Mycorrhizal associations change root functionality: a 3D modelling study on competitive interactions between plants for light and nutrients

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Summary

• Recent studies show that the variation in root functional traits can be explained by a two-dimensional trait framework, containing a 'collaboration' axis in addition to the classical fast–slow 'conservation' axis. This collaboration axis spans from thin and highly branched roots that employ a 'do-it-yourself' strategy to thick and sparsely branched roots that 'outsource' nutrient uptake to symbiotic arbuscular mycorrhizal fungi (AMF).

• Here, we explore the functionality of this collaboration axis by quantifying how interactions with AMF change the impact of root traits on plant performance. To this end, we developed a novel functional–structural plant (FSP) modelling approach that simulates plants competing for light and nutrients in the presence or absence of AMF.

• Our simulation results support the notion that in the absence of AMF, plants rely on thin, highly branched roots for their nutrient uptake. The presence of AMF, however, promotes thick, unbranched roots as an alternative strategy for uptake of immobile phosphorus, but not for mobile nitrogen.

• This provides further support for a root trait framework that accommodates for the interactive effect of roots and AMF. Our modelling study offers unique opportunities to incorporate soil microbial interactions into root functionality as it integrates consequences of belowground trait expression.

Introduction

Plants require multiple resources to grow and reproduce, and display considerable variation in traits related to the acquisition and conservation of these resources. A common hypothesis to explain this variation is the growth–survival tradeoff, which implies that combinations of linked traits map along an axis of functional strategies (Wright *et al.*, 2004). On one end of this axis, we find species with high resource acquisition resulting in fast growth but a short life span. On the other end of this axis, we find conservative strategies with slow growth but a long life span. This tradeoff in functional plant strategies has mainly been demonstrated for leaf traits. For example, acquisitive leaves have a high specific leaf area (SLA) and photosynthetic capacity, while conservative leaves have the opposite (Wright *et al.*, 2004; Poorter & Bongers, 2006). Recent attempts to apply this one-dimensional leaf economics spectrum (LES) to root traits have shown limited success (Kong *et al.*, 2016; Kramer-Walter *et al.*, 2016; Roumet *et al.*, 2016; Weemstra *et al.*, 2016).

Mycorrhizal fungi play a vital role in a recently proposed two-dimensional – rather than one-dimensional – belowground trait

framework aimed at functionally understanding root trait variation (McCormack & Iversen, 2019; Bergmann *et al.*, 2020). Next to the 'conservation' axis that compares to the classical one-dimensional economics spectrum analogous to the LES, a second 'collaboration' axis was proposed that reflects a range of strategies from 'do it yourself' vs 'outsourcing' of nutrient acquisition via mycorrhizal symbiosis (Bergmann *et al.*, 2020; Supporting Information Fig. S1). It is well known that the symbiosis between plants and arbuscular mycorrhizal fungi (AMF; Smith & Read, 2010; Kiers *et al.*, 2011) plays an important role in the diversity and productivity of plant communities through increased resource acquisition (Van der Heijden *et al.*, 1998; Vogelsang *et al.*, 2006), and only recently have we started to realize that these fungi are intrinsically related with root traits (Laliberté, 2017; Kuyper *et al.*, 2021). Root colonization by AMF is positively correlated with root diameter, and hence negatively correlated with specific root length (SRL) (Baylis, 1975; St John, 1980; Ma *et al.*, 2018; Bergmann *et al.*, 2020, but see Maherali *et al.*, 2016). This suggests that plants can rely either on their own root system for nutrient acquisition by having thin roots or on outsourcing of nutrient acquisition to AMF by having thick roots that increase mycorrhizal colonization (Baylis, 1975; Freschet *et al.*,

2021). The inclusion of the mycorrhizal symbiosis opens a second dimension in the root economics space that is key to understanding root trait variation (Bergmann *et al.*, 2020). However, we do not know how different strategies along the collaboration axis pay off when plants are competing in mixed stands for limited soil nutrients such as nitrogen (N) and phosphorus (P), which differ greatly in their availability in soils and mobility in the soil matrix.

In this study, we aim to further explore this 'collaboration' axis with a theoretical exercise that aims to gain a better understanding of how AMF affect the relationship between root traits and the performance of plants competing for above- and belowground resources. To this end, we developed a novel three-dimensional plant growth model that is designed to simulate competitive interactions driven by the basic mechanisms of light acquisition and nutrient acquisition by roots and AMF, which requires simulation of monospecific and mixed stands composed of multiple individually distinct plants. This functional–structural plant (FSP) modelling approach uses explicit representations of both shoot and root architecture and captures the dynamic interactions between plants through the feedback between changing plant phenotype and resource capture, both above and below ground (Evers *et al.*, 2018). The novelty of our approach lies in its focus on dynamic interactions between individually distinct plants through a functional representation of shoots, roots and AMF. This allows us to elucidate how root trait variation affects competitive interactions between plants with equal or differing trait values under nutrient-limiting conditions, and how AMF associations change these effects of root trait variation.

Materials and Methods

Functional–structural plant models typically simulate shoot architectural development and light capture (Prusinkiewicz & Lindenmayer, 1990; Kurth, 1994; Evers *et al.*, 2007) or root architectural development and nutrient uptake (Diggle, 1988; Pagès *et al.*, 1989; Lynch *et al.*, 1997; Dunbabin *et al.*, 2013). Yet, FSP models that explicitly combine both above- and belowground plant parts (Louarn & Faverjon, 2018; De Bauw *et al.*, 2020), or that describe the development of AMF colonization (Schnepf *et al.*, 2016; Zhou *et al.*, 2020) have seen only recent development. Here we seek to combine these elements in a novel mechanistic modelling approach that simulates competitive interactions between individual plants through the basic mechanisms of light acquisition by leaves and nutrient uptake by both roots and AMF. The aim of this approach is to gain a mechanistic understanding of how multidimensional plants interact with a multidimensional environment that includes abiotic conditions (nutrient availability) and biotic interactions (AMF and inter- and intraspecific competition) to shape individual plant performance. The model used in this study was developed in the modelling platform GROIMP (Hemmerling *et al.*, 2008) and was designed to simulate a generic annual dicot, for which we made use of pre-existing calibrations presented in Pagès *et al.* (2014) and de Vries *et al.* (2018), rather than presenting a calibration and validation based on new experimental data. As such, the model cannot be used to make detailed quantitative predictions, but can be used to assess qualitative effects of

