

# PLANT ROOTS

## THE HIDDEN HALF

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## Root Architecture-Wheat as a Model Plant

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### I. INTRODUCTION

Root characteristics play an important role in the development of new wheat germplasm with improved drought tolerance, nutrient and water uptake efficiency, lodging resistance, and tolerance to mineral toxicity. These traits are especially relevant for the adaptation of wheat to marginal environments, with increasing demand for wheat production at a time when water and phosphorus are becoming scarce commodities worldwide. This chapter describes the morphology, physiology, ecology, and function of wheat roots, and reviews the current status of knowledge regarding heritability and genetic diversity of root traits of wheat.

### II. MORPHOLOGY AND PHYSIOLOGY OF WHEAT ROOTS

Two root types are distinguished in cereals—the seminal roots (also called primary roots), which develop at the scutellar and epiblast nodes of the embryonic hypocotyl of the germinating caryopsis, and adventitious roots (also called shootborne, nodal, secondary, or crown roots), which subsequently emerge from the coleoptilar nodes at the base of the apical culm and tillers. These two categories of roots function in a complementary manner, and thus the root system must be considered as a whole. The number of seminal roots in cereals is usually five to seven but may reach 10.

However, not all primordia always develop. In wheat, three to six seminal roots normally emerge from the seed, but genetic variations exist among the various cultivars (Robertson et al., 1979). Seed size and seminal root number are positively correlated, although in some genotypes this is not the case. (O'Toole and Bland, 1987). The seminal roots constitute 1-14% of the entire root system. They grow and function throughout the whole vegetative period, and penetrate the soil earlier and deeper than the adventitious roots. The wheat crown root system develops on the lower shoot internodes, typically 1-2 cm beneath the soil surface. The seminal root system is very important for the establishment of wheat seedlings. Crown roots begin to develop only at the first foliar node, when the fourth mainstem leaf appears. Root axes (generally, two to four per node) then emerge from successive higher nodes (Klepper et al., 1984). The unique relationships between stem nodes and crown roots permits the establishment of correlations between shoot and root development (Klepper, 1991). The stage of development of the crown root system can be calculated from the phyllochron, which is the unit of time between equivalent growth stages of successive leaves. The phyllochron depends on the air temperature. In wheat, each phyllochron requires ~ 100 growing degree days (Rickman et al., 1984).

Adventitious roots mostly occupy the upper soil layers and their number depends mainly on the tillering ability of the plant. Root number and tillering thus are

positively correlated (Hockett, 1986). The ratio of seminal to adventitious roots is also altered by the degree of tillering, and consequently by interplant competition. A high-input ideotype of wheat is characterized by a low number of tillers, by a high harvest index, and by seminal root dependence. In contrast, low-input genotypes develop a larger root system, essentially based on adventitious roots exploring a greater soil volume. Indeed, research results at CIMMYT in Mexico showed that the number of tillers was positively correlated with root length density and grain yield of semidwarf bread wheat cultivars (BWs) grown under P deficiency in acid soils (Manske et al., 2000). Tiller numbers did not affect grain yield and root length density when P was amply available.

The average root radius of wheat plants ranges between 0.07 and 0.15 mm. The root length density (RLD) varies between 2 and 10 cm cm<sup>-3</sup> soil depending on the stage of plant development, soil depth, and environmental factors. The horizontal spread of the roots of a wheat plant is usually between 30 and 60 cm. However, under deficient moisture conditions, they invade lower horizons and have a greater vertical distribution (Mishra et al., 1999). The roots can be abundant at soil depths > 100 cm with some roots even reaching < 200 cm (Gregory et al., 1978).

Root hairs and extramatrical hyphae of vesicular-arbuscular and arbuscular mycorrhizal fungi (AMF) enlarge the effective absorbing surface area considerably. Root hairs have a diameter of 0.003-0.007 mm, a length of 3-13 mm, and a normal life-span of a few days. They emerge just behind the root tip, at the zone of root elongation. The root surface of a single wheat plant thus varies in terms of number, size, length, and life span of root hairs.

