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# Can modulations of nitrogen fertilisation and crop traits promote biological weed regulation through competition? A simulation study

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With the reduction of both herbicide and mineral fertiliser use for environmental reasons, crop–weed competition for nitrogen might increase in arable fields. Adapting nitrogen fertilisation and selecting crop species/varieties according to their nitrogen-nutrition traits could provide options to influence competitive relationships among plants. A simulation study was conducted to identify which nitrogen-fertilisation options and crop traits related to nitrogen nutrition have the greatest influence on weed impacts in the agroecosystem. We examined indicators of both weed harmfulness (i.e., crop grain yield loss due to weeds, field infestation by weed biomass, and weed seed production) and weed benefits (i.e., weed species richness and weed-based food offer for bees). Sensitivity analyses were performed using a process-based model (FLORSYS) simulating crop and weed growth and dynamics over the years based on information on the cropping system, pedoclimatic, and species traits. A maize monoculture from southwestern France was used as a case study. Different maize varieties (differing in their trait values related to nitrogen nutrition) were simulated under different scenarios of nitrogen fertilisation (application date and rate, crop residue management, and initial soil organic nitrogen) and weather. The analyses showed that nitrogen application rate and maize variety were the factors most influencing weed impacts on the agroecosystem. Decreasing nitrogen rates increased weed harmfulness and decreased maize yield potential (i.e., yield in the absence of weeds). The maize traits that both reduced weed harmfulness the most and increased maize productivity the most were low plant nitrogen demand, high root nitrogen uptake efficiency, and a specific leaf area (leaf area per unit leaf biomass) insensitive to plant nitrogen stress. These results are useful for better understanding the role of nitrogen in crop–weed competition and for identifying management strategies that promote biological weed regulation.

## KEYWORDS

weed, nitrogen, fertilization, trait, sensitivity analysis, model, cropping system

## 1 Introduction

Weeds are the most harmful pests in arable fields (Oerke, 2006), mainly because they compete with crops for resources (light, water, and nutrients) (Colbach et al., 2023). In conventional cropping systems, chemical inputs play a key role in ensuring crop yield and grain quality, with herbicides controlling weeds and fertilisers providing essential nutrients for crop growth. Health and environmental concerns have led to the development of agroecological cropping systems, with reductions in both herbicide and mineral nitrogen fertiliser inputs. This shift in farming practices may result in two major changes in crop–weed competition. First, a more abundant residual weed flora is expected, leading to more intense crop–weed competition. Second, competition for nitrogen could become more important, whereas light is generally the main resource for which crops and weeds compete in intensive and temperate agroecosystems (Wilson and Tilman, 1993; Cahill and James, 2002; van Breugel et al., 2012).

Past studies concluded that, from 1970 to 2000, increasing nitrogen fertilisation led to modifications of the weed flora (Fried et al., 2009). They reported increased competitiveness of nitrophilic species (e.g., species with a high growth potential, strong nitrogen uptake capacity, and large leaf area that shades neighbouring plants) at the expense of oligotrophic species (Fried et al., 2009; Moreau et al., 2013; Moreau et al., 2014). Reduced nitrogen fertilisation and crop species/varieties tolerant to low soil nitrogen could therefore be an option to influence crop–weed competition in cropping systems that rely less on chemical inputs. This strategy may be particularly useful to regulate the most nitrophilic species, which are considered the most harmful to crop production in conventional intensive cropping systems.

Many studies have highlighted nitrogen fertilisation management (both in terms of application rate and/or date) as a tool to manage crop–weed competition (Ditomaso, 1995; Liebman and Davis, 2000; Barberi, 2002; Rathke et al., 2006; Shekhawat et al., 2017).

Some studies reported that reducing nitrogen fertiliser rates suppressed weed growth more than crop growth (Ditomaso, 1995; Santos et al., 1998; Singh et al., 2017; Fracchiolla et al., 2018), whereas other studies found that increasing nitrogen rates promoted weed growth more than crop growth (Esposito et al., 2023; Raniro et al., 2023).

Some studies reported the opposite. Several of these studies showed that low nitrogen rates affected crop growth more than weed growth (Wilson and Tilman, 1993; Jornsgard et al., 1996; Tollenaar et al., 1997; Kirkland and Beckie, 1998; Evans et al., 2003a, Evans et al., 2003b; Kristensen et al., 2008; Tang et al., 2014; Jiang et al., 2018; Wang et al., 2019) (Karlsson et al., 2025). Other studies found that increasing nitrogen rates promoted crop growth more than weed growth (Wrocławowicz et al., 2023).

Finally, some studies reported no effects at all (Wells, 1979; Wilson and Tilman, 1993; Andersson and Milberg, 1998; Swanton et al., 1999; Otto et al., 2023).

The timing of fertiliser application was also proposed as a strategy for managing weeds, as plant nitrogen requirements vary over time depending on species and their interaction with the environment. However, similar to nitrogen application rate, early

fertilisation benefited either weed or crop growth depending on the study (Angonin et al., 1996; Liebman and Davis, 2000; Dhima and Eleftherohorinos, 2001; Harbur and Owen, 2004).

These differences in the outcome of crop–weed competition in response to modifications of nitrogen management depend on many factors interacting with the environment and management conditions, e.g., crop species/varieties, weed species/communities (with different relative emergence timings, capacities of resource uptake, responses to resource availability, etc.), weed and crop densities, weed management methods, and cropping systems (Brozović et al., 2021; Little et al., 2021; Rouge et al., 2022; Esposito et al., 2023; Dolijanović et al., 2025). All these interacting factors make it difficult to identify generic rules.

Mechanistic (i.e., process-based) models can increase genericity when investigating the effects of nitrogen fertilisation management and crop traits on weed regulation. By synthesising existing knowledge, such models are powerful tools for exploring a large number of prospective scenarios over the long term and across different environmental conditions (Colbach, 2010; Renton and Chauhan, 2017). As a complement to field experiments, which can explore only a limited number of scenarios, these models can perform many “virtual experiments” that are particularly useful for decorrelating the effects of numerous factors and identifying more general rules (Colbach et al., 2021).

FLORSYS (Colbach et al., 2021) is, to our knowledge, the most complete mechanistic model for simulating weed dynamics and crop yield over time based on cropping system, pedoclimatic, and species traits. The model operates with a daily time step, a 3D representation of each plant in the virtual field, and simulations of plant–plant competition for both light and nitrogen. It is, to our knowledge, the only model that allows the role of nitrogen fertilisation techniques and crop traits in weed dynamics and impacts to be deciphered.

The objectives of this paper were to identify which nitrogen fertilisation techniques and crop traits related to nitrogen nutrition most influenced weed dynamics, their impacts on crop production, and effects on agroecosystems. Both weed harmfulness and weed benefits were considered. Including weed-related services has become essential, as weeds are a key component of plant biodiversity and provide food for wild fauna in landscapes with intensive farming (Marshall et al., 2003). The final aim was to pinpoint fertilisation techniques and crop traits that decrease weed harmfulness, increase (or maintain) weed benefits, and maintain/increase potential crop yield (crop yield in the absence of weeds). To this end, multiannual and multispecies simulations were conducted using the FLORSYS model to perform sensitivity analyses (Saltelli et al., 2008).

