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Research Article

Modeling root loss reveals impacts on nutrient uptake and crop development

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Abstract

Despite the widespread prevalence of root loss in plants, its effects on crop productivity are not fully understood. While root loss reduces the capacity of plants to take up water and nutrients from the soil, it may provide benefits by decreasing the resources required to maintain the root system. Here, we simulated a range of root phenotypes in different soils and root loss scenarios for barley (Hordeum vulgare), common bean (Phaseolus vulgaris), and maize (Zea mays) using and extending the open-source, functional–structural root/soil simulation model *OpenSimRoot*. The model enabled us to quantify the impact of root loss on shoot dry weight in these scenarios and identify in which scenarios root loss is beneficial, detrimental, or has no effect. The simulations showed that root loss is detrimental for phosphorus uptake in all tested scenarios, whereas nitrogen uptake was relatively insensitive to root loss unless main root axes were lost. Loss of axial roots reduced shoot dry weight for all phenotypes in all species and soils, whereas lateral root loss had a smaller impact. In barley and maize plants with high lateral branching density that were not phosphorus-stressed, loss of lateral roots increased shoot dry weight. The fact that shoot dry weight increased due to root loss in these scenarios indicates that plants overproduce roots for some environments, such as those found in high-input agriculture. We conclude that a better understanding of the effects of root loss on plant development is an essential part of optimizing root system phenotypes for maximizing yield.

Introduction

Roots are vital plant organs that forage for nutrients and water, provide anchorage, and provide storage in some species. Because of soil degradation, adverse effects of global climate change and inadequate use of soil fertility inputs crops in many locations face challenges accessing adequate nutrients. Added to this, plants are in constant competition for the resources that are available, both below and above ground, and are constantly under threat from herbivory, root rots, disease and nutrient deficiency, as well as environmental stresses such as heat, cold, and drought. Their root systems are not exempt from these threats and root loss is prevalent in many species. A meta-analysis of 85 studies into the effects of 36 species of

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root-feeding insect herbivores on 75 plant species found that belowground herbivory led to an average reduction in root dry weight of 36.3% (Zvereva and Kozlov, 2012). Understanding root growth and functioning under such adverse conditions is vital for understanding a fundamental dimension of plant fitness, and has agricultural relevance in guiding the development of the more resilient, sustainable crops urgently needed in global agriculture (Lynch, 2019). Understanding the effects of root loss in this context is important because root phenotypes that are associated with high yields in controlled or high-input environments with minimal root loss might perform poorly in conditions where root loss is prevalent.

There is evidence root loss is not programmed, in contrast to leaves (Fisher et al., 2002). Root length does generally decrease during and after flowering, this could be because plants reduce investment in new roots during this stage of their development (Eissenstat and Yanai, 1997). Several external factors affect the prevalence of root loss. Drought increases root turnover and topsoil drying leads to rapid root dieback (Hayes and Seastedt, 1987). Although reducing soil temperature appears to have no clear effect on root longevity of quaking aspen (*Populus tremuloides*; King et al., 1999), increasing soil temperature has been found to increase root mortality in grasses (Forbes et al., 1997), white clover (*Trifolium repens*; Watson et al., 2000), and sugar maple (*Acer saccharum*; Hendrick and Pregitzer, 1993). The mean annual temperature was the most important variable explaining fine-root turnover in the global data set on root turnover of Gill and Jackson (2000), and it suggests a mean annual temperature increase of 10°C would lead to a 40%–90% decrease in root lifespan. There are many variables that vary with temperature and this makes it difficult to ascertain if the effect on root longevity is a direct consequence of temperature or something else such as pathogen activity or soil quality. It should also be noted that some studies found increasing temperature had no clear effect (Steele et al., 1997; Fitter et al., 1999). Similarly, the availability of soil nutrients appears to influence root lifespan but there are conflicting results. Some studies found that high nutrient availability coincides with short root lifespan (Pregitzer et al., 1995, 2000; Majdi and Kangas, 1997; Steingrobe et al., 2001), while others found the opposite (Alexander and Fairley, 1983; Pregitzer et al., 1993; Burton et al., 2000). Mycorrhizal associations seem to protect roots from a variety of factors, enhancing their longevity (Gange et al., 1994; Newsham et al., 1995; Espeleta et al., 1999). There are many organisms in the soil, some of which feed on roots (Weste, 1986), explaining why applying pesticides increases root lifespan considerably (Wells, 1999). Hence root longevity depends on the plant, herbivores, and pathogens.

Root loss, for whatever reason, means that any resources in the roots are lost and decreases the capacity of the root system to take up nutrients and water from the soil. This generally results in lower plant nutrient content, though compensatory growth can actually increase plant nutrient content (Kahler et al., 1985). Infestation by rootworm (*Diabrotica virgifera*) increases the prevalence of lodging in maize (*Zea mays*; Sutter et al., 1990). Root loss due to disease or pest infestation is associated with a reduction of yield in many species (Chiang et al., 1980; Kahler et al., 1985; Gorfu, 1993; Oyarzun, 1993; Urías-López and Meinke, 2001; Naseri, 2008; Al-Abdalall, 2010).

In some cases, root loss may have benefits for plant growth. The amount of resources invested in the production and maintenance of root systems is considerable, as evidenced by the fact that the dry weight of root systems can be larger than the dry weight of the shoots (Chapin et al., 1989; Fredeen et al., 1989; Levy et al., 2004). Under unstressed conditions, more than a fifth of all the carbohydrates produced by photosynthesis can be spent on root respiration (Poorter et al., 1990; Atkin et al., 1996); under phosphorus stress this can increase to >40% (Nielsen et al., 2001; Lynch and Ho, 2005), while >15% of the carbohydrates can be spent on root exudates (Hobbie and Hobbie, 2006). Roots that are lost do not have to be maintained and it is in this way that root loss can lead to a large reduction in resource expenditure. What further illustrates this is that the carbon cost of respiration necessary to maintain a root can exceed the carbon cost of growing the root in as little as 20 days (Eissenstat and Yanai, 1997). Thus, it is reasonable to suggest that root loss may be beneficial in some situations, because the soil surrounding older roots may be depleted of diffusion-limited resources like phosphorus and potassium. Low soil phosphorus concentrations were observed to lead to increased root turnover (Steingrobe et al., 2001). A previous root-system model predicted that root turnover increases the explored soil volume and therefore phosphorus and potassium uptake, although this model did not assign any cost to root turnover (Steingrobe, 2001, 2005; Steingrobe et al., 2001). Since nitrogen leaches down into the soil, it has been suggested that parsimonious root phenotypes, such as root systems subjected to moderate to high rates of root loss, are deeper and thus beneficial in conditions of suboptimal nitrogen availability (Lynch, 2013, 2019).

Root systems can differ greatly among plant species. Dicot root systems start from a primary root which develops into a taproot after which the root system grows through lateral root formation, and in some cases basal roots as in common bean (*Phaseolus vulgaris*). In contrast, monocots lack secondary growth and continually produce nodal roots of increasing diameter from shoot tissue. Many grass species, including principal cereal crops like wheat (*Triticum aestivum*), rice (*Oryza sativa*), and barley (*Hordeum vulgare*), form tillers, which grow root systems themselves in turn. As a result of crop breeding, modern maize lines rarely tiller. There are also interspecific and intraspecific differences in lateral branching rates, the number of lateral root orders and the number of adventitious roots that plants grow. It has been hypothesized that these differences in root architectural phenotypes, and the resulting differences in root system topology, lead to differences in susceptibility to root loss among species and phenotypes (Lynch, 2005).

One of the reasons why experimental research on root loss is limited in the literature is that it is difficult to study in the field. Studying roots in their natural environment is much harder than studying shoots, due to the difficulty of visualizing roots in situ within the soil, and studying dynamic processes such as root loss is particularly challenging. Invasive methods such as rhizotrons alter the local soil environment and allow one to study only a small part of the root system. To detect root loss, one needs to identify roots across multiple images. But it can also be difficult to determine if a given root has been lost or not, since roots and soil might shift around and determining the status of a root from visual inspection alone can prove difficult. Soil coring or excavating root systems only provide snapshots of root system development and even if recently deceased roots can be identified it is difficult to determine overall root loss rates. In addition to the difficulty of observing roots in soil over time, in the context of root loss, the presence and activity of soil biota, primarily root herbivores and pathogens, is critically important. It is challenging to impose realistic biotic stress in controlled environments, and in the field biotic stress is generally variable in time and space.

The substantial challenges associated with experimental studies of root loss make modeling useful. Not only does modeling permit precise control over root loss rates of specific root classes, which is all but impossible in field conditions, but it also allows access to information that would be very hard to obtain in field experiments, such as root development over time, nutrient uptake rates as well as the complete structure of the root system. Simulations also allow us to study a much larger array of phenotypes and environmental scenarios than would be possible in field experiments, without any factors such as the weather being out of our control. Currently, a number of different root system architecture models exist that simulate root growth and function (Diggle, 1988; Pagès et al., 2004; Wu et al., 2007; Javaux et al., 2008; Leitner et al., 2010; Dunbabin et al., 2013; Postma et al., 2017). We have used *OpenSimRoot* (Postma et al., 2017), the open-source successor of *SimRoot* (Lynch et al., 1997; Lynch and Postma, 2009), because it allows us to simulate resource acquisition and allocation as well as the effects of shortages. This makes it an ideal simulation model to study the impact of root loss. *(Open)SimRoot* has been used to simulate barley, bean, lupin (*Lupinus albus*), maize, rice, and squash (*Cucurbita pepo*) in a variety of settings (Ge et al., 2000; Walk et al., 2006; Postma and Lynch, 2011, 2012; Chen et al., 2011; Postma et al., 2014; Schneider et al., 2017; Rangarajan et al., 2018; Strock et al., 2018; Ajmera et al., 2022). *OpenSimRoot* simulates the geometry, growth, and nutrient uptake of root systems, as well as water and nutrient flows in the soil (Lynch et al., 1997; Postma et al., 2017). Because *OpenSimRoot* simulates the development of root systems through the application of growth and branching rules for each root class, it can simulate a wide variety of different root architectures. Additional functionality can be added with relative ease because of the modular structure (Schäfer et al., 2022). While there are some dependencies between modules, users are free to choose which modules are included in the simulation.

