



Towards an improved representation of the relationship between root traits and nitrogen losses in process-based models

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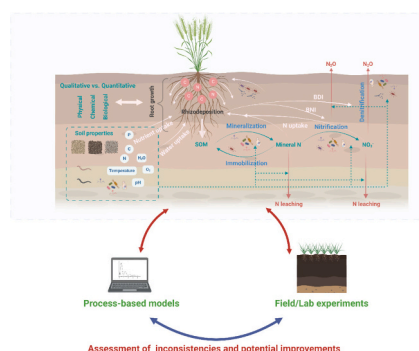
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HIGHLIGHTS

- Synthesis of relationships between plant traits and N losses from experiments.
- Survey of process-based models simulating crop growth and N losses.
- Sensitivity analysis with four well-known models to examine root trait vs N loss interactions.
- Model simulations do not capture empirical relationships between root traits and N losses well.
- Suggested model improvements include new traits that link N cycling and proxies for complex traits.

GRAPHICAL ABSTRACT



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ABSTRACT

CONTEXT: Nitrogen (N) application to crops is crucial to feed an increasing world population. Yet, much of this N is not taken up by crops, initiating a cascade of N losses with dire environmental and economic consequences. There is, therefore, a need to develop crops with traits that make them use N more efficiently, thereby reducing N losses. Process-based models have been used to design in-silico crops with desirable traits to maximize yield and increase climate resiliency, but few have been used with the perspective of reducing N losses.

OBJECTIVE: To examine the way process-based models capture interactions between root traits and N losses, and propose opportunities to improve model representation of observed relationships.

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Nitrogen pollution
Crop ideotype

METHODS: We synthesize the current knowledge on the relationships between plant traits and N losses based on experiments reported in the literature, conduct a survey of process-based models simulating crop growth and N losses, and run a sensitivity analysis with selected models (DSSAT, APSIM, DNDcCAN, Daisy).

RESULTS AND CONCLUSIONS: The results show that the relationships between root traits and N losses can be very strong in experiments, but model simulations do not capture the magnitude of these associations well. This is mainly due to the lack of a robust representation of the plant root mechanisms influencing N losses. Suggested model improvements include designing new functions to link root traits with key N-cycling processes supported by experimental evidence – such as root exudation of various compounds including biological nitrification inhibitors – and using easily observable morphological traits in process-based models as proxies to predict changes induced by plants on N-cycling by soil microbial communities.

SIGNIFICANCE: This work represents a key step towards designing novel root function-based ideotypes adapted to reduced fertilizer inputs while maintaining the same level of yield, and that is, therefore, potentially less harmful to the environment.

1. Introduction

Since the Green Revolution, the world has witnessed an unprecedented increase in nitrogen (N) fertilization owing to the increasing food demand of a growing global population and the goal of achieving zero hunger (Zhang et al., 2021; Gu et al., 2023). Indeed, a 5-fold increase in N inputs has contributed to the doubling of global food production (Tilman et al., 2002; Batty et al., 2017). However, on average only around 46 % of the N fertilizer applied to agricultural soils is utilized by plants, while a large fraction of the remaining N is lost from agroecosystems through nitrate (NO_3^-) leaching, ammonia (NH_3) volatilization, and nitrous oxide (N_2O) emissions (Zhang et al., 2015a, 2015b; Chang et al., 2021). These N losses can trigger a cascade of severe economic, social, and environmental consequences, including eutrophication, biodiversity loss, air pollution, stratospheric ozone depletion, global warming, and associated climate change (Reay et al., 2012; Springmann et al., 2018). The pressure to increase N fertilizer inputs will continue because global food demand is expected to increase by 35–56 % by 2050 (Van Dijk et al., 2021). This calls for an improved understanding of N cycling within the plant-soil-atmosphere continuum to better manage the adverse impacts associated with this vital nutrient on our ecosystems.

Plants can shape the fate of N losses in agroecosystems by influencing the main biotic and abiotic controls on N transformations in soils. Nitrogen losses through leaching and runoff are caused by rainfall or irrigation events that exceed the soil water retention or infiltration capacity, promoting NO_3^- movement with drainage water through the soil profile or flooding across the soil surface (Padilla et al., 2018). Most NO_3^- leaching losses occur outside of the growing season, consisting of NO_3^- not taken up by the crops or mineralized from crop residues and soil organic matter. Accordingly, the main mechanism by which plants can influence NO_3^- leaching is through the immobilization of N in plant biomass via N uptake and reducing soil drainage through water uptake. Nitrous oxide (N_2O) emissions are primarily produced through two microbial processes: nitrification and denitrification. Denitrification is stimulated under anaerobic conditions when soil is saturated with water, while nitrification is an aerobic process that involves two successive oxidation reactions. Soil carbon (C), mineral N, pH, and moisture content are the dominant driving factors regulating N_2O emissions (Lam et al., 2017; Harris et al., 2022). Plants can affect all these factors through various processes mediated by root biomass, root exudation, and soil water and N uptake (Bardgett et al., 2014; Abalos et al., 2019).

Innovative root research has begun to reveal the pivotal and yet overlooked importance of root traits as drivers of plant N uptake, particularly when soil N availability is low (Freschet et al., 2021). Root traits such as abundance and length of lateral roots and root hairs, root length density (RLD), specific root length (SRL), and root depth, affect the volume of soil explored by roots and the surface area for nutrient uptake, thereby influencing plant N acquisition (Abalos et al., 2018, 2019; Freschet et al., 2021). In turn, more efficient plant N uptake can

reduce N losses in the form of N_2O emissions (Abalos et al., 2014) and NO_3^- leaching (Fernandez Pulido et al., 2023). Other root traits such as rhizodeposited C from live roots and the C/N ratio of the rhizodeposits, regulate interactions with the soil microbial community and in particular with microbial guilds determining plant nutrient availability (Moreau et al., 2019). This emerging evidence suggests that there is potential to identify specific root traits – or suites of traits – representing an improved crop ideotype (model plant) for more efficient N uptake and reduced N losses.

Conventionally, plant traits are identified via field trials conducted under various agronomic and pedoclimatic conditions and used in breeding programs to develop new cultivars suitable for targeted environments and climatic conditions (Voss-Fels et al., 2019). However, these experiments are usually labor-intensive, time-consuming, and expensive, making it difficult to carry out long-term trials across multiple sites (Johnston and Poulton, 2018; Kephe et al., 2021). Process-based models that simulate the soil-plant-climate continuum have arguably become the best tools to overcome these challenges (Tsuji and Hoogenboom, 1998; Peng et al., 2020). These mechanistic models have played a determinant role for the design of new crop ideotypes able to cope with climate change (Rötter et al., 2015; Paleari et al., 2022; Getachew et al., 2023), and to optimize agricultural management practices to improve the economic and environmental sustainability of food production (e.g., best N fertilizer strategies to reduce N losses, modifying the sowing date to maintain or increase crop yield; Hunt et al., 2019; Kropp et al., 2019). These robust modelling frameworks combined with the empirical evidence supporting root traits as key drivers of N cycling may pave the way to redefine a plant ideotype for reducing N losses in agroecosystems.

The main objectives of this study are to explore how well process-based models capture the relationship between root traits and N losses, and to provide recommendations to overcome the identified limitations. Ultimately, this work will contribute to supporting the use of models to develop root trait-based ideotypes that improve N use efficiency (NUE) in the context of reduced N fertilizer rates, thereby supporting the sustainability of agroecosystems.

2. Plant traits and nitrogen losses: Empirical evidence

Root systems play a fundamental role in plant-soil interactions, particularly in N cycling through various direct and indirect pathways (Fig. 1). These plant-soil interactions significantly influence the transformation and movement of elements and compounds in soil ecosystems (Freschet et al., 2021). Roots can directly influence soil N cycling in three primary ways. First, they regulate N uptake by modifying their absorption surface area in response to available soil N (Duan et al., 2024), adjusting uptake rates through the upregulation or downregulation of N transporter activity (Jacquot et al., 2020), and altering root growth rates (Duan et al., 2024). Second, the roots of some plants can release biological nitrification inhibitors (BNI) and denitrification

inhibitors (BDI), which potentially reduce the rates of nitrification and denitrification processes in soil (Bardon et al., 2014; Sun et al., 2016). Third, roots could directly modify soil water dynamics through water uptake, which affects N leaching patterns (Ehdaie et al., 2010).

The indirect effects of roots on soil N cycling are more complex and occur through physical, chemical, and biological mechanisms. From a physical perspective, roots alter the soil microclimate, causing temperature fluctuations and shifts between aerobic and anaerobic conditions within soil macropores (Greiser et al., 2024). Additionally, root growth reshapes soil structure by increasing soil aggregation and porosity (Lucas et al., 2019). Chemically, roots influence soil substrate composition through rhizodeposition (the release of organic compounds into the soil) (Witzgall et al., 2024). Biologically, roots shape the soil microbial community by selectively recruiting specific microorganisms and providing resources through rhizodeposition, affecting soil microbiota's abundance, composition, and diversity (Tomazelli et al., 2024). These physical, chemical, and biological modifications occur simultaneously across temporal and spatial scales, creating complex interactions that affect soil N cycling through changes in substrate availability, abiotic conditions, and biotic factors.