parameter changes or qualitative differences between treatments that emerge from the mechanisms implemented in the model. Simulating interspecific competition would require that the model simulates large stands composed of multiple individually distinct plants. To balance the increased computation time of simulating these individually distinct plants, we implemented a coarser temporal and spatial resolution in the belowground part of the model compared with previous FSP models of root growth and development (Postma *et al.*, 2017) or root–mycorrhizal integration (Schnepf *et al.*, 2018).

Plant morphology

The morphology of the simulated plants was described using the root architectural parameters of *Pisum satvium* (pea) found in Pagès *et al.* (2014), and the shoot architectural parameters of *Brassica nigra* (black mustard) found in de Vries *et al.* (2018). This choice of model plants was driven by the availability of a parameter set that could be used for the model and these model plants are used solely to describe the root and shoot architectures. This means that any functional aspects that characterize these plants were not used for model calibration (i.e. the simulated plants do not make root nodules even though *P. satvium* does, and the simulated plants can form AMF associations even through *B. nigra* cannot).

The focus of the aboveground part of the model is to simulate the dynamics in competition for light through the positive feedback between light capture and plant growth as well as phenotypic plasticity to avoid shading through light-mediated shade avoidance responses (Fig. 1) (for a detailed model description see de Vries *et al.*, 2018). We made two changes to the shoot architectural part of the model described in de Vries *et al.* (2018) to reduce the computation time of the model: we removed the plant's ability to branch and we reduced the average number of possible phytomers from 29 to 23. These changes resulted in fewer simulated plant organs and an earlier flowering time, but allowed us to derive the generic principles of interaction that were investigated in this study.

We combined this dynamic shoot architectural model with a root architectural model based on the principles of ArchiSimple (Pagès *et al.*, 2014). This root architectural model allows for the dynamic simulation of root growth over time as a function of assimilate availability, but lacks any form of plasticity in physiological or morphological traits in response to the soil environment. In our model, we assume all roots to function as both absorptive and transportive roots, thereby accounting for the heterogeneous pool of functions among fine roots (McCormack *et al.*, 2015). However, we do make a distinction between three types of roots in our model from an architectural perspective: first-, second- and third-order roots (see Table S1; Methods S1). In this model, the third-order root is the first root to emerge from the seed kernel upon germination, and the diameter of this initial root determines the diameter of all other roots in the root system, following the architectural model by Pagès *et al.* (2014). The second-order roots are the lateral roots that emerge from the third-order root and together with the third-order root make up the root architecture that is explicitly represented in the model's
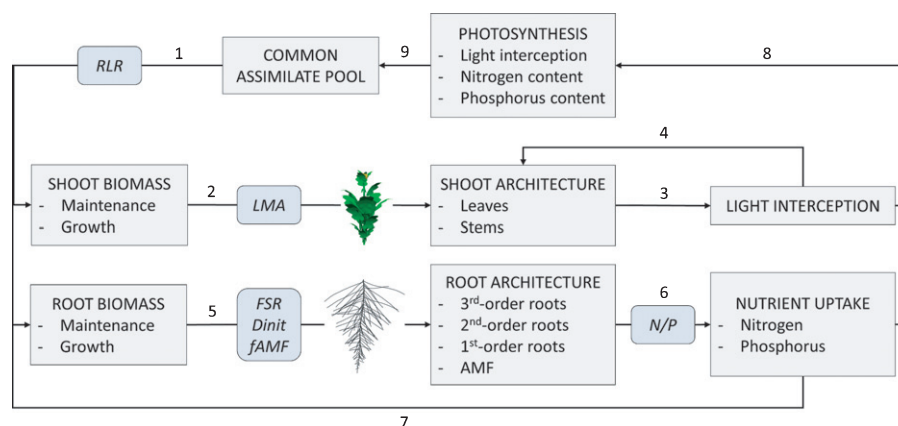
Fig. 1 Graphical model summary. At the start of a time step, the plant's trait value for the root : leaf mass ratio (RLR) drives the distribution of a common assimilate pool between root and shoot biomasses, which is used to pay for maintenance respiration and growth (1). The increase in shoot biomass is translated to growth of the shoot architecture, where the leaf mass per unit area (LMA) determines the size of the leaves (2). The shoot architecture determines light interception at the level of individual leaves, which is affected by the canopy structure as a whole, including the shoots of neighbouring plants (3). Light interception mediates plastic responses that determine stem elongation and the shape, size and insertion angle of leaves (4). The increase in root biomass is translated to growth of the root system, where the first : second-order root length ratio (FSR), the initial root diameter (Dinit) and the arbuscular mycorrhizal fungi (AMF) allocation fraction (fAMF) determine the shape of the root system and the division of biomass over third-, second- and first-order roots and AMF (5). The root architecture determines the amount of nitrogen (N) and phosphorus (P) taken up from the soil, which is affected by the nutrient availability in the soil (N/P) and the root architecture of neighbouring plants (6). Portions of the nutrients taken up by the root system are used for the construction of new biomass (7). The remaining N and P are distributed over the individual leaves, and combined with leaf-level light interception determine leaf-level photosynthesis (8). The assimilates produced by the leaves are then pooled and added to the common assimilate pool, to be used for growth in the next time step (9). For a detailed model description, see Supporting Information Methods S1 and de Vries *et al.* (2018).

three-dimensional environment. From the second-order roots emerge the first-order roots, which are represented numerically rather than explicitly. These first-order roots represent the finest roots of the root system, and the density of these is controlled with a parameter that denotes the length ratio between first- and second-order roots (FSR, m m^{-1}). Root hairs were implemented separately as part of the nutrient uptake model (see the nutrient uptake section as well as Methods S1).