With this study, we extend functional–structural plant models by adding a root loss module to *OpenSimRoot*. We present results from root system simulations of common bean (a dicot), barley (a tillering grass), and maize (a nontillering grass) subjected to various levels and types of root loss in different soil environments in order to study the effects of root loss on plant productivity in contrasting taxa, root phenotypes, and different environments.

Results

Root length

Total root length decreased for most soils and phenotypes under all types of root loss for all three species, with axial and general root loss associated with larger declines (Figure 1). In bean and maize, root loss led to an increase in root length for certain combinations of soil and phenotype. For barley, there was a positive relationship between tiller number and lateral branching density and total root length in most conditions. For bean and maize this was true, in many cases plants with low axial root number or low lateral branching density had greater root length than those with high axial root number or high lateral branching density. For plants subjected to lateral root loss, the amount of root length lost increased with increasing root loss intensity (Figure 2). When plants were subjected to axial or general (axial + lateral) root loss, we saw a similar pattern, but in several cases the amount of root length lost peaked at the medium root loss intensity. The phenotypes that had the greatest root length generally also had the greatest amount of lost root length.

Shoot dry weight

The effect of root loss on shoot dry weight depended on species, soil nitrogen and phosphorus availability, root loss type and, to a lesser extent, phenotype (Figure 3). Axial and general root loss led to larger reductions in simulated shoot dry weight than lateral root loss. On average, plants that lost 1% of their lateral roots every day, had their shoot dry weight reduced by 3%. Under the highest level of lateral root loss considered (5% loss per day), shoot dry weight was reduced by 16% (barley), 17% (bean), and 13% (maize) on average and the change in simulated shoot dry weight varied from a 17% increase to a 36% decrease (barley), 0% to 34% decrease (bean), and a 13% increase to a 39% decrease (maize). Under the highest level of axial and general root loss considered shoot dry weight was reduced by 58% (barley), 42% (bean), and 50% (maize) on average and the reduction in shoot dry weight varied from 19% to 86% (barley), 17% to 66% (bean), and 15% to 77% (maize) as compared to an environment without root loss. Root loss was more detrimental for plants of all three species in low phosphorus soils than in low nitrogen soils. For barley and maize, phenotypes with high lateral branching densities

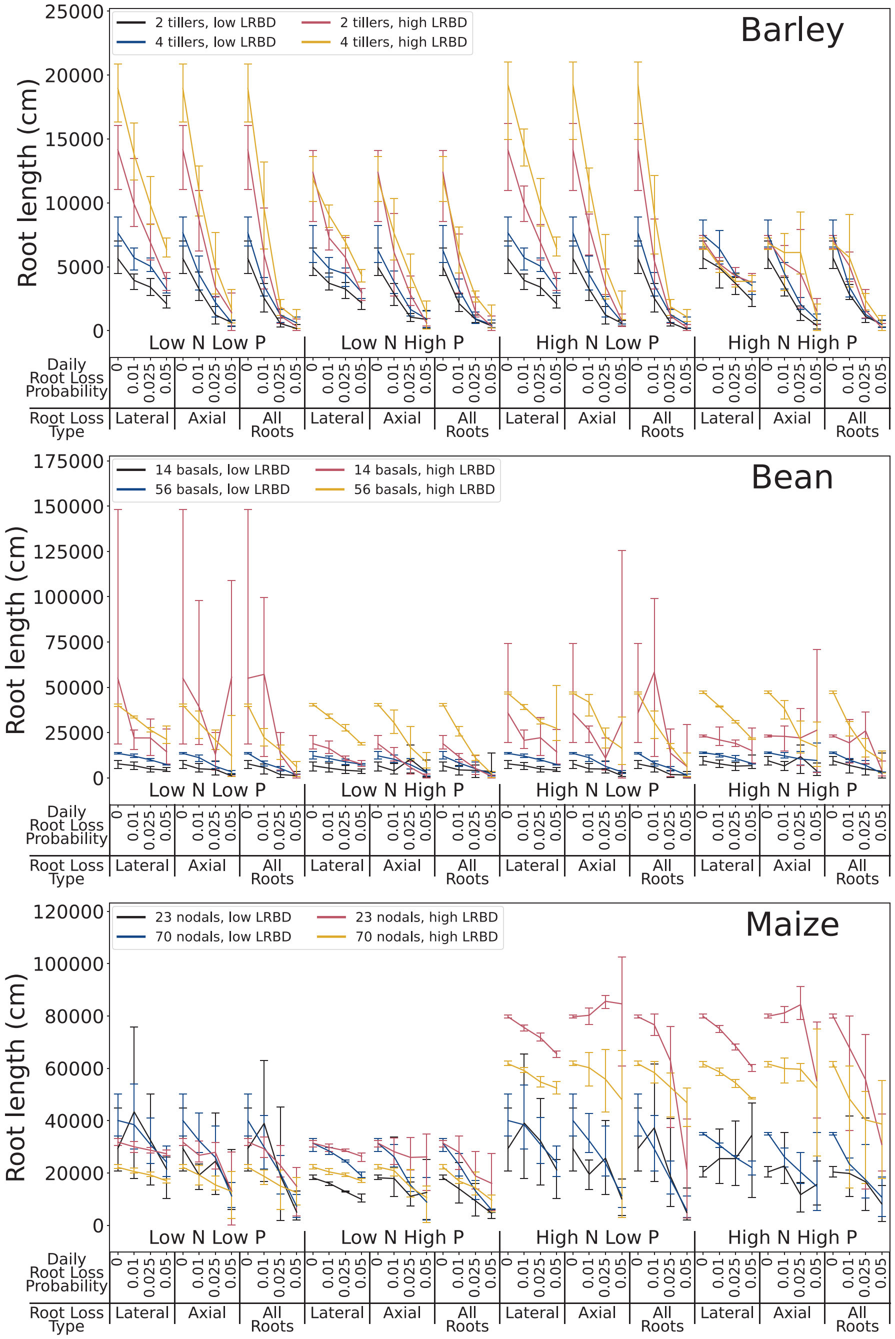

Figure 1 Mean root lengths at 80, 40, and 40 days, respectively, for barley, bean, and maize phenotypes. The bars indicate minimum and maximum values. Each panel is divided into four sections, one for each of the four different soils we considered. For every soil, we show the results for the three different types of root loss at four different intensities (which includes the case without any root loss). The legend in the top left shows which color corresponds to which phenotype. LRBD, lateral root branching density; N, nitrogen; P, phosphorus.

appeared more resistant to lateral root loss and saw an increase in shoot dry weight due to root loss in several soils.

For most combinations of species and soil there was a positive association between root dry weight and shoot dry weight (Figure 4). For barley and maize plants grown in a low nitrogen, high phosphorus soil and subjected to lateral root loss there was a slightly negative association between root dry weight and shoot dry weight. Maize plants grown in the high nitrogen, low phosphorus soil and subjected to lateral root loss also showed a negative association and for maize plants grown in the high nitrogen, high phosphorus soil subjected to lateral root loss the relationship between root and shoot dry weight was not clear. Bean plants showed a very clear positive association between root and shoot dry weight in all conditions. Relative shoot dry weight is negatively associated with the fraction of root length lost (Figure 5). Especially for axial and general root loss larger root loss fractions were associated with a larger decrease in shoot dry weight. Root loss was

