Using the ROOTMAP model of crop root growth to investigate root-soil interactions

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Abstract

Tailoring root systems to particular cropping environments is of interest in Australia's challenging cropping systems. The capacity to better match root systems to the environment in which they grow offers the potential to improve crop productivity. In this study, the ROOTMAP model of crop root growth was used to screen combinations of rooting traits and cropping environments, for identifying rooting traits important to crop productivity.

A sensitivity analysis method was used to investigate 30 parameters that describe root architecture, the cropping environment and agronomic management. Weed-free and weedy crops were modelled. Parameters were ranked in order of importance for water, nitrogen and phosphorus uptake.

Parameters controlling the efficient distribution of roots through soil (root system spread), and physiological parameters determining the rate of phosphate influx into roots, ranked highest for phosphate-limited scenarios. Modern high-yielding varieties reflect this characteristic, being efficient at capturing and utilising soil resources for a low investment in root and shoot biomass.

In contrast, the most important parameters for plants in competition with weeds were those controlling the intensity of soil foraging and rate of root system establishment, highlighting the importance of quickly and effectively occupying the soil volume during establishment if a crop is to out-compete weeds.

Key Words

crop root traits, ROOTMAP, nutrient uptake, root growth, crop-weed competition

Introduction

Variability is an inherent component of all biological systems. Plants grow in an environment of considerable spatial and temporal variability, even our notionally monoculture crops. The pressure to use crop varieties that maximise return (yield) is ever increasing, and in many cropping areas of the world it is the interaction between crop root systems and their soil environment that limits yields. This is particularly true in Australia, where drought, root disease, elemental toxicities and deficiencies, and soil structure (including the presence of hard pans), are some of the primary factors that limit the capacity of root systems to forage effectively for water and nutrients.

Crop root systems are therefore coming under greater scrutiny, and momentum is building in the area of breeding for specific root traits. However, there is still relatively little known about plant root systems and how individual rooting traits combine to produce a root system that enables optimum water and nutrient uptake from different cropping soils.

In this study, the ROOTMAP model of dynamic crop root growth was used to investigate the impact that a range of parameters (describing root architecture, water and nutrient uptake, soil, weather and agronomy) have on the water, nitrogen and phosphorus uptake by grain crops.

Methods

The ROOTMAP model of three-dimensional root growth (Diggle, 1988; Dunbabin et al., 2002) was used to investigate the contribution that a number of rooting traits make to water and nutrient uptake by grain-crops, grown with or without competition from weeds. The model considers soil water and nutrient dynamics, and root growth responses to these dynamics. ROOTMAP uses the balance between plant demand for resources and the capability of individual roots to supply soil resources, to drive allocation of assimilates and the resultant growth of each root tip, root branching and nutrient uptake.

For this study, a sensitivity analysis approach was used to assess the relative effect of a range of root traits on water, nitrate and phosphate uptake by grain crops. Due to the large number of parameters in many modern crop and root models, sensitivity analyses are not routinely applied to them. The Morris sensitivity approach (Saltelli et al. 2000; Morris 1991) was used and adapted to this study. It is a screening method that is computationally efficient and provides information on individual parameters and their interactions with other parameters. Most screening methods are a ‘one at a time’ approach, where one factor is changed at a time in turn, only allowing evaluation of the main effects. The value of the Morris (1991) approach is that it provides information on both the main effects and the interactions, without the computational cost of a full factorial analysis. Detailed factorial analyses can be applied to the subset of parameters identified by the screening method. The flexibility of this approach means that it could be used for the testing and evaluation of other parameter-intensive crop/plant models.

An extensive review of the literature for grain crops was undertaken to determine the realistic range for each parameter investigated. Thirty parameters were included in the analysis, covering root architecture, water and nutrient uptake, soil, agronomic and environmental parameters, involving over 2400 runs of the model. Parameters were ranked according to their sensitivity indices. A parameter was considered to have an important effect on water, nitrate and phosphate uptake if it had a sensitivity index (main effect) greater than 25% of the top-ranked index. The parameter ranking for interaction effects (not shown) was similar to that for the main effects. This is a characteristic of many biological models/relationships (Saltelli et al. 2000), which are typically highly non-linear, with important individual parameters interacting with other parameters. For a description of the highest-ranked parameters see Appendix 1.

