Large root systems: are they useful in adapting wheat to dry environments?

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This paper was presented at the 2nd International Workshop on Ecosystem Assessment and Management on 'Climate Change and Agricultural Ecosystem Management in Dry Areas' held from 19 to 25 July 2010 at Lanzhou University, Lanzhou, China.

Abstract. There is little consensus on whether having a large root system is the best strategy in adapting wheat (*Triticum aestivum* L.) to water-limited environments. We explore the reasons for the lack of consensus and aim to answer the question of whether a large root system is useful in adapting wheat to dry environments. We used unpublished data from glasshouse and field experiments examining the relationship between root system size and their functional implication for water capture. Individual root traits for water uptake do not describe a root system as being large or small. However, the recent invigoration of the root system in wheat by indirect selection for increased leaf vigour has enlarged the root system through increases in root biomass and length and root length density. This large root system contributes to increasing the capture of water and nitrogen early in the season, and facilitates the capture of additional water for grain filling. The usefulness of a vigorous root system in increasing wheat yields under water-limited conditions maybe greater in environments where crops rely largely on seasonal rainfall, such as the Mediterranean-type environments. In environments where crops are reliant on stored soil water, a vigorous root system increases the risk of depleting soil water before completion of grain filling.

Additional keywords: root biomass, root length, root length density, root system size, water capture.

Introduction

This paper questions whether a large root system contributes to improved adaptation in wheat (Triticum aestivum L.) to dry environments. A large root system in wheat is described as one that has large biomass, length and root length density (Hamblin and Tennant 1987). The first account of the role played by a root system with large biomass and root length in adapting wheat to dry environments was given by Aamodt and Johnston (1936). A major finding of their study was that the large root system of the wheat cultivar Pelissier was important in the avoidance of damage by drought in a dry season on the Canadian prairies. Since that time, there has been little consensus in the value of large root systems despite most assessments of the adaptation of crops to water-limited environments having the implicit idea that a large root system is able to collect more water, and produce more growth and yield. Reviews by Kramer (1969), Hurd (1974) and Jackson et al. (2000) have suggested that a deep, wide-spreading and much-branched root system is essential in the design of drought-tolerant crops. On the other hand, Passioura (1983) suggested that small root systems could

provide benefits in water-limited situations through improved water use efficiency. He reasoned that there would be an optimum root: shoot ratio above which further increases in root size would provide limited benefits but would also impose a cost on shoot growth by consuming biomass. This was demonstrated by Ma *et al.* (2008) in root pruning experiments in which water use efficiency was increased and a shift in water consumption to the post-anthesis period provided additional benefit through an increase in the harvest index.

There are several reasons for the contrasting conclusions on the value of root system size. The primary reason is that water supply in dryland farming systems is variable among environments and seasons, and imposes water stress at different stages of crop development. For crops which grow on soil water accumulated before sowing or early in growth, there is a significant benefit in conserving water for the reproductive phase (Richards and Passioura 1989; Morison *et al.* 2008). Alternatively, for crops growing under conditions of more uniform rainfall distribution, the ability to capture water and use it quickly may be beneficial (Turner and Nicolas 1987;

Moeller et al. 2009). Severely water-stressed crops leave substantial amounts of available water in the subsoil at maturity and few would argue that the root system was too small to capture soil water. However, for crops growing on stored soil water, there may be benefit if the root system expands slowly to allow soil water to be used later during the grain filling. In a controlled environment study, Passioura (1977) showed that the proportion of water consumed before and after anthesis was correlated with harvest index and hence yield. The benefit of using subsoil moisture late in the season has been demonstrated in the field by (Kirkegaard et al. 2007). Of course, the influence of the rainfall pattern interacts strongly with soil type in terms of its water holding capacity, the depth at which water is stored in the soil and the depth of soil that can be penetrated by the roots. Thus, a genotype that performs well in one water stress environment may not necessarily perform well in another environment or season. In terms of selection and breeding, this means that the target environment and dominant pattern of moisture stress needs to be defined and understood before an appropriate root morphology can be considered.

