\text{fixN2}_{dsi} = \text{no}$</p>	<ul style="list-style-type: none"> • legume_s = Parameter indicating whether a species is a legume or not • DD_d = Time from emergence to d day • Dminfix_s = Minimal date to start atmospheric nitrogen fixation for legume plants • fixN2_{dsi} = Indicates whether a plant can fix N₂ or not 	
(m) Plant nitrogen uptake	28	$\forall d, \forall s, \forall c, \forall i$ $\forall z \in [1, D_{dsc}]$	$\text{NpotUpt}_{dsiz} = \min(\text{Ndem}_{dsiz}, \text{Navailable}_{dsiz})$	<ul style="list-style-type: none"> • NpotUpt_{dsiz} = Potential plant nitrogen uptake 	
		$\forall d,$ $\forall z \in [1, D_{maxd}]$ $\forall x \in [1, \text{dim}_x]$ $\forall y \in [1, \text{dim}_y]$	$\text{NpotUptNonFixN2}_{dxyz} = \sum_{i=1}^n \text{NpotUpt}_{dsiz}$ <p style="text-align: center;"><i>if</i> $\text{fixN2}_{dsci} = \text{no}$ <i>if</i> $(x - \text{Psi}(x))^2 + (y - \text{Psi}(y))^2 \leq E_{dsiz}^2$</p> $\text{NpotUptFixN2}_{dxyz} = \sum_{i=1}^n \text{NpotUpt}_{dsiz}$ <p style="text-align: center;"><i>if</i> $\text{fixN2}_{dsci} = \text{yes}$ <i>if</i> $(x - \text{Psi}(x))^2 + (y - \text{Psi}(y))^2 \leq E_{dsiz}^2$</p>	<ul style="list-style-type: none"> • D_{maxd} = Depth of the deepest root system • dim_x = Field width on the x-axis • dim_y = Field width on the y-axis • $\text{P}_{si}(x)$ = Coordinate of the plant on the x-axis • $\text{P}_{si}(y)$ = Coordinate of the plant on the y-axis • $\text{NpotUptFixN2}_{dxyz}$ = Potential nitrogen uptake of N₂-fixating plants • $\text{NpotUptNonFixN2}_{dxyz}$ = Potential nitrogen uptake of non N₂-fixating plants 	
	29	$\forall d, \forall s, \forall c, \forall i$ $\forall z \in [1, D_{maxd}]$ $\forall x \in [1, \text{dim}_x]$ $\forall y \in [1, \text{dim}_y]$	<p>If $\text{NpotUptNonFixN2}_{dxyz} + \text{NpotUptFixN2}_{dxyz} \leq \text{VoxNconcBeg}_{dz}$</p>	$\text{NUpt}_{dsixyz} = \text{NpotUpt}_{dsiz}$	<ul style="list-style-type: none"> • NUpt_{dsixyz} = Actual plant nitrogen uptake
	30	$\forall y \in [1, \text{dim}_y]$	<p>Else if $\text{NpotUptNonFixN2}_{dxyz} \leq \text{VoxNconcBeg}_{dz}$</p>	<p>If $\text{fixN2}_{dsc} = \text{NO}$ then $\text{NUpt}_{dsixyz} = \text{NpotUpt}_{dsiz}$</p>	