## 2 Materials and methods

### 2.1 The “virtual-field” FLORSYS model simulating weed-crop dynamics over time

#### 2.1.1 A process-driven annual life cycle

FLORSYS (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014; Munier-Jolain et al., 2014; Colbach et al.,

2021; Moreau et al., 2021; Pointurier et al., 2021) is a process-based model simulating weed-crop dynamics over multiple years in a virtual field, with a daily time step. The model simulates a wide range of cropping systems, crop and weed species, and environmental conditions. Input variables include (1) a description of the simulated field (daily weather, latitude, and soil characteristics), (2) all management operations in the field (dates, tools, and options), and (3) the initial weed seed bank (species, density, age, and position in the soil layers).

These inputs and soil variables influence the annual life cycle of crops and weeds at a daily time-step. Plant phenology (e.g., flowering onset, maturity onset, and plant death) depends on temperature and the emergence season. Soil structure, temperature, and water potential control the pre-emergence stages, including surviving, dormant, and germinating seeds, as well as emerging seedlings. Emerging crop plants are positioned in the field according to the sowing pattern, whereas weeds are placed randomly in patches. Air temperature, soil nitrogen, and light available for each individual plant drive postemergence processes (photosynthesis, respiration, and growth). At plant maturity, part of the aboveground biomass is converted into seeds. Weed seeds are incorporated into the soil seed bank, while crop seeds are harvested to compute yield.

Life-cycle processes are influenced by dates, options, and tools of management techniques (tillage, sowing, herbicides, fertilisation, mechanical weeding, mowing, harvesting, irrigation) in interaction with the pedoclimate on the day of the operation. For instance, weed plant survival probability depends on management operations, the biophysical environment, weed stage, and weed morphology. Actual weed plant survival is determined stochastically by comparing the survival probability to a randomly generated value.

Each crop and weed species is described by a combination of parameter values (31 of which are presented in [Supplementary Table S1](#), section A online) characterising pre- and postemergent growth, nitrogen uptake, potential plant morphology, response to shading, and nitrogen limitation. The model is currently parametrised for 30 frequent and contrasting weed species and 33 crops (except for nitrogen competition; see [Section 2.1.3](#)).

### 2.1.2 Competition for light and nitrogen in a 3D individual-based canopy

Each individual plant is described in 3D: (1) aboveground, by a cylinder in which leaf area is distributed according to plant height, and (2) belowground, by a cylinder on top of a spilled cone in which root biomass is distributed. The field is discretised with voxels (3D pixels). Aboveground, incident light trickles down successive voxel layers depending on the leaf area within each layer. The light intercepted by a plant is converted into biomass and allocated to aboveground parts (increasing plant height and diameter) and belowground parts (similarly expanding root cones). Competition for light occurs when taller plants shade smaller ones or when plants have leaves in the same voxel. Belowground voxels can also contain roots from multiple plants. Competition for nitrogen occurs when the amount of nitrogen available in a voxel is insufficient for all plants with roots inside that voxel. In this case, individual plants

may experience nitrogen stress. This stress, along with shading, reduces biomass production, modifies biomass allocation among plant compartments (leaf, stem, root), and alters plant morphology (e.g., height and width per unit biomass, specific leaf area).

### 2.1.3 Species parameters underlying nitrogen competition

Plant nitrogen nutrition and competition in FlorSys were described by [Moreau et al. \(2021\)](#). Briefly, plant nitrogen uptake is simulated by confronting plant nitrogen demand with plant nitrogen supply.

Plant nitrogen demand is determined by the demand of the aboveground part (driven by daily leaf biomass and parameter  $cN_{req}$ , i.e., the optimal nitrogen amount in the plant aboveground part per unit of leaf biomass, in  $g \cdot g^{-1}$ ) and the belowground part (driven by daily root biomass and root nitrogen content). Plants decrease their root nitrogen content in response to nitrogen stress (driven by root biomass and parameter  $cRootN$ , i.e., the variation in root nitrogen concentration per additional nitrogen stress unit, in  $g \cdot g^{-1}$ ).

Plant nitrogen supply depends on root nitrogen uptake efficiency (parameter  $SNU_{max}$ , i.e., maximum amount of nitrogen that 1 g of root biomass can take up per day, in  $g \cdot g^{-1} \cdot day^{-1}$ ) and the daily available soil nitrogen to be shared among neighbouring plants. Soil-nitrogen availability varies with fertiliser application and mineralisation of soil organic matter, and it is simulated by the STICS soil submodel ([Brisson et al., 2009](#)) connected to FLORSYS.

Plant photosynthesis, aboveground plant morphology, and biomass allocation to roots vary daily with the nitrogen stress index of the plant. Thus, nitrogen-stressed plants reduce their specific leaf area, corresponding to leaf area per unit leaf biomass (parameter  $SLA_{muN}$ , dimensionless) and allocate more (or less, depending on the species) biomass to leaves at the expense of stems (parameter  $LBR_{muN}$ , dimensionless) ([Perthame et al., 2022](#)). Also, nitrogen-stressed plants allocate more biomass to roots at the expense of shoots (parameter  $rN$ , dimensionless). This parameter is not species-specific ([Pointurier et al., 2021](#)).

In total, FLORSYS includes six parameters related to nitrogen nutrition, five of which are species-specific. Among the 63 crop and weed species parameterised in FLORSYS, only seven species had these five species-specific nitrogen parameters determined from experiments. Default parameter values were assigned to the remaining species ([Moreau et al., 2021](#)).

### 2.1.4 Indicators of crop yield, weed harmfulness, and benefits

FLORSYS simulates crop yield and a set of weed-impact indicators for crop production and biodiversity ([Mézière et al., 2015](#)). This study used actual crop yield (from weed-inclusive simulations), potential crop yield (from weed-free simulations), and three indicators of weed harmfulness: crop grain yield loss due to weeds (i.e., the yield difference from weed-free vs. weed-inclusive simulations relative to weed-free yield), field infestation by weed biomass during the crop cycle, and annual weed seed production, as a proxy for the risk of future weed infestations. In addition, two indicators of weed benefits were used: weed species

richness (the number of weed species present during the cropping season) and weed-based food offer for domestic bees (depending on the appetite and density of flowering weed species).

### 2.1.5 Domain of validity

The FLORSYS version integrating only light competition, which considers nutrient availability is nonlimiting, was previously evaluated with independent field data at the French national scale, across a wide range of existing arable cropping systems, including maize monocultures in southwestern France. It showed that crop yields, daily weed species densities, and, in particular, densities averaged over the years were generally well predicted and ranked (Colbach et al., 2016; Pointurier et al., 2021).

Simulations run with the FLORSYS version integrating nitrogen nutrition and competition showed that predictions were in good agreement with knowledge of canopy functioning and crop–weed interactions, as well as with canopy nitrogen contents measured in the field (Moreau et al., 2021). Currently, the model only allows nitrogen fertiliser to be applied in a broadcast manner (i.e., no site-specific applications).

## 2.2 Simulation plan

### 2.2.1 Principle

We ran multiannual, multispecies weed simulations using the FLORSYS model. The aims were to determine the effects on crop yield and weed-impact indicators of:

- Nitrogen fertilisation (date and rate, crop residue management), initial soil organic nitrogen, and crop variety (differing in parameters related to nitrogen nutrition).
- Crop-variety parameters related to nitrogen nutrition.