In addition to aspects related to the adaptation value of the root systems, several experimental issues can also influence the conclusions. A major problem is that the difference between a 'large' and 'small' root system has not been described well. Parameters such as maximum rooting depth, spread of the root system, root length density, rate of root descent, number of axes or total root DW could all be taken as indication of root system size. Many of these parameters are often correlated across genotypes but this is not always the case (O'Brien 1979; Sanguineti *et al.* 2007) and the conclusions drawn will depend on which measures are used.

Furthermore, the capacity to assess the value of the size of the root system has often been limited by a restricted genotypic range in the size of the root system of the varieties assessed (Løes and Gahoonia 2004). The root systems of 'green revolution' wheat genotypes were smaller than earlier genotypes and landraces (Waines and Ehdaie 2007), a suite of *Rht* genes being shown to have a significant effect on root growth (Wojciechowski *et al.*)

2009). Landraces of barley (Hordeum vulgare L.) have also been shown to have larger root systems and greater seminal root length than cultivars (Grando and Ceccarelli 1995; Wahbi and Gregory 1995), with a historical analysis of Nordic barley breeding programs showing a long-term downward trend in seedling root weight (Bertholdsson and Brantestam 2009). In light of these results, comparisons between relatively contemporary cultivars may not capture the full genetic variation available within the species. The problem is compounded by environmental factors affecting root growth, such as acid subsoils, compaction layers, root diseases and predation (Tang et al. 2003; Higginbotham et al. 2004; Botwright Acuña et al. 2007). These factors can either limit the expression of root system size or differentially effect genotypes, compromising the capacity to assess the value of potentially different root systems.

Lessons from individual root traits for water capture

Since the O'Toole and Bland (1987) review, it has become clear that genotypic variation for root system characteristics and their function can be exploited to improve grain yields of crops when grown in environments prone to water deficit (Palta and Watt 2009). During the last 20-25 years, interest in identifying and evaluating root system traits that adapt wheat to water-limited environments has increased. Potential traits include increasing root distribution at depth to improve deep water capture (O'Brien 1979; Manske and Vlek 2002), depth of rooting to extract water from full soil depth (Hurd 1974), fast root elongation rates for deep water capture (O'Brien 1979), reducing the diameter of the xylem vessel in the seminal roots to conserve soil water (Richards and Passioura 1989), angle of seminal roots for extracting water from full soil depth (Nakamoto and Oyanagi 1994; Manschadi et al. 2006) and improve the root : shoot dry matter for improve water capture across the soil profile (Siddique et al. 1990; Reynolds et al. 2007) (Table 1).

Phenotypic screening for these potential traits has been conducted and, in the case of denser root distribution at depth

 Table 1. Root characteristics and their functional value for water uptake and increased yields under water deficit conditions (Adapted from Palta and Watt 2009)

Trait	Value	Phenotypic selection	Adoption ^A	Reference
Root distribution at depth (denser roots at depth)	Deep water capture	Selection of parents from several lines in root boxes, followed by selection for yield	No	O'Brien (1979); Manske and Vlek (2002)
Depth of rooting	Deep water capture	Phenotypic screen for several lines with a mini Rhizotron camera	Unknown	Hurd (1974)
Root elongation	Deep water capture	Phenotypic screen; root elongation measured with mini Rhizotron camera	No	O'Brien (1979)
Reduced diameter of the xylem vessel in the seminal roots	Conserves water	Phenotypic screen measuring vessel diameters	No	Richards and Passioura (1989)
Angle of seminal roots	Deep water capture	Phenotypic screen, angle of seminal root measure	No	Nakamoto and Oyanagi (1994)
Root: shoot ratio	Water extraction from soil depth	Phenotypic screen of many lines and selection of potential parents	No	Siddique <i>et al.</i> (1990); Reynolds <i>et al.</i> (2007)

^AAdoption by a public or commercial breeding company.