Ecologists are increasingly adopting trait-based approaches to characterize how plants interact with the soil for nutrient acquisition and storage, and to regulate ecosystem processes (Laliberté, 2017). These approaches enable the development of a quantitative, mechanistic understanding of biochemical processes by linking them to measurable plant traits (Bardgett et al., 2014). This framework offers valuable opportunities to incorporate physiological processes into process-based models, enhancing their predictive capability. These approaches are primarily based on the leaf and root economics spectrum, which postulate that plants with acquisitive traits and resource strategies invest in faster growth and resource uptake rates, coupled with shorter life spans and more susceptible tissues. In contrast, plants with conservative traits have lower water and nutrient requirements, and therefore reduced growth and respiration rates, resulting in a longer life span (Wright et al., 2004; Kong et al., 2019; Pan et al., 2020). Root traits can be architectural and morphological, physiological and chemical, and biotic (Table 1; Bardgett et al., 2014). Here, we provide qualitative and quantitative estimates of the relationship between root traits and N losses based on the available literature.

2.1. Methodology

We conducted a literature survey using Google Scholar by searching the following terms and their variations: root traits, plant traits, root architecture, root exudate, nitrogen use efficiency, NO_3^- leaching, N_2O emissions, nitrification, denitrification, functional genes related to N cycling (amoA-AOA, amoA-AOB, nirK, nirS, napA, napZ, and nosZ), and N uptake. Articles were included if they met the following criteria: (1) provided detailed information of experimental design, plant types, and extractable data for at least one root trait (independent variables) and one response variable (including N_2O emission, N uptake, and NO_3^- leaching); (2) if referring to different phenological stages, the growing season accumulated response variables and root traits at maturity were reported. A total of 24 studies were used for a qualitative assessment indicating the direction of the relationship between root traits and N losses (i.e., suitable for qualitative assessment), including 6 studies focused on nitrification and denitrification rates (Table 1), while 7 of those studies were further used for a more in-depth quantitative assessment of such relationships (Fig. 2). Regarding the functional genes related to N cycling, a total of 7 studies were used for a qualitative assessment (Table S1), and 3 of these studies contained detailed data suitable for quantitative analysis (Fig. 2).

We used the natural log-transformed response ratio ($\ln RR$) as a measure of effect size for the quantitative evaluation (Hedges et al., 1999) (eq. 1):

$$\ln RR = \ln \left(\frac{x_E}{x_C} \right)$$

Where x_C is the reference value, selected as the observation within a study with the greatest N loss (N_2O or NO_3^- leaching) or abundance of functional genes related to nitrification/denitrification, and x_E is the other observation (or observations) within a study with their corresponding root trait values. Results were back-transformed to “percentage of change” using the formula $[100 \times \{\exp(\ln RR) - 1\}]$ to ease interpretation.

2.2. Results of the literature survey

We identified a relatively wide range of root traits (27) associated with measurable changes in N losses (Table 1), and the mechanistic understanding of these associations is robust. For example, an increase

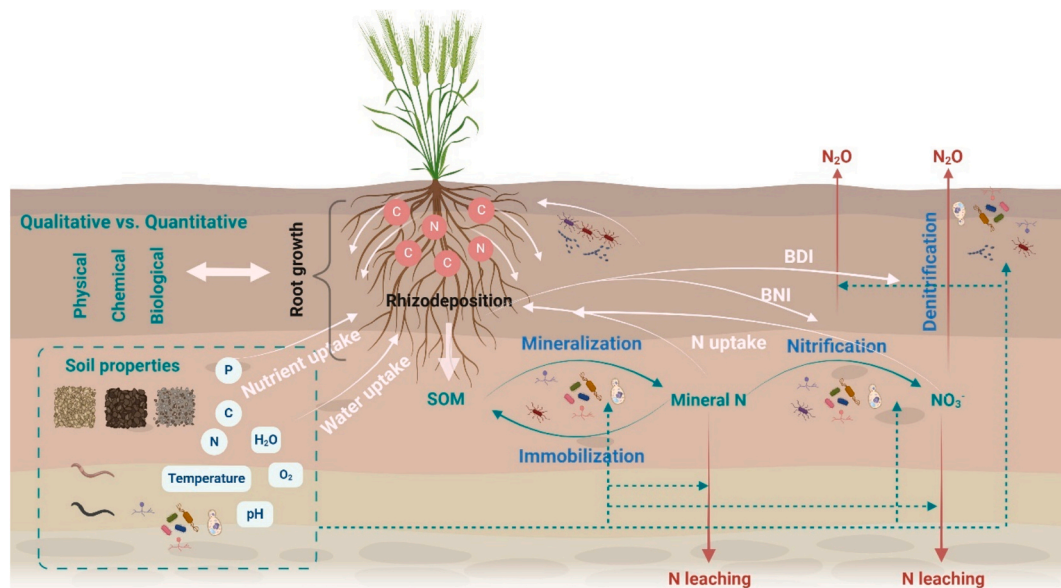


Fig. 1. Conceptual diagram depicting the relationships between roots and soil N cycling (SOM: soil organic matter; BNI: biological nitrification inhibitor; BDI: biological denitrification inhibitor).

Table 1

Qualitative summary of relationships between root traits and nitrogen losses and plant nitrogen uptake reported in experiments.

N cycling component	Root trait		Direction of N loss with increasing trait values	Scale	Plant/crop	References	
N ₂ O emission	Architectural and morphological	Root biomass	Increase Decrease	Field Greenhouse Mesocosm	Rice Grass	Baruah et al., 2010 Oram et al., 2020	
		Specific root length	Decrease	Greenhouse Mesocosm	Grass	Abalos et al., 2014, 2018; Oram et al., 2020; Fernandez Pulido et al., 2023	
		Root Diameter	Increase	Greenhouse Mesocosm	Grass	Abalos et al., 2014, 2018; Fernandez Pulido et al., 2023	
		Root length density	Decrease	Greenhouse Mesocosm	Grass	Abalos et al., 2018; Fernandez Pulido et al., 2023	
		Root dry matter content	Increase	Greenhouse Mesocosm	Grass	Fernandez Pulido et al., 2023	
		Root/shoot ratio	Increase	Greenhouse Mesocosm	Grass	Abalos et al., 2014	
		Root tissue density	Decrease	Greenhouse Mesocosm	Grass	Oram et al., 2020	
		Root C/N ratio	Decrease	Greenhouse Mesocosm	Grass	Oram et al., 2020	
		Root N concentration	Increase	Greenhouse Mesocosm	Grass	Oram et al., 2020; Fernandez Pulido et al., 2023	
		Root C concentration	Decrease	Greenhouse Mesocosm	Grass	Oram et al., 2020	
	Physiological and chemical	Deep root biomass	Decrease	Sand_tube	Wheat	Ehdaie et al., 2010	
		Shallow root biomass	Decrease	Sand_tube	Wheat	Ehdaie et al., 2010	
		Root/shoot ratio	Decrease	Sand_tube	Wheat	Ehdaie et al., 2010	
		Root/shoot ratio	Decrease	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022	
		0–0.3 m root biomass	Decrease	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022	
		0.3–1.0 m root biomass	Decrease	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022	
		0–0.1 m root biomass	Decrease	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		0.1–0.2 m root biomass	Decrease	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		> 0.2 m root biomass	Decrease	Greenhouse Mesocosm	Grass	Popay & Crush, 2011	
		Root biomass	Decrease	Sand_tube	Wheat	Ehdaie et al., 2010	
NO ₃ [−] leaching	Architectural and morphological	Root biomass	Decrease	Greenhouse Mesocosm	Grass	Popay & Crush, 2011; Moir et al., 2012	
		Root length density	Increase	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022	
		Maximum root depth	Decrease	Greenhouse Mesocosm	Grass	Fernandez Pulido et al., 2023	
		0–0.1 m root length	Increase	Sand_tube	Wheat	Ehdaie et al., 2010	
		0–0.1 m root length	Decrease	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		0.1–0.2 m root length	Decrease	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		> 0.2 m root length	Decrease	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		Root length	Decrease	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		0–0.1 m root diameter	Decrease	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		0.1–0.2 m root diameter	Increase	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
	Physiological and chemical	> 0.2 m root diameter	Increase	Greenhouse Mesocosm	Grass	Popay and Crush, 2010	
		Root diameter	Increase	Greenhouse Mesocosm	Grass	Popay & Crush, 2011; Fernandez Pulido et al., 2023	
		Root dry matter content	Decrease	Greenhouse Mesocosm	Grass	Fernandez Pulido et al., 2023	
		Specific root length	Increase	Greenhouse Mesocosm	Grass	Popay & Crush, 2011; Fernandez Pulido et al., 2023	
		Center of gravity of the root system	Decrease	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022	
		Root N content	Increase	Greenhouse Mesocosm	Grass	Fernandez Pulido et al., 2023	
		Physiological and chemical	Root C exudation	Increase	Controlled light exposure and soil moisture	Wheat, barley and ryegrass	Maurer et al., 2021
			Root N exudation	Increase	Controlled light exposure and soil moisture	Wheat, barley and ryegrass	Maurer et al., 2021
		Architectural and morphological	Specific root length	Decrease	Greenhouse Mesocosm	Grass	Cantarel et al., 2015
			Root N content	Increase	Greenhouse Mesocosm	Grass	Cantarel et al., 2015
Nitrification	Physiological and chemical	Root affinity for NH ₄	Increase	Greenhouse Mesocosm	Grass	Cantarel et al., 2015	
		Exudation of nitrification inhibitors	Decrease	Chamber	<i>Brachiaria humidicola</i>	Subbarao et al., 2007	
N uptake	Architectural and morphological	Root surface area	Increase	Chamber	Rice, Cotton	Chen et al., 2020; Iqbal et al., 2020	
				Hydroponic condition	Wheat	Zhang et al., 2015	

