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

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**Abstract**

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 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. To address this, 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, run a sensitivity analysis with selected models (DSSAT, APSIM, DNDCvCAN, Daisy) to examine the way they capture interactions between root traits and N losses, and propose opportunities to improve model representation of observed relationships. 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 developing 3D root components, integrating phenotyping and functional gene detection into process-based models, 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. Overall, this work represents a key step towards designing novel root function-based ideotypes adapted to reduced fertilizer inputs, and therefore potentially less harmful to the environment.

**Keywords:** Root characteristics; N2O emissions; Nitrate leaching; Nitrogen pollution; Crop ideotype

**Highlights:**

1. Synthesis of relationships between plant traits and N losses from experiments
2. Survey of process-based models simulating crop growth and N losses
3. Sensitivity analysis with DSSAT, APSIM, DNDCvCAN, Daisy to examine root trait *vs* N loss interactions
4. Model simulations do not capture effects of root traits on N losses well
5. Required model improvements include 3D, functional gene detection, proxies for complex traits

**1. Introduction**

Over the recent six decades, 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; Battye & Schlesinger, 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 (NO3-) leaching, ammonia (NH3) volatilization, and nitrous oxide (N2O) emissions (Zhang et al., 2015; 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% between 2010 and 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 capacity, promoting NO3- movement with drainage water through the soil profile or flooding across the soil surface (Padilla et al., 2018). Most NO3- leaching losses occur outside of the growing season, consisting of NO3- not taken up by the crops or mineralized from crop residues and soil organic matter. Accordingly, the main mechanism by which plants can influence NO3- leaching is through the immobilization of N in plant biomass via N uptake and reducing soil drainage through water uptake. Nitrous oxide (N2O) 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 N2O 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 N2O emissions (Abalos et al., 2014) and NO3- 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 labour-intensive, time-consuming, and expensive, making it difficult to carry out long-term trials across multiple sites (Johnston et al., 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 (Peng et al., 2020; Jägermeyr et al., 2021). 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; Tao et al., 2017; Paleari et al., 2022), 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; Azad et al., 2020). 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**

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 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 longer life spans (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, NO3- leaching, N2O emissions, nitrification, denitrification, 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 N2O emission, N uptake, and NO3- leaching); (2) if referring to different phenological stages, the growing season accumulated response variables and root traits at maturity were reported. A total of 19 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 10 of those studies were further used for a more in-depth quantitative assessment of such relationships (Fig. 1). 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):

Where is the reference value, selected as the observation within a study with the greatest N loss (N2O or NO3- leaching), and 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 × {exp(*lnRR*) -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 in architectural traits such as root depth can cause a reduction in NO3- leaching. This is because root depth indicates the vertical plant foraging capacity for nutrients and water, and since NO3- 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 NO3- leaching and N2O 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 N2O emission due to greater soil C availability stimulating denitrification (Abalos et al., 2019).

The quantitative assessment revealed the magnitude of some of the trait × N loss relationships (Fig. 1). Changes in root traits were associated with variations in N losses often exceeding 50%. In general, the relationship between root traits and N2O emissions was stronger than with NO3- leaching. Relatively modest increases of 10% in root biomass, root C/N ratio, and root tissue density can reduce N2O emissions by 2.3%, 4.3%, and 6.5% respectively, whereas the same increase in root N concentration can increase N2O emission by 4.1%. By contrast, 10% increases in root length, root/shoot ratio and root biomass can lower NO3- leaching by 2.3%, 1.1% and 1.3%, respectively. The relationships identified in our literature survey highlight the crucial importance of representing the associations between root traits and N losses in process-based models to ensure accurate simulations of N cycling in agroecosystems.

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

We identified 54 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 S1). 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 S1). Approximately 41 and 34 of the surveyed models can simulate NO3- leaching and N2O emission, respectively, 34 models can simulate both N losses, and only 24 models can simulate all seven functional processes including crop growth, root traits, soil C and N dynamics, soil water flow, NO3- leaching, and N2O emission (Table S1). Two spatial (plot and regional) and three temporal (hourly, daily and monthly) scales are covered by the 24 models covering all seven functional processes. The vast majority of models simulate at the plot scale (45) on a daily time step (45).

**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 S1: DSSAT, APSIM, DNDCvCAN, and Daisy. These models were selected for various reasons: (1) they can simulate at least six of the surveyed categories (Table S1); (2) they were initially developed with a different purpose, two of them to simulate crop growth (DSSAT and APSIM), and the other two with a stronger focus on soil properties (DNDCv.CAN 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 S2). 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 validated 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).

***General representation of N2O emissions in process-based models***

Nitrification and denitrification are the two processes linked to N2O emission in process-based models. Nitrification refers to the process of oxidation of NH4+ to NO3- and occurs under aerobic conditions. The first step in process-based models is to calculate the nitrification rate based on the extractable soil NH4+ and soil abiotic/biotic modifiers, which are model specific. Then, NO and N2O 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 NO3- to NO2-, NO, N2O and N2 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 NO3- or extractable C modified by abiotic or biotic factors. Then the second step is often to calculate the N2/N2O ratio based on oxidation of an electron donor (normally hydrogen) to reduce oxidized N substrates as a function of soil water content. The N2O gas flux from denitrification is the product of the denitrification rate and the N2O ratio. Most models follow these steps and incorporate the associated mechanisms to simulate soil N2O 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.