Mycorrhiza is the mutualistic association between soilborne fungi and roots of higher plants. The AMF derive their carbon compounds from the host plants and in return for a delivery of mineral nutrients to the host plant. Intercellular arbuscules are the main sites of nutrient and carbon exchange between the fungi and the host cytoplasm. Wheat roots are usually infected by soilborne vesicular-arbuscular and AMF (Young et al., 1985). The AMF extramatrical hyphae, which also extend several centimeters away outside of the roots into the soil rhizosphere, are 5-10 times thinner than the root hairs and explore an area around the root, which exceeds the zone of nutrient depletion around uninfected roots (Smith and Smith, 1990). The finer hyphae enter pores of soil aggregates not accessible to roots and root hairs. These hyphae absorb relatively immobile elements (P, Zn, Cu) in such inaccessible

fractions of the soil. This enables these fungi to benefit plants. Another advantage of mycorrhizae is that the extramatrical hyphae remain functional for a long time, and continue to provide an uptake pathway even when roots become suberized (Bowen et al., 1975). In field surveys conducted in India, Mexico, and Germany, with > 200 wheat genotypes grown in different soils and under different water and fertilizer

regimes, the roots were always infected by AMF (authors' unpublished information). In one trial in India, where sewage water was used for irrigation, AMF was absent (Liittger, 1996). AMF spores are sensitive to the accumulation of heavy metals.

### III. ECOLOGY AND FUNCTION OF WHEAT ROOTS

Extensive root growth is often required for improved growth of shoots and for higher yields in marginal environments. Complex feedback systems between roots and soil take place in the rhizosphere, which commonly comprises 20--30% of the topsoil volume. In compacted soils, roots are shorter, thicker, and more irregularly shaped than the thinner, fibrous roots that develop under noncompacted conditions (Dexter, 1987; Chapter 45 by Masle in this volume). Wheat produces finer roots per unit soil volume under conditions of low nutrient and water supply. Moreover, it exhibits a remarkable plasticity in root growth, adjusting to the soil nutrient and water status (Cholick et al., 1977; Vlek et al., 1996; Chapter 34 by Glass in this volume). Wheat plants can respond to nutrient and water stress via various mechanisms--alternations of root branching and root extension rates (Horst et al., 1996), increased rate of uptake per

unit root length or weight (Egle et al., 1999), higher root:shoot ratios (Manske, 1989; Hamblin et al., 1990), more and longer root hairs (Foehse et al., 1991), enhancement of root exudates (Neumann and Romheld, 1999), and AMF infection (Manske et al., 1995)--and by lowering demand for nutrients and water for growth. Each of these parameters can be altered by selection and breeding.

Roots tend to proliferate in the soil zones of more favorable nutrient and water supply, but avoid sites of hypoxia or toxic levels of minerals. As a result, wheat roots are more abundant in the upper soil layers which are better aerated and richer in nutrients than deeper horizons. Usually, 70% of the total root length are found in the 0-30 cm soil layer, where the nutrients are concentrated in most agricultural soils. The five

principal functions of roots are listed below and discussed in relation to wheat.

### A. Nutrient Uptake Efficiency

Wheat roots in the upper soil layers have an outstanding capability to absorb nutrients, and most of the nutrient requirements can be satisfied by these roots. Only a fraction of the nutrients are absorbed from the deeper soil (Bole, 1977). However, under P stress, roots will proliferate in the deeper soil profile, allowing access to residual, native P in the deeper soil layer in an Andisol in Mexico (cf. Manske et al., 2000).

The geometry of the root system is a key to improvement of nutrient uptake as it may be manipulated to maximize RLD in those places where nutrients and water are more readily available. Wheat plants can only extract immobile nutrients such as P from soil close to the root surface. The quantities extracted are limited by the concentration at the root-soil interface. The soil solution concentrations of phosphate are small ( $\approx 0.05 \text{ } \mu\text{g g}^{-1}$ ) compared to that of nitrate-N ( $100 \text{ } \mu\text{g g}^{-1}$ ). Very little of the phosphate is moved to the root by capillary water movement (F6hse et al., 1991). The wheat roots have to grow until they come in contact with unexplored soil from which they can extract phosphate. Therefore, root length is the major determinant of the absorbing surface area. Wheat genotypes with higher root length density are able to take up more P (Manske et al., 2000). This is most important in soils of low P availability. At low-P supply, the linear correlation between RLD and P uptake or grain yield is usually 0.50-0.60, but with adequate P supply this correlation is weaker (Manske et al., 1995, 2000).