To fulfil these aims, we performed two global sensitivity analyses. This method evaluates the variability of model outputs (here, crop yield and weed-impact indicators) in response to the simultaneous variation of model inputs (here, fertilisation, initial soil organic nitrogen, and crop nitrogen nutrition parameters) across their entire range of variation (Saltelli et al., 2008). By varying inputs simultaneously rather than successively, the global sensitivity analysis accounts for the interactions between inputs.

A simple cropping system was chosen as a case study to test the approach: a maize monoculture in Aquitaine (southwest of France). Maize monoculture is an intensive cropping system, widely practiced by farmers in this region (Jouy and Wissocq, 2011), and relies on high rates of nitrogen fertilisation: 182 to 202 kg N · ha<sup>-1</sup> applied to maize in 2017 in Aquitaine, while the mean rate applied to maize in France that year was 144 kg N · ha<sup>-1</sup> (Agreste, 2022). Weather data for the simulations were recorded at the Luxey weather station (X: 44.26667, Y: -0.51667, 99 m asl). The study determined whether modulating fertilisation management and maize traits (via variety choice) contributes to driving maize–weed interactions. This study is considered a proof of

concept; if the approach is validated here, it may be extended in the future to other cropping systems.

### 2.2.2 First sensitivity analysis of all factors related to nitrogen-fertilisation techniques

A virtual field network of maize monoculture was simulated with FlorSys using different combinations of (1) nitrogen application rates and dates, and crop residue management practices, (2) initial amounts of soil organic nitrogen, and (3) maize varieties differing in the values of the five species-specific nitrogen nutrition parameters (presented in Section 2.1.3). These parameter values were varied within the ranges observed for the eight to 10 species (depending on the parameter) parameterised for nitrogen nutrition in the model (Table 1).

The chosen cropping system was recorded during farm-field surveys used in a previous simulation study (Bürger et al., 2015). Maize was sown on 15 May and harvested on 14 October (list of operations in Supplementary Table S2, section B online). The field was tilled three times, including mouldboard ploughing, before sowing. Herbicides were applied the day after sowing, and the crop was irrigated. Nitrogen fertilisation was mineral (ammonium nitrate) and applied on a single date. No cover crop was present during winter fallow.

The fertilisation techniques that varied were nitrogen application rate and date, as well as crop residue management (either buried or exported) (Table 2A). Application rate varied from 0 to 400 kg N · ha<sup>-1</sup>. Nitrogen rates were chosen to be roughly ± 100% of the mean rate applied to maize in Aquitaine. Application dates varied from the day after sowing to 33 days after sowing. This time span is crucial for maize nitrogen absorption (Arvalis-infos, 2017). Later in the season, nitrogen uptake sharply decreases (Arvalis-infos, 2017), and increasing plant height hampers field access. Initial soil organic nitrogen was made to vary within ranges reported from fields (Brisson et al., 2003) (Table 2B).

Three maize varieties were simulated: one mean variety (V1 in Table 2C), defined using mean values for nitrogen nutrition parameters, and two contrasting varieties. As species-specific nitrogen nutrition parameters were not available for maize, these parameters were derived from measurements across eight to 10 crop and weed species. The two additional maize varieties (V2 and V3 in Table 2C) were defined using either the minimum or maximum values observed for nitrogen nutrition parameters across species, while respecting correlations among parameters (see principal component analysis in Supplementary Figure S2, section C.1 online). Variety V2 is characterised by a high aboveground nitrogen demand, whereas variety V3 is characterised by a high response of leaf biomass to nitrogen stress, a high belowground nitrogen demand, and a high root nitrogen uptake. For the three maize varieties, all other parameters (phenology, germination, emergence, competition for light, etc.) were unchanged and corresponded to actual maize. A total of 132 scenarios was created by combining these five factors based on Latin hypercube sampling (LHS) (McKay et al., 1979), using the randomLHS function of R (Author, 2019).

Each scenario was simulated over 10 years and repeated five times with five randomly chosen 10-year weather series (identical series for each scenario) drawn from climatic years between 2000 and 2006 in Aquitaine (INRAE Climatik platform). A typical regional weed seed

TABLE 1 Key species-specific parameters for nitrogen nutrition.

Parameter name	Meaning of the parameter	Unit	Range
cNreq <sub>s</sub>	Optimal amount of nitrogen in the vegetative aboveground part of the plant (leaf + stem) per unit of leaf biomass. It corresponds to the minimal value required to ensure maximal crop growth rate.	g <sub>shoot nitrogen</sub> ·g <sub>leaf biomass</sub> <sup>-1</sup>	[0.030, 0.111]
cRootN <sub>s</sub>	Additional root nitrogen concentration per additional nitrogen stress unit ([Supplementary Figure S1.C, Section A online]).	g <sub>root nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup>	[0.0107, 0.0400]
SNUmax <sub>s</sub>	Root nitrogen uptake efficiency (the maximum amount of nitrogen that 1 g of root biomass can take up per day).	g <sub>soil nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup> ·day <sup>-1</sup>	[0.0011, 0.087]
SLA_muN <sub>s</sub>	Response of specific leaf area (SLA) to nitrogen stress [Supplementary Figure S1.A, Section A online]. < 0: SLA decreases with nitrogen stress.	None	[- 1.54, 0]
LBR_muN <sub>s</sub>	Response of leaf biomass ratio (LBR) to nitrogen stress [Supplementary Figure S1.B, Section A online]. > 0, LBR increases with N stress, < 0: LBR decreases.	None	[- 1.21, 0.68]

Ranges of variation correspond to the species parameterised for nitrogen nutrition (between eight and 10 species per parameter) (Perthame et al., 2020; Moreau et al., 2021; Perthame et al., 2022).

TABLE 2 Range of variation of nitrogen fertilisation, initial soil organic nitrogen, and maize variety that were used to evaluate their influence on weed-impact indicators.

Variable	Unit	Range (Value for maize variety parameters)	
<b>A. Nitrogen fertilization</b>			
Nitrogen application rate	kgN·ha <sup>-1</sup>	[0, 400]	
Nitrogen application date	Days after sowing	[1, 33]	
Crop residue management	none	Burial or Export	
<b>B. Initial soil nitrogen</b>			
Initial soil organic nitrogen	kgN <sub>org</sub> ·ha <sup>-1</sup>	[48.9, 293.4]	
<b>C. Maize varieties (see Table 1 for meaning of parameters)</b>			
V1 (mean variety)	cNreq <sub>s</sub>	g <sub>shoot nitrogen</sub> ·g <sub>leaf biomass</sub> <sup>-1</sup>	0.0966
	cRootN <sub>s</sub>	g <sub>root nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup>	0.0234
	SNUmax <sub>s</sub>	g <sub>soil nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup> ·day <sup>-1</sup>	0.0491
	SLA_muN <sub>s</sub>	none	-0.13
	LBR_muN <sub>s</sub>	none	-0.85
V2 (virtual variety)	cNreq <sub>s</sub>	g <sub>shoot nitrogen</sub> ·g <sub>leaf biomass</sub> <sup>-1</sup>	0.111
	cRootN <sub>s</sub>	g <sub>root nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup>	0.0107
	SNUmax <sub>s</sub>	g <sub>soil nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup> ·day <sup>-1</sup>	0.0011
	SLA_muN <sub>s</sub>	none	-1.54
	LBR_muN <sub>s</sub>	none	-1.21
V3 (virtual variety)	cNreq <sub>s</sub>	g <sub>shoot nitrogen</sub> ·g <sub>leaf biomass</sub> <sup>-1</sup>	0.030
	cRootN <sub>s</sub>	g <sub>root nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup>	0.0400
	SNUmax <sub>s</sub>	g <sub>soil nitrogen</sub> ·g <sub>root biomass</sub> <sup>-1</sup> ·day <sup>-1</sup>	0.087
	SLA_muN <sub>s</sub>	none	0
	LBR_muN <sub>s</sub>	none	0.68

bank from Aquitaine was selected, consisting of 25 annual weed species currently included in FLORSYS (seed bank density per species is available in [Supplementary Table S3](#), section B online).