(continued on next page)

Table 1 (continued)

N cycling component	Root trait	Direction of N loss with increasing trait values	Scale	Plant/crop	References
	Root biomass	Decrease	Greenhouse Mesocosm	Rice	Fan et al., 2010
			Field	Maize	Mu et al., 2015; Guo et al., 2022
			Chamber	Rice, Cotton	Chen et al., 2020; Iqbal et al., 2020
	Root biomass (0–10)	Increase	Field	Maize, Rice	Ju et al., 2015; Mu et al., 2015; Yu et al., 2015; Chu et al., 2022; Guo et al., 2022
			Hydroponic condition	Wheat	Zhang et al., 2015
			Greenhouse Mesocosm	Grass, Rice, Sugarcane	Fan et al., 2010; Moir et al., 2012; Takaragawa et al., 2022
	Root biomass (10–20)	Increase	Sand_tube	Wheat	Ehdaie et al., 2010
			Field	Rice	Ju et al., 2015; Chu et al., 2022
			Field	Rice	Ju et al., 2015; Chu et al., 2022
	Root biomass (0–0.3 m)	Decrease	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022
			Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022
			Sand_tube	Wheat	Ehdaie et al., 2010
	Root biomass (0.3–1.0 m)	Decrease	Sand_tube	Wheat	Ehdaie et al., 2010
		Increase	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022
			Sand_tube	Wheat	Ehdaie et al., 2010
	Deep root biomass	Increase	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022
			Sand_tube	Wheat	Ehdaie et al., 2010
			Sand_tube	Wheat	Ehdaie et al., 2010
	Shallow root biomass	Decrease	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022
			Sand_tube	Wheat	Ehdaie et al., 2010
			Sand_tube	Wheat	Ehdaie et al., 2010
	Center of gravity of the root system	Increase	Greenhouse Mesocosm	Sugarcane	Takaragawa et al., 2022
			Sand_tube	Wheat	Ehdaie et al., 2010
			Field	Maize, Rice	Yu et al., 2015; Ju et al., 2015; Chu et al., 2022
	Root/shoot ratio	Decrease	Greenhouse Mesocosm	Grass, Sugarcane	Abalos et al., 2014; Takaragawa et al., 2022
			Chamber	Cotton	Iqbal et al., 2020
			Chamber	Cotton	Iqbal et al., 2020
	Root depth	Increase	Sand_tube	Wheat	Ehdaie et al., 2010
			Greenhouse Mesocosm	Grass	Abalos et al., 2014
			Chamber	Cotton, Rice	Chen et al., 2020; Iqbal et al., 2020
	Root Diameter	Increase	Field	Rice	Chu et al., 2022
			Field	Maize, Rice	Ju et al., 2015; Mu et al., 2015; Chu et al., 2022
			Field	Rice	Chu et al., 2022
	Root length density	Increase	Hydroponic condition	Wheat	Zhang et al., 2015
			Chamber	Rice, Cotton	Chen et al., 2020; Iqbal et al., 2020
			Chamber	Cotton	Iqbal et al., 2020
	Root length ratio	Decrease	Chamber	Cotton	Iqbal et al., 2020
			Chamber	Cotton	Iqbal et al., 2020
			Field	Rice	Chu et al., 2022
	Root thickness	Increase	Greenhouse Mesocosm	Grass	Abalos et al., 2014
			Field	Maize, Rice	Ju et al., 2015; Chu et al., 2022; Guo et al., 2022
			Field	Maize, Rice	Guo et al., 2022
	Specific root length	Increase	Hydroponic condition	Wheat	Zhang et al., 2015a, 2015b
			Greenhouse Mesocosm	Rice, Grass	Fan et al., 2010; Moir et al., 2013
			Chamber	Rice	Chen et al., 2020
	Root length	Decrease	Chamber	Rice	Chen et al., 2020
			Chamber	Cotton	Iqbal et al., 2020
			Chamber	Cotton	Iqbal et al., 2020
	Root tip number	Increase	Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
	Root density	Decrease	Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
	Root projected area	Increase	Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
	Root angle opening	Decrease	Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
	Root maximal width	Increase	Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022
			Field	Maize	Guo et al., 2022

in architectural traits such as root/shoot ratio can cause a reduction in NO_3^- leaching. This is because higher root/shoot ratio indicates a larger below-ground foraging capacity for nutrients and water, and since NO_3^- is highly mobile in the soil, it can easily be leached deep into the soil with percolating water (Thorup-Kristensen et al., 2020). Regarding morphological traits, an increase in root diameter can increase both NO_3^- leaching and N_2O emission, because high root diameter indicates a resource-conservative strategy, and therefore lower plant water and nutrient uptake capacity and higher soil availability of both resources. A greater C investment per unit of root length is required by larger-diameter roots, which must be coupled with a longer lifespan to ensure a favorable nutrient and water return on the higher C investment compared with smaller-diameter roots (Weemstra et al., 2016). In terms of chemical traits, an increase in root C exudation could increase N_2O emission due to greater soil C availability stimulating denitrification (Abalos et al., 2019).

The quantitative assessment revealed the magnitude of some of the trait \times N loss relationships (Fig. 2). Changes in root traits were

associated with variations in N losses and N-related functional genes often exceeding 50 %. In general, the relationship between root traits and functional genes was much stronger than with N_2O emissions or NO_3^- leaching. Relatively modest increases of 10 % in root biomass could increase the abundance of nirK gene copies by 67.4 %, while the same increase in root diameter could raise the abundance of AOB and nosZI by 14.3 % and 9.4 %. Increases of 10 % in root biomass, root C/N ratio, and root tissue density can reduce N_2O emissions by 2.3 %, 4.3 %, and 6.5 % respectively, whereas the same increase in root N concentration can increase N_2O emission by 4.2 %. Similarly, 10 % increases in root length, and root biomass can lower NO_3^- leaching by 5.7 %, and 2.0 %, respectively. The relationships identified in our literature survey highlight the benefits of representing the associations between root traits, functional genes and N losses in process-based models to ensure accurate simulations of N cycling in agroecosystems.