		If $(x-P_{si}(x))^2+(y-P_{si}(y))^2 \leq E_{dsiz}^2$	else $NUpt_{dsixyz} = (VoxNconcBeg_{dz} - NpotUptNonFixN2_{dz}) \cdot NpotUpt_{dsiz} / NpotUptFixN2_{dxyz}$	
	31		Else if $NpotUptNonFixN2_{dxyz} > VoxNconcBeg_{dz}$	If $fixN2_{dsc} = NO$ then $VoxNconcBeg_{dz} \cdot NpotUpt_{dsiz} / NpotUptNonFixN2_{dxyz}$ else $NUpt_{dsixyz} = 0$
	32	$\forall d, \forall s, \forall c, \forall i$ If $fixN2_{dsc} = no$	$missingN_{dsi} = \sum_{x,y,z} (NpotUpt_{dsiz} - Nupt_{dsixyz})$ if $(x-P_{si}(x))^2 + (y-P_{si}(y))^2 \leq E_{dsiz}^2$	<ul style="list-style-type: none"> missingN_{dsi} = Amount of nitrogen missing to the plant to meet its nitrogen requirement
	33	$\forall d \forall z$	If $NpotUptNonFixN2_{dxyz} + NpotUptFixN2_{dxyz} \leq VoxNconcBeg_{dz}$ Then $superfluousN_{xyz} = VoxNconcBeg_{dz} - \sum_{i=1}^n NUpt_{dsixyz}$ Else $superfluousN_{xyz} = 0$	<ul style="list-style-type: none"> superfluousN_{xyz} = Amount of nitrogen remaining in a soil voxel after nitrogen uptake by all plants
(n) Compensation	34	$\forall d, \forall s, \forall c, \forall i$ $\forall z \in [1, Dmax_d]$ $\forall x \in [1, dim_x]$ $\forall y \in [1, dim_y]$ If $\{(x-P_{si}(x))^2+(y-P_{si}(y))^2\} \leq E_{dsiz}^2$ If $fixN2_{dsc} = no$	If $x=1$ and $y=1$ and $z=1$ Then $missingN_{dsixyz} = missingN_{dsi}$ else $missingN_{dsixyz} = missingN_{dsix'y'z'}$	<ul style="list-style-type: none"> missingN_{dsixyz} = Amount of nitrogen missing to the plant to meet its nitrogen requirement when the loop is at voxel (x,y,z) missing$N_{dsix'y'z'}$ = Amount of nitrogen missing to the plant to meet its nitrogen requirement when the voxel loop is at voxel (x',y',z') (see Equation 37)
	35		If $missingN_{dsixyz} > 0$ and $superfluousN_{xyz} > 0$ Then $NavailableComp_{dsixyz} = \min(superfluousN_{xyz}; RBD_{dsiz} \cdot SNUMax_s)$ And $potentialComp_{dsixyz} = \min(missingN_{dsixyz}, NavailableComp_{dsixyz})$	<ul style="list-style-type: none"> NavailableComp$_{dsixyz}$ = Nitrogen available to plant to compensate the nitrogen it misses after first uptake potentialComp$_{dsixyz}$ = Potential compensative nitrogen uptake
	36		If $\sum_{i=1}^{n'} potentialComp_{dsixyz} \leq superfluousN_{xyz}$ Then $compensationN_{dsixyz} = potentialComp_{dsixyz}$ Else $compensationN_{dsixyz} = superfluousN_{xyz} \cdot potentialComp_{dsixyz} / \sum_{i=1}^{n'} potentialComp_{dsixyz}$	<ul style="list-style-type: none"> compensationN_{dsixyz} = Amount of nitrogen taken up by the plant for compensation
	37		If $y < dim_y$ then $y'=y+1$ Else if $x < dim_x$ then $x'=x+1$	