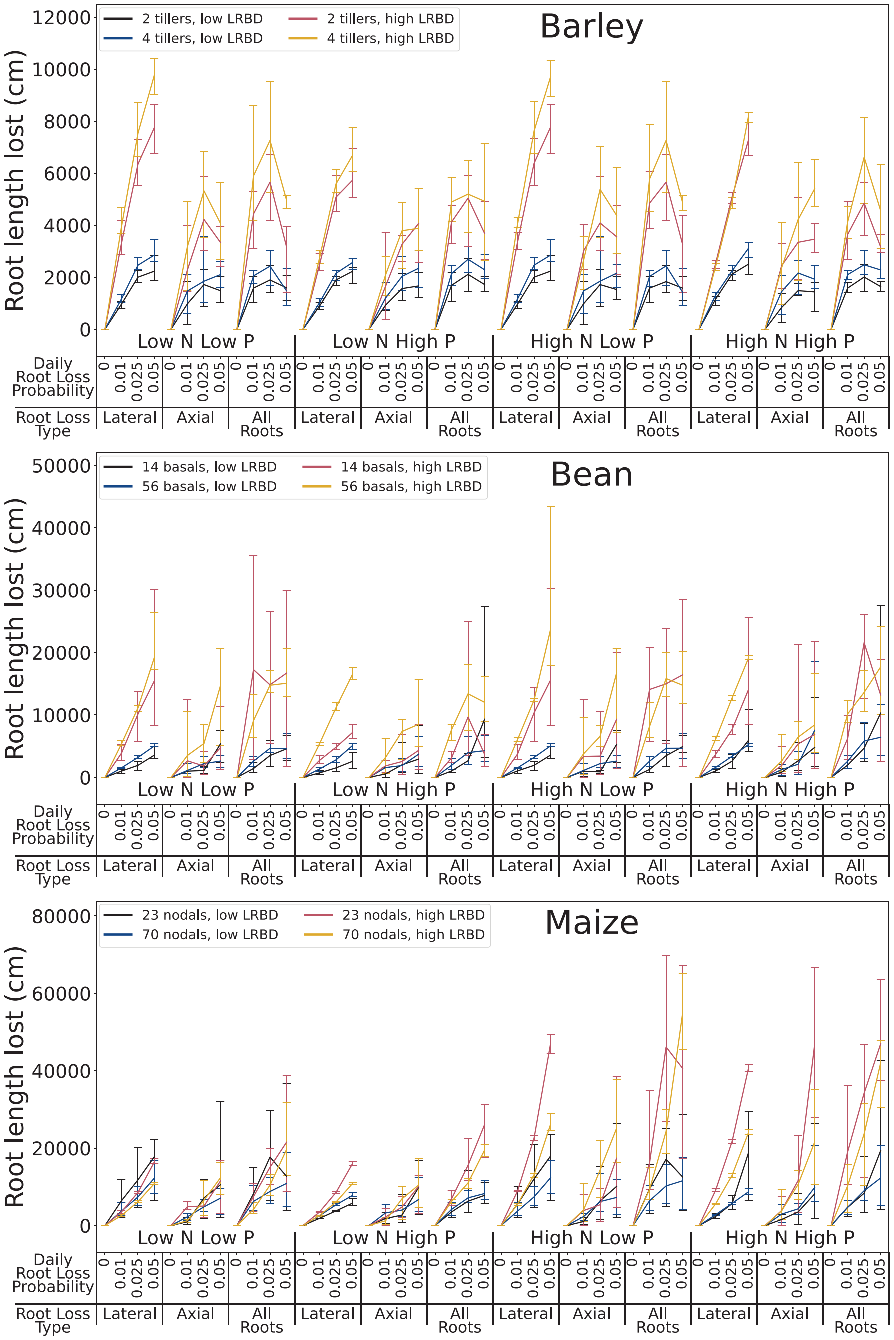

Figure 2 Mean root length lost at 80, 40, and 40 days, respectively, for barley, bean, and maize phenotypes. The bars indicate minimum and maximum values. Each panel is divided into four sections, one for each of the four different soils we considered. For every soil, we show the results for the three different types of root loss at four different intensities (which includes the case without any root loss). The legend in the top left shows which color corresponds to which phenotype. LRBD, lateral root branching density; N, nitrogen; P, phosphorus.

associated with greater shoot dry weight in several scenarios, especially in maize and barley plants subjected to lateral root loss.

Applying root loss to maize root systems led to distinct visual differences in their root systems at 40 days (Figure 6). Aggregate measures such as total root dry weight and shoot dry weight also showed large differences. The variance in root dry weight increased strongly due to root loss but at low levels of root loss, mean root dry weight at day 40 decreased only by a small amount. For the greatest intensity of root loss, mean root dry weight initially kept pace until declining around day 34. Shoot dry weight was reduced by root loss to 8.8 g, as compared to the plants grown without root loss, which had an average shoot dry weight of 23.8 g. Again, we observed an increase in variance with greater root loss, as with root dry weight.

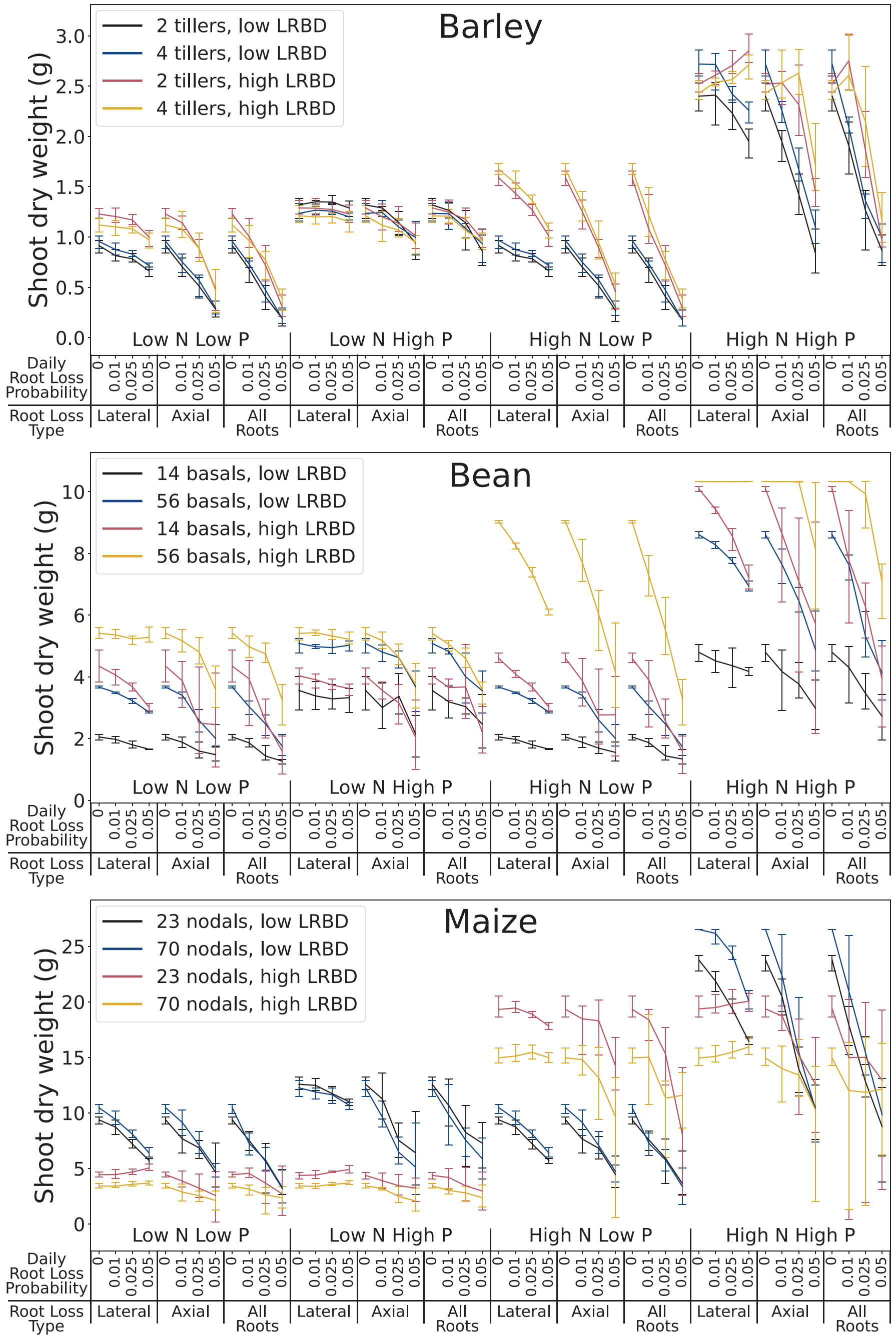

Figure 3 Mean shoot dry weights at 80, 40, and 40 days, respectively, for barley, bean, and maize phenotypes. The bars indicate minimum and maximum values. Each panel is divided into four sections, one for each of the four different soils we considered. For every soil, we show the results for the three different types of root loss at four different intensities (which includes the case without any root loss). The legend in the top left shows which color corresponds to which phenotype. LRBD, lateral root branching density; N, nitrogen; P, phosphorus.

Nutrient uptake

The greatest intensity of lateral root loss considered, on average reduced nitrogen uptake by 3% (barley), 4% (bean), and increased nitrogen uptake by 7% for maize, across all nutrient scenarios (Figure 7). In barley and maize, high branching phenotypes saw an increase in nitrogen uptake in soils with high nitrogen concentrations. At the highest intensity of root loss, axial and general root loss reduced nitrogen uptake by 25%–40% on average, though there are some cases where nitrogen uptake increased. For barley and bean, the reduction was as high as 60% in some cases, for maize this increased to 70%. In bean and maize, the greatest mean nitrogen uptake was attained in the high nitrogen, low phosphorus soil by plants affected by root loss.

Phosphorus uptake was reduced much more strongly by root loss than nitrogen uptake was, with average reductions

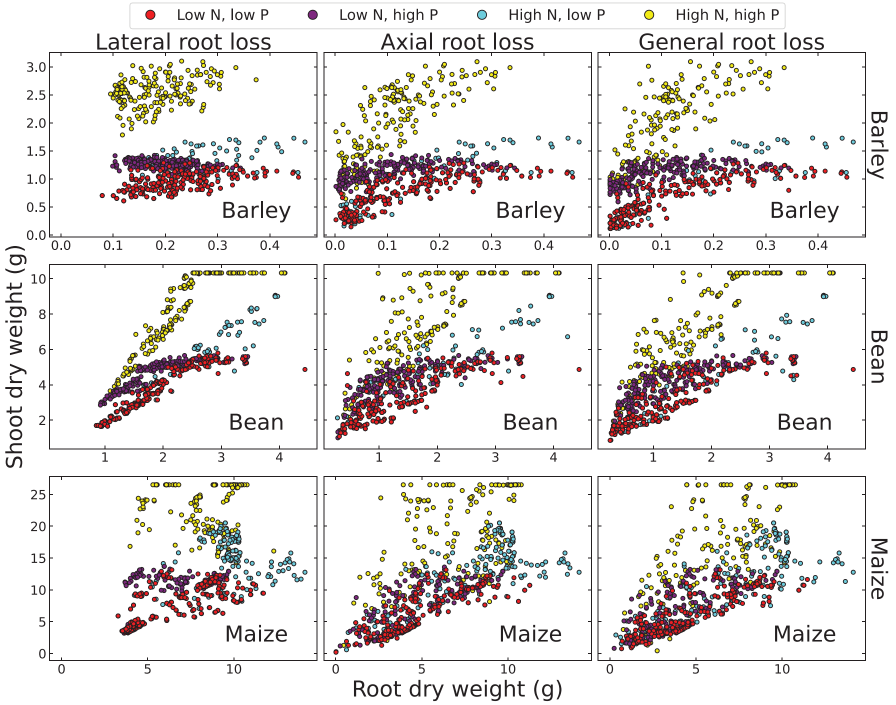

Figure 4 Root dry weight versus shoot dry weight of plants simulated using *OpenSimRoot*. Each row displays results for a different species, from top to bottom these are barley, bean, and maize. Each column displays results of plants subjected to a different kind of root loss, from left to right these are lateral, axial, and general root loss. Colors indicate soil nutrient concentrations. N, nitrogen; P, phosphorus.