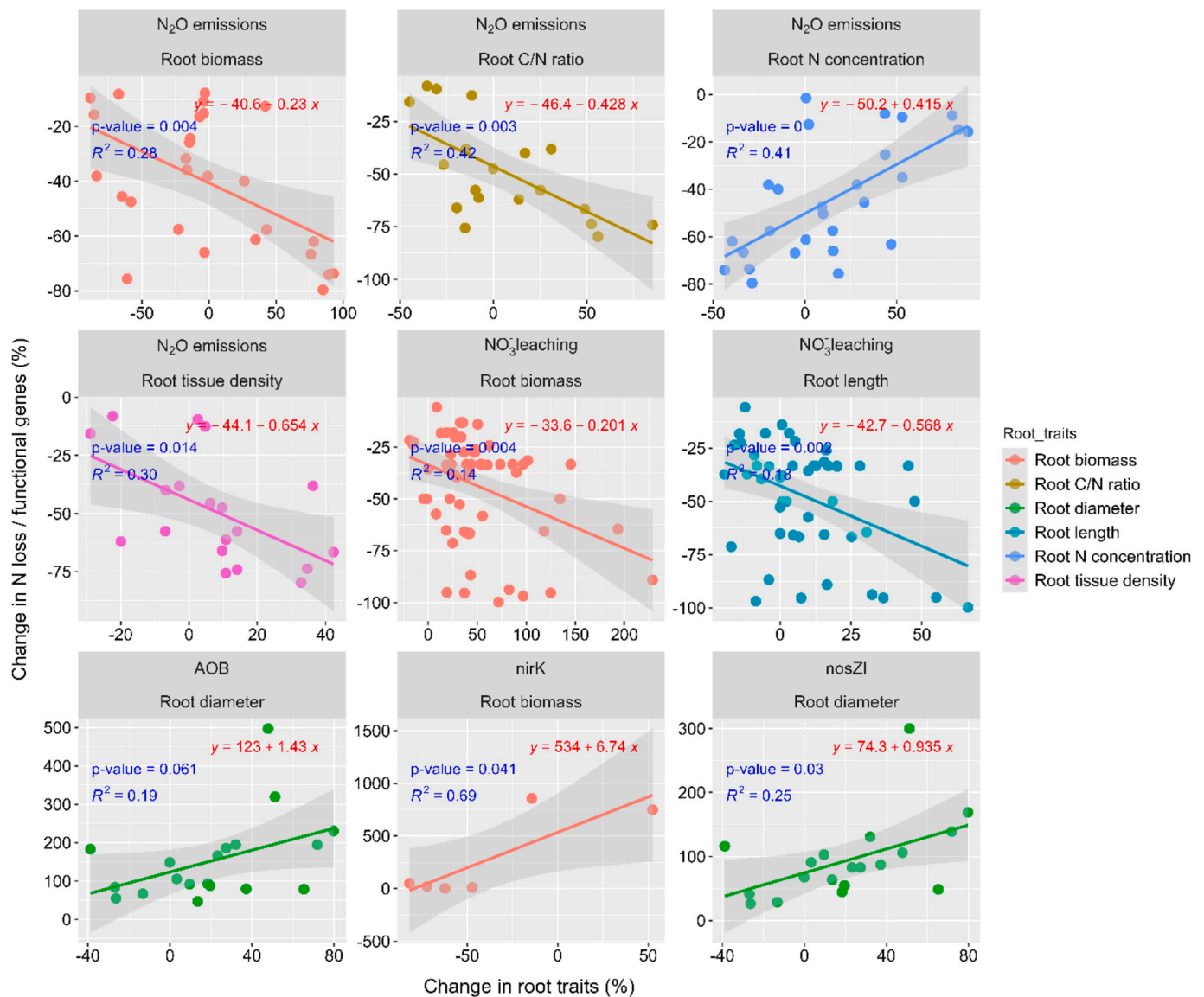


Fig. 2. Examples of quantitative relationships between nitrogen losses (N₂O emissions and NO₃⁻ leaching), N-related functional genes (AOB (amoA-AOB), nirK, and nosZI), and root traits based on metadata from experiments (Table 1). The units of the Y- and X-axis are relative changes (%).

3. Survey of process-based models simulating crop growth and nitrogen losses

We identified 55 widely used process-based models with the capacity to simulate crop growth, root traits, soil C dynamics, soil water flow, soil N dynamics, NO₃⁻ leaching, and/or N₂O emissions at different temporal and spatial scales (Table S2). All these models were initially developed with a focus on either soil processes or crop yield (Jones et al., 2003; Keating et al., 2003; van Ittersum and Donatelli, 2003). Soil-focused models were designed primarily to simulate C and/or N cycling and water movement across the soil-plant-atmosphere continuum, such as DayCent and DNDC, while crop-focused models were established to simulate crop growth and development, such as DSSAT. Over time, model developers have incorporated advances to encompass more features related to the dynamic processes of plant growth and soil nutrient cycling, and currently a large fraction of these models can simulate both crop growth and soil dynamics with reasonable accuracy. Based on the initial goals or the strengths of each model by the time they were launched, models can be categorized into three types: crop models, biogeochemical models, and agro-hydrological models (Table S2). Approximately 45 and 39 of the surveyed models can simulate NO₃⁻

leaching and N₂O emission, respectively, 39 models can simulate both N losses, and only 37 models can simulate all seven processes including crop growth, root traits, soil C and N dynamics, soil water flow, NO₃⁻ leaching, and N₂O emission (Table S2). Only 2 of the surveyed models incorporate N-related functional genes. Two spatial (plot and regional) and three temporal (hourly, daily and monthly) scales are covered by the 37 models that include all seven processes. The vast majority of models simulate at the plot scale (49) on a daily time step (50).

4. Understanding how current generation models simulate root traits and nitrogen losses

To acquire a deeper mechanistic understanding of the capacity of models to simulate root trait × N loss relationships, we focused on four of the more widely used models listed in Table S2: DSSAT, APSIM, DNDCvCAN, and Daisy. These models were selected for various reasons: (1) they can simulate at least six of the surveyed categories (Table S2); (2) they were initially developed with a different purpose, two of them to simulate crop growth, development, and yield (DSSAT and APSIM), and the other two with a stronger focus on soil properties (DNDCvCAN and Daisy); and (3) they cover a wide gradient of complexity in terms of

potential root traits to explore, from 4 in DNDCv.CAN to 21 in APSIM (Table S3). For each of the selected models, first we unfold the main links and interactions between plant traits and their impacts on soil processes related to N losses. Then, we collected already calibrated and evaluated datasets for model setups from individual studies, and all the required input data to run the models, covering climatic, soil and agricultural management information, in order to perform sensitivity analyses (more details below and in the supplementary information).

4.1. General representation of N_2O emissions in process-based models

Nitrification and denitrification are the two processes linked to N_2O emission in process-based models. Nitrification refers to the process of oxidation of NH_4^+ to NO_3^- and occurs under aerobic conditions. The first step in process-based models is to calculate the nitrification rate based on the extractable soil NH_4^+ and soil abiotic/biotic modifiers, which are model specific. Then, NO and N_2O emissions from nitrification are calculated as a constant proportion of nitrified N (Parton et al., 2001). By contrast, denitrification involves a series of reductive reactions from NO_3^- to NO_2^- , NO , N_2O and N_2 under anaerobic conditions, and requires an energy source from soil extractable C. Similar to nitrification, the first step of denitrification is also to calculate the denitrification rate based on the soil NO_3^- or extractable C modified by abiotic or biotic factors. Then the second step is often to calculate the N_2/N_2O ratio based on oxidation of an electron donor (normally hydrogen) to reduce oxidized N substrates as a function of soil water content. The N_2O gas flux from denitrification is the product of the denitrification rate and the N_2O ratio. Most models follow these steps and incorporate the associated mechanisms to simulate soil N_2O emissions from both nitrification and denitrification; yet they differ in specific modifying (driving) factors with soil temperature and water content generally being the most important.

4.2. General representation of NO_3^- leaching in process-based models

Losses via NO_3^- leaching are primarily linked to drainage using a cascade water flow approach in process-based models. When the soil water content exceeds the upper drained limit or field capacity (generally defined as the water content retained in soil at -0.1 bar, ranging from -0.06 to -0.33 bar for different soil types), the drainage flow in each soil layer is calculated based on the difference between saturation water content and the upper drained limit of the soil. Then, NO_3^- leaching is simulated based on the soil NO_3^- concentration and drainage flow in each soil layer. Most process-based models follow this principle to simulate NO_3^- loss, while differing in hydraulic parameters and drainage flow types. Some models use the Richards equation to simulate water flow, and some also include a retention process that slows NO_3^- leaching relative to the drainage flow. The soil NO_3^- concentration is, therefore, a key driver of NO_3^- leaching in most models, and this is in turn affected by the estimation on nitrification.

4.3. Model description and representation of plant trait \times N loss relationships

4.3.1. DSSAT

The Cropping System Model (CSM) of The Decision Support System for Agrotechnology Transfer (DSSAT; www.DSSAT.net) model has been used to reproduce crop growth and yield formation accurately under a wide range of climatic and management conditions (e.g., Liu et al., 2020; Cammarano et al., 2022; Dar et al., 2023). Five primary modules are embedded in the DSSAT-CSM structure: plant, soil-plant-atmosphere, soil, weather, and management. The latest DSSAT v4.8 also includes a greenhouse gas emissions (GHGs) module which makes it possible to simulate N_2O and methane emissions (Hoogenboom et al., 2019, 2021).