Root diameter and root hair abundance are other important determinants of P uptake efficiency in wheat (Jones et al., 1989). Genotypes with thinner roots showed improved P uptake (Manske et al., 1996a). At high P and ample water supply, root hairs are rudimentary, whereas under deficient conditions long root hairs are abundant (F6hse et al., 1991). Root hair length and density play a significant role in P acquisition, because they modify the P depletion profiles in the rhizosphere (Gahoonia et al., 1997). Root hair density, scored in plants grown in pot cultures with quartz sand, varied considerably among 19 BWs, and were positively correlated ( $r = .77$ ) with P uptake at anthesis when grown on a P-deficient calcareous Aridisol (Manske, 1997).

Vesicular-arbuscular and arbuscular mycorrhizal fungi (AMF) are also of importance for the uptake of nutrients that are relatively immobile-e.g., P

(Hayman and Mosse, 1971), Cu (Gildon and Tinker, 1983), and Zn (Swaminathan and Verma, 1979). The AMF infection improves P influx (P uptake per unit root length). Increased fertilizer doses reduce the infection by native AMF. With reduced fertilizer application in an irrigated field trial, improved AMF infection at the stage of tillering resulted in higher grain yields (Manske et al., 1995). In a P-fixing, acid Andisol, AMF infection rate was positively correlated with P uptake into wheat shoots ( $r = .47$ ) (Manske et al., 2000). However, this explains only 25% of the variance of P uptake. Other traits like RLD and phosphatases excretion by the roots were also important.

Roots induce changes in the pH of their rhizosphere. Carboxylic acids, especially citric and malic acid, are the major compounds in exudates of wheat roots that are responsible for this process. Compared with other monocots, wheat is highly resistant to lime-induced chlorosis caused by Fe deficiency. Under conditions of Fe deficiency, the roots release high amounts of chelating exudates (phytosiderophores), which form plant available Fe-phytosiderophore complexes and transport Fe to the roots (Marschner et al., 1986). Exudation promotes the dissolution of poorly available nutrients such as P (Neumann and Romheld, 1999) and Mn (Godo and Reisenhauer, 1980). Poorly available organic P in the soil, which commonly accounts for 40-50% of the total P supply to plants, can be utilized with the help of root phosphatases (Helal, 1990). Genotypic differences in root phosphatase, excreted or bound at the root surface, exist (McLachlan, 1980). The acid phosphatase activity at the surface of intact wheat roots was determined from 4-week-old plantlets of 42 bread wheats from the CIMMYT collection grown in P-free nutrient solution by the p-nitrophenyl assay (Tabatabai and Bremner, 1969). Results were positively correlated ( $r = .49$ ) with P uptake of those genotypes grown in the field on a P

deficient Andisol (Manske, 1997; Portilla et al., 1998), which indicates that the wheat plants could utilize organic P from the soil. The measurement of phosphate activity in nutrient solution is a nonsophisticated but reliable method to screen wheat germplasm for root phosphate activity.

### B. Drought Tolerance and Water Accessibility

The traits associated with high-uptake efficiency of water are similar to those for nutrient uptake efficiency. However, the soil water status is more dynamic in nature. Thus, a well-developed root system COID

bines the ability to reach residual moisture deep in the soil profile with a high degree of plasticity to adjust to rapid changes in topsoil water status. In rain-fed wheat, root length densities are much higher in drier years than in humid ones (Hamblin et al., 1990). Wheat grown on residual moisture depends on roots that reach the deep soil layers (Mian et al., 1993; Bai et al., 1997). Varietal differences in rooting depth of wheat were demonstrated (cf. Hurd, 1968). Droughttolerant semidwarf bread wheats formed more roots in the deeper layers (by the cultivars Pastor, Sujata Dharwar, Synthetic 2), whereas the nontolerant checks (Sonalika, Tevee2, Baviacora, and Pavon) had fewer roots in the deep soil (Table 1). Improved total root volume in the whole soil profile (0-100 cm) was not responsible for improved water use efficiency. RLD in the upper soil was even negatively correlated ( $r = -.70^{**}$ ) with grain yield, but not in the deeper soil. Scores for green stay were positively correlated ( $r = .69^{**}$ ) with RLD in deep soil layer (80-100 cm). Especially the high-yielding genotypes Sujat and Synthetic 1 stayed long green. Grain yield was not significantly related to RLD in the deep soil layer, because Check 3 and Synthetic 2 had high RLD in the deep soil, but low yield potential (Table 1). Therefore, breeding for improved drought tolerance

has to combine both high-yield potential and improved root systems.