This simulation plan was repeated without an initial weed seed bank to estimate potential yield (weed-free simulations). Crop yield loss due to weeds was calculated as the difference between the two series relative to the weed-free yield.

### 2.2.3 Second sensitivity analysis of maize parameters

A second virtual field network of maize monoculture was simulated with FlorSys, combining different maize parameters regarding nitrogen nutrition. The chosen cropping system was the same as described above, but nitrogen fertilisation variables were fixed. Ammonium nitrate was applied at a rate of  $220 \text{ kg N} \cdot \text{ha}^{-1}$  (Agreste, 2013) 1 month after sowing (15 June). Crop residues were buried. Initial soil organic nitrogen ( $48.9 \text{ kg N}_{\text{org}} \text{ ha}^{-1}$ ) was based on typical soils from the region (Bürger et al., 2015).

Only maize nitrogen nutrition parameters varied (Table 1) within the ranges observed in the species parameterised for nitrogen nutrition (Perthame et al., 2020; Moreau et al., 2021; Perthame et al., 2022). A simulation plan of 100 combinations of nitrogen nutrition parameters, respecting correlations among parameters (according to the PCA in [Supplementary Figure S2](#), section C.1 online), was carried out using LHS with the LHS<sub>corr</sub> function in R.

Each scenario was simulated over 10 years using five 10-year-long weather series, which were identical for all scenarios. Two simulation series were run: one starting with the same initial weed seed bank as in [Section 2.2.2](#), and the other without weeds, in order to calculate crop yield loss due to weeds.

## 2.3 Statistics

First, tradeoffs between weed harmfulness, crop yield, and weed benefits were studied using principal component analysis (PCA) and Pearson correlations.

The proportion of indicator variability (yield and weed-impact indicators) explained by the different simulation factors was then quantified. For both sensitivity analyses, we used linear models of indicators as a function of either nitrogen fertilisation techniques or maize parameters, as well as weather repetition, time since simulation onset, and double interactions between factors (the `lm` function of R). Only factors/variables significant at  $p < 0.05$  were retained in the final model after backward selection. Initial soil nitrogen content and nitrogen application date were discretised for interactions with continuous variables. Crop yield loss and weed seed production indicators were  $\log_{10}$ -transformed to ensure that residuals presented a normal distribution centred on zero and that variance was independent of the means. Nitrogen rate was  $\log_{10}$ -transformed in the models explaining weed seed production and weed-free yield, as yield does not increase linearly with increasing nitrogen rate (Simonin, 2017). A  $\log_{10}$ -transformation was also applied to the root nitrogen uptake efficiency parameter in the model explaining weed-free yield. Mean indicators were compared per maize variety and per crop residue

management option using a least-significant difference test (`lsd.test` function of R).

## 3 Results

### 3.1 Tradeoffs among indicators

A principal component analysis was performed for both sensitivity analyses. The aim was to determine whether modulating nitrogen fertilisation techniques (Figure 1) or maize parameters ([Supplementary Figure S3](#) [section C.3 online]) led to (in)compatibility between minimising weed harmfulness vs. maximising weed benefits vs. maximising maize production. Correlation analyses are detailed in [Supplementary Tables S4](#) (section C.2 online), [S5](#) (section C.3 online).

The first axes (dim1, dim2, and dim3) explained most of the variability of the indicators of weed impacts and crop performance among situations (i.e., nitrogen fertilisation strategy or variety  $\times$  weather repetition  $\times$  year), with 86.7% in [Figure 1](#) and 87.5% in [Supplementary Figure S3](#) [section C.3 online].

Situations with a high crop yield (from weed-inclusive simulations) were also those with low weed harmfulness (i.e., low crop yield loss due to weeds and low field infestation). Moreover, situations that achieved a high bee-food offer were also those with high weed species richness, but they did not systematically exhibit high or low crop yield, or high or low weed harmfulness. These findings suggest that it is possible to identify situations combining high weed benefits, high crop yield, and low weed harmfulness.

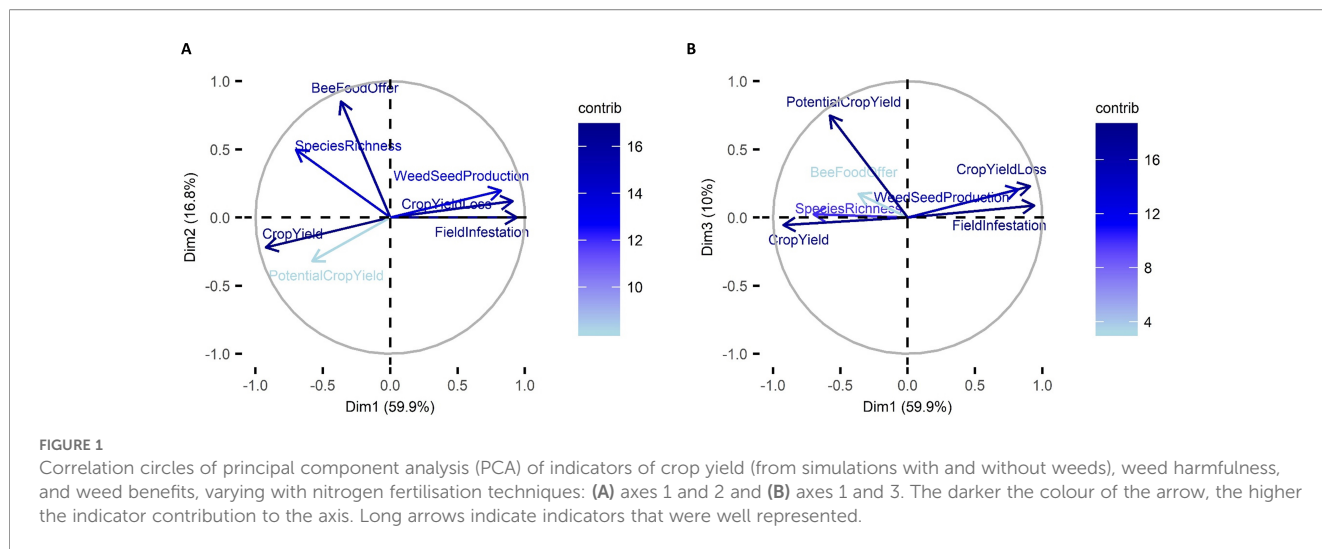
As harmfulness indicators and crop yield (in weed-inclusive field) were highly (negatively) correlated, we selected two weed harmfulness indicators (crop yield loss and weed seed production) for the sensitivity analyses in the following sections. We also retained weed-free crop yield and the two weed benefit indicators, weed species richness and bee food offer (except for the sensitivity to maize parameters).