Root : shoot integration

The above- and belowground model components interact through carbon and nutrient (N and P) source-sink dynamics (Fig. 1; see de Vries *et al.* (2018) for a detailed description of the source-sink model used to describe carbon allocation). These nutrients are tied to the plant growth model through the maximum rate of leaf-level photosynthesis, which is assumed to be limited by either N or P following an optimal N : P mass ratio of 15 : 1 (Aerts & Chapin, 1999). This link between nutrients and leaf photosynthesis functionally ties the root system to the leaves of the plant and therefore we conserve the ratio between root and leaf biomass (root : leaf mass ratio; RLR) as a functional trait to drive carbon allocation to the root system in response to increasing leaf biomass. The carbon allocated to the root system is invested into growth of the roots and the AMF hyphae, which are considered an extension of the root system.

Extraradical mycorrhizal fungal mycelia

For the representation of the AMF, we assume an exclusively mutualistic relationship with the host plant (i.e. we do not

consider cheating behaviour by either plant or AMF) and employ a phytocentric perspective where the root system and AMF are considered as a single functional unit. Hence, the extraradical mycelium is treated as an extension of the root system analogous to the first-order roots, both in theory (Hodge *et al.*, 2000) and in model implementation, using a parameter analogous to the FSR to simulate the AMF : root mass ratio (fAMF, g AMF g^{-1} root). The fungal hyphae act as a sink for C and as both a sink and a source of N and P. The simulated fungal hyphae differ from the simulated first-order roots in three traits only: the fungal hyphae have a smaller diameter, higher tissue density and lower minimum nutrient concentration (C_{min}) required for uptake (Silveira & Cardoso, 2004; see Table S2). Other differences between AMF and roots, such as differences in C, N and P requirements, were not considered in this study. For more details on the implementation of AMF in the model, see Methods S1.

Nutrient uptake

We implemented a simplified model of nutrient uptake that was designed to capture the functional differences between uptake of nutrients with different mobilities in the soil matrix by roots and AMF. To reduce computation time, we forwent the diffusion–convection and Michaelis–Menten equations that are commonly used to describe nutrient fluxes from the soil to the root (Barber & Cushman, 1981; Lynch, 2005). Instead, we assumed that roots and hyphae are able to take up all nutrients in their immediate vicinity within the model time step of 1 d. This assumption captures the plant's ability to change the nutrient uptake rate of its roots in response to nutrient conditions, which is a commonly reported means of increasing nutrient uptake under nutrient-

limiting conditions. In the model, the soil is divided into a three-dimensional grid of independent cells of $0.1 \times 0.1 \times 0.1$ m that contain plant roots, mycorrhizal fungal hyphae, as well as N and P that the roots and hyphae can take up and deplete (see Methods S1 for a detailed description of nutrient uptake). We assumed nutrients to be homogeneously distributed within a soil cell, and that there was no influx of additional nutrients over the course of the season, as would normally occur, through mineralisation or otherwise, and we did not consider any structural or textural properties of the soil matrix. Within these soil cells, we define a cylinder of soil volume around individual roots and hyphae from which nutrients are exploited (Hill *et al.*, 2010) using a nutrient uptake radius parameter. This parameter captures differences in the mobility of different nutrients that would otherwise emerge from diffusion–convection equations (Barber & Cushman, 1981). N (nitrate) hardly interacts with the mineral soil matrix and is therefore very mobile, represented by a large uptake radius, whereas P strongly interacts with the mineral soil matrix and is therefore far less mobile, and thus is represented by a small uptake radius (Li *et al.*, 1991; Gahoonia & Nielsen, 1997; see Table S2) that is affected by root hair length. With these assumptions the model can simulate differences in N and P uptake, depletion of nutrients at the level of individual roots, and depletion of nutrients at the level of the root system through depletion of well-rooted soil cells. These belowground model components, the function of root traits, and the interactions between root and shoot are described in detail in the Methods S1. The result is a whole-plant model that simulates plant growth as a function of light, N (as an example of a highly mobile nutrient) and P (as an example of a very poorly mobile nutrient) acquisition, from which internal resource tradeoffs and competitive interactions between plants emerge.

Simulations

We simulated plots of four by four plants at a density of 100 plants m^{-2}. Border effects in light conditions and their effect on plant growth were minimized by cloning the shoots 625 times to simulate a large field of 10 000 plants. At every time step, the light interception of each individual leaf was calculated by averaging the light interception of its 625 clones. Border effects in nutrient uptake were eliminated using periodic boundaries for the root system where a root exiting the soil volume of the plot grows into the plot on the other side of the soil volume, creating an infinite repetition of the soil and the simulated root systems. The simulations spanned a growing season of 100 d (31 March to 9 July), with a time step of 1 d. The average daily temperature, average daily insolation and solar angle were typical for the Netherlands at a latitude of $52°$.