and reduced diameter of the xylem vessel, extreme lines have been selected and grown in the field alongside the parents to estimate grain yield. However, none of these traits has been adopted by a commercial or public breeding organisation to date. There are three major reasons for the poor adoption of these potential traits. First, an important limitation to the utilisation of root traits is that very few have been rigorously validated under field conditions to demonstrate their capacity to increase water capture and grain yield. Field validation is critical for morphological root traits because the water and soil conditions in the field during the growing season are extremely difficult to replicate under controlled environment conditions such as in pots, hydroponics or root growth boxes. This will alter both the expression of root traits and their influence on plant performance. For example, it is known that plant growth and morphology, including both roots and shoots, can be modified by the volume available for root growth, independent of nutrition or moisture stress (e.g. Krizek et al. 1985; Peterson et al. 1991a, 1991b). The difficulties are accentuated when exploring root system traits that are expressed or become important later in the life cycle, such as around flowering or during grain filling, because of the limitations imposed by soil volume. As indicated earlier, the value of a trait will vary depending on the pattern of water deficit that the crop experiences and field validation thus needs to occur in the target environment both in terms of climate and soil type.

A second reason why potential traits have not been adopted is that the genetics of many individual root traits, such as the heritability and inheritance patterns, are poorly understood. This presents a significant impediment to the effective incorporation of individual root traits into breeding programs. Progress is being made (e.g. Sharma and Lafever 1992; Camargo and Ferreira-Filho 2005; Sanguineti *et al.* 2007; Sharma *et al.* 2010). However, while there are indications that many morphological individual root traits are controlled by single genes, others, including total root system size, are controlled by complex polygenic systems and are influenced by other plant growth traits such as growth rate, duration of the vegetative phase and dry partitioning of dry matter (Monyo and Whittington 1970; Lynch 2007).

Thirdly, for implementation in breeding programs, rapid and simple screening procedures are needed. Screening for individual root traits under field conditions is labour-intensive, subject to high variability and inefficient (Lynch 2007). However, screening methods used in controlled environments must yield results that are well correlated with performance under field conditions. As discussed above, this can be problematic. For example, Wojciechowski et al. (2009) showed that the effect of *Rht* genes on root growth was strongly positive in gel cultures but strongly negative in soil. Potential approaches for efficient phenotyping of root traits under controlled conditions have recently been reviewed by Gregory et al. (2009), who indicated significant emerging capability. However, field screening remains difficult. Surrogate approaches such as screening for differences in canopy temperature may prove important (Slafer et al. 2005). Marker assisted selection offers promise under both controlled and field conditions, although limitations exist for its use with complex traits (Reynolds et al. 2005; Slafer et al. 2005).

Regardless of the interest in these individual morphological traits and their functional implications for water capture and increased yields in water-limited environments, they do not describe a root system as large or small. For instance, the denser roots at depth characteristic of the root system of the Australian synthetic derivative wheat AUS33687 and the deeper seminal roots of AUS33435, another Australian synthetic derivative wheat, measured at ear emergence (Z59 in Zadoks' growth scale for cereals; Zadoks et al. 1974) when grown on a deep sandy soil at Wongan Hills, Western Australia (WA), do not describe these systems as large when compared with the root system of AUS33684 (Fig. 1). The root system of AUS33684 neither had seminal roots as deep as those of AUS33435 nor as dense a root at depth as AUS33687, but its root system had a profuse branching in the top 0.35 m of the soil profile. This root proliferation in AUS33684 led to a higher total root length density (in the 0.0-1.2 m soil layers) than in the other two genotypes (Fig. 2). Total root length density is considered to be directly related to the amount of water uptake and to indicate the size of the root system.

Invigorating the root system in wheat is increasing its size

Vigour in the root system of wheat has recently been increased in novel germplasm through indirect selection for greater leaf size (Richards and Lukacs 2002). Here greater 'early vigour' describes faster leaf area development to increase shoot biomass (Rebetzke and Richards 1999). The value of greater shoot vigour has primarily been thought to increase water use efficiency in Mediterranean environments through shading of the soil surface to reduce water loss through soil evaporation (Botwright *et al.* 2002).