Growth was simulated for 12 weeks, capturing the early establishment/growth phase in which it is important for crops to out-compete weeds (Lemerle et al. 2001).

Results and Discussion

The sensitivity analysis highlighted some important differences between the root traits that contribute to successful resource capture and growth in weedy crops, compared to weed-free crops. The highest-ranked root/plant parameters separate out into being of greatest benefit to weedy or weed-free crops (Fig. 1), suggesting that there is the potential for tailoring root traits to specific conditions.

For weedy crops, resource capture was controlled by a relatively small number of parameters (Table 1, Fig. 1). The highest-ranked rooting trait for water, nitrate and phosphate uptake was branch spacing (rooting density/proliferation). This parameter controls the intensity of soil foraging. Root growth rates (rate of root system establishment) also played an important role in resource acquisition. The ability to quickly (growth rate) and effectively occupy (rooting density) the soil volume during crop establishment is likely to be important for denying weeds water and nutrients (Lemerle et al. 2001).

For weed-free crops, the highest-ranked parameters were those controlling the efficiency with which soil resources can be acquired by a given length of root. The geotropism and deflection indices (Appendix 1) control how crop roots are distributed through the soil, while P uptake kinetics and uptake plasticity parameters determine the rate of phosphate influx into plant roots, and the degree to which this is up-regulated when the crop is nutrient-limited and the nutrient supply is heterogeneous.

For this study, realistic ranges for available soil P in Australian cropping soils were used, including representations of relatively P-rich soils. The fact that P uptake ranked as an important parameter for nitrate and water acquisition by weed-free crops (Fig. 1a,b) suggests that foraging for the least mobile, and often most limiting nutrient, may provide the best strategy for acquiring all soil resources. In ROOTMAP, the potential for P uptake at the root surface (P uptake kinetics) affects the rate and total amount of P taken up by the plant. When P is a limiting resource, uptake directly affects plant growth and the size and extent of the root system available for water and nitrate foraging. The density and spatial distribution of roots affects both the uptake of immobile phosphate ions and the uptake of the relatively mobile nitrate and water resources. Modelling and field studies have shown that nitrate uptake can be transport-limited in the field (Barber and Silberbush 1984; Brady et al. 1995; Kage 1997; Wiesler and Horst 1993, 1994), hence rooting traits that assist with the acquisition of immobile nutrients also increase nitrate uptake.

The rate at which root axes grow was more important for water and nitrate uptake than for phosphate uptake by weed-free crops (Tables 2, Fig. 1). Root extension and rooting depth play an important role in foraging for these dynamic resources that can move relatively quickly through the soil profile, and for which uptake from the subsoil can play an important role.

The physical occupation of soil space by roots is a less efficient method of accessing water and nutrients than strategic root placement and effective uptake, but it does deny weedy competitors of resources. Modern high-yielding varieties are efficient at capturing and utilising (uptake physiology) soil resources for the lowest cost (growth). Some crop/weed researchers (see Lemerle et al. 2001), have suggested that breeding for high-yielding (efficient) crops may have selected against weed-competitive traits. This modelling study suggests that root traits can be categorised according to their effect on resource capture in competition or competition-free scenarios. Further analysis is needed to identify the degree to which these traits are mutually exclusive (unique phenotypes for specific environments), or can co-exist (one-size fits all).

Table 1. Water, nitrate and phosphate uptake by modelled grain crops growing in competition with weeds. Parameters are ranked in order of their sensitivity index. All parameters greater than 25% of the top-ranked parameter are listed. See Appendix 1 for a description of each parameter.

Water	**Nitrate**	**Phosphate**
Branch spacing *Spatial Intensity*	Branch spacing *Spatial Intensity*	Branch spacing *Spatial Intensity*
Relative growth rate axes *Growth Rate*	Relative growth rate axes *Growth Rate*	Plant available water *Soil Parameter*
Plant available water *Soil Parameter*	N Mineralisation in Soil *Soil Parameter*	Soil mineral P *Soil Parameter*
Deflection Index Branches *Spatial Efficiency*		Relative Growth Rate Axes *Growth Rate*
Relative Growth Rate Branches *Growth Rate*		Soil organic P *Soil Parameter*
Plant Density *Spatial Intensity*		

Table 2. Water, nitrate and phosphate uptake by modelled grain crops growing as a weed-free monoculture. Parameters are ranked in order of their sensitivity index. All parameters greater than 25% of the top-ranked parameter are listed. See Appendix 1 for a description of each parameter.