Genetic factors also influence the spatial distribution of seminal and adventitious roots in wheat. The plagiogravitropic growth of the axes, from which the root emerges, determines the shape of the root system. The plagiogravitropic response of a nodal root depends on its diameter and on the position of the internode from which it emerges. The rooting depth is closely related to the growth angle of the seminal roots (Oyanagi et al., 1993).

### c. Lodging Resistance

Lodging is often caused by strong winds that affect plants with a poorly developed anchoring root system. The plants lean at an angle, though each of the stems remains rigid and straight. Lodging-resistant wheat is positively correlated with the spreading angle of roots (pin thus, 1967).

### D. Tolerance to Waterlogging

In considerably large areas of wheat cropping, yields are reduced due to waterlogging. Prolonged periods of rainfall combined with poor soil drainage often causes

Table 1 Grain Yield, Scores for Stay Green, and Root Length Density (RLD) at Different Soil Layers (0-100 cm) of 12 Wheat Genotypes with Different Drought Resistance Grown on Residual Moisture (one single irrigation at sowing time) in an Arid Environment in Northwest Mexico (means of six replication)

| Genotypes   | Grain yield |                   | RLD in diff. soil layers |                    |                      |
|-------------|-------------|-------------------|--------------------------|--------------------|----------------------|
|             | t ha-1      | Scorea stay green | 0-100 cm<br>cm cm-3      | 0-20 cm<br>cm cm-3 | 80-100 cm<br>cm cm-3 |
| Sonalika    | 2.29        | 1                 | 0.95                     | 1.92               | 0.40                 |
| Baviacora   | 2.51        | 3                 | 0.98                     | 1.85               | 0.43                 |
| Pavon       | 2.15        | 1                 | 1.11                     | 2.45               | 0.45                 |
| Nesser      | 2.07        | 2                 | 1.00                     | 1.82               | 0.45                 |
| Tevee       | 2.29        | 3                 | 0.88                     | 1.92               | 0.49                 |
| Seri        | 1.76        | 2                 | 1.08                     | 2.09               | 0.56                 |
| Check 3     | 0.71        | 5                 | 1.14                     | 2.71               | 0.61                 |
| Synthetic 1 | 2.44        | 4                 | 0.92                     | 1.76               | 0.65                 |
| Synthetic 2 | 2.15        | 5                 | 1.04                     | 1.89               | 0.68                 |
| Dharwar     | 2.20        | 3                 | 1.09                     | 2.25               | 0.70                 |
| Sujata      | 2.65        | 5                 | 0.88                     | 1.42               | 0.71                 |
| Pastor      | 2.52        | 3                 | 1.01                     | 1.62               | 0.72                 |
| Mean        | 2.15        | 3                 | 1.01                     | 1.97               | 0.57                 |
| LSD 5%      | 0.38        | 0.93              | 0.18                     | 0.72               | 0.24                 |

"Score stay green after anthesis; 1 < 5 for increasing green.

low pO<sub>2</sub> in the soil. Decreases in soil O<sub>2</sub> content, under flooded conditions, are often accompanied by increase in soil CO<sub>2</sub> and ethylene content. Such changes have detrimental effects on root and shoot growth of wheat. Waterlogging-tolerant wheat genotypes are less responsive to increased CO<sub>2</sub> and decreased O<sub>2</sub>. In part this is because roots of wheat, especially those of the waterlogging-tolerant genotypes, produce aerenchyma under conditions of hypoxia, a feature that helps them cope with such conditions (Huang et al., 1997).

#### IV. HERITABILITY AND GENETIC DIVERSITY OF ROOT TRAITS IN WHEAT

Information on the genetic background of a plant character is a prerequisite for effective breeding. Knowledge on heritability and inheritance pattern of wheat root characters is still limited, but indicates that those traits are controlled by a polygenetic system. The control of root systems is largely influenced by additive genetic systems, which allow progress to be made by selection on root quantity and depth of penetration (Monyo and Whittington, 1970). The partitioning of assimilates between roots and shoots appears highly dependent on the wheat genotype (Sadhu and Bhaduri, 1984). Over 32% of the total phenotypic variability for root:shoot ratio is conditioned by additive gene effects (Kazemi et al., 1979). Although this additive portion of the total variance is not especially high, the authors suggested that lines with favorable root:shoot ratios may be obtained from direct selection in early generations of wheat crossings. Moderate heritability values for the total root length (0.62) and root branching (0.42) have been reported (Monyo and Whittington, 1970).