Scenario studies

To test the effects of individual root traits on plant performance, we used plant biomass as a measure of plant performance and conducted a model sensitivity analysis of plant biomass to four key plant traits that we varied from a 20% decrease to a 20%

**Table 1** Four plant traits varied for a sensitivity analysis of the new functional–structural whole-plant model.

Parameter	Description	Units	Eqn
Dinit	Initial root diameter	m	S3
FSR	First : second order root length ratio	m m^{-1}	S6
RLR	Root : leaf mass ratio	g g^{-1}	S1
LMA	Leaf mass per unit area	g m^{-2}	–

increase with 10% increments (Fig. 1; Table 1). These traits were selected for their relationship with the outsourcing vs do-it-yourself axis (initial root diameter, Dinit, which is the primary determinant of SRL) the acquisition of N vs P (length ratio between first- and second-order roots; FSR), or the relative limitation by above- vs belowground resources (root : leaf mass ratio; RLR). We also included a leaf trait with a strong relation to the acquisition conservation axis (leaf mass per unit area, LMA; inverse of specific leaf area), as a proxy for root traits with a relation to that axis such as tissue density or N concentration. Plants are known to show plasticity in these four traits (i.e. SRL, FSR, RLR, LMA) in response to their environment, indicating that these traits play an important role in determining plant performance. To assess the role of these traits in determining plant performance and the outcome of competitive interactions, we opted to implement these traits as static parameters (i.e. the traits do not respond to the environment) and to conduct a sensitivity analysis. The sensitivity analysis was conducted both in monostands of a single genotype (i.e. intraspecific competition), and in mixtures of two genotypes that differed in a single parameter value (i.e. interspecific competition). In these mixtures, the two genotypes were distributed following a checkerboard pattern, such that every plant directly competed with four plants of the other genotype.

We tested the role of these traits in three scenarios. First, under nutrient-limiting conditions, we simulated plants growing in nutrient-poor soil where plant growth was limited by the availability of either N or P, at 350 µM N l^{-1} soil and 15 µM P l^{-1} soil, respectively ('Ctrl' in Figs 2, 3 and Table 2). These values reflect an optimal N : P mass ratio for plant tissues of 15 : 1 (Aerts & Chapin III, 1999) and were chosen to impose strong nutrient limitation to growth, assuming that no additional nutrients were added to the soil over the course of the growing season. The concentration of the other, nonlimiting nutrient was set to 10 times the low nutrient concentration, at 3500 µM N l^{-1} soil and 150 µM P l^{-1} soil, respectively. Second, to assess how the role of these traits changed with an increase in soil nutrient availability, we doubled the availability of the limiting nutrient (to 700 µM N l^{-1} soil and 30 µM P l^{-1} soil, '+N/P' in Figs 2, 3 and Table 2). Third, to assess how AMF alter the role of these traits, we allowed plants to invest carbon in AMF hyphal length to aid in the uptake of N and P ('+AMF' in Figs 2, 3 and Table 2). Each treatment combination was replicated 10 times to account for model stochasticity.

To test the importance of nutrient availability and of the costs of maintaining AMF associations for model behaviour, we also

Fig. 2 Cumulative whole-plant biomass in g (*y*-axis) of plants grown in monostands under either nitrogen (N) (a) or phosphorus (P)-limiting conditions as simulated by the model (b). Plant growth was simulated under three conditions; strong nutrient-limiting conditions (Ctrl); an increased nutrient availability treatment of a two-fold increase in soil N or P (+N/P); or through the inclusion of arbuscular mycorrhizal fungi (+AMF). Error bars show the SEMs.
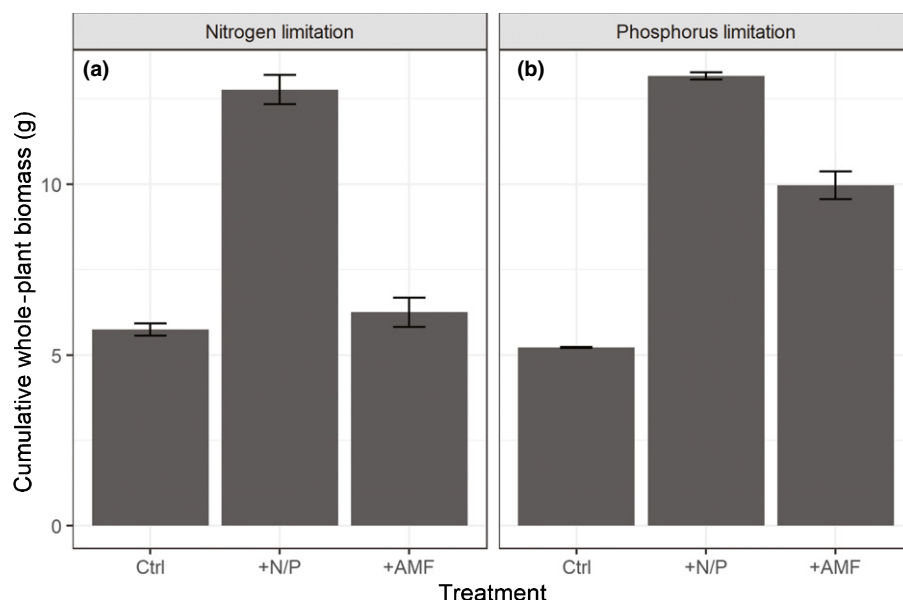
tested model sensitivity to nutrient availability and to the AMF : root mass ratio (fAMF, g g^{-1}). The nutrient availability was only tested in monostands as it is impossible to deliver a higher nutrient concentration to a selection of plants in a plot without affecting all plants in the plot. These analyses are reported in the supplementary material (Fig. S4), separate from the four plant parameters selected for the sensitivity analysis.

Output

All model output is generated at the level of individual plants. The primary analysed output variable of the model was cumulative whole-plant biomass (e.g. combined biomass allocated to seeds, shoot, roots and reserves) of one growing season, which was used as a proxy for individual plant performance. Other analysed output variables were SRL, root : shoot mass ratio, and total uptake of N and P. The results of the sensitivity analysis are reported by a value S that describes the model's sensitivity to each of the tested parameters in both the monostand and the mixtures. S shows the relative change in plant biomass caused by a change in the respective parameter. S is calculated using the value of the altered model parameter P (P_1), the default value for the model parameter (P_0), the biomass of the plants affected by the parameter change in either monostand or mixture (Bio$_1$, g), and the biomass of plants with the default parameter value of plants that grew in monostands (Bio$_0$, g), acting as a baseline to which the effect of a parameter change was compared (e.g. $S = 0$ when Bio$_1$ = Bio$_0$ and $P_1 = P_0$).

$$S = \frac{Bio_1 - Bio_0}{Bio_0} \times \frac{P_0}{P_1 - P_0} \qquad \text{Eqn 1}$$

Negative values of S indicate a negative relationship between the tested parameter and plant biomass, whereas positive values

indicate a positive relationship between the tested parameter and plant biomass. In Fig. 3, we report the absolute values for S, with the sign of S (e.g. positive or negative) presented as colours in the graph to allow for easy comparison of model sensitivity in different scenarios. All values reported in this paper are averages with error bars representing the SEMs.