### 3.2 Effect of nitrogen fertilisation techniques and maize variety on yield and weed impacts

Linear models explained most of the variability in weed-free yield and species richness (large total  $R^2$  in [Table 3](#)). More unexplained variability remained for crop yield loss due to weeds, weed seed production, and bee food offered from weeds (lower total  $R^2$ ). This was due to interactions with weather, interactions among factors beyond the second order (which were not included in the analysis of variance), and stochastic effects in FLORSYS.

For all indicators, weather repetition and/or time since simulation onset had a strong influence (% of total  $R^2$  for the analysed indicator is shown in [Table 3](#)). For weed-free crop yield, time since simulation onset had a minor effect, indicating only minor carryover effects.

Potential (i.e., weed-free) maize yield and crop yield loss due to weeds were the indicators most influenced by nitrogen-related factors. In contrast, weed-benefits indicators (species richness and bee food offer) were not strongly affected. Maize variety and nitrogen application



**TABLE 3** Percentage of total variance of yield and weed-impact indicators explained by simulation factors.

	Factor	% of total R <sup>2</sup>				
		Crop yield potential (from weed-free simulations) (dry yield t·ha <sup>-1</sup> )	Crop yield loss due to weeds (%)	Weed seed production (seeds·m <sup>-2</sup> )	Weed species richness (species number)	Bee food offer from weeds [0, 10] (dimensionless)
Variety and N fertilization modalities	Maize variety	1.5	5.5	1.2	0.6	0.2
	Crop residue management	2.9				
	N rate		12.3	0.1	0.0	0.2
	Initial soil organic N	1.3	2.4	0.4	0.3	0.3
	N date	4.4		0.2	0.1	0.5
	Maize variety × N rate	12.1	5.9	3.5	0.6	1.8
	Maize variety × initial soil organic N	1.1	0.9	0.4	0.1	0.9
	Maize variety × N date	3.4		0.4		0.4
	Residue management × N rate	1.9				
	Residue management × initial soil organic N					
	Residue management × N date	1.4				
	N rate × initial soil organic N	3.2	0.5	0.4		0.3
	N rate × N date	0.9				
	Initial soil organic N × N date	4.6		0.0		
Weather Repetition	59.9	32.0	50.0	8.5	39.0	
Time since simulation onset	1.2	40.4	43.1	89.7	56.3	
Total R <sup>2</sup> (dimensionless)	0.88	0.39	0.51	0.76	0.36	

Indicators of weed harmfulness and benefits are shown in red and green, respectively. Only factors significant at  $p \leq 0.05$  were retained. Cells were coloured from white (zero % of total variance) to dark yellow (highest % of variance). Gray cases indicate nonsignificant factors that were removed from the model. N, nitrogen. Purple numbers correspond to total R<sup>2</sup>, while black numbers are expressed as a percentage (%) of the total R<sup>2</sup>.

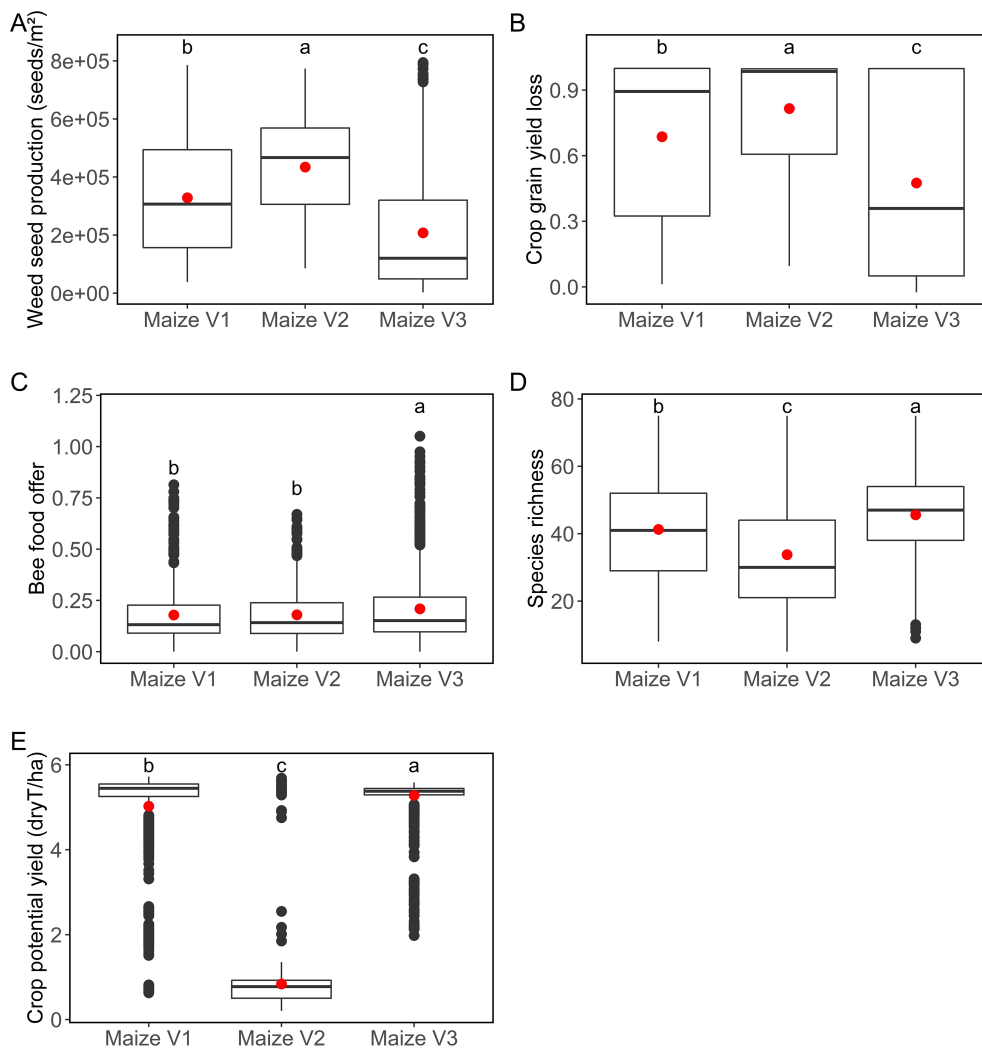
rate (as sole factors or in interaction, depending on the indicator) had the strongest effect. Nitrogen application date had a noticeable influence (as a single factor or in interaction with other factors) on maize potential yield only. All the other factors had a negligible influence.

We quantified the effects of nitrogen fertilisation rate and variety, which were the most influential factors according to the previous analysis. Mean potential (i.e., weed-free) maize yield, species richness, and bee food offer were highest for variety V3 (across all simulations), while mean crop yield loss and weed seed production were the lowest (Figure 2). Variety V2 showed the opposite features. Varieties V3 and V2 were thus the most and the least productive, competitive, and biodiversity-promoting maize varieties, respectively.

For two out of three varieties (V1 and V3), decreasing the nitrogen fertilisation rate decreased potential yield and species richness and increased crop yield loss due to weeds (Table 4). However, varietal differences were observed. Decreasing nitrogen application rate by 50 kg

$N \cdot ha^{-1}$  had the following effects: (1) potential (i.e., weed-free) yield decreased (by  $0.16 \text{ dry t} \cdot ha^{-1}$ ) for variety V1, whereas the effect was negligible for the other varieties (Table 4, line 3); (2) crop yield loss due to weeds increased for V1 and V3 (by 12% and 10%, respectively) and was not significant for variety V2; (3) the effect on weed seed production differed for varieties V2 and V3 (– 16% and + 10%, respectively) and was not significant for the variety V1; (4) species richness decreased much more for V1 than for V3 and increased for V2; and (5) the effect on bee food offer was negligible for all three varieties. Overall, variety V2 responded the most favourably to a reduction of nitrogen fertilisation rate (showing stable potential yield and crop yield losses due to weeds, reduced weed seed production, and increased weed species richness).