			Else if $z < D_{max,d}$ then $z' = z + 1$ Else calculation stops $missingN_{dsix'y'z'} = missingN_{dsixyz} - compensationN_{dsixyz}$	
(o) Nitrogen in plants after soil-nitrogen uptake	38	$\forall s, \forall c, \forall i, \forall d$ If $stage_{sc} \leq plantlet$	If $fixN2_{dsc} = no$ or $stage > cotyledon$ Then $N_{plant_{dsi}} = N_{plant_{d-1si}}$ $+ \sum_{(x,y,z)=(1,1,1)}^{(dim_x, dim_y, D_{dsc})} (NUpt_{dsixyz} + compensationN_{dsixyz}) + missingN_{dsi} \cdot PropTT_{plantlet_{dsi}}$ Else $N_{plant_{dsi}} = N_{plant_{d-1si}} + N_{dem_{dsi}}$	<ul style="list-style-type: none"> $PropTT_{plantlet_{dsi}}$ = Proportion of elapsed thermal time from beginning to end of plantlet stage
	39	$\forall s, \forall c, \forall i, \forall d$ If $(plantlet < stage_{sc} < maturity\ onset)$	If $fixN2_{dsc} = no$ Then $N_{plant_{dsi}} = N_{plant_{d-1si}} + \sum_{(x,y,z)=(1,1,1)}^{(dim_x, dim_y, D_{dsc})} (NUpt_{dsixyz} + compensationN_{dsixyz})$ Else $N_{plant_{dsi}} = N_{plant_{d-1si}} + N_{dem_{dsi}}$	
	40		If $N_{dem_{dsi}} > 0$ Then $N_{aboveground_{dsi}} = N_{aboveground_temp_{dsi}} + \sum_{(x,y,z)=(1,1,1)}^{(dim_x, dim_y, D_{dsc})} (NUpt_{dsixyz} + compensationN_{dsixyz}) \cdot AG_N_{dem_{dsi}} / N_{dem_{dsi}}$ And $N_{belowground_{dsi}} = N_{belowground_temp_{dsi}} + \sum_{(x,y,z)=(1,1,1)}^{(dim_x, dim_y, D_{dsc})} (NUpt_{dsixyz} + compensationN_{dsixyz}) \cdot BG_N_{dem_{dsi}} / N_{dem_{dsi}}$ Else $N_{aboveground_{dsi}} = N_{aboveground_{d-1si}}$ And $N_{belowground_{dsi}} = N_{belowground_{d-1si}}$	
	41	$\forall s, \forall c, \forall i, \forall d$ If $stage_{sc} \geq maturity\ onset$	$N_{plant_{dsi}} = N_{plant_{d-1si}}$	
(p) Nitrogen concentration in soil voxels and layers at the end of the day	42	$\forall d, \forall s, \forall c, \forall i$ $\forall z \in [1, D_{max,d}]$	$VoxN_{concEnd_{dz}} = VoxN_{concBeg_{dz}} - \sum_{(x,y,i)=(1,1,1)}^{(dim_x, dim_y, n)} (NUpt_{dsixyz} + compensationN_{dsixyz}) / (dim_x \cdot dim_y)$	<ul style="list-style-type: none"> $VoxN_{concEnd_{dz}}$ = Voxel nitrogen concentration at the end of the day
	43	$\forall d$ $\forall l \in [z \cdot vox_z, (z+1) \cdot vox_z - 1]$	$SoilN_{ConcEnd_{dl}} = VoxN_{concEnd_{dz}} / (vox^3 \cdot 10^{-5})$	<ul style="list-style-type: none"> $SoilN_{ConcEnd_{dl}}$ = Soil-nitrogen concentration per soil layer at the end of the day
(q) Plant nitrogen stress index	44	$\forall s, \forall c, \forall i, \forall d < maturity\ onset$	If $LBM_{dsi} > 0$, $N_{stress_{dsi}} = 1 - \frac{N_{aboveground_{dsi}} / LBM_{dsi}}{cN_{req}}$	

	45	$\forall s, \forall c, \forall i, \forall d$ If $\text{stage}_{sc} \geq \text{maturity}$ onset	$\text{Nstress}_{\text{dsi}} = \text{Nstress}_{\text{dsi-1}}$

Appendix 2: Parameters used in the nitrogen version of the plant growth submodel of FLORSYS

Corresponding equations are in **Appendix 1**. All the parameters are specific (i.e. their values depends on the species), except rN. The eight parameters that are specific to the nitrogen submodel (not in the previous FLORSYS version) are in red (bold).