Results

Model basics: effects of soil nutrient availability on plant performance

The simulated plants growing in control conditions (monostands with strong nutrient limitation) had an equal biomass under N- and P-limiting conditions, producing 5.75 ± 0.19 and 5.22 ± 0.02 g of biomass, respectively (Fig. 2, Ctrl). Increasing the nutrient availability of the soil had a positive effect on plant biomass, such that a two-fold increase in soil nutrient availability increased plant biomass to 12.69 ± 0.47 and 13.22 ± 0.11 g under N and P limitation, respectively (Fig. 2, +N/P). The inclusion of mycorrhizal fungi had no effect on plant biomass under N-limiting conditions (Fig. 2a, +AMF), as the plants were already able to deplete the soil of available N in the absence of AMF. Conversely, mycorrhizal fungi had a positive effect on plant performance under P-limiting conditions, increasing plant biomass to 10.26 ± 0.31 g (Fig. 2b, +AMF). This can also be attributed to the AMF having a lower C_{min} for P uptake (minimum nutrient concentration at which uptake can take place) than plants, implying that mycorrhizal plants both enlarge the soil volume from which P can be taken up and increase the amount of P that can potentially be taken up from that soil volume. The SRL was highly sensitive to changes in root traits, in particular Dinit (Fig. S2), ranging from 236.8 ± 0.24 m g^{-1} at a high
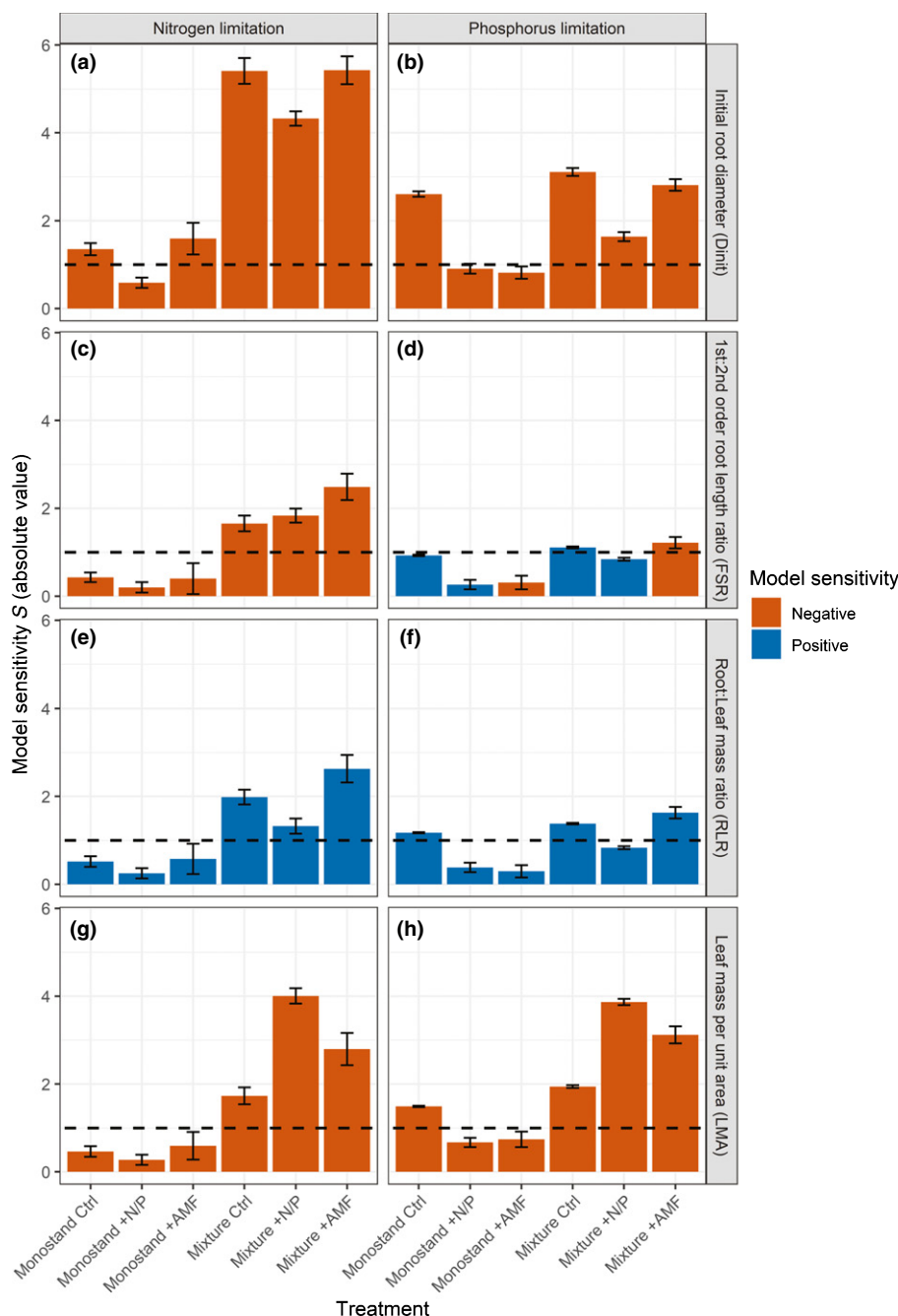
Fig. 3 Model sensitivity analysis of four tested parameters – initial root diameter (Dinit) (a, b), first : second-order root length ratio (FSR) (c, d), root : leaf mass ratio (RLR) (e, f) and leaf mass per unit area (LMA) (g, h) – under either N- (a, c, e, g) or P-limiting conditions (b, d, f, h) in four treatment combinations (x-axis: monostands and mixtures grown under nutrient-limited control conditions (Ctrl), with increased nutrient availability (+N/P), or including mycorrhizal fungi (+AMF)). The model sensitivity is defined as the relative effect of a parameter change on individual plant biomass (the y-axis shows absolute values of model sensitivity S; see Eqn 1 in text), with the dotted line representing a model sensitivity of 1 (e.g. where a parameter change shows a 1 : 1 proportional effect). Values above that line indicate disproportionally strong effects, and values below that line indicate disproportionally small effects. A negative sensitivity (red) indicates that an increase in a parameter value leads to a decrease in individual plant biomass. A positive sensitivity (blue) indicates that an increase in a parameter value leads to an increase in individual plant biomass. Error bars show the SEMs.