In conclusion, reducing the nitrogen fertilisation rate generally decreased maize performance (in terms of potential crop yield, crop yield loss due to weeds, and promotion of weed species biodiversity). Overall, across the simulated situations, varieties V3 and V2 performed



**FIGURE 2** Mean performances of the three maize varieties. (A, B) Weed harmfulness, (C, D) weed benefits, and (E) potential yield indicators for the three maize varieties. V1 is a variety with mean parameter values, V2 is characterised by a high aboveground nitrogen demand, and V3 is characterised by a high response of leaf biomass to nitrogen stress, a high belowground nitrogen demand, and a high root nitrogen uptake. Boxplots show the minimum, third quartile, median, first quartile, and maximum values for each indicator (with outliers defined as values outside four times the interquartile range). Red points show means. Same letters indicate that the means are not significantly different.

TABLE 4 Variation of potential (i.e., weed-free) maize yield and weed-impact indicators in response to nitrogen-fertilisation techniques and variety.

N°	Factor		Factor variation	Effect of factor variation on indicators									
				Potential (i.e. weed-free) yield (dry t·ha <sup>-1</sup> )		Crop yield loss (%)		Weed seed production (seeds·m <sup>-2</sup> )		Species richness (number of species)		Bee food offer (dimensionless)	
Theoretical range of variation of indicators				[0, +∞]		[-100, 100]		[0, +∞]		[0, 75]		[0, 10]	
1	Time since simulation onset		+ 10 years	+ 0.094		× 2.61		×2.75		- 43.2		- 0.203	
2	N date		↘ 32 days							+ 1.6			
3	Maize variety × N rate	V1	↘ 50 kgN·ha <sup>-1</sup>	- 0.16	c	× 1.12	a	× 1	b	- 0.60	c	0	b
		V2		0	a	× 1	c	× 0.84	c	+ 0.50	a	- 0.006	c
		V3		- 0.007	b	× 1.10	b	× 1.10	a	- 0.15	b	+ 0.007	a
4	Maize variety × initial soil organic N	V1	↘ 50 kgN <sub>org</sub> ·ha <sup>-1</sup>	0	c	× 1.11	a	× 0.95	a	- 0.84	b	0	a
		V2		+ 0.051	b	× 1.03	b	× 0.92	b	- 0.28	a	0	a
		V3		+ 0.086	a	× 1.11	a	× 0.96	a	- 0.51	a	- 0.013	b
5	Maize variety × N date	V1	↘ 32 days	- 0.62	a			× 1.21	a			+ 0.041	b
		V2		- 0.37	b			× 1	b			0	a
		V3		- 0.77	a			× 1.28	a			+ 0.025	b
6	Residue management × N rate	Burial	↘ 50 kgN·ha <sup>-1</sup>	- 0.065	b								
		Export		0	a								
7	Residue management × N date	Burial	↘ 32 days	- 0.70	a								
		Export		- 0.47	b								
8	N rate × initial soil organic N	Low <sup>1</sup>	↘ 50 kgN·ha <sup>-1</sup>	0	a	× 1.09	a	× 0.98	a			0	a
		Medium <sup>1</sup>		0	a	× 1.07	b	× 0.97	b			- 0.003	b
		High <sup>1</sup>		- 0.041	b	× 1.06	c	× 0.98	a			- 0.003	b
9	N rate × N date	Early <sup>2</sup>	↘ 50 kgN·ha <sup>-1</sup>	- 0.017	b								
		Medium <sup>2</sup>		0	a								
		Late <sup>2</sup>		0	a								

(Continued)

TABLE 4 Continued

N°	Factor	Factor variation	Effect of factor variation on indicators				
			Potential (i.e. weed-free) yield (dry t·ha <sup>-1</sup> )	Crop yield loss (%)	Weed seed production (seeds·m <sup>-2</sup> )	Species richness (number of species)	Bee food offer (dimensionless)
Theoretical range of variation of indicators			[0, +∞]	[-100, 100]	[0, +∞]	[0, 75]	[0, 10]
10	Initial soil organic N × N date	Early <sup>2</sup>	0		× 0.96		
		Medium <sup>2</sup>	+ 0.08		× 0.94		
		Late <sup>2</sup>	+ 0.10		× 0.93		

Indicators of weed harmfulness and benefits are shown in red and green, respectively. Due to the log<sub>10</sub>-transformation, variation of harmfulness indicators is expressed as a ratio (×), whereas it is expressed as a difference for the other indicators (±). For a given factor, two variations followed by the same letter are not significantly different, and slopes that are not significantly different from 0 (or 1 for ratios) are indicated; slopes were compared using the ln function of R. Cells are coloured from red for the highest deterioration of indicator value (i.e., the strongest decrease of biodiversity and yield or the strongest increase of weed harmfulness) to green for the greatest improvement of indicator value (vice versa). Gray cases indicate nonsignificant factors that were removed from the model. V1 is a variety with mean parameter values; V2 is characterised by a high aboveground nitrogen demand; and V3 is characterised by a high response of leaf biomass to nitrogen stress, a high belowground nitrogen demand, and a high root nitrogen uptake.

<sup>a</sup>Initial soil organic N low [48.9, 97.8], medium [107.6, 195.6], and high [205.4, 293.4] kg<sub>Storg</sub>·ha<sup>-1</sup>.

<sup>b</sup>N application date early [1, 11], medium [12, 22], and late [23, 33] days after sowing.

the best and the worst, respectively. When nitrogen fertilisation was lowered, variety V2 showed the most favourable response.

### 3.3 Effect of maize parameters on yield and weed-related indicators

To better understand these differences among varieties, we analysed the effect of each nitrogen-nutrition parameter on maize potential yield, as well as on weed harmfulness and benefits (Table 5). As in the first sensitivity analysis, linear models explained most of the variability in species richness (large total R<sup>2</sup> in Table 5), while more unexplained variability remained in crop yield loss, weed seed production, and potential (weed-free) yield.

In the first sensitivity analysis, weather repetition and/or time since simulation onset had the strongest influence for all indicators except potential crop yield (large % of total R<sup>2</sup> for the analysed indicator in Table 5).

Overall, the most influential nitrogen nutrition parameters for potential (i.e., weed free) yield and weed harmfulness (crop yield loss due to weeds and weed seed production) were aboveground nitrogen demand per unit leaf biomass (cNreq<sub>s</sub>), root nitrogen uptake efficiency (SNUmax<sub>s</sub>), and the response of specific leaf area to nitrogen stress (SLA\_muN<sub>s</sub>) (see partial R<sup>2</sup> values). The hierarchy of the parameters depended on the indicators. For instance, potential yield was mostly influenced by SNUmax<sub>s</sub>, while cNreq<sub>s</sub> and SLA\_muN<sub>s</sub> were minor factors. The opposite was observed for weed harmfulness indicators. All parameters had a weak influence on weed species richness.