In DSSAT-CSM, only saturated flow is considered for drainage, and

the drainage rate is controlled by hydraulic parameters, including soil water saturation content and drained upper limit. Soil NO_3^- concentration and the drainage flow determine NO_3^- leaching. Soil abiotic factors, including soil temperature, water, and pH, are the modifiers for nitrification rate. The N_2O emission is estimated as a fraction (0.001) of nitrification. The DSSAT-CSM model provides two methods for denitrification: CERES denitrification (Godwin and Singh, 1998) and Century denitrification (Gijssman et al., 2002). In the CERES module, soil extractable C, NO_3^- concentration, temperature and water factors are accounted for in calculating the denitrification rate. Then N_2O emissions are calculated based on the soil NO_3^- content and a given N_2/N_2O ratio modified by soil water content. By contrast, in the Century denitrification module, the denitrification rate is calculated based on soil heterotrophic respiration (CO_2), NO_3^- , and soil water content. The N_2/N_2O ratio is calculated based on the ratio of NO_3^- to CO_2 and modified by soil water content. Plant traits in DSSAT-CSM are specific at the crop/species level. In terms of the general representation of N losses and plant traits across crops in DSSAT-CSM, traits linked to crop N uptake modify soil NO_3^- and NH_4^+ content and associated N losses, and the soil water flow is influenced by plant water uptake that in turn is affected by changes in root length density and potential N and water demand. Belowground, root senescence can add litter to the soil and affect the soil fresh organic matter pool, further affecting soil mineralization and immobilization and, thus, both soil C and N pools. Aboveground, the leaf area index (LAI) regulates evapotranspiration and, therefore, to soil water content (Fig. 3).

4.3.2. APSIM

The Agricultural Production System Simulator (APSIM) is a comprehensive mechanistic model which has been used for various purposes (Holzworth et al., 2014). APSIM is structured around plant, soil, and management modules, covering multiple crops and many soil processes including a water balance, N transformations, and soil pH, as affected by management practices (Pasley et al., 2021).

In APSIM, NO_3^- dissolved in water can move to deeper soil layers via saturated or unsaturated water flow. The saturated and unsaturated water flows are calculated based on soil water retention capacity and hydraulic parameters, including drained upper limit, saturated water limit, 15 bar lower limit (water content at wilting point), hydraulic conductivity, and drainage and diffusivity rate constants. Nitrification is assumed to follow Michaelis-Menten kinetics (Godwin and Jones, 1991). The nitrification rate is modified by soil water, temperature, and pH. The NO and N_2O emissions from nitrification are calculated as a fixed proportion of nitrified N (Parton et al., 2001). For denitrification, APSIM adds an extra temperature factor to adjust the potential denitrification rate. The N_2O from denitrification is then calculated based on the N_2 to N_2O ratio (Del Grosso et al., 2000). Plant traits are linked to N losses through N uptake, water uptake by adjusting root parameters, and plant nutrient and water uptake capacity, further indirectly affecting the dynamic N cycling process through the soil water and temperature factors. Root litter left in the soil affects the soil fresh organic matter pool, further affecting soil N mineralization and immobilization processes and thus both soil C and N pools (Fig. 4).

4.3.3. DNDCv.CAN

The Canadian version of DNDC (Denitrification - Decomposition model: DNDCv.CAN; available at <https://github.com/BrianBGrant/DNDCv.CAN>) has been used to estimate the effects of climate and management strategies on crop growth, soil C and N dynamics, especially for NO_3^- leaching and N_2O emission (Smith et al., 2013, 2020; Abalos et al., 2016). DNDCv.CAN utilizes most of the same C and N cycling framework as the original DNDC (DNDC95) model (Li et al., 2012), including four of the main sub-models: soil/climate, crop vegetation, decomposition, and denitrification. The decomposition sub-model is composed of four main C pools (litter, labile humus, passive humus, and microbial biomass). Each of these has its own fixed C/N

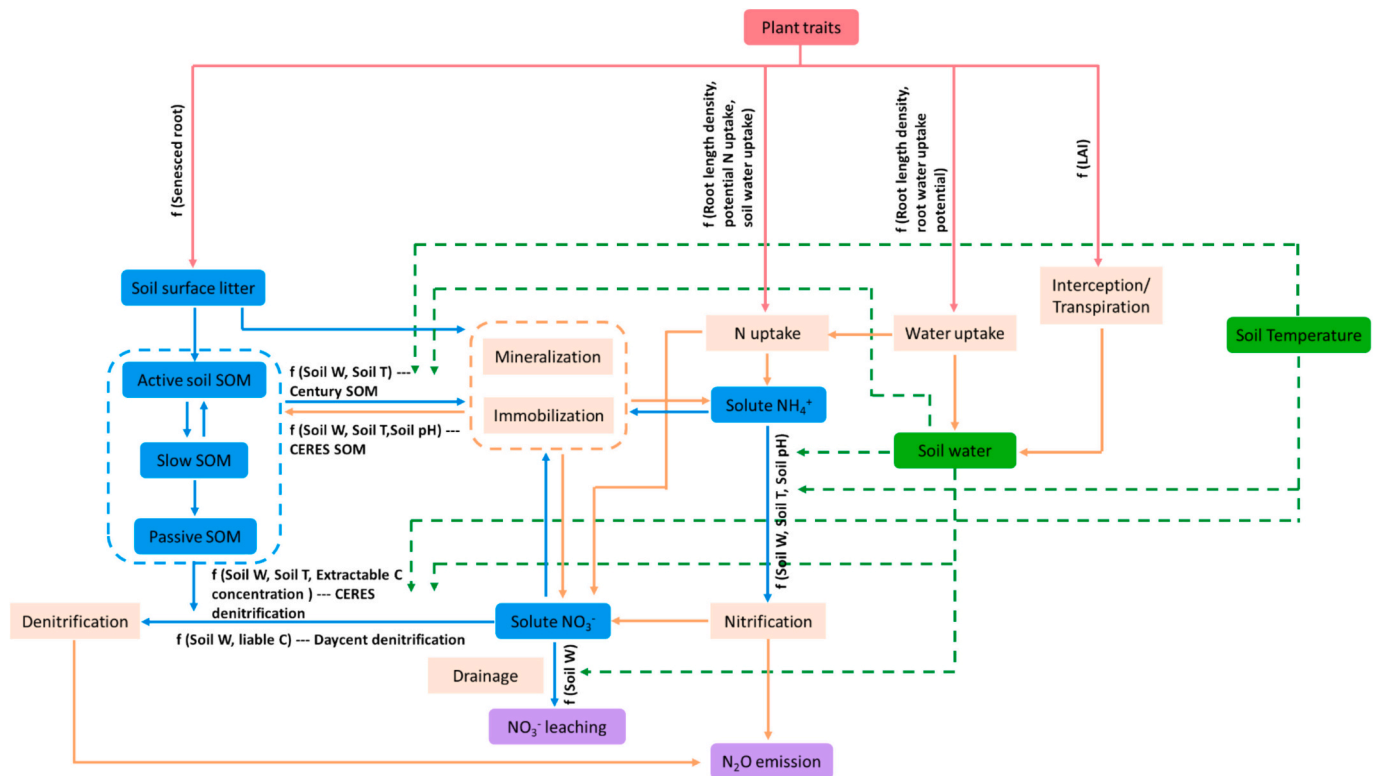


Fig. 3. Conceptual diagram depicting the potential effects of plant traits on nitrogen losses described in the Cropping System Model of DSSAT. The red color box indicates plant traits; red solid arrows indicate the possible impact of plant traits; blue color boxes indicate the soil substrates; blue solid arrows indicate the possible biochemical processes in which the substrates are directly involved; green boxes indicate soil abiotic factors and green dashed arrows indicate possible processes affected by abiotic factors; light orange boxes indicate process related to soil C, N and water dynamics; light orange solid arrows indicate possible consequence of changes in processes; purple boxes indicate the N losses. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ratio and base decomposition rate. These rates are influenced by a combination of soil texture, soil moisture, soil temperature, and soil N (Smith et al., 2008). The initial status of the available NO_3^- and soluble C is provided by the decomposition sub-model. The denitrification sub-model predicts the consumption of NO_3^- and generates soil fluxes of NO , N_2O , and N_2 depending on the microbial biomass of denitrifiers, pH, redox potential (Eh), soil water content, soil organic C, soil temperature, and the concentration of the corresponding N oxides (Fig. 4; Smith et al., 2008; Li et al., 2012).

The DNDC model uses an anaerobic balloon concept to regulate the nitrifier and denitrifier populations. This representation of aerobic and anaerobic soil volumes contrasts with other models such as APSIM and DayCent, that only model bulk soil properties. The nitrifier and denitrifier populations are controlled by soil Eh via the Nernst equation and the reaction rates (i.e., nitrification or denitrification) is calculated by the Michaelis-Menten Equation (modified by the concentration of substrates in reaction). The nitrification rate is calculated based on soil NH_4^+ concentration, the biomass of nitrifiers, and soil pH. Abiotic factors including soil temperature and moisture can also affect the nitrification rate by regulating the growth of nitrifiers. The N_2O emission induced by denitrification is the result of the production, consumption, and diffusion of gases within the anaerobic balloon. The consumption rate for the N oxides is calculated by the relative growth rate of denitrifiers, maximum growth rate on N oxides, maintenance coefficient on N oxides, denitrifier biomass, N concentration of all N oxides, and pH and temperature factors (Li et al., 2000). Leaching losses of NO_3^- in DNDCv.CAN are derived from the bulk water flux between soil layers, the soluble NO_3^- concentration, and a small amount of preferential N movement which can be parameterized through the user interface (Smith et al., 2020). Plant traits, including plant water demand, root shape function,

and root depth, affect the soil water flow and the adsorption and desorption of NH_4^+ to clay particles impacting N movement (Li et al., 2006). Plant traits controlling water and N uptake capacity directly affect the N substrate concentrations in the soil, and root architecture parameters, including the rooting depth and the vertical distribution of root biomass regulate plant access to soil water and N, which can lead to differences in the vertical distribution of these elements within the soil. Root exudates affect the soil organic matter pool, and aboveground traits such as LAI affect soil temperature, which can be important for denitrification and nitrification processes (Fig. 5).