Hexaploid wheat has > 90% genetic duplication. High levels of genetic duplication reduce the likelihood of natural or spontaneous single gene recessive variation of any given rooting characteristic. This reduces also the narrow-sense heritability for multigenic characteristics. Narrow-sense heritability for root length ranged between 0.38 and 0.46.

Zhang et al. (1999a) analyzed the genetic behavior of apparent tolerance to aluminum toxicity in triticale crosses as measured by root regrowth of seedlings after exposure to Al stress in nutrient solutions. Their results suggested that Al tolerance is of polygenetic inheritance. The moderate high value of estimates of heritability and genetic advance showed that this method could be used in a breeding program aimed at greater

Al tolerance. There exist no association between Al and Mn tolerance measured in nutrient solution, and selective breeding for tolerance to acid soils has to focus on both stress tolerances (Zhang et al., 1999b).

Screening experiments with wheat have shown considerable genotypic variability in AMF colonization and efficiency (Bertheau et al., 1980; Manske, 1990; Kapulnik and Kushnir, 1991; Hetrick et al., 1992). Old wheat cultivars rely more on symbiosis than modern wheats (Manske, 1990). In comparison between landraces from Asia and the United States, the Asian ones showed higher root colonization levels of AMF (Hetrick et al., 1992). Both the extent of AMF infection and the degree of benefit from AMF are plant heritable traits (Manske, 1990; Vlek et al., 1996). High AMF efficiency of a wheat variety can be transferred by crossing to a nonefficient one (Manske, 1990; Diederichs and Manske, 1991). Depending on the crossing combination and environment, recessive, intermediate, dominant inheritance modes, plasmatic effects, effects of heterosis, and even a change of dominance within the same genotypes in different environments were found (Manske, 1989, 1990; Diederichs and Manske, 1991).

#### A. Differences Among Wheat Genotypes of Different Ploidy Level

Bread wheat *Triticum aestivum* is an allopolyploid species with three different genomes (A, B, D) and 42 chromosomes ( $2n = 6x = 42$ ). In a pot experiment with 57 wheat genotypes of different ploidy level grown on an acid, P-deficient soil, almost all wheat genotypes benefited from the AMF inoculation. However, AMF inoculation effects varied between and within the three ploidy levels of wheats (Table 2). The di- and tetraploid genotypes were more dependent upon AMF than the hexaploid ones. When grown in a sterilized soil, without AMF, the di- and tetraploid genotypes formed little biomass and almost no kernels. Inoculation with the AMF fungus *Glomus manihot* drastically improved growth. There was a strong enhancement in total root length with AMF, especially with spelt, tetra- and diploid wheats. Within the hexaploid group, the landraces, spelt wheats, and their wild relatives were most responsive to AMF inoculation (Table 2). Some of the inoculated high-yielding varieties formed also very large root systems. Kapulnik and Kushnir (1991) showed that the response of hexaploid wheat to AMF is controlled by factors of the A and B genomes which are epistatic over those located in the D genome. They also found

Table 2 Aboveground Biomass at Maturity and Total Root Length at Anthesis of 34 Hexaploid Wheat Genotype?

| Groups                  | n  | Total root length (cm/pot) |        |        |         | Biomass dry weight (g/pot) |        |         |        |
|-------------------------|----|----------------------------|--------|--------|---------|----------------------------|--------|---------|--------|
|                         |    | FeP04                      |        | MCP    |         | FeP04                      |        | MCP     |        |
|                         |    | -AMF                       | +AMF   | -AMF   | +AMF    | -AMF                       | +AMF   | -AMF    | +AMF   |
| Hexaploid               |    |                            |        |        |         |                            |        |         |        |
| High-yielding varieties | 25 | 195 ab                     | 293 cd | 531 a  | 990 d   | 581 c                      | 624 cd | 3673 be | 5359 e |
| Landraces               | 10 | 236 be                     | 346 d  | 685 ab | 1196 de | 660 c                      | 778d   | 4531 d  | 5909 f |
| Spelt wheats            | 9  | 183 ab                     | 349 d  | 767 be | 1153 de | 538 be                     | 808 e  | 7393 be | 4674 d |
| Tetraploid              | 16 | 196 ab                     | 482 e  | 631 a  | 892 cd  | 299 a                      | 579 c  | 2889 a  | 3313 b |
| Diploid                 | 6  | 158 a                      | 345 d  | 982 d  | 1246 e  | 365 a                      | 670 d  | 3991 c  | 3349 b |

a < b for  $P = .05$ , separately for each P regime. n = number of genotypes.