More recent evidence from recurrent selection lines for greater leaf vigour suggests that greater shoot vigour may contribute partly or fully to greater root vigour (X. Chen 2010, unpubl. data). The characteristics of a vigorous root system are early and fast



Fig. 1. Rooting patterns of three synthetic derivate wheat cultivars illustrating the desirable traits for root distribution at depth (AUS33687) and depth of rooting (AUS33435) in comparison with a larger root system (AUS33684). Measurements were made at ear emergence (Z59) on breeding plots at Wongan Hills, WA.



Fig. 2. Average root length density (in the soil volume 0-1.2 m soil profile) of three synthetic derivate wheat cultivars, AUS33687, AUS33435 and AUS33684, grown on a deep sandy soil at Wongan Hills, WA. Measurements were made at ear emergence (Z59) by coring the 0-1.2 m soil profile using a hydraulic drill. Bars indicate \pm s.e. of the mean of four replicates.

extension, early and profuse proliferation, high root biomass and high root length density (Liao *et al.* 2006; Palta and Watt 2009). So it is not surprising that leaf and root vigour are related. When 12 genotypes of wheat, including current commercial cultivars and breeding lines differing in leaf vigour, were grown in glass-walled root boxes, differences in shoot biomass at stem elongation (Z31) were closely related to variation in root biomass ($R^2 = 0.95$; y = 0.0088 + 2.14x) (Fig. 3). This suggests that increasing vigour in the shoot can also increase vigour in the root system and therefore, shoot biomass potentially offers the possibility of being a surrogate characteristic of vigour in the root system.



Fig. 3. Relationship between shoot and root biomass measured at stem elongation (Z31) in 12 wheat genotypes grown in glass-walled boxes filled to a depth of 1.0 m with soil obtained from a field site, packed to a bulk density of ~1.53 g cm⁻³. The linear regression fitted to shoot biomass is y=0.0088+2.14x ($r^2=0.95$).

Total root length density and root biomass (Waines and Ehdaie 2007; Ehdaie et al. 2010) are indicators of the size of a root system. A vigorous root system which has large biomass, length and root length density is then considered as a large root system. The early bred lines with vigorous root systems such as Vigor18 and B18, selected by Drs R. Richards and G. Rebetzke at CSIRO Plant Industry (Rebetzke and Richards 1999; Richards and Lukacs 2002), had 50-70% more root biomass and 33-83% greater root length, and captured 42-60% more nitrogen than non-vigorous commercial cultivars at stem elongation (Z31; Liao et al. 2006). However, the root elongation rates of the seminal roots and hence the depth of rooting was similar to the nonvigorous commercial cultivars (Liao et al. 2006). This indicates that the main advantage of the vigorous root system of these lines was early in the season, facilitating crop establishment and growth, and improving the capture of water and nitrogen (Liao et al. 2006; Palta et al. 2007; Palta and Watt 2009). Early in the season, capture of water and nitrogen is important in improving grain yields in wheat grown on deep sandy soils in Mediterranean-type climates where end-of-season drought (terminal drought) often occurs (Palta and Fillery 1995). Less advantage was seen around flowering and grain filling when deeper rooting was required to capture additional water, particularly when watering was withheld from 50% anthesis to simulated terminal drought (J. Palta, unpubl. data). This is not surprising, since the root system of wheat often fails to take up all the available deep soil water because root growth stops owing to the lack of available time (Passioura 1983). Root growth runs out of time because it often slows down when less photosynthetic fixed carbon is invested in root growth from ear initiation (Davidson et al. 1990; Palta and Gregory 1997) and ceases from flowering when grain filling becomes the major sink for carbon from current assimilation and stem reserves (Gregory et al. 1978). Consequently, root proliferation and elongation of the seminal roots before flowering is critical in increasing the



Fig. 4. Changes with time in the mean axis length of the seminal roots of cultivar Janz, breeding line Vigor18, and recurrent selection lines (RSL) 37-6, 38-19 and 92-11, grown in specialised glass-walled root boxes. Measurements were made by root mapping every 3 days, beginning at 4 days after sowing (DAS) and ending at 25 DAS. Vertical bars represent the (P=0.05).