Water	**Nitrate**	**Phosphate**
Geotropism Index Branches *Spatial Efficiency*	Geotropism Index Branches *Spatial Efficiency*	Deflection Index Axes *Spatial Efficiency*
P uptake kinetics *Nutrient Uptake Efficiency*	P uptake kinetics *Nutrient Uptake Efficiency*	Branch Angle *Spatial Efficiency*
Plant available water *Soil Parameter*	Branch spacing *Spatial Intensity*	Geotropism Index Axes & Branches *Spatial Efficiency*
Branch spacing *Spatial Intensity*	Plant Density *Spatial Intensity*	P Uptake Plasticity *Nutrient Uptake Efficiency*
Plant Density *Spatial Intensity*	Relative growth rate axes *Growth Rate*	N Mineralisation in Soil *Soil Parameter*
Soil mineral P *Soil Parameter*	Plant available water *Soil Parameter*	Deflection Index Branches *Spatial Efficiency*
Relative growth rate axes *Growth Rate*	N Mineralisation in Soil *Soil Parameter*	N Uptake Plasticity *Nutrient Uptake Efficiency*
Soil organic P *Soil Parameter*	Soil organic P *Soil Parameter*	P uptake kinetics *Nutrient Uptake Efficiency*
		Plant available water *Soil Parameter*
		Soil mineral P *Soil Parameter*