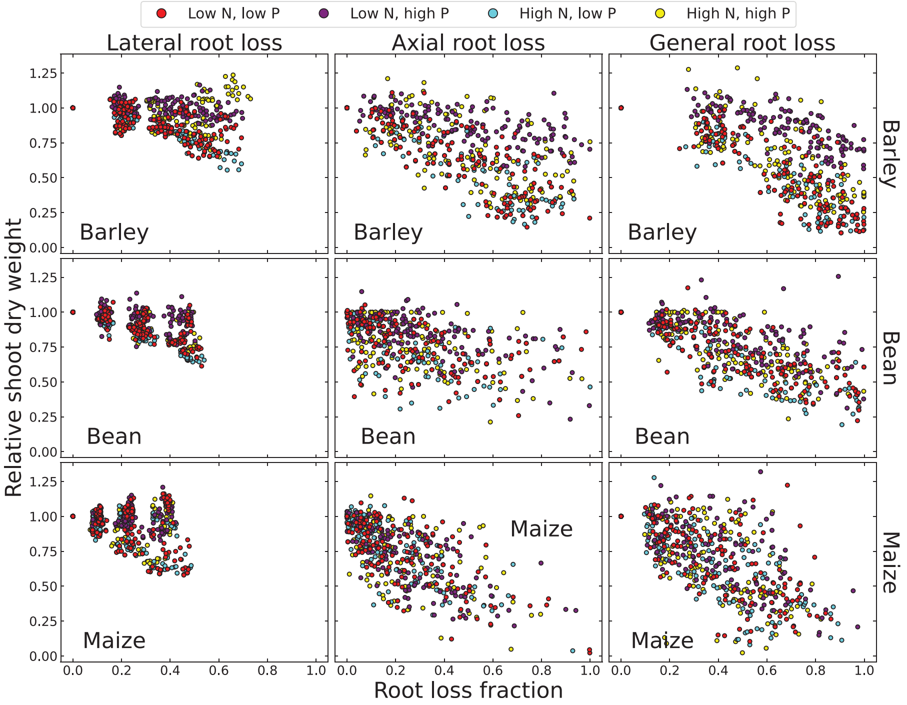

Figure 5 Root loss fraction, the root length lost as a fraction of total root length, versus relative shoot dry weight, the shoot dry weight as compared to the reference case without root loss. Each row displays results for a different species, from top to bottom these are barley, bean, and maize. Each column displays results of plants subjected to a different kind of root loss, from left to right these are lateral, axial, and general root loss. Colors indicate soil nutrient concentrations. N, nitrogen; P, phosphorus.

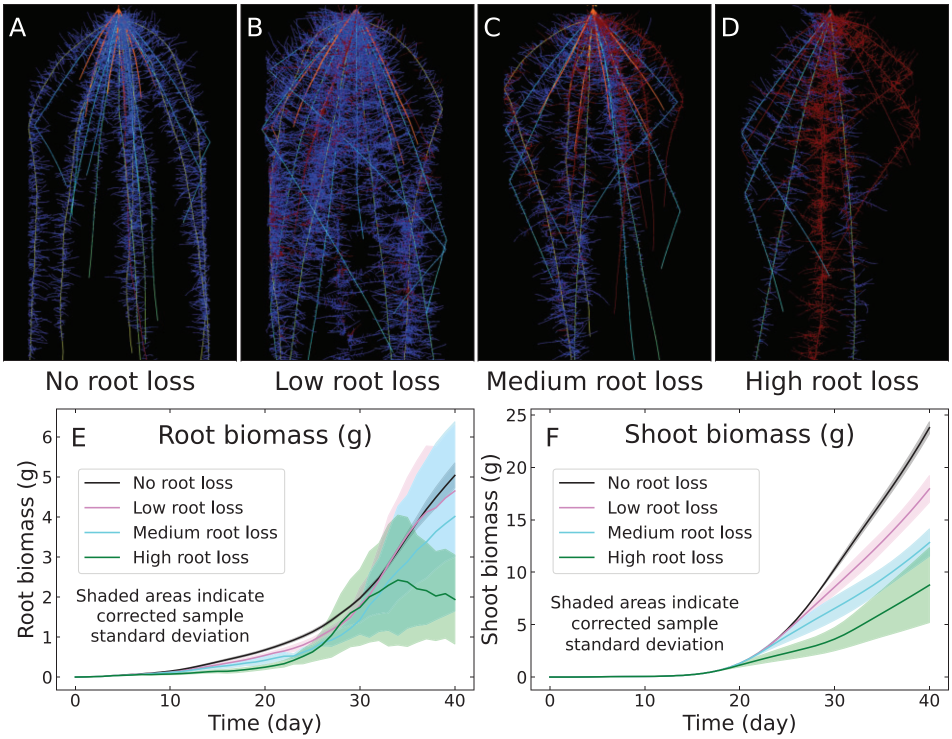

Figure 6 The effect of different levels of root loss on maize root systems with the same axial root number and lateral root branching density. A, A maize root system after 40 days in the high nitrogen, low phosphorus soil, without any root loss. (B–D) show similar root systems but grown under general root loss at low, medium, and high intensity, respectively. The different colors indicate different root classes and red roots have been lost. E, The mean root dry weights over time of five repetitions of the maize simulations displayed in (A–D) with the shaded areas indicating corrected sample standard deviation. F, The mean shoot dry weights over time of five repetitions of the maize simulations displayed in (A–D) with the shaded areas indicating corrected sample standard deviation.

of 30% (barley), 31% (bean), and 20% (maize) when subjected to the greatest intensity of lateral root loss (Figure 8). Axial and general root loss led to reductions in phosphorus uptake of up to 70%.

We define nutrient uptake efficiency as micromole nutrient taken up from the soil per square centimeter of root surface per day. Nitrogen uptake efficiency increased for all phenotypes of all three species in every soil under every type of root loss compared with no root loss (Figure 9). In barley, nitrogen uptake efficiency increased much more under axial or general root loss than under lateral root loss, while in bean and maize the increases were similar for each type of root loss. The effect of root loss on phosphorus uptake efficiency depended on species, phenotype, and soil phosphorus content (Figure 10). In barley and maize, phosphorus uptake efficiency increased under axial and general root loss, while the picture was more mixed in bean, with many phenotypes showing no improvement. In barley, the phosphorus uptake efficiencies of many phenotypes were not affected by lateral root loss. In bean, lateral root loss reduced phosphorus uptake efficiency for all phenotypes and soil conditions. In maize, the high branching phenotypes increased uptake efficiency under lateral root loss in many conditions while the other phenotypes showed small decreases or no effect.

Discussion

We have cast a wide net with this simulation study, covering both a mobile (nitrogen) and immobile (phosphorus) nutrient, monocot (barley and maize) and dicot (bean) species, tillering (barley) and non-tillering (bean and maize) species, different types of root loss and root system traits we deemed relevant. Our simulations showed that the effect of root loss on plant development depends on environment, root loss type, and the root system architecture. Root loss was much more detrimental for plants that were subjected to phosphorus stress than plants that were subjected to nitrogen stress. Axial root loss was much more detrimental to plant development than lateral root loss. Root phenotypes with many lateral roots were somewhat buffered against root loss but were generally not the optimal phenotypes for shoot dry weight. There was a clear relationship between the fraction of total root length that was lost and the associated reduction in shoot dry weight and the final root and shoot dry weights were strongly associated. Somewhat surprisingly, in many scenarios, root loss led to an increase in shoot dry weight.

Root loss and stochasticity

OpenSimRoot simulations contain stochasticity. The angles at which laterals emerge, variations in root growth direction