Decreasing root nitrogen uptake efficiency (SNUmax<sub>s</sub> by 0.086 g · g<sup>-1</sup> · day<sup>-1</sup>) and leaf area per unit leaf biomass in response to nitrogen stress (SLA\_muN<sub>s</sub> by 1.54) increased crop yield loss due to weeds (by 52% and 77%, respectively) and weed seed production (by 50% and 84%, respectively) (Table 6, lines 3 and 4). It also reduced species richness (by four and seven species, respectively). A decrease in SNUmax<sub>s</sub> additionally reduced potential maize yield (by 3 dry t · ha<sup>-1</sup>). In contrast, decreasing aboveground nitrogen demand per unit of leaf biomass (cNreq<sub>s</sub> by 0.081 g · g<sup>-1</sup>) had opposite (and beneficial) effects on all the indicators: it increased potential crop yield and weed benefits and reduced weed harmfulness (Table 6, line 1).

To conclude, a maize variety combining high root nitrogen uptake efficiency (SNUmax<sub>s</sub>), low nitrogen demand per unit leaf biomass (cNreq<sub>s</sub>), and stable leaf morphology (leaf area per unit leaf biomass) regardless of plant nitrogen stress (SLA\_muN<sub>s</sub>) achieved the best performance, with high maize productivity and weed benefits and low weed harmfulness.

## 4 Discussion

### 4.1 An original approach to decipher the effects of nitrogen fertilisation techniques and variety traits on weed harmfulness and benefits

This study performed sensitivity analyses using a process-based model (FLORSYS) simulating crop and weed growth and dynamics

TABLE 5 Percentage of total variance of yield and weed-impact indicators explained by simulation factors.

Factor		% of total $R^2$			
		Potential (i.e., weed-free) maize yield (dry $t \cdot ha^{-1}$ )	Crop yield loss due to weeds (%)	Weed seed production (seeds $m^{-2}$ )	Weed species richness (species number)
N nutrition parameters	Aboveground N demand per unit leaf biomass (cNreq <sub>s</sub> )	4.0	27.2	10.0	0.6
	Root N content in response to N stress (cRootN <sub>s</sub> )	0.4		0.2	0.02
	Root N uptake efficiency (SNUmax <sub>s</sub> )	72.5	6.6	5.4	0.5
	Response of specific leaf area to N stress (SLA_muN <sub>s</sub> )		12.1	12.4	1.5
	Response of leaf to shoot biomass ratio to N stress (LBR_muN <sub>s</sub> )	1.1	0.5	1.0	0.1
Weather repetition		21.1	17.5	39.7	3.3
Time since simulation onset		0.8	36.1	31.2	94.0
Total $R^2$ (dimensionless)		0.40	0.34	0.50	0.87

Indicators of weed harmfulness and benefits are in red and green, respectively. Only factors significant at  $p \leq 0.05$  were kept. Cells were coloured from white (zero % of total variance) to dark yellow (highest % of variance). Gray cases indicate nonsignificant factors that were removed from the model. N, nitrogen. Purple numbers correspond to total  $R^2$ , while black numbers are expressed in % of total  $R^2$ .

TABLE 6 Variation of weed-free yield and weed-impact indicators in response to modification of maize parameters related to nitrogen nutrition.

No.	Factor	Factor variation	Effect of factor variation on indicator variation			
			Potential (i.e., weed-free) yield (dry $t \cdot ha^{-1}$ )	Crop yield loss due to weeds (%)	Weed seed production (seeds $m^{-2}$ )	Weed species richness (species number)
Theoretical range of variation of indicators			[0, + ∞]	[- 100, 100]	[0, + ∞]	[0, 75]
1	Aboveground N demand per unit leaf biomass (cNreq <sub>s</sub> )	↘ 0.081 $g \cdot g^{-1}$	+ 0.54	× 0.43	× 0.58	+ 4.28
2	Root N content in response to N stress (cRootN <sub>s</sub> )	↘ 0.03 $g \cdot g^{-1}$	+ 0.16		× 0.93	+ 0.69
3	Root N uptake efficiency (SNUmax <sub>s</sub> )	↘ 0.086 $g \cdot g^{-1} \cdot day^{-1}$	- 3.23	× 1.52	× 1.50	- 3.83
4	Response of specific leaf area to N stress (SLA_muN <sub>s</sub> )	↘ 1.54		× 1.77	× 1.84	- 6.67
5	Response of leaf biomass ratio to N stress (LBR_muN <sub>s</sub> )	↘ 1.89	+ 0.29	× 1.13	× 1.19	- 1.71

Indicators of weed harmfulness and benefits are shown in red and green, respectively. This analysis investigates the effect of decreasing parameter values from the maximum to the minimum values observed in the parameterised species. Due to the  $\log_{10}$ -transformation, variation of harmfulness indicators is expressed as a ratio (×), whereas it is expressed as a difference (±) for the other indicators. All the slopes are significantly different from 0 (or 1 for ratios); slopes were compared to 0 using the lm function of R. Cells are coloured from red for the highest deterioration of indicator value (i.e., the strongest decrease of biodiversity and yield or the strongest increase of harmfulness) to green for the greatest improvement of indicator value (vice versa). Gray cases indicate nonsignificant factors that were removed from the model.

over the years from information on the cropping system, pedoclimate, and species traits (Colbach et al., 2021). A maize monoculture from southwestern France was used as a case study. Different maize varieties (differing by their trait values related to nitrogen nutrition) were simulated in different scenarios of nitrogen fertilisation (application date and rate, crop residue management, and initial soil organic nitrogen) and weather conditions. Weed impacts were analysed in terms of both harmfulness on crop production (i.e., crop grain yield loss due to weeds, field infestation by weed biomass, and weed seed production) and benefits for biodiversity (i.e., weed species richness, weed-based food offer for bees).

The present study constitutes a proof of concept of a novel approach using a mechanistic model simulating crop–weed dynamics to decipher the effects of fertilisation techniques, initial soil organic nitrogen, and crop traits related to nitrogen nutrition on crop productivity and weed impacts.

Until now, the effect of nitrogen management on weeds has been mainly studied under real field conditions, making it difficult (nearly impossible) to disentangle complex interactions (see the many references quoted in Section 1). In particular, this approach makes it difficult to (1) discriminate the effects of weed-flora context, pedoclimate, and cropping system from the effects of nitrogen management and crop traits, given the usual adaptation of management techniques to the other factors and the numerous interactions among all factors, and (2) quantify the impacts of weeds on crop productivity and biodiversity (which are difficult to measure in the field) over the long term. In this study, the model was used as a virtual field to investigate weed impacts on crop productivity and biodiversity over the long term under numerous combinations of nitrogen-related factors and a multispecies weed flora.

Thanks to this simulation approach, which allows disentangling complex interactions (Colbach, 2010; Renton and Chauhan, 2017), this study is, to our knowledge, the first to attempt to disentangle the effect of each nitrogen-related factor on the impacts of weeds.

## 4.2 Reducing the nitrogen fertilisation rate globally decreased the potential crop yield and increased the harmfulness of weeds

This novel approach was essential to rank the nitrogen fertilisation techniques according to their influence on weed harmfulness and benefits in the analysed maize monoculture case study. While nitrogen application date and initial soil organic nitrogen had minor effects, nitrogen rate was the most influential factor. The novelty of this finding, along with the associated scarcity of references in the literature, makes the comparison to other studies difficult. However, past in-field studies focussed much more frequently on the effect of nitrogen fertilisation rate on weeds than on fertilisation date (Perthame, 2020). This observation could implicitly suggest that modulating nitrogen rate is considered more effective than modulating nitrogen date, as null effects are rarely published (Anonymous Editorial, 2019).