***General representation of NO3- leaching in process-based models***

Losses via NO3- leaching are primarily linked to drainage using a cascade water flow approach in process-based models. When the soil water content exceeds the field saturation water content, the drainage flow in each soil layer can be calculated based on the gap between saturation water content and the upper drained limit (i.e., water content at field capacity) of the soil. Then, NO3- leaching can be simulated based on the soil NO3- concentration and drainage flow in each soil layer. Most process-based models follow this principle to simulate NO3- loss, while differing in hydraulic parameters and drainage flow types. Some models may also include some retention processes that slow the NO3- leaching relative to the drainage flow. The soil NO3- concentration is therefore a key driver of NO3- leaching in most models, and this is in turn affected by the estimation on nitrification.

***4.1. Model description and representation of plant trait × N loss relationships***

***DSSAT***

The Decision Support System for Agrotechnology Transfer (DSSAT) model has been used to reproduce crop growth and yield formation accurately under various climatic and management conditions (e.g., Cammarano et al., 2022; Liu et al., 2022). Five primary modules are embedded in the DSSAT 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 N2O and methane emissions (Hoogenboom et al., 2019, 2021).

In DSSAT, 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 NO3- concentration and the drainage flow determine NO3- leaching. Soil biotic factors, including soil temperature, water, and pH, are the modifiers for nitrification rate. The N2O emission is estimated as a fraction (0.001) of nitrification. The DSSAT model provides two methods for denitrification: CERES denitrification and DayCent denitrification. In the CERES module, soil extractable C, NO3- concentration, temperature and water factors are accounted for in calculating the denitrification rate. Then N2O emissions are calculated based on the soil NO3- content and a given N2/N2O ratio modified by soil water content. By contrast, in the DayCent denitrification module, the denitrification rate is calculated based on soil heterotrophic respiration (CO2), NO3-, and soil water content. The N2/N2O ratio is calculated based on the ratio of NO3- to CO2 and modified by soil water content. In terms of the representation of N losses and plant traits in DSSAT, traits linked to crop N uptake modify soil NO3- and NH4+ 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) is linked to potential evapotranspiration and therefore to soil water content (Fig. 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, NO3- dissolved in water can move to deeper soil layers with saturated or unsaturated water flows. 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 & Jones, 1991). The nitrification rate is modified by soil water, temperature, and pH. The NO and N2O 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. 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. 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 NO3- leaching and N2O 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 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 NO3- and soluble C is provided by the decomposition sub-model. The denitrification sub-model predicts the consumption of NO3- and generates soil fluxes of NO, N2O, and N2 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 NH4+ 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 N2O 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 NO3- in DNDCv.CAN are derived from the bulk water flux between soil layers, the soluble NO3- 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 NH4+ on 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 the denitrification and nitrification processes (Fig. 4).

***Daisy***

The soil-plant-atmosphere system model Daisy is an explanatory, mechanistic, and physically based model (Abrahamsen & 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 to the drainage is calculated by the flow towards the drainage above and below the drainage level, adjusting by an average of the conductivities of the saturated layers above and below the drainage level (Mollerup et al., 2014; Holbak et al., 2021). Solute NH4+ concentration, temperature and potential pressure factors are taken into account for calculating nitrification rate. The fraction of the nitrified NH4+ that becomes N2O is given as a constant with a default value of 0.02. The denitrification rate is calculated using CO2 respiration rate as a proxy and solute NO3- modified by the soil temperature and water factors. The N2O emission from denitrification is currently not simulated by Daisy, but ongoing work is underway to develop this model component. Plant traits affect N2O emissions from nitrification in a similar way by affecting the concentration of substrates (soil C, NH4+, NO3-) and abiotic factors (soil water, and temperature), as described for the other models above (Fig. 5).

***4.2. Sensitivity analysis***

***4.2.1. 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, N2O emissions, and NO3- 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 validated with, along with all the required input data including climatic, soil, and agricultural management information. A description of the models’ setups is provided in Table 3; 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 2), according to the results of the sensitivity analysis for each model for a wide range of traits (Table S2). 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 NO3- leaching losses that occurred after crop harvesting. All the analyses were conducted using R version 4.2.2. (R Core Team, 2022).

***4.2.2. 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. The changes ranged from -20% to 9.4% for crop N uptake, from -9.1% to 18.6% for NO3- leaching, and from -5.4% to 8.3% for N2O emissions (Fig. 6). The most responsive traits for crop N uptake, NO3- leaching, and N2O 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 2), and root shape function parameter in DNDCv.CAN, 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. 6). 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 N2O emissions and NO3- leaching. By contrast, in APSIM an increase of this trait caused only a marginal effect on crop N uptake and a slight increase of N2O emissions.

Pearson correlation analysis revealed that, in general, there was a strong negative relationship between changes in crop N uptake and changes in N losses for all models (Fig. S1). This indicates that the main pathway by which changes in root traits modify N losses in the models is by controlling the amount of N retained in the crop biomass.