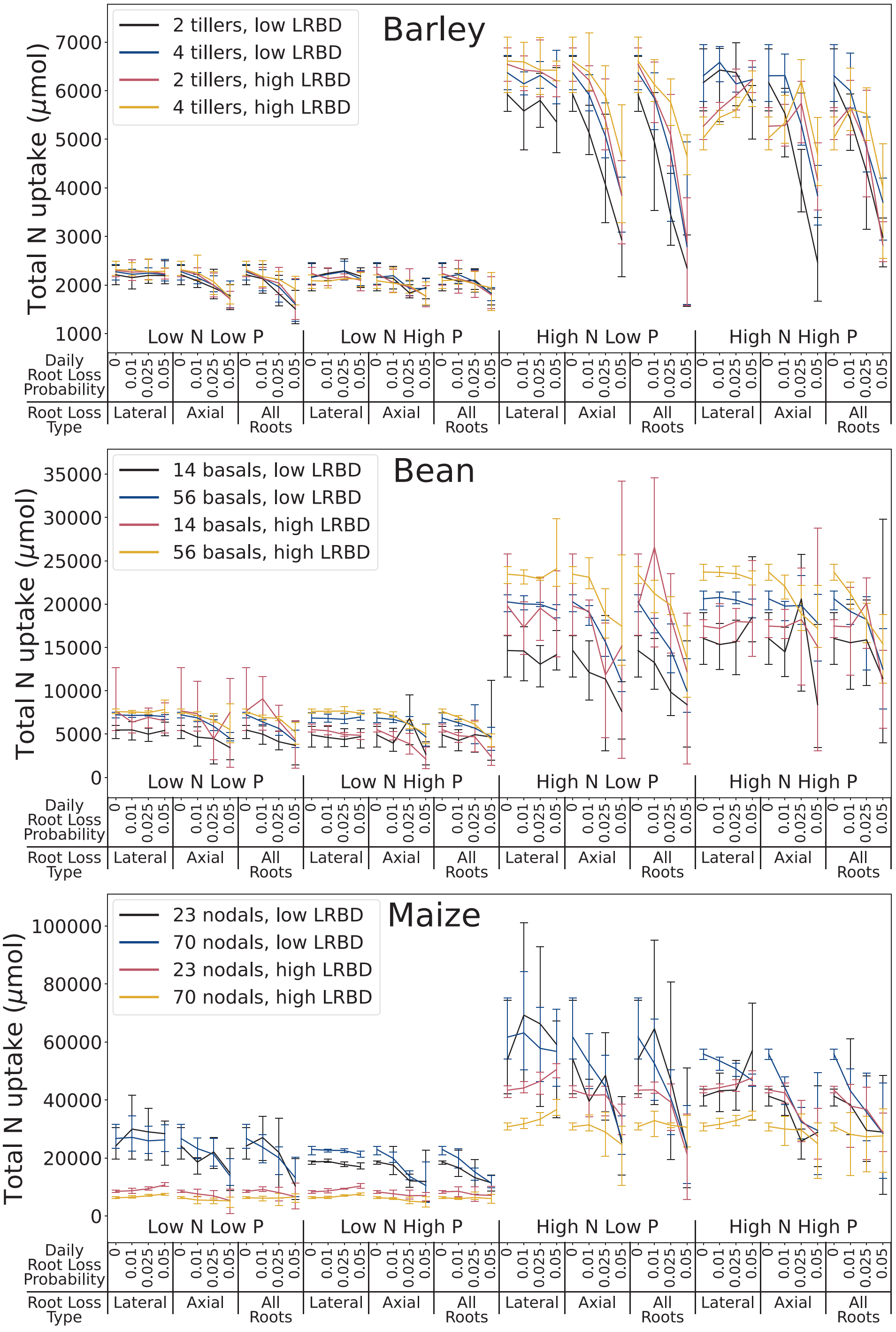

Figure 7 Mean nitrogen uptake at 80, 40, and 40 days, respectively, for barley, bean, and maize phenotypes. The bars indicate minimum and maximum values. Each panel is divided into four sections, one for each of the four different soils we considered. For every soil, we show the results for the three different types of root loss at four different intensities (which includes the case without any root loss). The legend in the top left shows which color corresponds to which phenotype. LRBD, lateral root branching density; N, nitrogen; P, phosphorus.

and root elongation rate are all pseudorandom processes. One can see the effects of these sources of random variation on output variables by looking at the cases without root loss in Figures 1–3 and 8–10. With the introduction of randomized root loss we have introduced another source of random variation. As can be observed from the same figures, the randomized root loss increases the variation in output variables in most cases, especially when it involves the loss of axial roots. One reason for the greater variation under axial root loss is that while on average, a constant percentage of roots is lost per day, this can vary at different times. The variation in the daily rate of root loss will be smaller if the

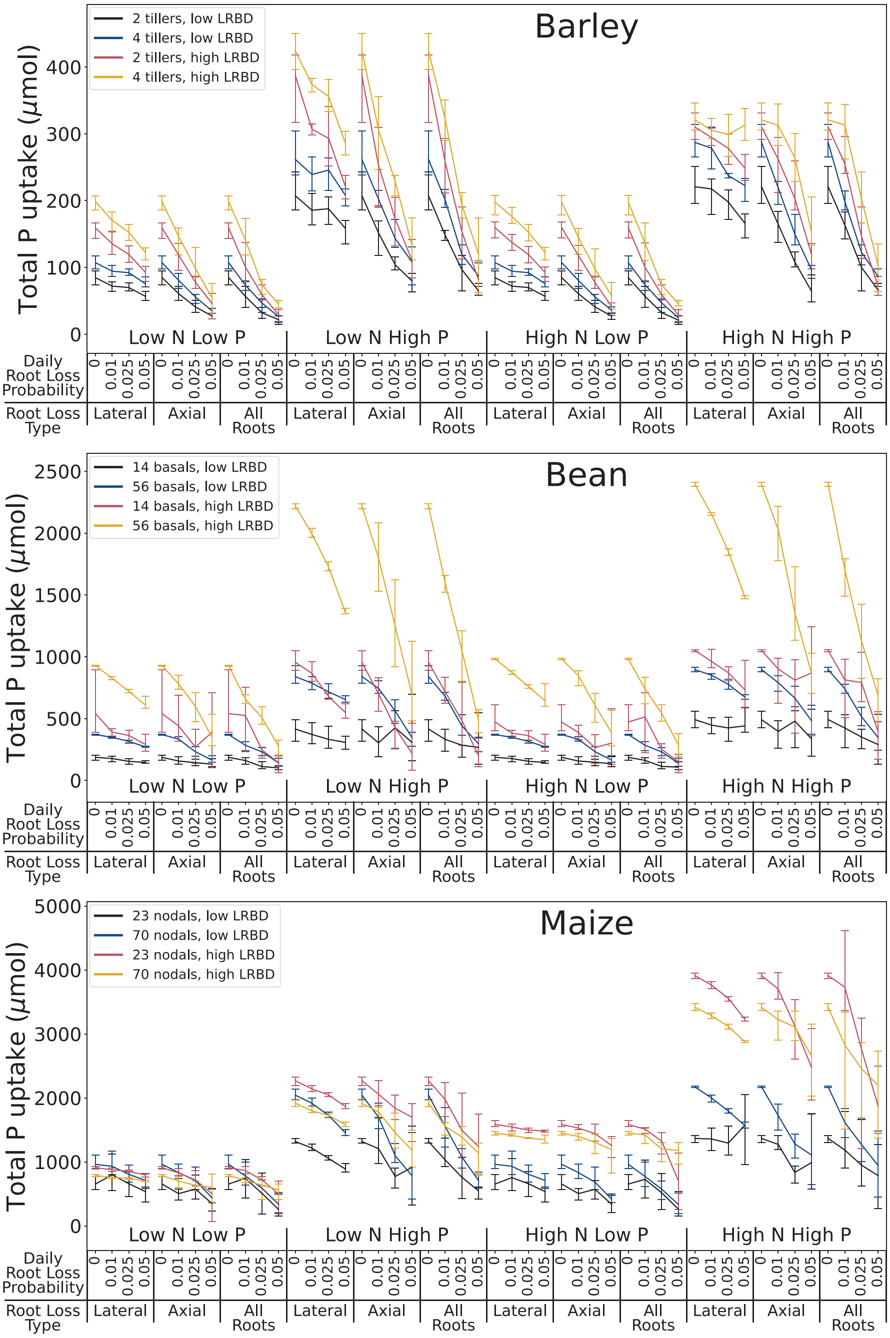

Figure 8 Mean phosphorus uptake at 80, 40, and 40 days, respectively, for barley, bean, and maize phenotypes. The bars indicate minimum and maximum values. Each panel is divided into four sections, one for each of the four different soils we considered. For every soil, we show the results for the three different types of root loss at four different intensities (which includes the case without any root loss). The legend in the top left shows which color corresponds to which phenotype. LRBD, lateral root branching density; N, nitrogen; P, phosphorus.

number of roots affected by the relevant type of root loss is larger (just as how you are more likely to get 4 tails in 10 coinflips than 400 tails in 1,000 coinflips). This means that axial root loss will lead to larger variations in root length than lateral root loss.

Another reason why axial root loss leads to larger variance then lateral root loss is the following. A root which is lost very soon after emergence will lead to a small loss of invested resources, this is larger if the root is lost at later stages of growth. The total carbon cost of root maintenance increases with root lifespan, while root construction costs are frontloaded. Furthermore, while total nutrient uptake of a root increases over time, the uptake rate will decrease as surrounding soil gets depleted of nutrients. For a root in a given environment, this means there is some optimal lifespan where nutrient uptake per amount of carbon invested