Parameter	Definition	Unit	Method of calculation
r1 _s	Parameters to predict root biomass as a function of total plant biomass. r1 _s and r2 _s are specific parameters, and rN is a non-specific parameter accounting for the effect of nitrogen stress on biomass allocation to roots.	g root biomass · g total biomass ⁻¹	Pointurier et al. (2021)
r2 _s		dimensionless	
rN		dimensionless	
cNε_{b,s}	Response rate of maximal radiation use efficiency to nitrogen stress for species s	dimensionless	Set at 1 for all species in accordance with Brisson et al. (1998)
cNreq_s	Optimal amount of nitrogen in the vegetative aboveground part of the plant (leaf+stem) per unit of leaf biomass for species s. It corresponds to the minimal value required to ensure maximal crop growth rate.	g aboveground nitrogen · g leaf biomass ⁻¹	Perthame et al. (2020)
cRootN_s	Response rate of root nitrogen concentration to nitrogen stress index for species s	g root nitrogen · g root biomass ⁻¹	Section S4 of the Supplementary material online
Dminfix_s	Minimal date to start atmospheric nitrogen fixation for legume species s	°C.day	Section S4 of the Supplementary material online
ε _{btotmax_s}	Maximal gross radiation use efficiency for species s when nitrogen does not limit photosynthesis (N _{stress_{dsi}} is ≥ 0). This coefficient is used to convert intercepted light into total plant biomass (above- and below-ground) (respiration is not subtracted)	g plant biomass · MJ ⁻¹	Colbach et al. (2014b) and Brisson et al. (1998)
legume _s	Parameter indicating whether a species s is a legume or not	dimensionless	YES or NO from the literature
LBR0 _s	Leaf to aboveground biomass ratio in optimal growth conditions for species s	g leaf biomass · g aboveground biomass ⁻¹	Munier-Jolain et al. (2014) and Colbach et al. (2020)
LBR_mu _{s,x}	Response parameter of leaf to aboveground biomass ratio to shading index for species s at stage x	dimensionless	Munier-Jolain et al. (2014) and Colbach et al. (2020)
LBR_muN_s	Response parameter of leaf to aboveground biomass ratio to nitrogen stress index for species s		(Perthame et al., submitted-a)
SLA0 _s	Specific leaf area in optimal growth conditions for species s	cm ² leaf area · g leaf biomass ⁻¹	Munier-Jolain et al. (2014) and Colbach et al. (2020)
SLA_mu _s	Response parameter of specific leaf area to shading index for species s	dimensionless	Munier-Jolain et al. (2014) and Colbach et al. (2020)
SLA_muN_s	Response parameter of specific leaf area to nitrogen stress index for species s		(Perthame et al., submitted-a)

SNU_{max,s}	Maximum specific nitrogen uptake for species s (i.e. maximum amount of nitrogen that 1 gram of root biomass can take up per day)	g soil nitrogen · g root biomass ⁻¹ · day ⁻¹	Section S4 of the Supplementary material online
----------------------------	--	--	--

Appendix 3: State variables used in the nitrogen version of FLORSYS

Corresponding equations are in **Appendix 1** and **Appendix 5**. The variables that are specific to the nitrogen submodel (not in the previous FLORSYS version) are in red (bold).