Fig. 5. Total root biomass and root length measured at booting (Z45) in the commercial wheat cultivars Janz, Westonia, Wyalkatchem, the breeding line Vigor18 and the recurrent selection lines 50–4, 37–6, 38–19 and 92–11. The genotypes were grown in glass-walled boxes filled to a depth of 1.0 m with soil obtained from a field site, packed to a bulk density of ~1.53 g cm⁻³. Bars indicate \pm s.e. of the mean of four replicates.

capture of available deep water, although post-flowering root growth in wheat has been observed in the cultivar SeriM82 (Manschadi *et al.* 2006).

Improving the elongation rate of seminal roots

An S1 recurrent selection program was initiated by Dr G. Rebetzke at CSIRO Plant Industry to accumulate favourable alleles for early vigour and indirectly for root vigour, from across 20 international lines with unrelated pedigrees and thereby assumed to contain different alleles for greater early vigour. Briefly, the process followed internating of the original parents at random for two cycles before allowing specimens to self-pollinate. Approximately 6000 progeny, representing 60 random crosses, were sized to a common seed weight and then sown under favourable conditions. When seedlings developed four leaves, they were measured for leaf width, and the largest 50% (~3000 lines) were selected for transplanting to small pots. Plants were then allowed to grow under favourable conditions until maturity. Harvested seed from all 3000 lines were sized to a common weight and then sown in a replicated study. Seedlings were grown under favourable conditions until the fourth-leaf stage, when leaf widths were measured. The two most vigorous lines in each cross were retained and allowed to grow until flowering, whereupon they were intermated at random to initiate the second cycle of recurrent selection for greater early vigour. This process was repeated four times to generate Cycle four progeny. The 400 most vigorous selected lines during Cycle four were seed-sized to a common weight before sowing in 50 cm deep tubes containing a 80:20 sand : compost soil mix. These were then grown in favourable conditions until emergence of the fourth leaf, when they were harvested for leaf area and root determination. Four lines (37-6, 38-19, 50-4 and 92-11) were selected as producing very vigorous shoot and root growth (G. Rebetzke, unpubl. data).

The four recurrent selection lines (RSL) were grown together with Vigor18 and three current commercial cultivars in glasswalled boxes filled to a depth of 1.0 m with soil obtained from a field site, packed to a bulk density of ~1.53 g cm⁻³ for comparison of their root systems. The mean axis length of the seminal roots measured by root mapping every 3 days, beginning at 4 days after sowing (DAS), was greater in the RSLs than in Vigor18 (one of the original parents used in the recurrent selection program) and the cultivar Janz (Fig. 4). The rate of elongation of the axes was 2.05-2.16 cm d⁻¹ in Janz and Vigor18, and 2.74-290 cm d⁻¹ in the RSLs. Total root length at stem elongation (Z45) in the RSLs was



Fig. 6. Average canopy temperature between 1200 hours and 1400 h measured at anthesis for the commercial cultivar Janz, breeding line Vigor18 and the recurrent selection lines 37–6, 38–19 and 92–11. The genotypes were grown on a deep sandy soil at CSIRO Floreat, WA. Bars indicate \pm s.e. of the mean of four replicates.



Fig. 7. Relationship between canopy temperature measured in the field between 1200 hours and 1400 h at anthesis and (*a*) total root biomass and (*b*) total root length measured at booting (Z45) in plants grown in glass-walled boxes filled to a depth of 1.0 m with soil obtained from a field site, packed to a bulk density of ~1.53 g cm⁻³. The linear regressions fitted to canopy temperature are y=32.99-1.198x ($r^2=0.97$) for root biomass and y=34.61-24.22x ($r^2=0.98$) for total root length.

