Breeding more productive grain crops - could selecting the right rooting traits help?

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Abstract

Root systems and their interactions with the below-ground environment are difficult to study. As a result, root research has typically lagged behind that carried out on above-ground parts of crop plants. Modern advances in computing technology are allowing 3D root architectural models to play a role in below-ground investigations. ROOTMAP is one such model, and has been used to investigate the influence that lupin root systems can have on water and nitrate distributions and nitrate leaching in field soils.

Simulating a wide range of root architectures, ROOTMAP predicted that to reduce nitrate leaching to depth below lupin crops, a trade-off between surface and subsoil rooting density is required, with high rooting density in the topsoil alone insufficient to minimise leaching. Simulated plants that rapidly established a relatively high density of roots in the topsoil, reduced total nitrate leached with the break of season rains. Further increases in topsoil root density were, however, a poor investment of internal assimilates. A shift in resource allocation to subsoil root growth as the season progressed, gave plants a second chance to acquire nitrate previously leached to depth, and proved the most successful strategy for reducing total annual losses of nitrate.

Given the ability to investigate rooting traits and quantify potential benefits of one rooting form over another, root modelling can be used to identify desirable root traits for which genotypes can then be screened. ROOTMAP is currently being used to investigate below-ground competition between wheat and annual ryegrass for both mobile (eg. water, nitrate) and immobile (eg. phosphorus) soil resources. This work will aid in the identification of key rooting traits that confer a competitive advantage to wheat.

Key Words

Root architecture, root modelling, below-ground competition, nutrient uptake, nitrate leaching, lupins.

Introduction

While root systems acquire the majority of the essential elements required for crop growth, the role that root trait selection could play in crop breeding programs has not been fully explored. Current breeding techniques rely on the selection for above-ground characters. While this process may be indirectly selecting for desirable rooting traits, given the large and varied role that root systems play some breeding objectives may be better met by directly targeting particular rooting characters. However, the link between root form and function and crop productivity is not well understood and is inherently difficult to study. It is for this reason that root models are increasingly being used to help identify potentially valuable rooting traits. Modern three-dimensional root architectural models (eg. 1,2,3,4) are gradually being developed to better represent real root systems responding to their non-uniform soil environment. This is allowing root modelling to generate valuable hypotheses about the roles root form and function play in plant productivity (5), providing the potential to have a direct influence on plant breeding efforts. This paper reviews recent work that highlights the link between root systems and plant productivity, including published and unpublished work from the authors, and a brief discussion of work currently in progress.

The use of root modelling to investigate the link between rooting traits and plant productivity

Since a large number of the resources required by a plant are found below-ground, the form and function of root systems has a direct influence on plant productivity. Root architecture has, for example, been closely linked with the acquisition of immobile ions, with root length density in topsoil layers found to be important for increasing phosphorus uptake by wheat (6), and topsoil exploration important for phosphorus acquisition by common bean (7). The ability to compete below-ground with other species is closely linked to characters such as root density and surface area, root growth plasticity and nutrient uptake plasticity (8). Below-ground competition, as driven by rooting traits, often has a greater influence on plant productivity than above-ground competition (9).

Root modelling has been used to help investigate the relationship between root architecture and plant productivity. Ge *et al.* (10) modelled the contribution of a range of root characteristics (root growth angles, adventitious rooting, lateral branching, root hair length and density, and plasticity in these characters) to topsoil foraging and P acquisition efficiency by common bean (11). Dunbabin (5) used root modelling to show the role that root growth and nutrient uptake plasticity plays in the capture of nitrate, while Robinson (12) modelled the important role that root proliferation can play when two root systems are competing for nitrate.

The well demonstrated link between root function and plant productivity is now starting to be exploited in breeding programs. Selection of P efficient parents with enhanced topsoil foraging ability has resulted in new cultivars that have a higher yielding capacity on low P soils (see 11). Marker-aided selection using quantitative trait loci (QTL) tagging of desirable traits, may accelerate this type of work in the future. A considerable amount of research is now emerging which identifies QTL's for rooting characters. Work on Arabidopsis has identified single genes that are involved exclusively in post-embryonic root formation (see 13), and the identification of rooting QTL's for a number of species, including rice (14) and maize (15) has been carried out. This increase in the identification of rooting QTL's in parallel with the improved capacity of root growth models to represent real root systems, presents the opportunity to link the two technologies for improved breeding outcomes.