a25 *Triticum aestivum* (15 high-yield varieties and 10 landraces), 9 spelt wheats (6 *T. spelta*, 1 *T. vavilovii*, 1 *T. compactum*, 1 *T. spaerococcum*), 17 tetraploid genotypes (8 entries of *T. durum*, 4 *T. turgidum*, 3 *T. diccocom*, 1 *T. diccoides*, 1 *T. araraticum*), and 6 diploid genotypes (3 *T. monococcum*, 2 *T. tauschii*, 1 *T. urartu*) grown in pots in an acid, P-fixing, sterilized soil, with (+ AMF) and without (-AMF) inoculation by *Glomus manihot*. The plots were fertilized with iron phosphate (FeP04) or monocalciumphosphate (MCP).

a high AMF colonization and response in *T. timopheevii* var. *araraticum*, which has an *AAGG* genome. The latter could not be confirmed by Hetrick et al. (1992) when using a different AMF inoculum.

### B. Old, Tall vs. Modern, Semidwarf Cultivars

Genetic diversity in root characteristics is well documented for bread wheat (MacKey, 1973; O'Brien, 1979) and for durum wheat (Motzo et al., 1993). Many wild forms and landraces of wheat possess large root systems, but tend to lodge because of their tall culms (Manske, 1989; Vlek et al., 1996). There is concern that breeding for improved yield potential under high-input conditions would result in germplasm with smaller root systems. This was checked with 44 historically important lines released by CIMMYT during the last 45 years grown under conditions of adequate nutrient and water supply. Grain yield was increased on the average by 50.4 kg ha<sup>-1</sup> y<sup>-1</sup> over the years, but the absolute values of root length density were not significantly changed (Fig. 1) (Manske, 1997). Selection for adaptation to acid soils, low-P conditions, and tolerance to Al toxicity have resulted into superior semidwarf bread wheats. The modern semidwarf lines had improved grain yield, P uptake, and root length density at low and high P input conditions (Table 3) (Manske et al., 1996b). This demonstrates that yield potential can be increased by wheat breeding without adverse effects on root length.

### C. Influence of Dwarfing Genes

The dwarfing genes *Rht-B1b* and *Rht-D1b* (with the former designations *Rht1* and *Rht2*, respectively), incorporated singly or together, are in the background of most of the successful wheat cultivars in use today. *Rht-B1c* (former *Rht3*) reduces culm length more than *Rht-B1b* and/or *Rht-D1b*. It is often used in physiological studies, but has not been incorporated into com

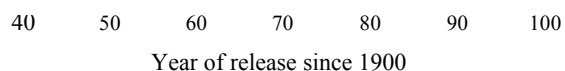


Figure 1 The effect by the year of release on root length density (RLD) in the upper soil layer (0-20 cm) of 44 important CIMMYT lines released since 1942, grown on an alkaline soil with nutrients and water amply supplied. Means of three replicated plots.

Table 3 Grain Yield and Root Length Density (at the 0-20 cm soil depth) of Eight Semi dwarfs and Eight Tall Wheat Lines Grown on a P-exhausted Alkaline Soil with Irrigation

|                     |                    | High-P regime |        | Low-P regime |        |
|---------------------|--------------------|---------------|--------|--------------|--------|
|                     |                    | Semidwarf     | Tall   | Semidwarf    | Tall   |
| Grain yield         | kg/ha              | 6240 b        | 4598 a | 4539 b       | 3169 a |
| Root length density | cm/cm <sup>3</sup> | 7.7 b         | 6.6 a  | 10.4b        | 8.7 a  |

a < b for P = .05, separately for each P regime.

Plants were fertilized with 35 kg P ha<sup>-1</sup> applied as superphosphate. Average of eight tall and eight semidwarf wheats.

mercial cultivars. The extent of rooting can be modified by selection during breeding, irrespective of the dwarfing genes (MacKey, 1973; Gale and Yousefian, 1985). McCaig and Morgan (1993) found no significant relationships between dwarfing genes and root dry matter. Similar results were obtained in our own

8 experiments with 28 semi- and double-dwarf hexaploid wheat genotypes containing *Rht-B1b* and/or *Rht-D1b* or *Rht-B1c*.