4.3.4. Daisy

The soil-plant-atmosphere system model Daisy is an explanatory, mechanistic, and physically based model (Abrahamsen and Hansen, 2000; Hansen et al., 2012). The model simulates water, heat, C and N balances, and crop growth in the root zone (Hansen et al., 2012). The three main modules are bioclimate, vegetation, and soil. The root system in the vegetation module is characterized by root weight, rooting depth, and root density distribution. The decomposition of soil organic matter is affected by soil temperature, soil water content, and soil clay content. This decomposition results in flows of organic matter between pools based on the C in each pool, and the corresponding N is calculated based on a fixed C/N ratio in each pool, then net N mineralization or immobilization are simply derived from the N balance of the pool changes.

In Daisy, the water flow is calculated by the flow towards the drainage above and below the groundwater level, adjusting by an average of the conductivities of the saturated layers above and below the drainage level (Møllerup et al., 2014; Holbak et al., 2021). Solute NH_4^+ concentration, temperature and water potential pressure factors are taken into account for calculating nitrification rate. The fraction of the

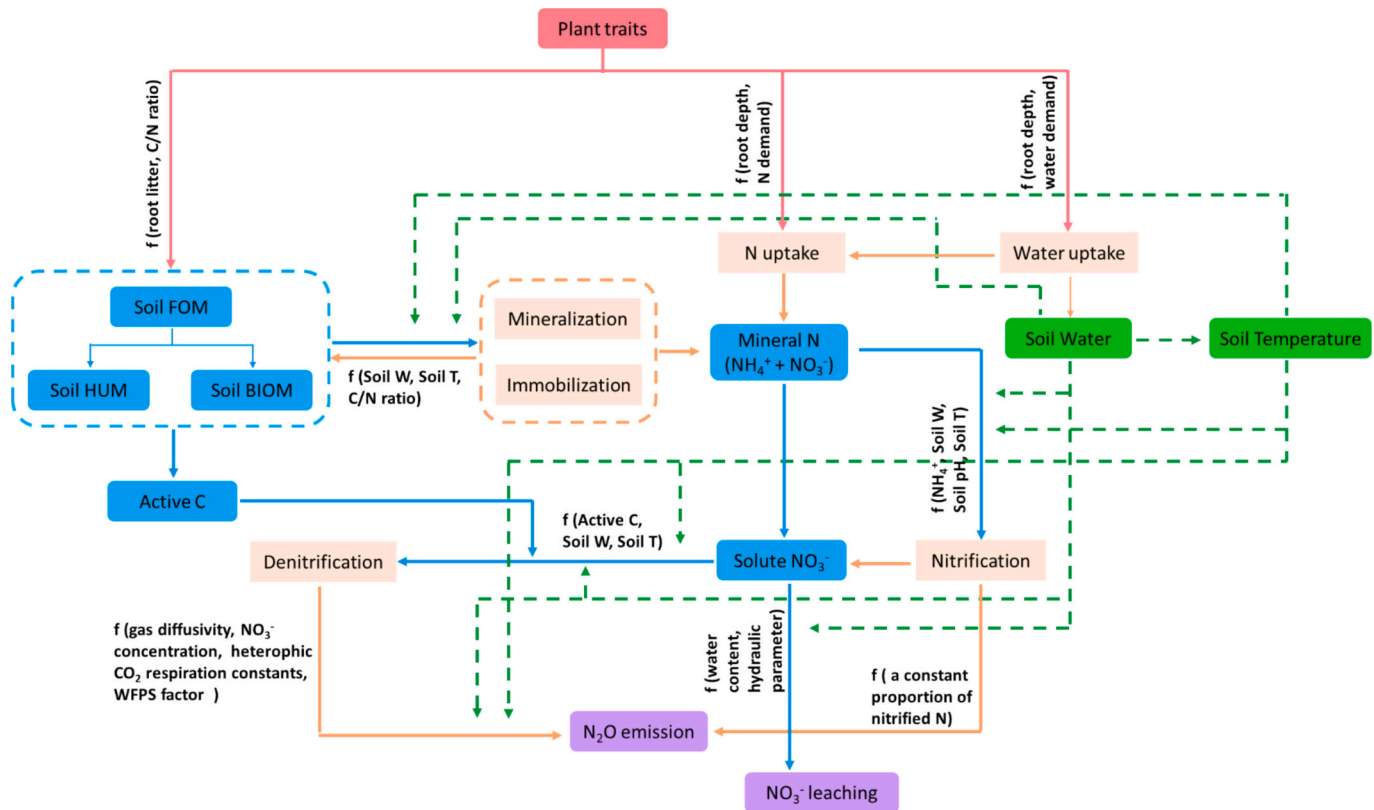


Fig. 4. Conceptual diagram depicting the potential effects of plant traits on nitrogen losses described in APSIM. The red color box indicates plant traits; red solid arrows indicate the possible impact of plant traits; blue color boxes indicate the soil substrates; blue solid arrows indicate the possible biochemical processes in which the substrates are directly involved; green boxes indicate soil abiotic factors and green dashed arrows indicate possible processes affected by abiotic factors; light orange boxes indicate process related to soil C, N and water dynamics; light orange solid arrows indicate possible consequence of changes in processes; purple boxes indicate the N losses. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

nitrified NH_4^+ that becomes N_2O is given as a constant with a default value of 0.02. The denitrification rate is calculated using CO_2 respiration rate as a proxy and solute NO_3^- modified by the soil temperature and water factors. The N_2O emission from denitrification is currently not simulated by Daisy, but ongoing work is underway to develop and add this component into the model. Plant traits affect N_2O emissions from nitrification in a similar way by affecting the concentration of substrates (soil C, NH_4^+ , NO_3^-) and abiotic factors (soil water, and temperature), as described for the other models above (Fig. 6).

4.4. Sensitivity analysis

4.4.1. Approach

For each of the four models (DSSAT, APSIM, DNDCvCAN, and Daisy) we performed a one-factor-at-a-time sensitivity analysis (Lenhart et al., 2002), by testing a set of different values for the parameters related to root traits in each model, and extracting the simulated effects on crop N uptake, N_2O emissions, and NO_3^- leaching. The sensitivity of each root parameter was tested by setting a range from -40% to 40% of the default value with intervals of 5% , and the default value of each parameter was taken as the baseline to calculate the percentage change in N losses and N uptake compared to the percentage change of each root parameter. To benchmark the models, we utilized model setups from experimental datasets that the models had previously been calibrated and evaluated with, along with all the required input data including daily weather, soil, and agricultural management information. A description of the models' setups is provided in Table 2; further details of the field experiments and the articles reporting the calibration and validation of each model can be found in the Supplementary Information. We selected the four most responsive traits in each model to

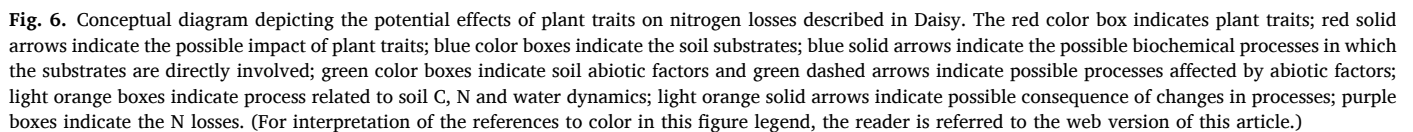
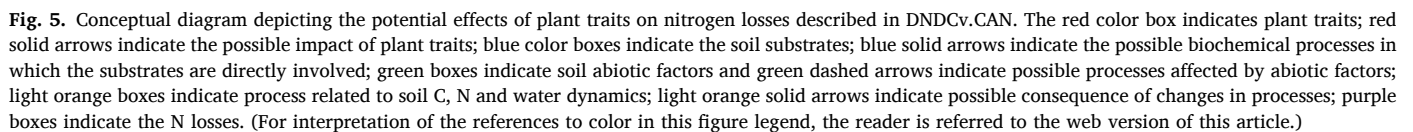
represent the magnitudes and directions of the interactions between root traits and N loss (Table 3), according to the results of the sensitivity analysis for each model for a wide range of traits (Table S3). The models were assessed over a single growing season and non-growing season period that spanned from sowing to sowing so as to calculate the annual N losses and capture any NO_3^- leaching losses that occurred after crop harvesting. All the analyses were conducted using R version 4.2.2. (R Core Team, 2022).