Dinit to 581.7 ± 0.19 m g^{-1} at a Dinit. The root : shoot mass ratio was less directly controlled by root trait values and more an emergent property of several mechanisms, and ranged from 0.22 (1% quantile) to 0.87 (99% quantile). The root : shoot mass ratio was higher under N-limiting conditions than under P-limiting conditions, and was positively correlated with all four of the tested parameter values (Fig. S3). Both the simulated values for SRL and the root : shoot mass ratio were within the range commonly reported for herbaceous plants (Monk, 1966; Mommer *et al.*, 2012; Poorter *et al.*, 2012; Schroeder-Georgi *et al.*, 2016), but were not under active regulation in response to the environment, as would be the case in real plants.

Model sensitivity: effects of trait variation on nutrient uptake and biomass

The results showed a negative sensitivity of plant biomass to changes in Dinit (Fig. 3a,b) and LMA (Fig. 3g,h), and a positive sensitivity of plant biomass to changes in RLR (Fig. 3e,f) in all treatment combinations. In addition, the results showed a negative sensitivity of plant biomass to changes in FSR under N limitation, and a positive sensitivity under P limitation in the absence of AMF (Fig. 3c,d). An increase in nutrient availability increased model sensitivity to changes in LMA (Fig. 3g,h, +N/P), while it decreased model sensitivity to the root-related traits (Dinit, FSR, RLR; Fig. 3, +N/P).

Table 2 Soil nutrient concentrations used for the control (Ctrl), increased nutrient availability (+nitrogen/phosphorus (+N/P)) and arbuscular mycorrhizal fungi (+AMF) treatments.

Treatment	Nutrient treatment	N concentration (μM N l^{-1} soil)	P concentration (μM P l^{-1} soil)
Ctrl	N limitation	350	150
	P limitation	3500	15
+N/P	N limitation	700	150
	P limitation	3500	30
+AMF	N limitation	350	150
	P limitation	3500	15

Nutrient limitation is determined by the availability of N vs P; growth is limited by N at N concentrations of 350 and 700 μM N l^{-1} soil, and is limited by P at P concentrations of 15 and 30 μM P l^{-1} soil.

In monostands, the model generally showed a sensitivity of plant biomass that was at most proportional to the changes in the four tested parameters (i.e. an increase in a parameter leading to an equal increase or decrease in plant biomass; Fig. 3, monostands), as a result of the symmetry of competitive interactions between plants with the same trait values. In mixtures, the model generally showed a disproportionate sensitivity of plant biomass to the changes in the four tested parameters (Fig. 3, mixtures), as a result of the asymmetry of competitive interactions between plants with differing trait values. A few notable exceptions to these general observations were observed. First, the model showed a proportional sensitivity to changes in FSR under P limitation in mixtures (Fig. 3d, mixtures). Second, the model showed a disproportional sensitivity to changes in Dinit under P limitation in monostands (Fig. 3b, monostand Crtl). This can be attributed to a positive feedback loop between nutrient uptake and plant growth that is especially prevalent with the acquisition of P. This positive feedback loop was caused by the lack of nutrient influx during the season in combination with the small uptake radius of P, which led to the plants having to grow their root system continuously to take up more P. This feedback loop can also be seen in the model's sensitivity to changes in nutrient availability, where the model showed a disproportionally large positive response to an increase in nutrient availability that was particularly prevalent in P-limiting conditions and decreased with increased nutrient availability (Fig. S4).

The inclusion of AMF did not affect model sensitivity under N-limiting conditions in monostands, but it decreased model sensitivity to all tested parameters under P-limiting conditions in monostands (Fig. 3, monostand +AMF). In mixtures, the inclusion of AMF led to either no change or a small increase in model sensitivity (Fig. 3, mixture +AMF). The most notable effect of AMF was how they completely changed the way first-order roots affected plant biomass, going from a trait that positively affected plant biomass to a trait that negatively affected plant biomass (Fig. 3d, +AMF). The model showed a negative sensitivity to a change in the investment in AMF under N limitation, and a positive sensitivity under P limitation (Fig. S4). However, even in mixtures, the sensitivity of the model to an investment in AMF exerted a proportional effect under both N- and P-limiting

conditions (Fig. S4), contrasting the strong disproportional effects of other traits in mixtures.