The use of ROOTMAP to identify rooting characters important for nitrate capture by lupins

ROOTMAP (4, 16) is a root architecture model that has been used to represent root system dynamics at three scales: i) simulating glasshouse trials (4); ii) simulating field-grown lupins (17); and iii) running hypothetical 'what-if' experiments (5). ROOTMAP has performed well at both the glasshouse and field scales, satisfactorily predicting, over two seasons, the root growth (R^2=0.90), soil nitrate (R^2=0.86) and soil water (R^2=0.72) dynamics under field grown lupins (*L. angustifolius* L.) on a deep sandy soil in the Western Australian wheat-belt (17), and also reproducing ($R^2 = 0.98$) the root growth and nitrate uptake plasticity of lupins locally supplied with nitrate and grown in a controlled environment (4).

Given the success at representing root dynamics observed in the glasshouse and field, ROOTMAP was then used to investigate the ability of a range of actual and theoretical root architectures to capture nitrate leaching through a sandy soil profile (5, unpublished). The aim of this work was to determine whether it may be possible to select lupin species with root systems that have an enhanced ability to capture nitrate (5). Due to their high capacity to fix N_2, lupins have a low utilisation of mineralised N, resulting in some of the highest rates of nitrate leaching and soil acidification under any grain crop grown in the deep sandy soils of the WA wheat-belt. Any reduction in nitrate leaching would help slow the rate of topsoil acidification under lupins, while increasing nitrate uptake would reduce the excess cation uptake and hence excess hydrogen ion exudation thought to cause the high rates of subsoil acidification under lupin crops (see refs in 5).

A number of root architectures were investigated and were graded from the classic herringbone root system (first order branches only) to the dichotomous type of root architecture (highly branched) (see Fig. 1). Included were root types representative of actual *L. angustifolius* and *L. pilosus* root systems. All simulated root systems fixed N_2. All soil and rainfall parameters were those applied in a previous field modelling exercise, derived from a deep-sand field site in the Western Australian wheat-belt (Moora,

30?38'34"S, 116?43'36"E) in 1995 (5). All modelled plants were grown under identical conditions so that they could be directly compared, and simulations were run until 108 days after sowing. Each plant was given the same total supply of resources through time for root growth, maintenance and N_2 fixation, making each root system a true "cost-equivalent" arrangement of roots at any point in time, thus allowing a direct comparison of their nitrate acquisition efficiency.
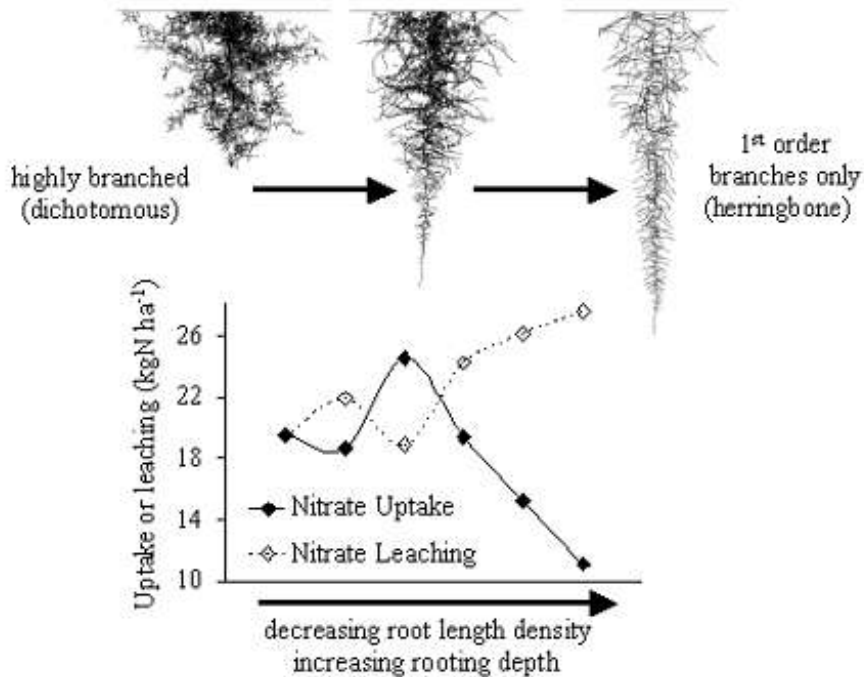

Figure 1. The change in total nitrate uptake and nitrate leached below 1.5 m, with changing root architecture from shallow and dense (dichotomous) to deep and sparse (herringbone), over 108 days under simulated field conditions.

