Genetic Opportunities to Improve Cereal Root Systems for Dryland Agriculture

Richard A. Richards

CSIRO Plant Industry, Canberra, ACT 2601, Australia

Abstract: Understanding the major limitations to root growth is very important if we are to maximize water and nutrient use and increase yields. Limitations may be insufficient rooting depth, root diseases, nutrient deficiencies, toxicities and soil hardness. An understanding of these limitations will lead to more precisely identifying traits for which to select and breed. Examples of successfully overcoming limiting factors to improve crop performance by breeding and selection are given for cereal cyst nematodes in wheat, soil acidity and salinity. The importance of altered crop management practices to reduce limitations is also stressed. These have resulted in a more effective and healthier root system, which results in more water use and greater yields. Opportunities to genetically increase the size of the root system in dryland systems where water and nutrients are not all used by the crop are given.

Keywords: Breeding, Root growth, Root health, Root physiology, Water uptake, Wheat.

Plant growth and grain yield are affected by many soil factors such as dryness, hardness, alkalinity, acidity, salinity, nutrient limitation and soil-borne diseases. Identifying important genetic variation in plant roots to overcome some of these limitations is thus important to improve crop growth and yield.

Faster and more extensive root growth is believed to be important for good plant growth under most adverse soil conditions. Such a root system is expected to extract more available soil water if it is dry, increase nutrient uptake, escape some root diseases and be competitive with weeds thereby resulting in higher yields. These should also promote more sustainable agricultural systems by reducing leakage of water and nutrients. Nevertheless, a faster growing root system may not always be desirable as in some water-limited environments slower root and shoot growth may be important so that water is available for grain filling (Passioura, 1972).

In the past, progress to genetically alter root systems has been slow for several reasons. The most notable is that it is difficult to select for root system traits. Also, to know what to select for has not always been clear. Root systems can be altered through management practices as well as by genetics and both must be considered when identifying the most effective ways to maximize water and nutrient use and to escape root diseases. Changes in management practices can be very powerful and adoption can be much quicker than breeding as the development of new varieties may take ten to twenty years.

Management Practices to Improve the Root System of Cereals

Management practices should be considered first as these can often be adopted quickly and often have greater effects than genetic changes to root systems. The best example of altering crop management that result in healthy root systems is the use of break crops. For example, canola used as a break crop in Australia improves root health where wheat is the dominant crop (Angus et al., 1991; Kirkegaard et al., 1994; Gardner et al., 1998). Growing canola in the rotation leads to healthier cereal root systems that extract more water and nutrients from the soil in cereal crops. Responses to nitrogen can also be greater. A 10% yield benefit as a result of canola in the rotation is not uncommon in cereal growing regions in Australia (Angus and van Herwaarden, 2001). Other examples are precision placement of seed to avoid disease such as crown rot when planting into wheat stubble, also narrow points to reduce rhizoctonia infection in cereals.

An important management practice to increase root growth, root depth and nutrient uptake in cereals is to extend the growth duration (Gomez-Macpherson and Richards, 1995; Batten et al., 1999). Wheat roots, on average, grow 1cm deeper per day in the field from sowing to flowering (Kirkegaard and Lilley, 2007). Thus, if water is available, root depth can be simply increased by extending growth duration and so by planting a month earlier but keeping anthesis date the same, root depth may increase about 30cm. A variety which has a genetic delay to flowering may also be required to achieve an extended vegetative duration.
Choosing varieties that have genes for vernalisation response may therefore be important. In some environments, sowing cereals just one week earlier can have a significant impact on yield (Anderson, 1992). One of the reasons earlier sowing may be important is that it enables crops to access water deeper in the profile then this water can contribute very significantly to grain yield. For example, for wheat in Australia it has been estimated that extraction of an extra 10 mm of water from deep in the profile may contribute an extra 350 kg per hectare of grain when it is dry (Angus and van Herwaarden, 2001). An extended vegetative duration is also important for increasing nutrient acquisition and this is likely to be due to a larger root system and access to a greater volume of soil (Batten et al., 1999). Another management option that may be important to increase root length density at depth is to increase sowing density.

