

Crop mineral nutrition under drought conditions

Zed Rengel

Introduction

Climate change will result in increased variability of precipitation. Moreover, many areas in the world (e.g. Western Australian wheat belt) are projected to have reduced rainfall, causing more frequent and longer droughts. Hence, in rain-fed agriculture, measures designed to increase the capacity of roots to take up water and nutrients from soil with limited water availability are needed. This review will concentrate on 1) breeding for improved root architecture and function, 2) fertiliser placement to encourage root proliferation deeper in the soil profile, and 3) hydraulic lift of water from wet into dry soil via roots.

Breeding for improved root architecture and function

Complex plant structures like roots have two developmental pathways: (i) intrinsic (governing the basic architecture and the limits of plasticity) that is determined genetically for a particular species, and (ii) response pathway determined by environmental cues (Malamy 2005). These two pathways combine in intricate ways to create a highly complex 3-D root structure influenced by genetics as well as the availability of resources in the heterogeneous soil environment (Baddeley et al. 2007). Although diffusion coefficients of nutrient ions are reduced in dry soil, many reports suggest that the uptake of soil immobile nutrients is predominantly affected by reduced root growth as soil dries out (Crabtree et al. 1998; Rose et al. 2008).

Root systems are fundamental to crop productivity (Dunbabin 2007; Malamy 2005). In Australia, crop root systems are poorly adapted to soils, resulting in yields averaging only 50 percent of the potential, with the major limiting factors being poor soil water holding capacity and nutrient deficiencies (Rengasamy 2002; Wong and Asseng 2006). Growing cultivars tolerant to soil-related stresses would be an economically- and environmentally-favourable solution most readily adopted by farmers (Rengel 2005). Hence, successful crop genotypes in the future will need to have enhanced efficiency of capturing water and nutrients from the increasingly hostile soil environments (De Dordodot et al. 2007).

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Targeted development of crop genotypes with increased efficiency of water use (Liu et al. 2007; Manschadi et al. 2006; Ober et al. 2005) and nutrient capture (Rengel 2005) hinges on a better understanding of root structure and function (Wang & Smith 2004). In soybean genotypes, increased capacity to take up water from deep (1.1 m) soil horizons in the field was linked to increased yield potential (Ober et al. 2005); similar connection was made for upland rice (Kondo et al. 1999) and also wheat in western and southern Australia (Wong and Asseng 2006).

Because genetic loci for root properties overlap with those associated with crop productivity in the field (Steele et al. 2007), identifying genetic loci and eventually molecular markers to facilitate marker-assisted selection for root traits will result in the selection of genotypes with higher productivity in the field based on more efficient capture of water and nutrients (De Dorlodot et al. 2007). Indeed, marker-assisted selection for the root-related genetic loci has been used to alter root architecture and increase grain yield in the field-grown rice (Steele et al. 2007) and also to increase root size and grain yield in maize (Landi et al. 2005). However, wide-scale use of root-related genetic information in breeding is hampered by relatively small mapping populations and inaccurate phenotyping (De Dorlodot et al. 2007).

Phenotyping of root traits in breeding programs is presently hindered by the structural and functional complexity of root systems in heterogeneous soil environments (Doussan et al. 2003; Pierret et al. 2006; Valizadeh et al. 2003), requiring multidisciplinary analysis of root functioning in soil, characterisation of factors limiting soil-root interactions in specific environments, and identification of root parameters that represent potential solutions. These requirements can be met by modelling, providing that models: (i) are 3-D and time-dynamic, (ii) integrate biological, physical and chemical processes occurring in soil, (iii) enable simulations of scenarios beyond those directly observed, and (iv) are capable of simulating these scenarios in a dynamic environments that vary in time and space (De Dorlodot et al. 2007).

It is still unknown which phenotypic traits are desirable in achieving increased efficiency of water and nutrient capture from the drying soil environments (Walk et al. 2006). However, defining optimal root systems can be done via simulation computer models, eg. ROOTMAP as an interactive model of root structure and function (Dunbabin et al. 2002b). ROOTMAP excellently matches the patterns of root growth and nutrient uptake observed in the field (Dunbabin et al. 2002a) and is uniquely able to search for optimality of root structure and function regarding nitrate and P capture in variable seasonal conditions (Dunbabin et al. 2003; 2004; 2006).