The dwarfing genes showed no effect on total root length and AMF infection, although the variation in total root length was large. The few root studies with near-isogenic lines showed contradicting results (Siddique et al., 1990; Miralles et al., 1997), because root growth varies with genetic background, growing conditions, and stage of development (Bush and Evans, 1988). In a field trial with near-isogenic lines carrying different combinations of the genes *Rht-B1b*, *Rht-D1b*, and *Rht-B1c* in two varietal backgrounds, the analysis of root length density in the upper soil layer (0-20 cm depth) revealed some effects of the *Rht* alleles (Table 4). The introduction of *Rht-B1b* or *Rht-B1c* was associated with lower RLD at the stage of tillering in both cultivars. In addition, *Rht-D1b* reduced root length density in the Mexican culti

8 var Nainari 60. The double dwarfs had RLD similar to

the tall controls in both cultivars at tillering. Between tillering and anthesis, *Rht-B1b* and *Rht-B1c* genotypes enhanced their RLD, so that at anthesis no differences between *Rht* alleles were present (Table 4). The *Rht-B1c* genotypes had lower grain yields but thick roots (data not shown), which is related to a surplus of assimilates during stem elongation. The assimilates were translocated to the roots due to the lack of alternative sinks (Miralles et al., 1997).

#### D. Effect of 1 8/1 R Translocation

Many high-yielding wheat cultivars carry the IB/IR translocated segment from rye. Substantial yield increases occurred in germplasm containing the IB/ IR translocation (Villareal et al., 1995). Rye has a larger root system than wheat, and a segment of rye chromosome may enlarge the wheat root system. Genotypes with the IB/IR translocation performed better on an acid soil, having more grains per spike. They also had thinner roots and higher RLD, two traits that enhance root surface area (Table 5). However, the same germplasm showed no advantage of the IB/IR translocation under better soil conditions or irrigation. In the latter location, this was confirmed

Table 4 Effect of Dwarfing Genes (*Rht-B1b*, *Rht-D1b*, Double Dwarfs of the Two Genes; *Rht-B1c*) and Tall Control on Root Length Density (cm cm<sup>-3</sup> soil) of the Bread Wheat Cultivars Nainari and Maringa

|                | Nainari | Maringa | Mean(dwarfing genes) |
|----------------|---------|---------|----------------------|
| Tall control   | 3.7 e   | 3.1 b   | 3.4 b                |
| <i>Rht-B1b</i> | 2.9 b   | 2.0 a   | 2.5 a                |
| <i>Rht-D1b</i> | 2.7 ab  | 3.0 b   | 2.9 ab               |
| Double dwarf   | 3.3 be  | 2.6 ab  | 3.0 ab               |
| Rht-Ble        | 2.7 ab  | 2.1 a   | 2.4 a                |
| Mean           | 3.1 b   | 2.6 a   |                      |

a < b for P = .05, separately calculated for cultivar, dwarfing genes, and interactions.

Roots were measured at the 0-20 cm soil layer at tillering time. Data present an average over two crop cycles in Mexico, with nutrients and water amply supplied.

Table 5 Effect of IB/IR Translocation (26 lines), IB/IB, Without Translocation (14 lines) on Grain Yield, Root Surface Area, and Root Diameter (0-20 cm soil layer), CIMMYT Wheat Lines Grown on Acid Andisol in Mexico Under Rainfed Condition, with 35 kg P ha<sup>-1</sup> Applied as Superphosphate

|      | n  | Grain yield<br>(kg/ha) | Root surface area (cm <sup>2</sup> /sample) |          |              | Root diameter (Jlffi) |
|------|----|------------------------|---|----------|--------------|-----------------------|
|      |    |                        | Tillering                                   | Anthesis | Postanthesis | Tillering             |
| IBIB | 14 | 2391 a                 | 1959 a                                      | 11867 a  | 9354 a       | 173 b                 |
| IBIR | 26 | 2622 b                 | 2159 a                                      | 14769 b  | 11446 b      | 164 a                 |

a<b for  $P = .05$ .

n = number of genotypes.

sample = roots from 12000 cm<sup>3</sup> soil volume.

by studies with near-isogenic lines carrying the IB/IR in different varietal backgrounds (Manske and Vlek, unpublished data). Further studies, especially in marginal environments, are necessary to elucidate the effect of the IB/IR translocation.