This simulation exercise showed that i) root architecture (the cost-equivalent arrangement of roots) can influence the total amount of nitrate leached to depth over a growing season (even for N_2-fixing plants) and that ii) in order to maximise uptake and minimise leaching in environments with high leaching potential, root systems need to represent a trade-off between density of roots in the topsoil layers and extension of root length into the subsoil. The simulated root architecture that both maximised uptake and minimised leaching (Fig. 1, middle part) quickly developed a high rooting density (up to three orders of branching) in the topsoil. This enabled a relatively fast depletion of nitrate from the surface mineralisation zone before a series of heavy early season rainfall events (occurring 20-60 days after sowing, see 5) caused substantial nitrate leaching. In addition to topsoil growth, this root system also invested resources into subsoil root growth, thereby providing an opportunity to acquire sources of nitrate previously leached to depth. It is interesting to note that in these simulations, there was an initial increase in nitrate leaching as topsoil root density decreased, but total rooting depth was not sufficient to capture nitrate leached to depth (Fig. 1).

This modelling exercise clearly identified the requirement for lupins to rapidly develop root density in the topsoil early in the season in order to minimise the nitrate lost in early leaching events when plants are still young, and to then go on to divert subsequent resources into subsoil exploration. These findings could now be used to screen for lupin genotypes that have a higher rooting density, but similar total rooting depth to the current *L. angustifolius* varieties, testing their capacity to reduce nitrate leaching in both glasshouse and field trials. These findings could then be incorporated into a breeding program that aims to reduce the degree of nitrate leaching and subsequent rate of soil acidification under lupin crops (18).

Using ROOTMAP to identify below-ground competition between grain crops and weeds

The root architectural model ROOTMAP is a particularly powerful tool for investigating root interactions since it can identify the behaviour of individual roots at any point in time and space. This enables the dynamic root responses to the temporally and spatially variable soil environment to be accurately mapped. Figure 2 is a representation of the way that the model can not only represent whole rooting strategies, but can also focus in on any point in the 3D soil environment and derive information at any point in time about factors such as a) the local soil properties, b) the number and length of roots each plant has in that local soil volume, and c) the amount of water and nutrient that each plant is acquiring from that soil volume and hence the relative competitive success of each rooting strategy. This capability is valuable for investigating inter root-system competition, which can be particularly important when plants are small and canopy interactions are not yet significant. ROOTMAP will be used to help identify rooting traits that are likely to confer a competitive advantage to grain-crop varieties over weedy species, improving the productivity of grain-crop varieties. This work will cover root investigation at all three levels from theoretical experiments, to glasshouse and field trials with associated simulation. A variety of grain-crop species will be investigated, with a particular focus on below-ground competition between wheat and annual ryegrass.
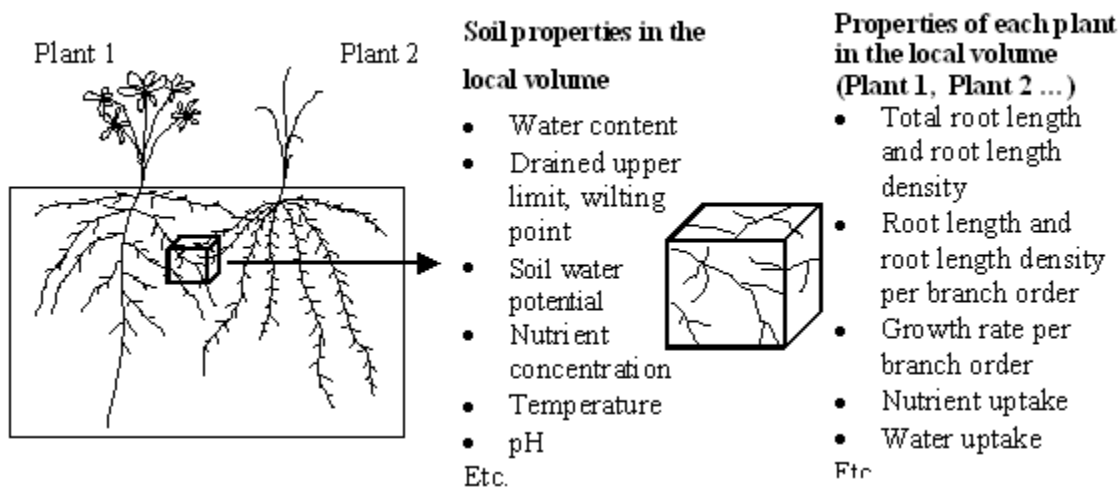

Figure 2. Representation of some of the plant and soil properties that ROOTMAP can summarise at any point in time and three-dimensional space.

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