Manipulating root distribution in the soil profile by fertiliser placement

In water-limited environments where the topsoil is prone to drying, placing

fertilisers deeper in the soil profile could increase nutrient acquisition by plants because fertilisers would be in the moist soil for a longer part of the growing season (Ma et al. 2009). There are many reports on the yield benefit from deep fertiliser placement (Crabtree 1999; Hocking et al. 2003; Jarvis and Bolland 1991). However, the effectiveness of deep fertiliser placement is influenced by soil texture, tillage, fertilising history, nutrient mobility, and crop species. In addition, when subsoils feature toxicities such as boron or salt, increasing root proliferation into the subsoils by placing fertilisers deep may exacerbate toxicity problems (Ma et al. 2009).

Roots can respond to localised nutrient availability by increasing the rate of nutrient uptake, and/or by root proliferation in the enriched zones. Frequently, the combination of these two is involved in the plastic responses of a root system to heterogeneous nutrient conditions (Dunbabin et al. 2001a; b). Compared with uniformly mixed fertiliser, root proliferation occurs in the vicinity of a fertilised band (Ma et al. 2007; Trapeznikov et al. 2003), but not too close because of toxicity caused by high nutrient concentrations (Zhang and Rengel 1999; 2002).

Hydraulic lift of water from moist deep soil layers into dry shallow layers

In agricultural systems with little soil mixing (no-till or minimum tillage) and placement of fertilisers near the seed, vertical stratification of nutrients may occur (with accumulation of nutrients in the topsoil (Howard et al. 1999). Between rainfall events, nutrients in the topsoil could become unavailable as the soil dries. In such instances, hydraulic lift may play a vital role in nutrient acquisition (Rose et al. 2008).

Hydraulic lift is defined as the root uptake of soil water from areas of high water potential (generally subsoil) and subsequent release into areas of low water potential (generally topsoil) by roots at night (Caldwell et al. 1998). Hence, hydraulic lift may maintain the root function and nutrient uptake in relatively dry soil. Hydraulic lift could be maintained even in soils that are as dry as having only 1 percent (w/w) moisture (Rose et al. 2008). There are however, both positive (Liebersbach et al. 2004; Rose et al. 2008; Valizadeh et al. 2003; Wan et al. 2000) and negative reports (Crabtree et al. 1998) with respect to hydraulic lift facilitating nutrient uptake from relatively dry soils.

Overnight, pearl millet lifted up to 27 g kg⁻¹ soil (Vetterlein and Marschner 1993) and wheat ~25 g kg⁻¹ soil (Valizadeh et al. 2003), but canola only 2-3 g kg⁻¹ soil (Rose et al. 2008). This difference might have been caused by differential root density (greater in case of highly branched root system of cereals vs. taprooted system of canola). Increased localised supply of P fertiliser (compared with nil fertiliser) resulted in wheat plants lifting more water and taking up more P (Valizadeh et al. 2003).

Conclusions

The importance of enhanced plant capacity to take up water and nutrients from soil is becoming increasingly important in rain-fed agriculture, especially in areas that are getting drier due to climate change and as water resources become scarcer and more expensive. A long-term strategy to dealing with such problems is to breed new cultivars with enhanced root architecture and function for particular drying environments. In addition, deeper fertiliser placement and enhanced plant capacity for hydraulic lift might contribute to increased uptake of nutrients from drying soil.

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Phosphorus acquisition efficiency: Root morphology and physiology

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Western Australia was a part of Gondwanaland, and some of the most ancient parts of the Earth's crust can be found here. The rocks are up to 3.6 billion years old, with some of the sediments being as old as 4.3 billion years. Other parts of the landscape originated more recently from calcareous marine deposits. Therefore, the soils of Western Australia are amongst the most heavily leached and nutrient-impooverished in the world. Moreover, the soils on lateritic profiles tightly bind phosphate, so that, phosphorus (P) is also poorly available to plants that are not adapted to these conditions. The southwest of Western Australia is also one of the world's hotspots of higher plant species diversity. Therefore, this environment offers a unique opportunity to study plant adaptations to nutrient-poor conditions.

A relatively large proportion of species from the P-poor environments in Western Australia cannot produce an association with mycorrhizal fungi, but instead, produce 'root clusters'. Root clusters are an adaptation both in structure and in functioning; they release large amounts of exudates, in particular carboxylates. Root-cluster-bearing Proteaceae in Western Australia occur on the most P-impooverished soils, whereas the mycorrhizal Myrtaceae tend to inhabit the less P-impooverished soils in this region.

The functioning of 'proteoid' root clusters in Proteaceae and Fabaceae has received considerable attention. 'Dauciform' clusters in Cyperaceae have been explored less, but they appear to function in a similar manner as 'proteoid' clusters. Research on the physiology of 'capillaroid' root clusters in Restionaceae has yet to be published.