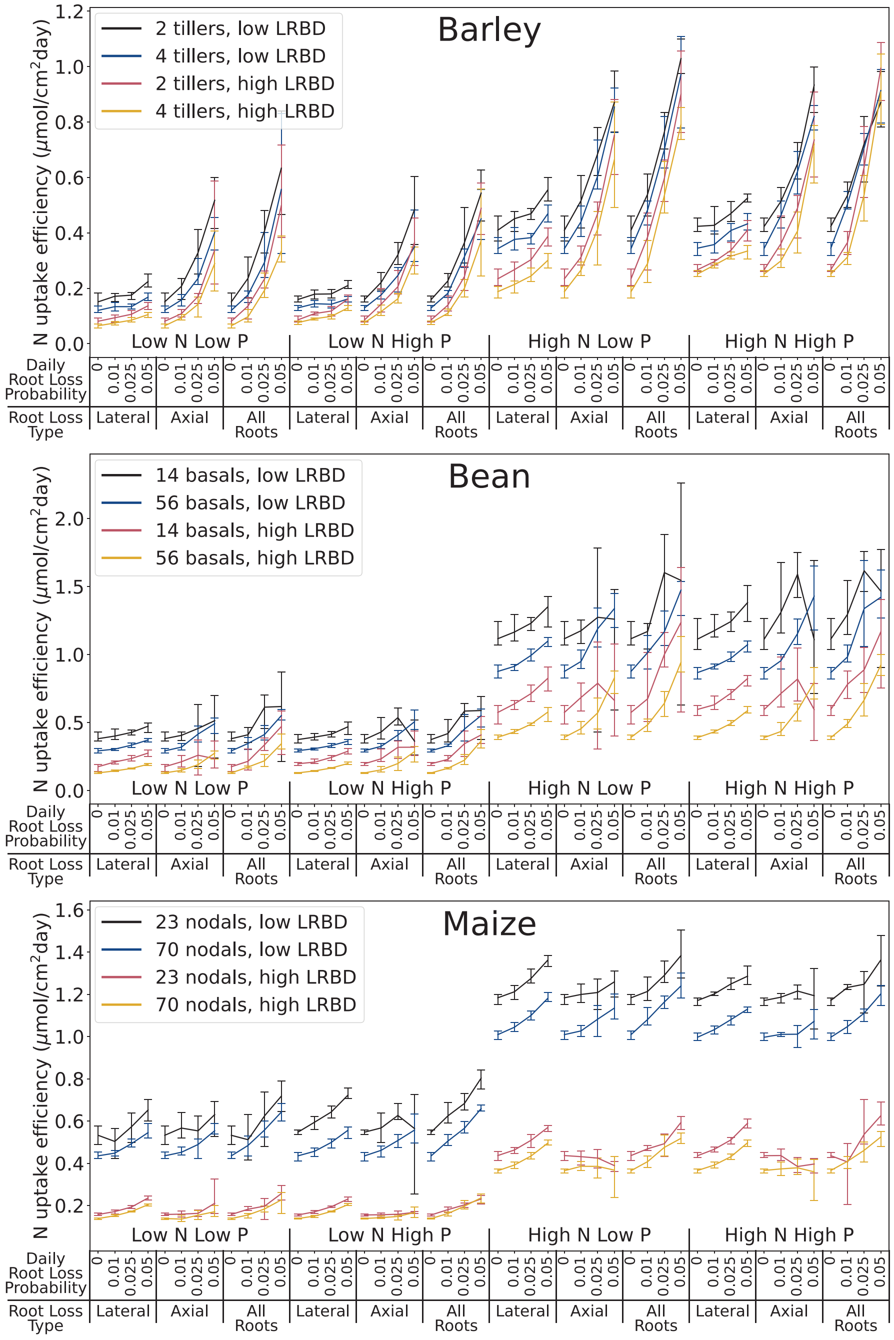

Figure 9 Mean nitrogen uptake efficiency, defined as uptake per root surface area per day, at 80, 40, and 40 days, respectively, for barley, bean, and maize phenotypes. The bars indicate minimum and maximum values. Each panel is divided into four sections, one for each of the four different soils we considered. For every soil, we show the results for the three different types of root loss at four different intensities (which includes the case without any root loss). The legend in the top left shows which color corresponds to which phenotype. LRBD, lateral root branching density; N, nitrogen; P, phosphorus.

is maximized (Eissenstat and Yanai, 1997). This means that the time at which a given root is lost determines the effect it has on the plant overall. Since axial roots have more root mass subtending from them than lateral roots, one expects any variation due to root loss timing to be correspondingly greater.

While for some of the simulated scenarios in our dataset the variation due to random effects is larger than the variation due to root loss, phenotype or environment, the fact that we see broadly similar trends across species and phenotypes makes it unlikely that the trends we observe are the product of random chance. For example, we see a consistent effect of axial root loss reducing shoot dry weight in all species and environments and root loss is more detrimental in low P soils than in low N soils.

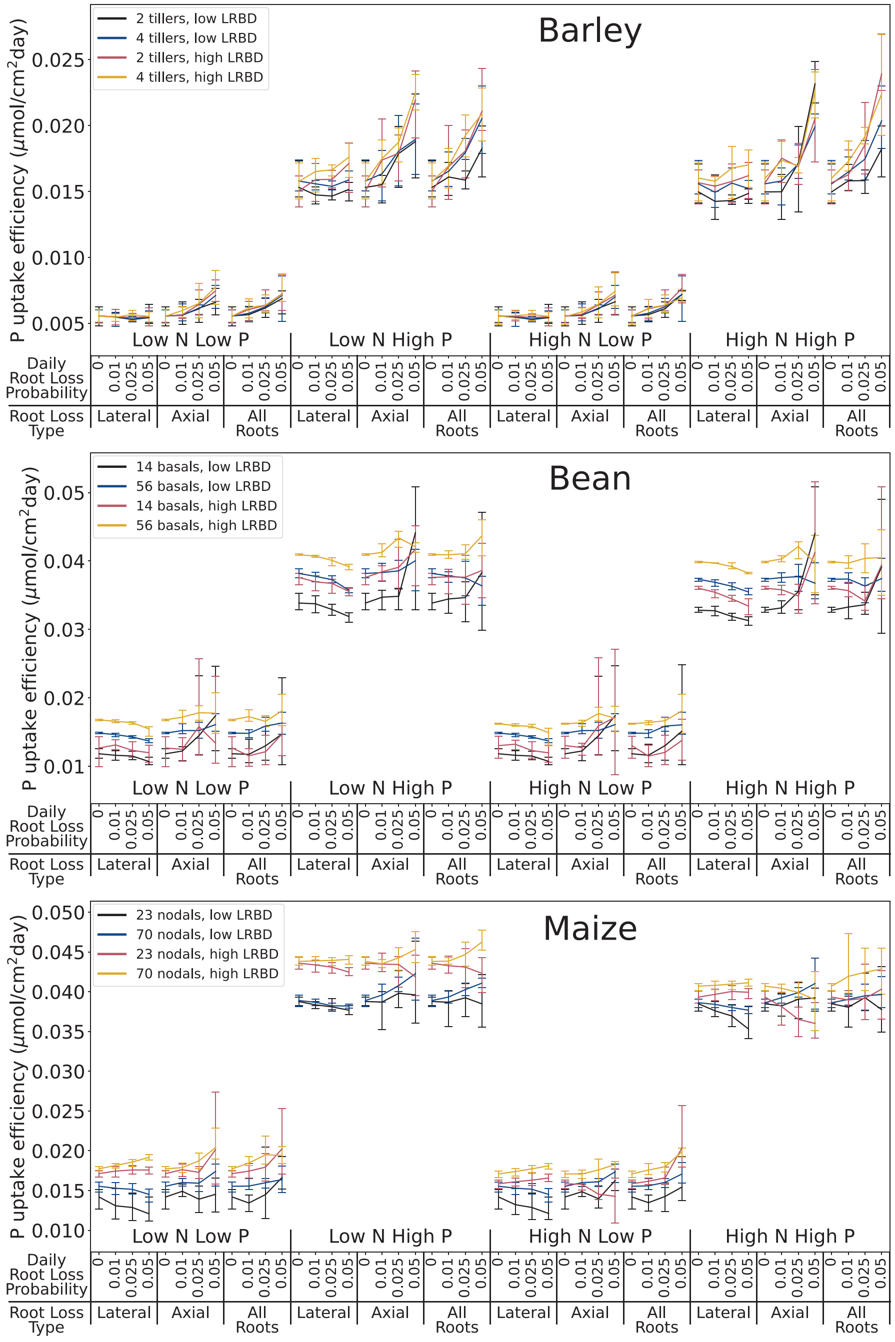

Figure 10 Mean phosphorus uptake efficiency, defined as uptake per root surface area per day, at 80, 40, and 40 days, respectively, for barley, bean, and maize phenotypes. The bars indicate minimum and maximum values. Each panel is divided into four sections, one for each of the four different soils we considered. For every soil, we show the results for the three different types of root loss at four different intensities (which includes the case without any root loss). The legend in the top left shows which color corresponds to which phenotype. LRBD, lateral root branching density; N, nitrogen; P, phosphorus.

Agreement of simulation results with empirical data

Although *OpenSimRoot* captures many key processes related to soil resource capture by roots, it inevitably simplifies and omits processes that have not been prioritized in its design. In this context, we note that *OpenSimRoot* results reported here match reasonably well with empirical results in the literature. For example, root loss caused by root rot in barley reported 80.8%, 69.2%, and 46.2% reductions in root dry weight coupled to 37.6%, 25.7%, and 16.5% reductions in shoot dry weight, respectively (Al-Abdalall, 2010). These percentages match up with our barley results, despite the simplifications we have made in our modeling assumptions and the many differences between the simulated and real plants and their environments.

Other studies have quantified the effects of root loss on yield. One study found that root loss due to root rot reduced yield by up to 50% in peas (*Pisum sativum*) (Oyarzun, 1993) and several found these reductions could go as high as 90% in bean (Gorfu, 1993; Naseri, 2008). Root loss due to corn rootworm (*Diabrotica virgifera*) reduced maize yield between 13.5% and 50% (Chiang et al., 1980; Kahler et al., 1985; Urías-López and Meinke, 2001). While we have not simulated yield directly, we saw reductions in shoot dry weight due to root loss that were of similar magnitude as those in the studies mentioned above. Assuming that shoot dry weight and yield show similar trends in response to root loss, our results suggest that root loss is more detrimental to yield when phosphorus, rather than nitrogen, is the primary limitation on plant growth. Likewise, assuming root loss can be contained to just the lateral roots, based on our results, yield reduction should be minimal. One study found that quantifications of root damage as a consequence of corn rootworm were not a good predictor of maize yields, while root dry weight was a much better predictor (Spike and Tollefson, 1989). This is in line with our observations that shoot dry weight associates with surviving root dry weight in most of the scenarios we considered (Figure 4).

Some studies found that the susceptibility of barley plants to root rot decreased as the number of tillers increased and plants exposed to root rot had higher yield if they had more tillers (Duczek and Jones-Flory, 1993). Our data do not show this, in fact for barley specifically the number of tillers appeared to have a very small impact on the shoot dry weight response to root loss (Figure 3). One possible explanation for this mismatch is that we applied root loss as a certain probability for each root to be lost, which means the amount of roots lost scales with the size of the root system while in the real world this is not necessarily the case.

Plants can sustain high lateral root loss fractions with only small reductions in shoot dry weight

Many of the plants we simulated had little reduction in shoot dry weight even with root loss fractions of 40% or greater (Figure 5). This happened most often with loss of lateral roots. When subjected to axial root loss, however, a small amount of root loss could have a substantial effect on shoot dry weight. Of course, lateral roots are easier to replace than axial roots and each axial root that is lost also means loss of any subtending laterals. Thus, the loss of an axial root often entails the accompanying loss of a substantial fraction of the root system, from which our simulated plants had more difficulty recovering. Should one or more axial roots be lost early during development, this means nutrient uptake and root growth rates are reduced, which results in fewer new roots. This positive feedback has a compounding effect that effectively set the plant's development back some days.