Discussion

Root trait functionality in association with AMF

Here we show that Dinit and LMA are more important to plant performance than FSR and RLR. A decrease in Dinit led to a disproportional increase in plant biomass in mixtures, as the benefits of increased resource acquisition through increased SRL were not offset by the presence of negative feedbacks that would affect thinner roots in reality (e.g. shorter root life span, lower resistance against pathogens, etc.). Essentially, a decrease in Dinit in the model represents an increase in root proliferation rate at no extra cost (i.e. it increases SRL while total root biomass remains the same, leading to increased root length), making it a very beneficial trait from the perspective of nutrient acquisition. For much the same reasons that resulted in a negative sensitivity to changes in the Dinit, a decrease in LMA represents an increase in leaf area and subsequently in light foraging potential, whereas it does not incur costs in the form of a decreased light absorptance of the leaf or a decreased resistance against herbivores or pathogens. Moreover, the Dinit is more important under low-nutrient conditions, where nutrients are the most limiting resource, and the LMA is more important in high-nutrient conditions, where light is the most limiting resource. This also explains the reduction in model sensitivity to changes in RLR under increased nutrient conditions, which decreases nutrient limitation and therefore decreases the importance of producing roots compared with leaves. These results reflect the theory on functional equilibria (Poorter et al., 2012), showing that the impact of a trait on plant performance is dependent on the availability of the resource whose acquisition it affects.

We also show that mycorrhizal associations change the functionality of first-order roots under P limitation but not under N limitation. This difference between the role of first-order roots in N- and P-limiting conditions can be attributed to the way we assumed first-order roots contribute to the uptake of N and P. The first-order roots are assumed not to make an additional contribution to the N uptake of second-order roots, which is mass flow-limited and therefore the depletion zone around the roots is expected to extend well beyond the first-order roots. Conversely, the first-order roots are expected to contribute to P uptake, which is diffusion-limited and therefore the depletion zone around the roots is expected to extend just beyond the length of the root hairs. This advantage of first-order roots in P-limiting conditions disappeared in the presence of AMF, indicated by the negative model sensitivity (Fig. 3d, monostand +AMF). This can be attributed to the AMF being more efficient in taking up P than the first-order roots owing to the mycorrhizal hyphae having a smaller diameter and a lower C_{min} (Silveira & Cardoso, 2004; Freschet et al., 2021) than the first-order roots. The AMF and roots were equally efficient in taking up N, so the addition of AMF did not increase total N uptake of the plant as the roots were already able to deplete the soil of its N in the absence of

AMF. The first-order roots are thus beneficial to plant performance when the plant has to acquire P by itself, but they reduce plant performance when the plants can outsource P acquisition to AMF. Our model therefore supports a two-dimensional root economics space that includes mycorrhizal interactions (Bergmann *et al.*, 2020).

While our model simulated annual dicots, the mechanistic nature of the modelling approach allows us to generalize our conclusions and speculate on the relevance of the results for other plant functional groups. In tree species, AMF have been hypothesized to alter the functional relation of root traits along the acquisition–conservation axis (Weemstra *et al.*, 2016) as AMF associations correlate with root traits that have traditionally been linked to resource conservation strategies, such as a large root diameter, low SRL and long life (Brundrett, 2002; Bergmann *et al.*, 2020). Arbuscular mycorrhizal fungi may help trees to 'escape' from the classical conservation–acquisition axis by providing a more efficient alternative to roots in the acquisition of immobile nutrients (mainly P; Raven *et al.*, 2018). Our model provides evidence to support this hypothesis as the presence of AMF increased the uptake of P and changed the qualitative effect of the first-order root density on plant performance under P limitation from positive to negative. Conversely, graminoid species have been shown to fit a one-dimensional root economics space (Roumet *et al.*, 2016). Graminoids are characterized by the absence of secondary growth and therefore have thinner roots and a higher SRL than dicots. This suggests that graminoids can rely more on their own root system than on AMF for their nutrient acquisition, which is in line with large-scale experiments that reported lower AMF colonization in monocots vs dicots (Cornwell *et al.*, 2001; Weishampel & Bedford, 2006). This is consistent with our results that show plants benefiting from a thin root system in the absence of AMF, despite the fact that our model does not simulate the root architecture of a graminoid.

Root phenotypic plasticity

In contrast to our simulated plants, real plants react to temporal and spatial heterogeneity of nutrients in the soil with a myriad root physiological and morphological responses (Hodge, 2004). These responses integrate both local and systemic signals (Boer *et al.*, 2020) and are strong determinants of the plant's competitive ability under nutrient-limiting conditions (Fort *et al.*, 2014). Root architectural responses to maximize P acquisition include a highly branched root system (Niu *et al.*, 2013) and long root hairs (Bates & Lynch, 1996), while a sparsely branched root system is optimal for the acquisition of N (Lynch, 2013). Our results reflect these optimal phenotypes by showing that first-order roots benefit the plant under P-limiting conditions but decrease plant performance under N limitation. Plants can exhibit the root architectural phenotype that optimizes the acquisition of the most limiting nutrient in response to the soil nutrient conditions (Linkohr *et al.*, 2002). However, the extent to which plants show these plastic responses varies greatly between species (Kembel *et al.*, 2005; Mommer *et al.*, 2011), especially in

a competitive environment (Mommer *et al.*, 2012; Ravenek *et al.*, 2016). In the future, our model can be extended to simulate the phenotypic plasticity of root systems morphology to the availability of nutrients that differ in their mobility in the soil matrix (e.g. N and P), to capture the variation in these responses and their consequences for plant performance.