4.4.2. Results of the sensitivity analysis

The magnitude of the changes in N cycling in response to modifications in root traits was similar for all four models (Fig. 7). The changes ranged from -20% to 9.4% for crop N uptake, from -9.1% to 18.6% for NO_3^- leaching, and from -5.4% to 8.3% for N_2O emissions. The most responsive traits for crop N uptake, NO_3^- leaching, and N_2O emission were root length weight ratio in DSSAT, and root penetration rate for Daisy, which are traits indicating how fast the root grows into deeper soil layers (Table 3), and root shape function parameter in DNDCvCAN, which considers the root distribution across the soil profile (Smith et al., 2020).

We observed that the relationships between changes in root traits and N losses and crop N uptake in the model simulations were mainly linear (Fig. 7). Some traits showed little effect on N pools, such as initial root depth in APSIM, and maximum root/shoot ratio in Daisy. However, sometimes the same traits showed divergent responses across models. For example, in DSSAT an increase in root depth growth rate caused higher crop N uptake and lower N_2O emissions and NO_3^- leaching. By contrast, in APSIM an increase of this trait caused only a marginal effect on crop N uptake and a slight increase of N_2O emissions.

Pearson correlation analysis revealed that, in general, there was a



In general, we found that N losses did not respond strongly to changes in root traits in most process-based models. A variation in root

Table 2

General information of the dataset setups for the sensitivity analysis with process-based models.

Models	Crop	Site	Soil texture	Nitrogen input (kg/ha)	Water regime	Reference
DSSAT	Spring barley	Dundee (56.45°N, 3.07°W)	Loam	120	Irrigated	Cammarano et al., 2019
APSIM	Spring barley	Foulum (56.30° N, 9.35° E)	Sandy loam	140	Rainfed	Vogeler et al., 2023
DNDCv.CAN	Spring barley	Quebec (48.85°N, 72.54°W)	Silty clay	70	Rainfed	Jégo et al., 2024
Daisy	Winter wheat	Foulum (56.30° N, 9.35° E)	Sandy loam	150–165	Rainfed	Gyldengren et al., 2020

Table 3

Main root traits in a selection of dynamic models (APSIM, DNDCvCAN, DSSAT, and Daisy) with potential effects on nitrogen losses.

Trait Category	Trait	Models	Default values	Units
Architectural and morphological	Initial root depth	APSIM	100	mm
	Maximum root depth	APSIM, DNDCv.CAN	1000; 1.51	mm; m
	Root depth growth rate	APSIM, DSSAT**	(0, 5.0, 30, 30, 30, 30, 0.0, 0.0, 0.0, 0.0, 0); 3.0	mm/d; cm/d
	Root fraction of total biomass	DNDCv.CAN	0.15	fraction
	Maximal root/shoot ratio	Daisy	c(0.5, 0.5, 0.25)	ratio per developmental stage (sowing, flowering, and maturity)
	Density distribution of root shape*	DNDCv.CAN	5	function number
	Root length weight ratio	DSSAT	0.98	cm/g
Physiological and chemical	Penetration rate parameter of root	Daisy	1	mm/dg C/d
	NO ₃ ⁻ uptake/root length	DSSAT	0.006	mg/cm
	Conversion efficiency of root	Daisy	0.69	g DM-C/g Ass-C
	Fraction of assimilate for growth to root	Daisy	c(0.5, 0.45, 0.4)	fraction per developmental stage (sowing, flowering, and maturity)
	Root respiration fraction	DSSAT	0.4	fraction
	Critical root N concentration	APSIM	0.02	gN/gDM
	Root C/N ratio	DNDCv.CAN	85	ratio

* The density distribution of root shape in DNDCv.CAN ranges from 1 to 8.

** For DSSAT, all root parameters are based on barley using the CERES module.

trait values from −40 % to 40 % induced changes in NO₃⁻ leaching or N₂O emissions that did not exceed ±20 % of the default scenarios (Fig. 7). Among all traits represented in APSIM, architectural and morphological traits such as maximum root depth and root depth growth rate tended to cause weaker responses than physiological and chemical traits such as critical root N concentration. By contrast, architectural and morphological traits such as root shape function parameter and root length-weight ratio tended to cause stronger responses than physiological and chemical traits such as root C/N ratio and fraction of assimilate for growth to root in the other three models.

5. Comparison between model simulations and experimental results

Experiments at the plot/field scale aim to represent actual agricultural production systems. Yet, the use of process-based models is often necessary to overcome the spatial, temporal, and geographic limitations of field experiments, and to integrate research from multiple disciplines at multiple locations. The use of process-based models for informing the design of more efficient agroecosystems that can better utilize applied N and assist in the development of crop varieties with higher NUE and lower N losses, requires that the capacity of models to simulate N cycling in response to changes in root traits is adequate. Wherever serious deficiencies or inadequate representations of relevant processes are identified, models need to be improved before they can be applied for crop ideotype design. Here we show the current understanding of the linkage between roots and soil N cycling in the real-world and in process-based models, emphasize the strong relationships between certain root traits and N losses found in experiments, present the most sensitive root traits in commonly used dynamic models, and highlight the large inconsistencies found between empirical evidence and model representations.

Our analysis revealed a notable disconnect between root traits

studied in field experiments (Table 1, Fig. 2) and those parameterized in process-based models (Fig. 7, Table S3). Models typically focus on traits related to root growth rates, penetration depth, and resource assimilation efficiency. In contrast, field experiments predominantly examine functional traits associated with root architecture, morphology, physiology, and biology. This misalignment between modelled and measured traits creates a significant barrier to integrating experimental data with process-based models for an improved understanding of the relationships between root traits and N losses.

The magnitude of the observed effects sometimes diverged strongly between experimental results and modelling estimations for the same root traits. For example, our analysis of the available results showed that NO₃⁻ leaching or N₂O emission changed by 50 % in response to changes in some root traits (Fig. 2), whereas the maximum effects in the models only reached 18.6 % (Fig. 7). The direction of the observed effects also differed in some instances between the experimental results and simulations. For example, with an increase in root C/N ratio, NO₃⁻ leaching and N₂O emission estimated by the DNDCv.CAN model showed a flat trend without obvious changes (Fig. 7). Conversely, observations from experiments show that an increase in root C/N ratio may induce a strong reduction in N₂O emission (Fig. 2), although the empirical evidence is still scarce, and further experiments are required to validate these findings. These results further support that an improved representation of root traits in process-based models may open new opportunities for improving N cycling simulations, help to improve estimates of N₂O emissions and N loading to rivers and estuaries, and develop crops/crop cultivars that acquire N more efficiently.

Our survey confirmed that current process-based models capture several key root-soil interactions, including N and water uptake, root litter/exudate contributions to soil organic matter, and their effects on abiotic factors such as soil temperature and water content. However, the survey also revealed key fundamental gaps, in particular in relation to soil microbial communities mediating soil N transformations. For