**Breeding Strategies to Improve Root Systems**

Important root system traits that have a high heritability should be targeted first in breeding. These are likely to be controlled by single genes. There are several success stories where single genes have been used to increase resistance to root disease or limit the impact of a chemical property of the soil which in turn improves water use and yield. There are perfect molecular markers for resistance to cereal cyst nematode (Ogbonnaya et al., 2001) and so resistant plants can be identified from healthy seeds or young seedlings without the need for infection. A healthy root system achieved by incorporating genetic resistance to root diseases contributes to increased rooting depth and extent and hence to increased extraction of water and nutrients from deeper layers.

Selecting for acid soil tolerance in wheat is another success story that improves water uptake, nutrient absorption and yield in acid soils. Wheat is generally sensitive to acid soils; elegant work in both Japan and Australia (Delhaize et al., 1995; Delhaize and Ryan, 1995; Matsumoto, 2000; Ma et al., 2001; Osawa and Matsumoto, 2001; Sasaki et al., 2004) has been responsible for identifying the mechanism for acid soil tolerance in wheat and the gene responsible. No adverse effects of this gene in different genetic backgrounds have been detected.

Improving salt tolerance in durum wheat is another example where single genes that alter root function may be important (Munns, 2005). Durum wheat, which is an allotetraploid, is the most sensitive temperate cereal species to salinity, whereas hexaploid wheat is very tolerant as it has a gene on chromosome 4D that is responsible for keeping sodium out of the plant. Durum wheat lacks the D genome and thus is salt sensitive. A salt tolerant durum wheat landrace has been identified (Munns et al., 2003) and two different genes that control salt tolerance in this landrace have been identified (Munns et al., 2003). Molecular markers for these genes have now been identified (Lindsay et al., 2004). One gene is responsible for keeping sodium out of xylem vessels in the roots (Davenport et al., 2005). The second gene controls keeping sodium out of the leaf laminar.

In each of the above examples major genes have been identified that can be used in breeding. However, most root system traits are likely to be controlled by multiple genes and the heritability of traits may therefore be low as well as difficult to measure. This raises the question as to whether it may also be possible to alter root systems by selecting for aboveground traits. Extending the duration of the pre-flowering period mentioned earlier is one such example. There is evidence that inhibiting tillering in cereals may be another (Duggan et al., 2005). Most cereals produce an excessive number of tillers as often only half the tillers that emerge become fertile. If tillering is reduced, then resource allocation changes (Duggan...
et al., 2005). A major gene that reduces excessive tiller production in wheat has been identified on chromosome 1A (Richards, 1988; Spielmeyer and Richards, 2004). Both controlled environment data (Hendricks unpublished, 2004; Duggan et al., 2005 unpublished) and field data (see Richards et al., 2007) have demonstrated that lines possessing the tin gene have an increased root length. Fig. 1 shows the root to shoot ratio in near-isogenic lines differing in a gene that restricts tillering. It shows that just after the beginning of tillering more carbon is allocated to roots than to shoots in the low tillering line relative to its free tillering near-isogenic counterpart. This appears to be an example where reduced aboveground growth has resulted in enhanced belowground growth which was also noted by Gomez-Macpherson et al. (1998).

There is some evidence that aboveground vigour may be related to root system vigour (Table 1). A breeding line, Vig 18, developed by combining traits contributing to early aboveground vigour (Richards and Lukacs, 2002) has been shown to have greater root vigour in direct drilled soils (Watt et al., 2003) and in root boxes (Liao et al., 2004) when compared with the widely grown commercial wheat Janz. Table 1 show a substantial increase in total biomass of Vig 18 over Janz when grown in an outdoor lysimeter system. This is associated with a significant increase in root biomass, root length, root surface area as well as a significant increase in total nitrogen per plant.