Variable	Definition	Unit
ABM _{dsi}	Aboveground biomass of plant i of species s on day d	g biomass·plant ⁻¹
AG_Ndem_{dsi}	Aboveground nitrogen demand of plant i of species s on day d	g nitrogen·plant ⁻¹
BG_Ndem_{dsi}	Belowground nitrogen demand of plant i of species s on day d	g nitrogen·plant ⁻¹
BMacb _{dsi}	Biomass of plant i of species s on day d that is above the cutting bar at mowing or harvest	g biomass·plant ⁻¹
BMexp_{dsi}	Biomass of plant i of species s on day d that is exported at harvest	g biomass·plant ⁻¹
compensationN_{dsixyz}	Amount of nitrogen taken up for compensation by plant i of species s on day d in voxel (x,y,z)	g nitrogen·plant ⁻¹ ·voxel ⁻¹
D _{dsc}	Depth of root system of cohort c of species s on day d (calculated from root system depth in mm then converted into voxels by dividing by (vox·10))	number of voxels
DD _d	Time from emergence to d day	°C·day
Dmax _d	Depth of the deepest root system on day d	number of voxels
ΔABMresp _{dsi}	Aboveground biomass lost by respiration of plant i of species s on day d	g biomass·plant ⁻¹
ΔRBMresp _{dsi}	Root biomass lost by respiration of plant i of species s on day d	g biomass·plant ⁻¹
ΔTBM _{dsi}	Daily accumulated total biomass of plant i of species s on day d (root + aboveground biomass)	g biomass·plant ⁻¹
E _{dsil}	Root system lateral radius of plant i of species s on day d in soil layer l	cm
E _{dsiz}	Root system lateral radius of plant i of species s on day d at depth z	Number of voxels
effectLBR_{dsi}	Global effect of shading and nitrogen stress on leaf to aboveground biomass ratio for plant i of species s on day d	dimensionless
effectSLA_{dsi}	Global effect of shading and nitrogen stress on specific leaf area for plant i of species s on day d	dimensionless
εb _{dsi}	Effective gross radiation use efficiency of plant i of species s on day d. This is the coefficient of conversion of intercepted light into total plant biomass (above- and below-ground) (respiration is not subtracted)	g biomass·MJ ⁻¹
fixN2_{dsi}	Indicates whether a plant i of species s on day d can fix N ₂ or not	dimensionless
LA _{dsi}	Leaf area of plant i of species s on day d	cm ² ·plant ⁻¹
LBM _{dsi}	Leaf biomass of plant i of species s on day d	g biomass·plant ⁻¹
LBR _{dsi}	Leaf to aboveground biomass ratio of plant i of species s on day d	g leaf biomass·g ⁻¹ aboveground biomass