Size asymmetry in nutrient competition

Comparing monostands and mixtures shows that the competitive interactions simulated by the model were size-asymmetric. Asymmetric competition is the unequal division of resources between plants relative to their size, meaning that larger individuals take a disproportionate share of the available resources compared with their size and thereby suppress the growth of smaller individuals (Weiner, 1990). One of the requirements of size-asymmetric competition is for the resource to be 'pre-emptive' (Schwinning & Weiner, 1998), meaning that the acquisition of that resource by one individual denies the acquisition by another individual. Light is the prime example of such a 'pre-emptive' resource, leading to size asymmetry in competitive interactions between plants, which has been demonstrated in game-theoretical models (Falster & Westoby, 2003), individual based models (Dybzinski *et al.*, 2011; de Vries *et al.*, 2019), and in experiments (Ejrnæs *et al.*, 2006). In addition to light, N was another 'pre-emptive' resource in our model as it was quickly depleted from the soil, leading to strong size-asymmetric competition under N-limiting conditions. Conversely, P was not so easily depleted from the soil and therefore did not show this competitive size asymmetry. P limitation did lead to a high model sensitivity to changes in the Dinit in both monostands and mixtures, which indicates that this sensitivity is directly caused by a positive feedback loop between root system growth and P uptake rather than being an indirect effect of competition. Competition for belowground resources is generally considered more size-symmetric than competition for light (Schwinning & Weiner, 1998; Cahill & Casper, 2000). However, size asymmetry in belowground competition has been predicted in other modelling studies (Gersani *et al.*, 2001; O'Brien *et al.*, 2005) and size-related root traits allowed competitive suppression of neighbouring plants in an experimental grassland (Semchenko *et al.*, 2018). Our results suggest that nutrient availability and mobility play an important role in determining symmetry of competitive interactions for the nutrient in question.

Limitations and further perspectives

This modelling approach takes a step towards mechanistic integration of AMF in FSP models, but still lacks several mechanisms that play an important role in plant–plant–AMF interactions. First, our model simulates AMF as an extension of the root system, rather than as individual organisms with their own fitness that actively mediate the C/N/P exchange with their plant hosts. Our model treats roots and AMF additively; that is, that there is no effect of AMF on root biomass. However, studies have suggested that mycorrhizal plants generally have a lower root : shoot mass ratio than nonmycorrhizal plants (Zhang *et al.*, 2011;

Veresoglou *et al.*, 2012). While the model posits a lower C_{min} for P uptake for AMF than for roots, it has the same C_{min} values for N uptake for both structures. However, a smaller C_{min} for N uptake for AMF could explain why most plants with thin roots still maintain the mycorrhizal symbiosis, as in mixed stands they could otherwise be outcompeted by mycorrhizal plants (Kuyper & Kiers, 2014). We also modelled plants and AMF having similar nutrient requirements, but this could be modified in a further extension of our model that could, for instance, assign AMF biomass a higher N concentration than roots. Under conditions of (strong) N limitation, mycorrhizal plants could then perform more poorly than nonmycorrhizal plants, as has been shown for several grasses (Püschel *et al.*, 2016). Furthermore, plants are typically colonized by several AMF species, which are in turn connected to several individual plants of potentially different species in common mycorrhizal networks (Newman, 1988; Smith & Read, 2010). This has led to a debate on the mechanisms of C/N/P exchange between these different partners and their role in maintaining the mutualistic relationship between plants and AMF (Johnson *et al.*, 1997, 2015; Kiers & Van der Heijden, 2006; Bever *et al.*, 2009; Corrêa *et al.*, 2014, 2015; Werner *et al.*, 2018). This complexity of the C/N/P exchange between plants and AMF has also made it difficult to generalize the role of AMF in mediating the outcome of competitive interactions between plants of the same or different species. Some studies show that shared mycorrhizal networks have little effect on the competitive interactions between plants (Stanescu & Maherali, 2017b; Milkereit *et al.*, 2018), while other studies show that shared mycorrhizal networks intensify intraspecific competition and alleviate interspecific competition (Moora & Zobel, 1996; Walder *et al.*, 2012; Stanescu & Maherali, 2017a; Weremijewicz *et al.*, 2018). Second, our model simplifies soil processes that can have profound effects on AMF functioning, nutrient stoichiometry and competitive interactions between plants, such as soil water status (Augé, 2001; Al-Karaki *et al.*, 2004) and mineralization of nutrients (Aerts, 2003). Third, our model does not include the plastic responses that allow plants to navigate this complex web of interactions with the soil, AMF and competing plants to optimize their C/N/P acquisition. Future developments might see the use of mechanistic FSP models to shed light on the mechanisms that drive these complex three-way interactions among plants, AMF and the soil environment.

Concluding remarks

Our work is a first step towards a whole-plant FSP modelling approach that provides opportunities to explore belowground plant–plant and plant–microbe interactions in a way that was not possible before, either experimentally or with previous (modelling) approaches. We included plant–mycorrhizal fungus interaction into a mechanistic modelling framework that aims to simulate how multidimensional plants interact with multidimensional environments that include both abiotic conditions and biotic interactions to shape plant fitness. Our modelling results support the notion that the collaboration of plants with AMF provides an alternative strategy to a highly branched root system

for the uptake of low-mobility (e.g. P) but not high-mobility (e.g. N) nutrients. This provides further support for a functional root economics space that accommodates the interactive effect of roots and mycorrhizal fungi, as proposed by Bergmann *et al.* (2020). Future developments should see validation of the model on experimental data that covers a range of species that adopt different strategies in the root economics space. This is needed to further elucidate the dynamics of plant–plant and plant–soil interactions, and to advance our understanding of the role of mycorrhizal fungi in extending root trait variation and the functioning of root traits.

Author contributions

JdV, JBE and LM conceived the idea for this project. JdV, JBE, JvR, TWK and LM designed the model outline. JdV coded the model and conducted the simulations with input from JBE. All authors were involved in data interpretation of model outcomes in the different scenarios. JdV wrote the first draft of the manuscript. All authors commented on and agreed with the final version of the manuscript. There are no conflicts of interest to declare.

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Data availability

The model code and data generated by the model are publicly available at http://dx.doi.org/10.17632/rfs4drbzn8.1.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Schematic representation of the two-dimensional root economics space framework.

Fig. S2 Model sensitivity of the SRL.

Fig. S3 Model sensitivity of the root : shoot ratio.

Fig. S4 Model sensitivity of the nutrient availability and the investment in AMF.

Methods S1 A detailed description of the FSP model used in this study.

Table S1 A list of indices used in the model description.

Table S2 A list of model parameters, their values and units.

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