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 trait values from -40% to 40% induced changes in NO3- leaching or N2O emissions that did not exceed ±20% of the default scenarios (Fig. 6). 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 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.

Indeed, the magnitude of the observed effects sometimes diverged strongly between experimental results and modelling estimations. For example, changes of 40% in the root C/N ratio led to a 0.1% reduction of N2O emissions in DNDCv.CAN; however, a mesocosm experiment reported that a gradient of root C/N ratio values was associated with changes in N2O emissions of 40% (Oram et al., 2020). Moreover, our analysis of the available results showed that NO3- leaching or N2O emission changed 50% in response to changes in some root traits (Fig. 1), whereas the maximum effects in the models only reached 18.6% (Fig. 6). The direction of the observed effects also differed in some instances between the experimental results and simulations. For example, with an increase in root/shoot ratio, NO3- leaching and N2O emission estimated by the Daisy model showed a flat trend without obvious changes (Fig. 6). Conversely, observations from experiments show that an increase in root/shoot ratio may induce a strong reduction in NO3- leaching (Fig. 1), although the empirical evidence is still scarce, and further experiments are required to validate these findings. These findings 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.

**6. The way forward**

Our literature survey illustrated that in some instances the data behind the N loss-root trait relationships had a skewed distribution, and that a large fraction of the empirical evidence is provided by mesocosm/pot experiments. More model-oriented and comprehensive types of field experiments are required, in which root traits related to resource investment such as root N concentration, root tissue density, specific root length and root diameter, should be routinely measured and documented to increase the empirical evidence for drawing stronger conclusions and to develop mathematical representations in models. 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 NO3- and NH4+ 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.

We now know that root traits are key drivers of soil organic matter stabilization and C sequestration (Poirier et al., 2018). For example, root length density, mycorrhizal association and rhizodeposition contribute to microaggregation, and together with hemicellulose and soluble compounds, to macroaggregation. Root depth distribution is the most important trait regulating subsoil C storage and stabilization (Poirier et al., 2018). Since soil water, C and N cycling are intrinsically intertwined, the interactive effects of root traits on both cycles should be simultaneously evaluated in order to incorporate sound mechanistic relationships into process-based models. This will avoid providing recommendations that incur trade-offs with respect to the greenhouse gas balance, and instead promote synergies, because higher root length density, mycorrhizal association, as described in this study, and hemicellulose (Abalos et al., 2022), are linked to both lower N2O emissions (and N losses in general) and increased soil C storage.

In addition to better capturing the functioning of root traits, developing a 2D or 3D root component in the models may increase the robustness of root simulations. For example, the model SPACSYS has a 3D root trait module allowing to incorporate important root parameters frequently overlooked in other process-based models, such as root branching and elongation directions and rates. By better representing the spatial configuration of the root system, 3D models may be better suited to test the potential impacts of diverse root system phenotypes on resource use efficiency and N losses (Bingham and Wu, 2011). To support the implementation of this model improvement, future empirical studies should provide detailed and spatially explicit assessments of the root system in order to parameterize and validate the 3D models. Non-invasive 3D measurement methods including neutron tomography, X-ray tomography, and magnetic resonance tomography can provide the required data on root system architecture.

Integrating phenotyping and functional gene detection into process-based models can speed up the development of new crop ideotypes when relevant root traits are identified (Wang et al., 2019). Advancing this research field requires determining the genetic control behind root anatomy phenotype and developing a robust association between key genes/QTLs and model input parameters, including further links to gene expression pathways. Models improved in such manner would facilitate the modelling of genotype × environment × management (G×E×M) interactions, including testing for dependencies between genes/QTLs that may result in undesirable phenotypes (e.g., root phenotypes that enhance soil exploration at the expense of reduced yield).

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, S1, and 2). 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 N2O emissions compared to bare soil and soybean (Subbarao et al., 2009).

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). For example, plants can stimulate denitrification via the release of organic compounds by rhizodeposition, stimulate microbial mineralization of soil organic N to enhance crop N uptake, and establish mutualistic relationships with arbuscular mycorrhizal fungi that reduce N2O emissions from soil (Moreau et al., 2019). Using easily observable morphological traits as proxies of these biological interactions may be an avenue to incorporate them in process-based models. For instance, the distance exudates travel from the root surface declines exponentially with root diameter (Finzi et al., 2015), whereas the rate of root exudation is linearly related to specific root length and negatively to root diameter (Guyonnet et al., 2018).

Our review is focused on a general understanding of the representation of root traits and N losses in models, which justifies the use of calibrated datasets for the simulations. Yet, 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. If soil N is limited, a change in root traits might not influence N losses significantly. The same might be true if the soil has a large N surplus. The strongest impact can be expected in situations where the soil is in a slight N surplus, and a change in plant traits could then have a sizeable impact on the residual soil N pool. Accordingly, different traits can be important in different situations, even when applying the same model. Testing the sensitivity of the model traits under more varied conditions and with shared datasets for all models is an obvious next step to support the design of suitable crops in tune with the site-specific pedoclimatic and agricultural management context.

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.

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