The relatively small effect on shoot dry weight of sustained lateral root loss at rates as high as 5% per day suggest that plants have evolved to deal with root loss. High lateral branching density could be an adaptation to environments where root loss rates are high, in addition to improving uptake of immobile nutrients. Fields used for high intensity modern agriculture are highly controlled environments compared to the conditions in which plants evolved. Especially when fertilizers and pesticides are used, one would expect crops to lose substantially fewer roots per day than they would in the wild. Assuming that increasing root growth is an adaptive response to root loss, this implies that crops produce too many roots for high input agricultural systems, wasting resources to hedge against environmental stresses which are absent. Similar to how dwarf crop varieties provide higher yield by not having to expend resources on competing for sunlight by growing tall, perhaps yield can be increased by reducing root growth where possible. In fertilized and irrigated fields, smaller root systems should still be able to acquire the resources needed for crop development, while reducing the amount of carbon and nutrients spent underground.

On differences between species

One question that might arise when comparing the effect of root loss on barley, bean, and maize is whether we can draw any conclusions about the effects of root loss on monocots as compared to dicots, or tillering versus nontillering species. We should first note that because the barley plants were simulated for 80 days, while the bean and maize plants were simulated for 40 days, the simulated plants did not suffer the same total levels of root loss. This is because losing a certain fraction of the root system every day for 80 days results in a far greater total root loss fraction than if this only happened for 40 days. While there were soil-dependent differences in shoot dry weight reductions when we compare barley at 40 days to barley at 80 days, the shoot dry weight reductions averaged over all soils and phenotypes are very similar (Table 1).

On average, bean is slightly more resistant to axial root loss than barley and maize (Table 1). One possible explanation for this is that for the bean plants, all of the axial roots emerge in the first 10 days after germination, while for barley and maize only a small fraction of all axial roots has emerged in the same timeframe. More precisely, for the phenotype with medium axial root number, 24 out of 24 axial bean roots have emerged by day 10, versus 6 out of 29 for barley, and 9 out of 58 for maize. This means that losing a few axial roots early on represents a much larger root loss fraction for barley and maize than for bean, and we have seen that root loss fraction is associated with shoot dry weight reduction (Figure 5). On the other hand, it seems reasonable to assume that continuous production of new axial roots is a good strategy to deal with axial root loss (Rubio and Lynch, 2007). However, growing new roots requires investing nutrients and carbon so nutrient-stressed plants (which can be a consequence of losing roots) will have less ability to grow new roots. Since total nutrient uptake is a function of how long the root has existed, i.e. root length duration (Nord and Lynch, 2008), growing roots

Table 1 The average shoot dry weight, relative to the shoot dry weight without root loss, for each type of root loss for barley at 40 days, barley at 80 days, and bean and maize at 40 days

Root loss	Barley at 40 days	Barley at 80 days	Bean at 40 days	Maize at 40 days
Low lateral	0.98	0.97	0.96	0.97
Medium lateral	0.93	0.92	0.90	0.94
High lateral	0.85	0.84	0.83	0.87
Low axial	0.89	0.88	0.92	0.90
Medium axial	0.71	0.71	0.77	0.75
High axial	0.39	0.47	0.63	0.54
Low general	0.87	0.86	0.89	0.86
Medium general	0.63	0.62	0.72	0.69
High general	0.34	0.37	0.53	0.47

earlier rather than later generally leads to higher nutrient uptake.

Lateral root loss has little effect on nitrogen uptake but axial root loss does

Nitrogen uptake efficiencies increased under root loss, which is consistent with previous findings that parsimonious root systems are better adapted for nitrogen uptake (Postma et al., 2014; Zhan and Lynch, 2015; Rangarajan et al., 2018, Guo and York, 2019). For plants of all three species which were not subjected to phosphorus stress, shoot dry weight associated strongly with total nitrogen uptake, indicating that nitrogen availability was the primary limit for growth (Figures 3 and 7). Total nitrogen uptake is also an important factor in plant development and when main axes were lost, total nitrogen uptake declined substantially, to the point where plants were not able to develop any substantial shoot dry weight. While plants that lose a lot of roots might be able to take up more nitrogen per day per root surface area, they are not able to explore enough soil volume to gather all the nutrients they need for development. In our simulations, root loss was also associated with more shallow root systems, which are not able to access nitrogen that has leached into deeper soil domains. Since lateral root loss had little effect on the shoot dry weight of nitrogen-stressed plants (Figure 3), the costs and benefits of root loss balanced out. The resources invested in these laterals, nutrients, and carbon, were lost but the carbon spent on root system maintenance decreased and the nitrogen uptake efficiency increased. This was true for all phenotypes we considered.

Phosphorus stress is compounded by root loss

Root loss increased phosphorus uptake efficiency for most combinations of species, phenotype, and soil, even though it declined for some bean and maize phenotypes. Since phosphorus uptake depends strongly on root surface area, soil phosphorus availability, soil exploration volume, and root length duration (Silberbush and Barber, 1983; Nord and Lynch, 2008; Jia et al., 2018; De Bauw et al., 2019), and competition between roots is small, it is not surprising that root loss decreases phosphorus uptake efficiency. The increases in phosphorus uptake efficiency were greatest in barley plants subjected to axial or general root loss, and these plants also saw the biggest decrease in average rooting depth, which means that a bigger proportion of the root systems of these plants was situated in the topsoil, where phosphorus is more plentiful (Lynch and Brown, 2001).

Previous modeling studies found that root turnover was beneficial for phosphorus uptake in P deficient soils because loss of roots followed by regrowth lead to better exploitation of undepleted soil areas by roots (Steingrobe, 2001, 2005; Steingrobe et al., 2001). However, the model used in these studies did not consider carbon and nutrient costs associated with growing and maintaining roots, nor did it take into account loss of nutrients associated with root loss. In contrast, our results show a reduction in net phosphorus uptake for almost every combination of soil, species, phenotype, and type and intensity of root loss and reductions in shoot dry weight in every environment where phosphorus is limiting, suggesting that the tradeoff between giving up existing root length and exploring new soil is usually not favorable when resource costs are taken into account. In *OpenSimRoot*, root regrowth is limited by available resources so a plant suffering from phosphorus deficiency will not be able to regrow a large amount of root length. Additionally, while root loss does reduce the carbon costs of root maintenance, it takes at least 20 days for this to equal the carbon cost of growing a new root (Eissenstat and Yanai, 1997). So, root loss frees up only a small amount of carbon available for new root growth. Also, in our model the nutrients invested in a root segment are lost upon root loss so if a root does not take up more than the nutrients invested in it before being lost, it is a net loss to the plant. Finally, if the buffer power of a soil is high, the soil might not be meaningfully depleted of phosphorus during the simulated timeframe and the benefits of exploring new soil may thus be small. More detailed studies are needed to determine under what conditions the tradeoffs of root turnover are beneficial for nutrient uptake.

Implications for crop management and breeding

In low-phosphorus soils, root loss should be prevented if possible, considering the substantial decline in predicted shoot dry weight we observed. Axial root loss is detrimental, regardless of the environment, especially for bean and maize. For barley grown in a low-nitrogen, high-phosphorus soil, the shoot dry weight reduction due to axial root loss is less pronounced. This reflects the larger number of axial roots produced by tillering grasses in comparison with dicot and nontillering grass species. The effect of lateral root loss depends on species and phenotype as well as environment. For high branching barley and maize plants grown without phosphorus limitations, lateral root loss increases shoot dry weight, so preventing lateral root loss is not beneficial. That this is not true for bean could be due to symbiotic nitrogen fixation in bean, which increases the utility of lateral roots.

Given the large number of environmental factors influencing root loss, it is rarely possible to prevent it entirely. A relevant question then is which root phenotypes should be selected in order to maximize shoot dry weight. Phenotypes with higher lateral branching densities are more resilient to lateral root loss, however this does not mean they are also the phenotypes with the greatest shoot dry weight in all environments (Figure 3). In most environments the top performers are very similar across the different root loss intensities. Even when different phenotypes respond differently to an increase in lateral root loss intensity, as is true for the high-branching maize phenotypes, this is generally not enough to make them a top performer, since the difference in shoot dry weight without any root loss was very large to begin with.

Further research

While the use of *OpenSimRoot* enabled us to explore a large range of scenarios, its limitations should be acknowledged. The barley *OpenSimRoot* model has been parameterized for 80 days, while bean and maize have been parameterized for ∼40 days. Additionally, *OpenSimRoot* is not yet capable of simulating the processes relevant for flowering and seed setting, meaning we could not directly predict yields and had to rely on shoot dry weight as a proxy for fitness. *OpenSimRoot* has recently been coupled with the ORYZA_v3 crop model to simulate the effect of root phenotypes on rice yields in past and future climates (Ajmera et al., 2022); this approach may be useful in the present context as well. It would be interesting to study the interactions between root loss and a wider selection of traits and environments. In order to focus on the influence of root loss on plant nutrient uptake and growth, we assumed that root loss was equally likely for every root of the affected root classes. It would also be useful to simulate the effects of root loss from contrasting stress agents. Root loss caused by hypoxia, soil drying, fungal disease, and insect herbivores have contrasting spatiotemporal patterns and often have more severe effects on specific root classes. For example, soil drying and many diseases and herbivores damage roots in surface soil layers rather than the subsoil. Loss of shallow roots may severely reduce phosphorus capture but may have less effect, or may even benefit, the capture of subsoil resources. In contrast, root loss cause by hypoxia is more common in deep soil domains, which may affect water and nitrate capture more than phosphorus capture.