More precisely, our findings showed that decreasing nitrogen rate globally deteriorated maize performance: it decreased potential crop yield (and, to a much lesser extent, weed species richness) while increasing crop yield losses due to weeds. These findings are concordant with studies on maize showing that decreasing nitrogen rate disfavoured crop growth more than weed growth (Tollenaar et al., 1997; Evans et al., 2003a, Evans et al., 2003b; Abouziena et al., 2007), even though some studies reported no effect of fertilisation rate on weed flora (density and species composition) (Swanton et al., 1999). This decrease in potential crop yield with decreasing nitrogen rate could result from crop breeding practices that select crop—and especially maize—varieties for high soil-nitrogen availability (Ciampitti and Vyn, 2012). The increase in weed harmfulness suggests that maize could be more penalised than weeds and may be related to the relative nitrophily of maize vs. weeds in our simulation study (Moreau et al., 2013, Moreau et al., 2014). The reduction of species richness with decreasing nitrogen application rate that we observed here disagrees with long-term field observations of Fried et al. (2009). However, the convergence between the two studies is difficult to analyse. (1) First, Fried et al. conducted their study on sunflowers in diverse rotations (and not on maize monoculture). (2) Second, they compared species richness across different time periods (1970 vs. 2000) rather than between nitrogen-fertilisation treatments, as in our study and most other studies, assuming that the observed differences were primarily due to a general increase in nitrogen fertilisation by farmers. However, other changes in cropping practices over the 30-year period could also explain the results reported by Fried et al.

## 4.3 A key role of crop traits related to nitrogen nutrition

Our study demonstrates the key role of maize variety for potential crop yield (i.e., yield without weeds) and weed harmfulness. In particular, the most productive and competitive maize varieties, across the tested scenarios, were characterised by low nitrogen demand per unit leaf biomass ( $cN_{req}$ ), high root nitrogen uptake efficiency ( $SNU_{max}$ ), and stable specific leaf area in response to nitrogen stress ( $SLA_{\mu N}$ ). Logically, a low nitrogen demand per unit leaf biomass, as well as a high root nitrogen uptake efficiency, allows fulfilling plant needs more easily, increasing plant competitive advantage (Ditomaso, 1995; Singh et al., 2017). In parallel, maintaining leaf area per unit of leaf biomass, even in the case of plant nitrogen deficiency, allows the plant to maximise its leaf area for a given biomass and therefore to maintain a large area for both (1) light interception for plant photosynthesis (promoting plant growth) and (2) shading of neighbouring plants (promoting competitive ability for light with weeds) (Moreau et al., 2013, Moreau et al., 2014; Colbach et al., 2019).

## 4.4 Can nitrogen fertilisation and maize traits contribute to weed management?

Altogether, our study suggested that crop varieties (with respect to their nitrogen nutrition traits) and nitrogen fertilisation rate can

be used as levers to drive potential yield as well as weed harmfulness (but not weed benefits, which were little influenced by these levers). Our findings highlighted the need to judiciously coordinate the choice of crop varieties and nitrogen fertilisation rate. In the context of reducing chemical inputs, the results suggested that, for the studied cropping system, a reduction in both herbicide and nitrogen fertiliser use might lead to a dead end in weed management, at least in cropping systems similar to the one studied here.

Note that we only varied the nitrogen-related parameters, while other plant traits might interact with their effects. Furthermore, additional sensitivity analyses would help determine whether the most influential crop nitrogen-nutrition parameters depend on, e.g., weed species seasonality or response to shading.

The present study was conducted with virtual maize varieties, artificially defined by combining trait values. Future work should screen real maize genetic resource collections to quantify the variability of the three most influential nitrogen-related traits. Additionally, our study was conducted in only one pedoclimate (from one French region), and the robustness of our conclusions across different pedoclimates should be tested. This study focussed on one particular, very simple cropping system (maize monoculture), chosen as a proof of concept to test our approach. In the future, the approach developed here will be applied to diversified cropping systems. The ultimate aim is to provide guidelines for breeding more productive and competitive crop varieties, which remain marginally developed and released to date (Sardana et al., 2017).

In the next steps, it would be useful to analyse whether, in addition to reducing nitrogen rate, localising nitrogen fertilisers on the sowing row (rather than broadcasted) could help promote crop vs. weed growth. Localising nitrogen on the crop row has been shown to efficiently promote crop vs. weed growth for different crop species, such as wheat, soybean, and alfalfa (Ditomaso, 1995). Although the relevance of this technique for maize–weed competition has, to our knowledge, not been evaluated, the large interrow width of maize makes it a good candidate for implementing this approach.

## 5 Conclusion

By using a mechanistic model simulating weed dynamics, the present study constitutes a proof of concept that enables us to decipher the effects of nitrogen fertilisation and nitrogen-related crop traits on the outcome of crop–weed competition. Our approach allowed identification of how changes in nitrogen-fertilisation techniques affect yield, weed harmfulness, and benefits, as well as which nitrogen-related crop traits enhance crop competitiveness against weeds. In the present case study, nitrogen application rate and maize variety were the factors influencing weed impacts on crop production and biodiversity the most. Decreasing nitrogen rates increased weed harmfulness for crop production and also reduced maize yield potential. The maize traits that both minimised weed harmfulness and maximised maize

productivity were a low plant nitrogen demand, a high root nitrogen uptake efficiency, and a specific leaf area (leaf area per unit leaf biomass) that was insensitive to plant nitrogen stress. These research results are highly significant for the biological control of weeds and the sustainable development of agriculture. Applying this approach to other production contexts could provide guidelines for farmers and varietal breeding, helping to identify optimal nitrogen-fertilisation strategies and the key traits to target for promoting weed control.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Author contributions

LP: Conceptualization, Formal analysis, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing. DM: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing. TM: Methodology, Writing – original draft, Writing – review & editing. NC: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

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## Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2026.1690014/full#supplementary-material>

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### SUPPLEMENTARY TABLE 1

Example of species parameters for characterising pre-emergent growth, plant growth, potential morphology, response to shading, root growth and other parameters.

### SUPPLEMENTARY FIGURE 1

Schematic representation of three nitrogen nutrition parameters.

### SUPPLEMENTARY TABLE 2

List of cultural operations for the simulated maize monoculture in Aquitaine.

### SUPPLEMENTARY TABLE 3

Initial seed bank at the onset of simulation.

### SUPPLEMENTARY FIGURE 2

Correlations circles of Principal Component Analysis (PCA) results with five key parameters related to nitrogen nutrition.

### SUPPLEMENTARY TABLE 4

Pearson correlations (in bold) among yield or weed-impact indicators varying with fertilisation techniques, initial soil organic nitrogen and maize variety.

### SUPPLEMENTARY FIGURE 3

Correlations circles of PCA results with yield indicators (actual and potential), weed harmfulness (field infestation, weed seed production, crop yield loss due to weeds) and biodiversity indicators (bee food offer, species richness) varying with maize parameters related to nitrogen nutrition.

### SUPPLEMENTARY TABLE 5

Pearson correlations (in bold) among yield indicators or weed-impact indicators varying with maize parameters related to nitrogen nutrition.

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