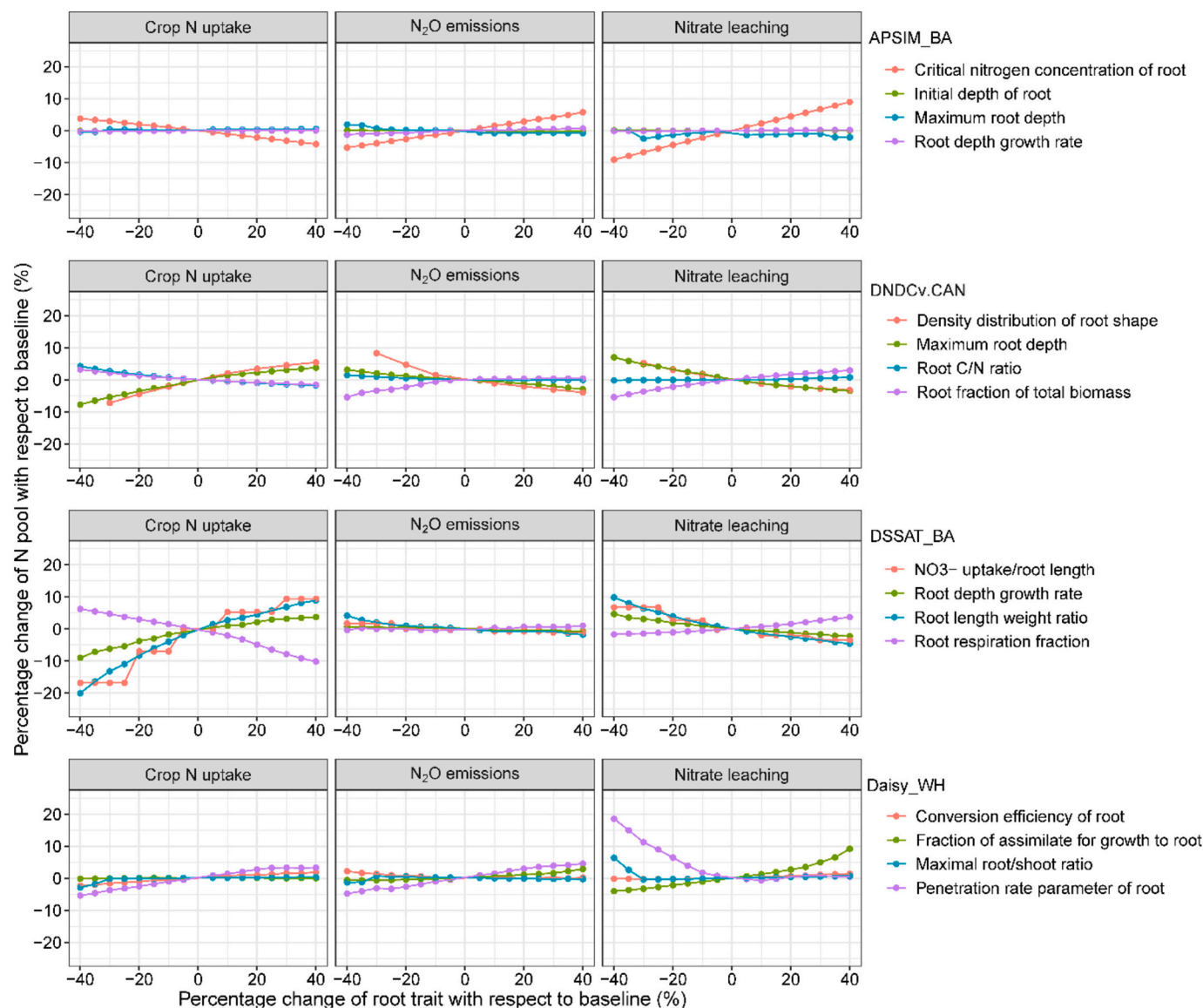


Fig. 7. Sensitivity analysis showing the potential effects of key root traits on nitrogen losses and crop nitrogen uptake in the models APSIM, DNDCvCAN, DSSAT, and Daisy, for spring barley (BA) or winter wheat (WH).

example, only 4 % of models incorporate quantification and characterization of microbial functional genes in the nitrification and denitrification pathways, even though the abundance of these genes can help inform N cycling process rates and associated N losses. Furthermore, none of the models simulate the production and release through the roots of biological nitrification inhibitors (BNIs) and biological denitrification inhibitors (BDIs).

6. Limitations and implications

Our research synthesis revealed a significant mismatch between experimental studies and process-based models in representing root traits associated with N cycling. To address this divergence, a broad screening of root traits may be required to distinguish traits that are crucial for N-cycling from those with minimal impact. Accordingly, we propose creating a comprehensive global dataset through multi-institutional collaboration among root, soil, crop scientists, and model developers, inspired by the coordinated efforts of the Agricultural Model Intercomparison and Improvement Project (AgMIP). By implementing standardized protocols for data collection, unified data-sharing

mechanisms, and consistent measurement methodologies, this initiative aims to produce a “platinum dataset” accessible to all contributors. Such a dataset would help standardize root trait measurements, align experimental and modelling approaches, identify root traits with the strongest impacts on N cycling, and bridge the gap between experimental and modelling communities.

The influence of root traits on N-cycling varies significantly across plant species, genotypes, environmental conditions, and management practices. Our quantitative analysis illustrates the high variability behind the relationship between root traits and N cycling, as evidenced by experimental results. To reduce this uncertainty, targeted experiments focusing on identified root traits of specific species should be conducted across diverse environments, management practices, and climate scenarios. These systematic investigations will help uncover the primary factors driving the observed variations in root trait impacts on N cycling, enabling the development of empirical or mathematical functions that can be integrated into process-based models.

Given our review's focus on understanding the representation of root traits and N losses in models, the use of calibrated datasets for simulations is justified. However, each individual dataset used in our study can

introduce different partitioning along the N loss pathways, and unique soil textures and soil characteristics can also influence these changes. For instance, when soil N is limited, changes in root traits may have negligible effects on N losses. Similarly, in soils with a large N surplus, the impact of root traits may be minimal. The most pronounced effects are likely in conditions of slight N surplus, where changes in plant traits could significantly influence the residual soil N pool. Accordingly, different traits can be important in different situations among various plant species, genotypes, environment, and management combinations, even when applying the same model. To deepen our understanding, the next logical step is to evaluate the sensitivity of model traits under a broader range of conditions, leveraging shared datasets across all models. This comprehensive approach will aid in designing crops with optimized root traits, tailored to specific pedoclimatic conditions and agricultural management practices.

From the perspective of experimental research, both well-described but also less well-studied suites of root traits should be considered in future studies to provide more detailed observational data for developing, calibrating, and validating models (Table 4). This is because classical morphological root traits are not necessarily the ones that explain best the influence of plants on N cycling (Freschet et al., 2021). Other indicators of root N uptake which are more complex to measure, including net and maximum NO_3^- and NH_4^+ uptake rates, must be better documented. The amount, rate, and composition of root exudates, both in terms of C and N compounds, are other challenging root traits to determine that may be of key importance to unfold the role of plants on N losses.

A root trait that may be particularly important in terms of consequences for N losses is the biological exudation of nitrification and denitrification inhibitors. To date, no model incorporates this root trait, although several experiments have shown the potential impacts on N cycling of this trait (Table 1, and S3). For example, the secondary metabolites from *Fallopia spp* led to a 92 % biological denitrification inhibition (BDI) and 52 % respiration inhibition in 15 stains of denitrifying bacteria (Bardon et al., 2014). Another study showed that *Brachiaria* pastures can suppress soil nitrifier populations, reducing c. 75 % ammonium-oxidation rates and N_2O emissions compared to bare soil and soybean (Subbarao et al., 2009). Future field studies validating these results under realistic field conditions and with comparisons using the same crop with and without the capacity to inhibit nitrification will provide the basis for the required model improvements.

The mechanisms by which root traits regulate the microbial communities involved in N cycling are also not captured by process-based models, among other reasons, due to the exclusion of root and rhizosphere microbiome interactions (Saleem et al., 2018; Herms et al., 2022). The abundance of N-related functional genes has been shown to be strongly associated to N_2O production (Prosser et al., 2020; Grassmann et al., 2022), and N_2O consumption (Xu et al., 2020; Kim et al., 2022). Our study shows that root traits are very closely associated with N-related functional genes. Accordingly, using easily observable morphological traits as proxies of these biological interactions may be an avenue to incorporate them in process-based models.

Although process-based plant-soil models are inherently imperfect in capturing the intricacies of the systems they simulate, they remain among the most effective tools for quantifying the impacts of crop management on agricultural sustainability. Ongoing model enhancements, specifically targeting the incorporation of root mechanisms and traits, will contribute significantly to advancing research efforts in improving crop NUE and reducing N losses at the farm scale.

CRediT authorship contribution statement

Huan Liu: Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization. **Brian B. Grant:** Writing – review & editing, Software, Data curation. **Ward N. Smith:** Writing – review & editing, Software, Data curation. **Cheryl H. Porter:**

Table 4

Research needs for improving model representation of the relationship between root traits and nitrogen losses.

Item	Action
Experiments – Screening root traits	Screening root traits from both process-based models and experimental studies
Experiments – Genotype × Environment × Management interactions	Identifying driving factors behind variability in root traits' impact on N cycling
Experiments – complex traits	Include complex indicators of root N uptake such as net and maximum NO_3^- and NH_4^+ uptake rates
Experiments – common traits	Document resource investment traits (e.g., root N concentration, specific root length) more consistently
Biological exudation of nitrification and denitrification inhibitors	Explore opportunities to incorporate this important root trait into process-based models
Soil microbial communities	Incorporate functional genes into process-based models to inform N cycling process rates
Use proxies for traits	Use easily observable root morphological traits in process-based models as proxies to predict changes induced by plants on soil microbial communities related to N cycling

Writing – review & editing, Methodology. **Davide Cammarano:** Data curation. **Iris Vogeler:** Writing – review & editing, Software, Data curation. **Gerrit Hoogenboom:** Methodology. **Johannes W.M. Pul-lens:** Software, Methodology. **Jørgen E. Olesen:** Writing – review & editing. **Marco Bindi:** Writing – review & editing. **Mikhail A. Semenov:** Writing – review & editing. **Per Abrahamsen:** Writing – review & editing, Software, Methodology. **Reimund P. Rötter:** Writing – review & editing. **Uttam Kumar:** Writing – review & editing. **Diego Abalos:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.agsy.2025.104400>.

Data availability

Data will be made available on request.

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