It is of interest that increased plant height is not related to longer roots in wheat (Cholick et al., 1977), although in barley there is evidence that recently bred dwarf barleys have a more extensive root system than older, taller barleys (Chloupek et al., 2006).

### The Cereal Root System and Opportunities for Improvement

Temperate cereals have a dual root system. Seminal roots emerge from the seeds at the time of germination. When plants have around four main stem leaves a secondary root system develops. These are nodal roots and they appear from culm nodes and they have a different anatomy from seminal roots. When the nodal roots appear, the seminal root can already be 40cm deep in the soil. Thus, to increase water extraction from deeper soil layers, attention should be on the seminal roots. The nodal roots can be ignored, although they are important for nutrient and water acquisition in the top 30 cm of soil.

Wheat generally only produces three seminal axes whereas barley usually produces around five or six. This small number of axes is responsible for water and nutrient use from deeper soil layers late in the season. This raises the question as to whether it is possible to genetically increase the number of seminal axes in wheat. Doubling the number from three to six should increase root density and possibly improve the chances of water and nutrient extraction particularly late in the season when these resources are particularly important. Significant variation in the number of seminal axes is evident in wheat (Robertson et al., 1979; Richards and Passioura, 1981) and also in barley (Grando and Ceccarelli, 1995).

Another way to increase rooting depth may be to increase the rate of elongation of the seminal roots. Little is known about genetic variation in elongation rate of the seminal axes. Evidence for genetic variation in rate of seminal root elongation is presented in Richards et al. (2007). An increased total root length can also be achieved by more or longer branches arising from the seminal axes. The tiller inhibitor gene mentioned earlier increases root branching (Duggan et al., 2005; Richards et al., 2007). Some breeding lines originating from crosses between high and low vigour wheat genotypes also show very substantial increases in root branching compared with commercial wheat varieties (Liao et al., 2004, Table 1).

Potential therefore exists to identify important genetic variation in the number of seminal axes, the rate of root elongation, and the extent of root branching. It is likely that these components of root vigour are controlled by different genes. If this is the case, then these three traits could be pyramided which could substantially increase the size and extent of the root system.

Effective screening methods are required for breeding to improve root system traits. This is not easy and little research has been conducted to evaluate or validate root traits and their impact on growth and yield. Success in breeding for root traits has come about when the limitation is well understood such as for acidity or salinity discussed earlier. However, other limitations in root systems are more complex, such as not being able to extract soil water deep in

---

**Table 1.** Plant biomass and total N uptake by Vig 18 and Janz grown in an outdoor lysimeter system at tillering (35 DAS). Table adapted from Liao et al. (2004).

|          | Total biomass (g plant⁻¹) | Root biomass (g plant⁻¹) | Root length (m plant⁻¹) | Root surface area (cm² plant⁻¹) | Depth of rooting (m) | Total N (mg N plant⁻¹) |
|----------|---------------------------|--------------------------|-------------------------|---------------------------------|---------------------|------------------------|
| Janz     | 0.23                      | 0.10                     | 11.5                    | 39                              | 0.89                | 7.90                   |
| Vigour 18| 0.49                      | 0.21                     | 21.5                    | 71                              | 0.91                | 17.48                  |
| l.s.d. (P=0.05) | 0.09                  | 0.05                     | 3.23                    | 8.86                            | N.S.                | 2.10                   |
the soil profile and not usually available to crops, or water that escapes from the root zone in light-textured soils. Soils are rarely uniform and hence roots do not grow uniformly in them. Roots of annual plants often grow in pre-existing channels that may have formed from earlier vegetation or down other paths of least resistance such as soil cracks (Watt et al., 2006). It will therefore be very important to carefully validate any screening method, which is usually conducted in controlled environments, with results from the target cropping region.