missingN_{dsi}	Amount of nitrogen missing to the plant i of species s on day d to meet its nitrogen requirement	g nitrogen · plant ⁻¹
missingN_{dsixyz}	Amount of nitrogen missing to plant i of species s on day d to meet its nitrogen requirement when the voxel loop is at voxel (x,y,z)	
missingN_{dsix'y'z}	Amount of nitrogen missing to plant i of species s on day d to meet its nitrogen requirement when the voxel loop is at voxel (x',y',z')	
Naboveground_{dsi}	Amount of nitrogen in the aboveground part of plant i of species s on day d	g nitrogen · plant ⁻¹
Naboveground_temp_{dsi}	Amount of nitrogen in the aboveground part after remobilisation from belowground part of plant i of species s on day d	g nitrogen · plant ⁻¹
Navailable_{dsiz}	Nitrogen available in an average voxel at depth z to plant i of species s	g nitrogen · plant ⁻¹ · voxel ⁻¹
NavailableComp_{dsixyz}	Nitrogen available in voxel (x,y,z) to plant i of species s on day d to compensate the nitrogen it misses after first uptake	g nitrogen · plant ⁻¹ · voxel ⁻¹
Nbelowground_{dsi}	Amount of nitrogen in the belowground part of plant i of species s on day d	g nitrogen · plant ⁻¹
Nbelowground_temp_{dsi}	Amount of nitrogen in the belowground part after remobilisation to aboveground part of plant i of species s on day d	g nitrogen · plant ⁻¹
nbVoX_{dsiz}	Number of voxels colonized by roots of plant i of species s on day d at depth z	number of voxels
Ndem_{dsi}	Nitrogen demand of plant i of species s on day d	g nitrogen · plant ⁻¹
Ndem_{dsiz}	Nitrogen demand of plant i of species s on day d in an average voxel at depth z	g nitrogen · plant ⁻¹ · voxel ⁻¹
NUpt_{dsixyz}	Actual nitrogen uptake of plant i of species s on day d in voxel (x,y,z)	g nitrogen · plant ⁻¹ · voxel ⁻¹
Nplant_{dsi}	Total amount of nitrogen of plant i of species s on day d	g nitrogen · plant ⁻¹
NpotUpt_{dsiz}	Potential nitrogen uptake of plant i of species s in voxels at depth z on day d (estimated without considering that the voxel can be occupied by roots of several plants)	g nitrogen · plant ⁻¹ · voxel ⁻¹
NpotUptFixN2_{dxyz}	Potential nitrogen uptake of a N ₂ -fixating plant i of species s in voxels at depth z on day d (estimated without considering that the voxel can be occupied by roots of several plants)	g nitrogen · plant ⁻¹ · voxel ⁻¹
NpotUptNonFixN2_{dxyz}	Potential nitrogen uptake of a non N ₂ -fixating plant i of species s in voxels at depth z on day d (estimated without considering that the voxel can be occupied by roots of several plants)	g nitrogen · plant ⁻¹ · voxel ⁻¹
Nstress_{dsi}	Nitrogen stress index of plant i of species s on day d. A value close to 0 indicates an optimum nitrogen nutrition. Positive (resp. negative) values reflect a nitrogen-limitation (resp. excess), with nitrogen-limitation (resp. excess) increasing with increasing (resp. decreasing) Nstress _{dsi} value	dimensionless
NstressEffectLBR_{dsi}	Effect of nitrogen stress index on leaf to aboveground biomass ratio for plant i of species s on day d	dimensionless
NstressEffectSLA_{dsi}	Effect of nitrogen stress index on specific leaf area for plant i of species s on day d	dimensionless
NUpt_{dsixyz}	Actual plant nitrogen uptake of plant i of species s on day d in voxel (x,y,z)	g nitrogen · plant ⁻¹ · voxel ⁻¹
PAR_{dsi}	Photosynthetically active radiation intercepted by plant i of species s on day d	MJ

potentialComp_{dsixyz}	Potential compensative nitrogen uptake of plant i of species s on day d in voxel (x,y,z) (estimated without considering that the voxel can be occupied by roots of several plants)	g nitrogen·plant ⁻¹ ·voxel ⁻¹
PropTTflo _{dsi}	Proportion of elapsed thermal time from beginning to end of flowering for plant i of species s on day d	°C.day·(°C.day) ⁻¹
PropTTplantlet _{dsi}	Proportion of elapsed thermal time from beginning to end of plantlet stage for plant i of species s on day d	°C.day·(°C.day) ⁻¹
P _{si} (x)	Coordinates of plant i of species s on the x-axis	voxel
P _{si} (x,y)	Coordinates of plant i of species s	voxel
P _{si} (y)	Coordinates of plant i of species s on the y-axis	voxel
Qres _{ds}	Quantity of crop residues of species s on day d	g biomass
RBD _{dsil}	Root biomass of plant i of species s on day d in soil layer l	g biomass·cm ⁻³
RBD _{dsiz}	Root biomass of plant i of species s on day d in an average voxel at depth z	g biomass·plant ⁻¹ ·voxel ⁻¹
RBM _{dsi}	Root biomass of plant i of species s on day d	g biomass·plant ⁻¹
RBR _{dsi}	Proportion of root biomass in total plant biomass of plant i of species s on day d	g root biomass·g total biomass ⁻¹
SBM _{dsi}	Seed biomass of plant i of species s on day d	g biomass·plant ⁻¹
ShadeEffectLBR _{dsi}	Effect of shading index on leaf to aboveground biomass ratio for plant i of species s on day d	dimensionless
ShadeEffectSLA _{dsi}	Effect of shading index on specific leaf area for plant i of species s on day d	dimensionless
SI _{dsi}	Cumulated shading index since plant emergence	dimensionless
SLA _{dsi}	Specific leaf area of plant i of species s on day d	cm ² leaf area·g leaf biomass ⁻¹
SoilNConcBeg_{dl}	Soil-nitrogen concentration per soil layer l of 1-cm thickness before plant nitrogen uptake	g nitrogen·m ⁻³ (per cm sol layer)
SoilNConcEnd_{dl}	Soil-nitrogen concentration per soil layer l of 1-cm thickness after plant nitrogen uptake	g nitrogen·m ⁻³ (per cm sol layer)
superfluousN_{xyz}	Amount of nitrogen remaining in a soil voxel (x,y,z) after nitrogen uptake by all the plants with roots in this voxel	g nitrogen·voxel ⁻¹
TBM _{dsi}	Total biomass of plant i of species s on day d (above- and below-ground biomass)	g biomass·plant ⁻¹
temperature _d	Mean air temperature on day d	°C
VoxNconcBeg_{dz}	Soil voxel nitrogen concentration in an average voxel at depth z at the beginning of day d (before plant nitrogen uptake)	g nitrogen·voxel ⁻¹