Scenarios where root loss depends on local soil conditions, such as oxygen or water availability, are also possible fruitful future avenues of research. There was also no assumption of physiological mitigation strategies by the plant. Older, thicker and more suberized roots are less vulnerable to a range of stresses that might lead to root loss. Modeling different root loss rates based on root diameter would introduce an interesting tradeoff, where thinner roots are more efficient at taking up nutrients, due to their increased surface-to-volume ratio, but also more susceptible to root loss. However, with just three types of root loss at three intensities, three plant taxa, four different soils, and two traits that were varied, this study represents results from 5,400 simulations, each requiring between 1 and 48 h of processing time to complete, and each using up to 20 GB of computer memory. Considerable computing resources are needed for more extensive simulation studies.

Conclusions

We used the functional structural plant/soil model *OpenSimRoot* to simulate the effects of root loss on the development of barley, common bean, and maize. Our simulations showed that the effect of root loss on plant development depends on environment, root loss type, and the root system architecture. This complex picture suggests that management and breeding strategies aimed at minimizing root loss-related yield reduction requires an approach tailored to the soil conditions and the type and severity of root loss. Crops grown in a controlled, high-input agricultural context will not benefit from growing extra roots to hedge against root loss while this is an essential strategy in low-nutrient environments where pests or disease lead to substantial root loss. Studies which link causes of root loss, such as root pests, diseases, and abiotic stresses, to the root system architecture and soil conditions may help us improve crop productivity in a wide variety of environments.

Materials and methods

OpenSimRoot

OpenSimRoot is an open-source version of *SimRoot* that is under continuous development (Postma et al., 2017). The source code can be downloaded from https://gitlab.com/rootmodels/OpenSimRoot.

In *OpenSimRoot* each root is simulated as a number of vertices connected by edges. Root tips are simulated by vertices with time-dependent coordinates, called growthpoints. The speed of a growthpoint is defined by the base growth rate specified in the XML input file and correction factors such as nutrient stresses, carbon supply, and local nutrient availability. The direction in which a growth point moves is determined according to rules relating to gravitropism, the emergence angle of roots and a stochastic contribution. Other vertices have static locations and are placed in the paths of growthpoints as they move. The length of a root is equal to the distance the growthpoint traveled, not the sum of distances between vertices.

New roots are created according to branching rules which specify the distance or time between subsequent branchings. Branches emerge from what are called xylem poles and the specified number of xylem poles as well as the twisting of the root determine the radial angles at which new branches can emerge. The XML input file specifies both the axial branching angle as well as the types of roots that can branch from a certain root class. Each root class has their own parameters, such as growth rates, branching rates, etc.

OpenSimRoot contains a simple, abstract shoot model in which the shoot is represented by state variables rather than an explicit geometric model. A simple photosynthesis model determines the rate of carbon production based on the leaf area and the carbon fixation rate. The carbon requirements are based on the growth and respiration rates of the roots, costs associated to root exudates, and nitrogen uptake and the requirements of the shoot. If the amount of produced carbon is greater than the amount required, leftover carbon is stored in a labile pool for later use. If the amount of produced carbon is smaller than the amount required, root growth rates are reduced, with the growth rates of higher order roots being reduced first.

The hydrology module in *OpenSimRoot* consists of three models that are linked together. One is a simplified implementation of the SWMS model in C + + which simulates water transport through the soil by numerically solving the Richards' equation (Simunek et al., 1995). The Richards' equation is:

$$\frac{d\theta}{dt} = \nabla\left[K(\theta)\nabla\left(h(\theta)+z\right)\right] - S$$

Here, θ is the volumetric water content, t is time, $K(\theta)$ is the hydraulic conductivity tensor, $h(\theta)$ is the matrix head, z is the elevation above some reference point, and S is a sink term that represents the water uptake by roots. Evapotranspiration, which is a term that includes the evaporation of water from the soil and transpiration by the plants, is simulated by the Penman–Monteith equation (Penman, 1948; Monteith, 1965, 1981; Allen et al., 1998). The water uptake rates of root segments are simulated assuming steady-state flow through the roots in order to calculate the water potentials for every root segment (Doussan, 1998).

Root loss module

Root loss is simulated by deactivation of root segments. The time of root loss can be determined in a number of different ways, see below, and once this time has passed, the root segments in question are considered lost. These root segments do not take up any more nutrients or water, do not count toward total root length, root mass, etc., do not respire, or need any other resources. Any root subtending from a deactivated root will be deactivated as well. If a root segment is lost, the deactivation is propagated downwards towards the apex. Of course, deactivated root tips stop growing.

The root-loss module keeps track of the root length that has been lost during the simulation and the amount of carbon that has been lost. It also simulates the loss of nutrients in the tissues of the lost roots by subtracting this from the nutrient pool. The amount of nutrients lost is calculated by assuming that nutrients are distributed homogeneously in the plant tissue, weighted by the minimal and optimal nutrient contents in each tissue, depending on nutrient stress levels. The stress factor is calculated as follows:

$$S(U) = \begin{cases} 0 & \text{if } U \leq P_m \\ \dfrac{U - P_m}{P_o - P_m} & \text{if } P_m \leq U \leq P_o \\ 1 & \text{if } U \geq P_o \end{cases}$$

Here, $S(U)$ is the stress factor for the nutrient under consideration, U the amount of that nutrient currently in the plant (initial seed content plus uptake up to now minus nutrients lost up to now), P_m the minimal nutrient content of the plant, and P_o the optimal nutrient content of the plant. The amount of nutrients lost by the plant, L_σ, when a segment σ is lost is equal to:

$$L_\sigma(S) = \begin{cases} (1-S)\sigma_m + S\sigma_o & \text{if } S \leq 1 \\ U\sigma_o & \\ P_o & \text{if } S = 1 \end{cases}$$

Here, $L_\sigma(S)$ is the amount of nutrients lost when segment σ is lost, S is the stress factor as defined above, σ_m is the minimal nutrient content of segment σ, and σ_o is the optimal nutrient content of segment σ. Partial nutrient remobilization can be simulated by adding a parameter set to the appropriate remobilization value R. Then the amount of nutrients lost per segment, $K_\sigma(S)$ will be calculated according to the expression:

$$K_\sigma(S) = \left(L_\sigma(S) - \sigma_m\right)(1-R) + \sigma_m$$

Here, $L_\sigma(S)$ is defined as above. With maximum remobilization ($R = 1$), the plant will lose σ_m per segment, the minimal nutrient content needed for the tissue to function.

The time of root loss can be determined for each segment individually or for entire roots at once, and each root class can be assigned different root loss probabilities or lifetimes. Root loss time can be determined based on a distribution of root lifetimes, such as a uniform or normal distribution, or a daily probability of root loss. If a daily probability is chosen, the probability can be modified based on depth in the soil. Because of the modular structure of *OpenSimRoot*, it is straightforward for anyone familiar with C + + to add additional plugins that define the probability of root loss based on local soil conditions, the water or nutrient status of the plant or root characteristics such as root diameter or age.

Simulated scenarios

Three crop species, barley (*Hordeum vulgare*), bean (*Phaseolus vulgaris*), and maize (*Zea mays*), were simulated in a variety of scenarios. The parameters used in our simulations either come from previous *(Open)SimRoot* publications or were estimated from the literature. Parameters used in previous publications mostly come from field or greenhouse experiments and results from many of these publications

Table 2 An overview of the two traits: LRBD and axial root number, that were varied for all three species and the values used in the simulations

Phene	Barley	Bean	Maize
LRBD	1.6, 2.5, 5 branches/cm	2, 4, 6 branches/cm	2, 5, 20 branches/cm
Axial root number	2, 3, 4 tillers	4, 12, 16 basal roots 10, 25, 40 hypocotyl born roots	11, 18, 36 nodal roots 12, 34, 34 brace roots

A factorial design was used, which means that every combination of values for these two traits was simulated.

have been verified in experiments. As summarized in Table 2, for each species, the following two traits were varied:

- Lateral root branching density.
- Axial root number. For barley, tiller number is varied; for bean, basal and hypocotyl root numbers are varied and for maize nodal and brace root numbers are varied.

All of these phenotypes, nine for each species, were simulated in a variety of environments. They were simulated in four different nutrient environments, high and low availability for both nitrogen and phosphorus. Each phenotype was subjected to three different types of root loss: lateral root loss, axial root loss, and a combination of both types of root loss. Root loss was simulated by assigning to each root of the relevant root type a daily probability of that root being lost. All three of these types of root loss were simulated at three different levels of severity, with roots having a 1%, 2.5%, or 5% daily probability of being lost. A control simulation without any root loss was also done. Each simulation was repeated five times with different seeds of the random number generator. This is because root loss, root branching, and root growth direction all include a stochastic component.

An introduction to running simulations with *OpenSimRoot* can be found in Schäfer et al. (2022). Instructions on how to recreate the XML input files and the *OpenSimRoot* executable used to generate the data for this article can be found at: https://gitlab.com/rootmodels/OpenSimRootPapers/-/tree/master/ErnstDSchafer-2022-RootLossAndNutrientUptake. The code used for the simulations in this article has git commit hash 1d82c5b5de2148c6b95df7b99b54c1eaf03212c1 in the *OpenSimRoot* repository. It can be downloaded from https://gitlab.com/rootmodels/OpenSimRoot/-/tree/1d82c5b5de2148c6b95df7b99b54c1eaf03212c1.

OpenSimRoot is currently only able to simulate vegetative growth and species are only parameterized for a certain number of days. Because of this, we cannot simulate flowering and grain filling and hence yield. Even though the empirical relationship between shoot dry weight and yield, called harvest index, varies depending on a number of factors including environment, field management, and plant water status (Unkovich et al., 2010), shoot dry weight is the best proxy we have available.

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