47–78% greater than in the three current commercial cultivars and 9.3–29% greater than Vigor18 (Fig. 5). Total root biomass of the RSLs was 68–113% greater than the commercial cultivars and 8.8–38% greater than Vigor18 (Fig. 5). This indicates that elongation rates of the seminal roots and, presumably, the depth of rooting was improved as the root system of wheat was enlarged by genetically increasing leaf vigour.

Canopy temperature measured by infrared thermometry is a method for estimating crop water and heat stress in wheat (Blum et al. 1989; Reynolds et al. 1998). Under conditions of droughtstress, wheat genotypes with lower midday canopy temperatures had a better plant water status (Blum et al. 1989). Average canopy temperature measured between 1200 hours and 1400 hours at anthesis was 1.5-3.6°C lower in the RSLs than in Vigor18 and 3.6–5.7°C lower than in the cultivar Janz (Fig. 6). The genotypes were grown in rain-fed conditions and by the time the RSLs were at anthesis, the top 0.7 m of the soil profile was already dry. Therefore it is likely that the low canopy temperature of the RSLs, particularly 92-11 and 38-19, reflected water extraction at deeper layers compared to the other genotypes. Preliminary analysis indicates that the lines 92-11 and 38-19 accessed 9.5 and 7.2 mm more soil water, respectively, than the cultivar Janz, and yielded 0.50 and 0.35 t ha⁻¹, respectively, more than Janz (X. Chen, unpubl. data). In a recent crop simulation model exercise, Lilley and Kirkergaard (2010) quantified the predicted benefits of modifying wheat root systems in the variable Australian climate for a range of soils and crop management scenarios. They demonstrated that wheat varieties with faster and more efficient root growth provided significant yield benefits (0.3 to 0.4 tha^{-1}) at all of the sites tested and such traits would rarely result in yield reduction.

The measured canopy temperature in the field at anthesis was closely related to root biomass ($R^2 = 0.97$; y = 32.99 - 1.198x) and total root length ($R^2 = 0.98$; y = 34.61 - 24.22x) measured at booting (Z45) in plants grown in glass-walled root growth boxes (Fig. 7). Increasing the vigour of the root system and hence its size lowered the canopy temperature because the crop had a better plant water status, as the roots were accessing more water. Canopy temperature potentially offers the possibility of

phenotyping wheat lines non-invasively in the field for the size of the root system.

The contribution of vigorous root systems in wheat to increased yield under water-limited conditions depends on the pattern of development of the water deficits in the target environment. For instance, in environments where wheat is mostly grown on stored soil water, such as in north-eastern Australia, vigorous root systems run the risk of exhausting the soil water before completing grain filling and hence reducing yield. In a quantitative analysis of root adaptive traits for southern Queensland, Australia, Manschadi et al. (2006) demonstrated that the wheat genotype SeriM82 was tolerant to terminal drought because its compact, uniform and deep root architecture reduced water use early in the season and increased access to water from deeper soil layers during the grain filling. In Mediterranean-type environments where crops depend mostly on in-crop rainfall, vigorous root systems are critical for increasing growth, pre-anthesis water use and yield if they also have deep seminal roots.

Conclusions

Despite the increasing interest in individual morphological root traits and their functional implications for water capture under water-deficient conditions, there is still little consensus on whether a large root system contributes to wheat adaptation in water-limited environments. This is because the individual root traits, which include the depth of rooting, root elongation rate, root distribution at depth, diameter of the xylem vessel, angle of seminal roots and root: shoot dry matter ratio, do not adequately describe a root system as large or small. We believe that increasing root vigour in wheat will increase the total size of the root system, as greater vigour encapsulates early and fast rates of root extension, and early and profuse root proliferation correlates to an increase in root biomass and root length density. Furthermore, a vigorous or large root system contributes to adaptation in dry environments and dry seasons where crop growth depends on seasonal rainfall. However, a large root system may be of less value in environments where crop growth is dependent on stored

soil water where access to more soil water runs the risk of exhausting soil water before completing grain filling.

Acknowledgements

We thank Professor Neil C. Turner and Dr Helen Bramley for critically reading the manuscript.

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Manuscript received 28 January 2011, accepted 24 March 2011