Root-cluster growth in species of the Cyperaceae, Fabaceae and Proteaceae is systemically stimulated when plants are grown at a very low P supply, and suppressed when leaf P concentrations increase. Proteoid root clusters in Fabaceae and Proteaceae and dauciform clusters in Cyperaceae are short-lived structures, and both release large amounts of carboxylates during an 'exudative burst' at rates that are considerably faster than reported for non-specialised roots of a wide range of species. Root clusters play a pivotal role in mobilisation of P from P-sorbing soil.

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Because the world P reserves are being depleted whilst vast amounts of P are stored in fertilised soils, there is a growing need for crops with a high efficiency of P acquisition. Some Australian native species as well as some existing crops have traits that would be highly desirable for future crops. The possibilities of introducing P-acquisition efficient species in new cropping and pasture systems are currently being explored. In addition, possible strategies to introduce traits associated with a high P-acquisition efficiency into future crop species are considered promising.

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Potassium nutrition and its effect on quality and post harvest properties of potato

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Potato is a high-value crop with world-wide significance. Potato production was increasing continuously during the past decades. Today, China, Russia and India are the leading potato producers. The annual per capita consumption of potato is 31.3 kg. The potato is a multi-purpose crop widely used as table potato, for processing (crisps, chips), as seed potato and for starch production and other industrial uses (plastics, alcohol, energy). Application of potassium to potato improves the quality parameters such as starch content, contents of protein, citric acid, ascorbic acid, storage attributes such as shell strength and resistance to tuber damage as well as resistance to black spot incidence and after cooking discoloration.

Potassium is important in many physiological processes that contribute to tuber quality, and countering stresses. Some of them are:

- production, translocation, conversion and storage of carbohydrates through enzyme activation
- water use efficiency – potatoes grown with adequate K supply use less water per kg of tubers and withstand drought periods
- resistance to stress (frost, heat impact) and diseases
- tuber quality and processing characteristics.

The distribution of K varies largely in different parts of potato. About 76 percent K is accumulated in tubers, 18 percent in leaves, 4 percent in stem, and 2 percent in roots. Potassium sufficiency-level varies in different parts of potato plant. At bud stage K-sufficiency (K- percent of dry matter) range varies from 4.5 to 7.0 percent, at start of flowering from 4.0 to 6.4 percent, at end of flowering from 3.7 to 6.1 percent and at tuber formation from 3.5 to 5.7 percent. Potato is a heavy feeder of potassium. A crop with tuber yield of 40 t ha⁻¹ removes about 300 kg K ha⁻¹, out of which 250 kg is removed by tubers.

Occurrence of black spots is a serious quality-reducing factor in potato. The formation of black spots depends on both external and internal factors. The external factor includes growing conditions eg. site, fertilization, water supply, harvest conditions, post harvest treatment and storage conditions. Variety and

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maturity of tubers are another important factors. Among internal factors are free phenolic acids, organic acids (pH), other phenolic compounds and activities of enzymes besides mineral content.

The importance of K for the tuber quality is due to the fact that K is involved in the formation of free phenolic amino acids, organic acids (pH) and other phenol compounds. Potassium induced formation of citric acid for example prevents tubers from the occurrence of black spots by inhibiting the formation of grey ferric complexes inside the tuber tissue. The discoloration occurs due to combination of Fe with chlorogenic acids, which under oxidized conditions forms grey coloured ferric complexes. By increasing the foliar K content from 2 to 4 percent through adequate K supply, black spot incidence can be reduced by more than 50 percent.

Potassium nutrition has a strong influence on starch formation in tubers. In a comparative study it was found out that moderate SOP (K_2SO_4) doses increased starch content, whereas high MOP (KCl) supply resulted in a very low K content of starch in tubers.

Reducing sugars are known to be problematic during tuber processing because they induce undesired browning of chips and crisps. However, there is a strong negative correlation between K content and the amount of reducing sugars in tubers. Therefore an adequate K supply significantly decreases the content of reducing sugars in tubers. It also ensures a better coloration of potato chips. Field trials in Germany proved that SOP was more effective in preventing enzymatic discoloration than did MOP.

K fertilization is also an important means to increase the frost resistance in cold growing regions. Tuber weight losses during storage was significantly reduced by sufficient K supply during the growing period.

The field experiments testing different K rates showed that most of the relevant potato quality and post harvest parameters were positively influenced by K. In most cases, SOP was the more efficient K source in comparison to MOP.