VoxNconcEnd_{dz}	Soil voxel nitrogen concentration in an average voxel at depth z at the end of day d (after plant nitrogen uptake)	g nitrogen·voxel ⁻¹
---------------------------------	--	--------------------------------

Appendix 4: Input variables for representing the below-ground part of the simulated field in FLORSYS

Variables	Definition	Unit
vox	Soil voxel edge size (cubic voxels)	cm
dim _x	Field width on the x-axis	Number of voxels
dim _y	Field length on the y-axis	Number of voxels

Appendix 5: Equations of the occasional processes occurring in the nitrogen version of FLORSYS

Equations with d: day in days, s: species, i: individual, c: cohort (all plants of the same species emerging the same day).

Process	#	When	Equation	Variables (for details, see Appendix 3)
Plant nitrogen loss	46	$\forall s, \forall c, \forall i, \forall d$	$N_{aboveground_{dsi}} = \frac{ABM_{d-1si} - ABM_{dsi}}{ABM_{d-1si} - RBM_{dsi}} \cdot N_{aboveground_{d-1si}}$ $N_{belowground_{dsi}} = \frac{RBM_{d-1si} - RBM_{dsi}}{RBM_{d-1si}} \cdot N_{belowground_{d-1si}}$	<ul style="list-style-type: none"> • $N_{aboveground_{dsi}}$ = Amount of nitrogen in the aboveground plant part • ABM_{dsi} = Aboveground plant biomass • $N_{belowground_{dsi}}$ = Amount of nitrogen in the belowground plant part • RBM_{dsi} = Plant root biomass
Crop biomass return to soil	47	$\forall s = \text{crop}, \forall c, \forall i, \forall d$	<p>(1) If d=tillage or herbicide date, $Q_{res_{ds}} = \sum_{i=1}^n TBM_{dsi}$</p> <p>(2) If d=mowing date, $Q_{res_{ds}} = \sum_{i=1}^n TBM_{dsi} - \sum_{i=1}^n BM_{acbd_{dsi}}$</p> <p>(3) If d=harvest date, $Q_{res_{ds}} = \sum_{i=1}^n TBM_{dsi} - \sum_{i=1}^n BM_{exp_{dsi}}$ with $BM_{exp_{dsi}} = SBM_{dsi}$ or RBM_{dsi} or $BM_{acbd_{dsi}}$</p>	<ul style="list-style-type: none"> • $Q_{res_{ds}}$ = Quantity of crop residues • TBM_{dsi} = Total plant biomass • $BM_{acbd_{dsi}}$ = Plant biomass above the cutting bar at mowing or harvest • $BM_{exp_{dsi}}$ = Plant biomass exported at harvest • SBM_{dsi} = Seed biomass