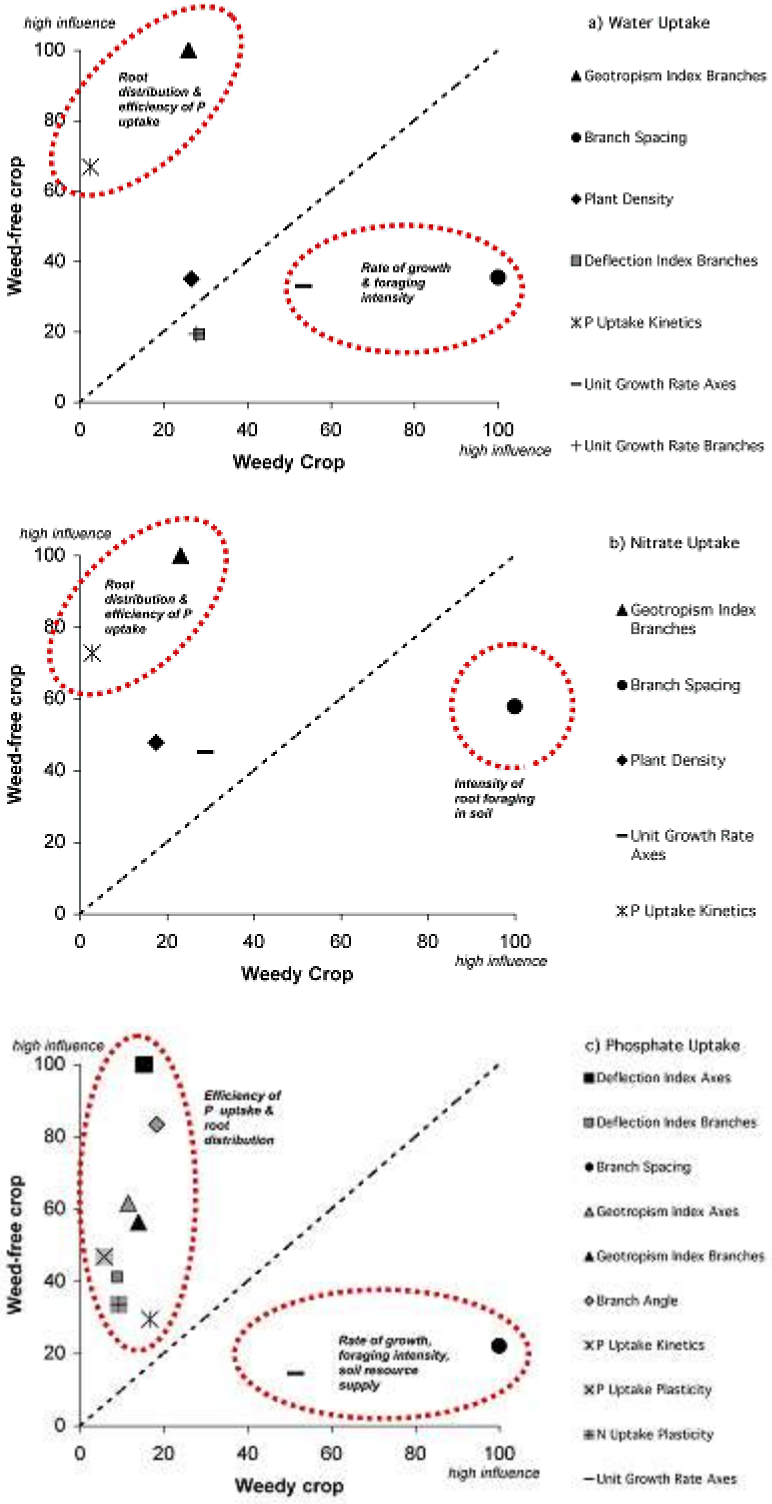

Figure 1. Sensitivity indices of root/plant parameters important for a) water, b) nitrate and c) phosphate uptake by weed-free or weedy grain crops. Indices are expressed as a percentage of the highest ranked index.

Conclusion

This modelling study has suggested that root traits can be clustered into functional groups that relate to specific cropping scenarios. These results highlight the potential for modelling to be used as a trait selection tool. Lynch and Brown (2001) identified gravitropic trajectory (root system spread) and root branching (intensity of soil foraging) as the two most important root traits for phosphorous efficiency in common bean, using root modelling. They determined that the angle of axes from the horizontal was a robust measure of gravitropic trajectory, and used this for screening a large number of cultivars at the seedling stage. From this work, P efficient bean cultivars were developed for growth on P-deficient soils. A similar process could be adopted for tailoring grain-crop root systems to Australian cropping soils. This modelling study suggests that the traits important for resource capture by crop roots separate out distinctly into those of greatest benefit in weedy/competition conditions (intensity/competition parameters) and those important for weed-free crops (efficiency parameters). This subset of parameters could be investigated with further detailed modelling and with glasshouse experiments, with the potential for screening genotypes for target rooting characteristics.

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Appendix 1. Brief Description of the 12 model parameters that ranked as having the highest importance for water, nitrate and phosphate uptake by grain-crops. For further detail see Diggle (1988) and Dunbabin et al*.* (2002).

Spatial Intensity – parameters affecting rooting density / intensity of foraging:

- Branch spacing (mm) – distance between root branches.
- Plant Density (plants/m^2).

Spatial Efficiency – parameters affecting the way roots are distributed through soil:

- Branch angle (deg) – angle at which root branches grow out from their parent root.
- Deflection index – multiplier (0-1) controlling the probability that a root tip will continue in its current direction of growth, or will deviate from that over time.
- Geotropism Index – multiplier (0-1) controlling the effect of gravity on root growth.

Nutrient Uptake Efficiency – parameters affecting plant capacity for nutrient uptake at the root surface:

- N and P uptake plasticity – the degree to which nutrient inflow is up- or down-regulated in response to plant nutrient demand and the proportion of the root system with access to the nutrient. Unique value for N and P uptake.
- P uptake kinetics (pmol.m^{-1}.s^{-1}) – value of I_{max} used in the Michaelis-Menten equation describing the uptake capacity of the crop plant. See Appendix 1.

Growth Rate – rate of root colonisation of soil:

- Relative Growth Rate (?m.mol^{-1}.s^{-1}) – potential growth rate of root axes or branches when supplied with a unit of assimilate for growth.

Soil Parameters – site specific soil parameters:

- N Mineralisation in soil (?gN.g^{-1}_{soil}.s^{-1}) – Rate of N mineralisation in soil.
- Plant Available Water (v.v^{-1}) – distribution of plant available water in the soil profile.
- Soil Mineral P (?gP/gsoil) – distribution of plant available P in soil.
- Soil Organic P (?gP/gsoil) – distribution of organic P in soil.