For success in breeding, it will be important to determine precise and fast screening methodologies that are repeatable, and have a high heritability. If this is not possible, but QTL’s can be identified through careful phenotyping, then these must be robust across breeding populations and account for a significant proportion of the genetic variation. Most importantly, they will have to be validated in field grown plots.

Acknowledgement

I am greatly indebted to Dr Terauchi Takayoshi, Crop Science Laboratory, Department of Crop Science and Agronomy, Graduate School of Agriculture, Hokkaido University, Sapporo for his dedicated help in completing this manuscript.

References

Andersson, W.K. 1992. Increasing grain yield and water use of wheat in a rainfed mediterranean type environment. Aust. J. Agric. Res. 43 : 1-17.

Angus, J.F. and van Herwaarden, A.F. 2001. Enhancing WUE in dryland and rainfed crop production. Agron. J. 93 : 290-298.

Angus, J.F., van Herwaarden, A.F. and Howe, G.N. 1991. Productivity and break crop effects of inter-growing oilseeds. Aust. J. Exp. Agric. 31 : 669-677.

Batten, G.D., Fettell, N.A., Mead, J-A. and Khan, M.A. 1999. Effect of sowing date on the uptake and utilization of phosphorus by wheat (cv Osprey) grown in central New South Wales. Aust. J. Exp. Agric. 39 : 161-170.

Chloupek, O., Forster, B.P. and Thomas, W.T.B. 2006. The effect of semi-dwarf genes on root system size in field grown barley. Theor. Appl. Genet. 112 : 779-786.

Cholick, F.A., Welsh, J.R. and Cole, C.V. 1977. Rooting patterns of semi-dwarf and tall winter wheat cultivars under dryland field conditions. Crop Sci. 17 : 637-639.

Davenport, R., James, R.A., Zakrisson-Plogander, A., Tester, M. and Munns, R. 2005. Control of sodium transport in durum wheat. Aust. J. Exp. Agric. Res. 45 : 1367-1374.

Delhaize, E., Ryan, P.R. and Randall, P.J. 1993. Aluminium tolerance in wheat (Triticum aestivum L.). II. Aluminium-stimulated excretion of malic acid from root apices. Plant Physiol. 103 : 695-702.

Delhaize, E. and Ryan, P.R. 1995. Aluminium toxicity and tolerance in plants. Plant Physiol. 107 : 315-321.

Duggan, B.L., Richards, R.A. and van Herwaarden, A.F. 2005. Agronomic evaluation of a tiller inhibition gene (tin) in wheat : II. Growth and partitioning of assimilate. Aust. J. Agric. Res. 56 : 179-186.

Gardner, P.A., Angus, J.F, Pitson, G.D. and Wong, P.T.W. 1998. A comparison of six methods to control take-all in wheat. Aust. J. Agric. Res. 49 : 1225-1240.

Gomez-Macpherson, H. and Richards, R.A. 1995. Effect of sowing time on yield and agronomic characteristics of wheat in south-eastern Australia. Aust. J. Agric. Res. 46 : 1381-1399.

Gomez-Macpherson, H., Richards, R.A. and Masle, J. 1998. Growth of near-isogenic wheat lines differing in development. II. Plants in a simulated canopy. Ann. Bot. 82 : 323-330.

Grando, S. and Ceccarelli, S. 1995. Seminar root morphology and coleoptile length in wild (Hordeum vulgare ssp. Spontaneum) and cultivated (Hordeum vulgare ssp. Vulgare) barley. Euphytica 86 : 73-80.

Kirkegaard, J.A., Gardner, P.A., Angus, J.F. and Koetz, E. 1994. Effect of Brassica break crops on the growth and yield of wheat. Aust. J. Agric. Res. 45 : 529-545.

Kirkegaard, J.A. and Lilley, J.M. 2007. Root penetration rate—a bench mark to identify soil and plant limitations to rooting depth in wheat. Aust. J. Exp. Agric. 47 : 590-602.

Liao, M., Fillery, I.R.P. and Palta, J.A. 2004. Early vigorous growth is a major factor influencing nitrogen uptake in wheat. Func. Plant Biol. 31 : 121-129.

Lindsay, M.P., Lagudah, E.S., Hare, R.A. and Munns, R. 2004. A locus for sodium exclusion (Nax1), a trait for salt tolerance, mapped in durum wheat. Func. Pl. Biol. 31 : 1105-1114.

Ma, J.F., Ryan, P.R. and Delhaize, E. 2001. Aluminium tolerance in plants and the complexing role of organic acids. Trends in Plant Sci. 6 : 273-278.

Matsumoto, H. 2000. Cell biology of aluminum toxicity and tolerance in higher plants. Int. Rev. Cytologia. 200 : 1-46.

Munns, R., Hare, R.A., James, R.A. and Rebetzke, G.J. 2000. Genetic variation for improving the salt tolerance of durum wheat. Aust. J. Agric. Res. 51 : 69-74.

Munns, R., Rebetzke, G.J., Husain, S., James, R.A. and Hare, R.A. 2003. Genetic control of sodium exclusion in durum wheat. Aust. J. Agric. Res. 54 : 627-635.

Munns, R. 2005. Genes and salt tolerance : bringing them together. New Phytol. 167 : 645-663.

Ogbonnaya, F.C., Subrahmanyam, N.C., Moullet, O., de Majnik, J., Eagles, H.A., Brwon, J.S., Eastwood, R.F., Kollmorgen, J., Appels, R. and Lagudah, E.S. 2001. Diagnostic DNA markers for cereal cyst nematode resistance in bread wheat. Aust. J. Agric. Res. 52 : 1367-1374.

Osawa, H. and Matsumoto, H. 2001. Possible involvement of protein phosphorylation in aluminium-responsive malate efflux from wheat root apex. Plant Physiol. 126 : 411-420.

Passioura, J.B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23 : 745-752.

Richards, R.A. and Passioura, J.B. 1981. Seminal Root Morphology and Water Use of Wheat II. Genetic Variation. Crop Sci. 21 : 253-255.

Richards, R.A. 1988. A tiller inhibitor gene in wheat and its effect on plant growth. Aust. J. Agric. Res. 39 : 749-757.

Richards, R.A. and Luakacs, Z. 2002. Seedling vigour in wheatsources of variation for genetic and agronomic improvement. Aust. J. Agric. Res. 53 : 41-50.

Richards, R.A., Watt, M. and Rebetzke, G.J. 2007. Physiological traits and cereal germplasm for sustainable agricultural systems. Euphytica 154 : 469-425.
Robertson, B.M., Waines, J.G. and Gill, B.S. 1979. Genetic variability for seedling root numbers in wild and domesticated wheats. Crop Sci. 19 : 843-847.

Sasaki, T., Yamamoto, Y., Ezaki, B., Katsuahara, M., Ahn, S.J., Ryan, P.R., Delhaize, E. and Matsumoto, H. 2004. A wheat gene encoding an aluminum activated malate transporter. Plant J. 37 : 645-653.

Spielmeyer, W. and Richards, R.A. 2004. Comparative mapping of wheat chromosome 1AS which contains the tiller inhibition gene (tin) with rice chromosome 5S. Theor. Appl. Genet. 109 : 1303-1310.

Watt, M., McCully, M.E. and Kirkegaard, J.A. 2003. Soil strength and rate of root elongation alter the accumulation of Pseudomonas spp. and other bacteria in the rhizosphere of wheat. Func. Plant Biol. 30 (5) : 483-491.

Watt, M., Kirkegaard, J.K. and Passioura, J.B. 2006. Rhizosphere biology and crop productivity. Aust. J. Soil Res. 44 : 299-317.