#### V. COST-BENEFIT ANALYSIS

A cost-benefit analysis of the wheat root system is essential for the elucidation of its function. The partition of the assimilated carbohydrates among shoots, roots, and grains is determined by the plant genotype and by environmental factors such as climate, soil conditions, and the availability of mineral nutrients and water. It is also determined by the demand for carbohydrates by microbial associations in the roots of the host plants. Carbon allocated to the roots and used for construction and maintenance is considered the currency for such an analysis. Wheat root dry matter deposited in the soil was estimated as being equal to the dry weight of grain produced (Samtsevich, 1965). Wheat uses 52-67% of the carbohydrates translocated to the roots for root respiration (Lambers et al., 1996).

The benefits of large RLD generally diminish in irrigated wheat with high fertilizer input. Root length density of wheat germplasm grown with irrigation in

India, Bangladesh, and Mexico was significantly and positively correlated with grain yield in only 50% of the cases (Table 6). A positive correlation occurred in most cases when the fertilizer was reduced. However, in Trial 2 in India and Trial 4 in Mexico, with the recommended rate of fertilizer applied, RLD and grain yield were negatively correlated. If the demand for carbohydrates by large root systems is not compensated by improved P and water acquisition, the roots may become yield limiting.

Plant growth response to VAM infection also depends on the balance between the costs and benefits of symbiosis. The energy required to build and maintain an extensive AMF-infected root system needs to be offset by the improved nutrient uptake of the plant, a condition that may apply in marginal soils. From the plant's side, AMF fungi are strong competitors for assimilates, which is especially relevant if C availability for growth and grain filling is limited. Depending on the host plant genotype or on P supply, 4-14% of the photosynthates are allocated to AMF-infected roots (Harris and Paul, 1987). Response of plant growth to AMF usually declines as stress conditions are relaxed, e.g., as sufficient nutrients are supplied. The enhanced uptake of P is gained at the cost of host photosynthate utilized by AMF. However, if P becomes nonlimiting and photosynthate utilization by AMF is not curtailed,

Table 6 Phenotypic Correlation Between Grain Yield and Root Length Density (RLD) in the Upper Soil Layer (0-20 cm) at Tillering Time and Early Anthesis

|                       | India                         |      |                              |        | Mexico                     |       | Bangladesh                |          |                           |       |
|-----------------------|-------------------------------|------|------------------------------|--------|----------------------------|-------|---------------------------|----------|---------------------------|-------|
|                       | Trial 1 (n = 20)<br>half full |      | Trial 2 (n = 9)<br>half full |        | Trial 3 (n = 30) -<br>P +P |       | Trial 4 (n = 20)<br>-P +P |          | Trial 6 (n = 12)<br>-P +P |       |
| RLD at tillering      | 0.28                          | 0.04 | -0.16                        | -0.80b | 0.51b                      | -0.05 | 0.52b                     | -0.54*** |                           |       |
| RLD at early anthesis | -0.17                         | 0.00 | 0.11                         | 0.16   | 0.50b                      | 0.03  | 0.41a                     | -0.16    | 0.45*                     | -0.10 |

Significant by t-test:  $ap < .05$ ,  $bp < .001$ ; - data not assessed; n = number of genotypes.

the AMF plant may become carbon limited, a situation that leads to parasitic effects of AMF (Vlek et al., 1996).

## VI. OUTLOOK

The root system of wheat has received far less attention by plant biologists and plant breeders than the aboveground shoot. This is particularly true for field experiments. Nevertheless, a considerable part of the research to date has dealt with the analysis of the genotypic variation of root traits. Wheat breeders have only rarely selected for root properties, mainly for resistance to root diseases. However, "roots" mean far beyond the mere tissues of that organ. The importance of AMF in regulating the water and nutrient uptake by plants under stress, and improving their resource acquisition efficiency as well as yields, has been documented. In spite of that, no practical means exist to produce a viable inoculum of the obligate symbiotic AMF in order to introduce effective strains on a field scale (Heinzemann, 1994).

The lack of suitable nondestructive methods to observe growth and development of intact root systems in situ is one of the reasons for an inadequate knowledge of root system phenology and inheritance. Many of the methods are too expensive to allow for routine genetic studies. The advances in our knowledge of root characteristics have largely been made with relatively simple, but time-consuming, methods. Techniques like minirhizotron, image analysis systems, and root washing machines have been developed, and although they are often more precise and faster, they are expensive and/or unsuitable for field studies with many genotypes (cf. Box, 1996; Chapter 18 by Polomski and Kuhn in this volume). However, those techniques combined with biotechnological methods may lead to new knowledge about the mode of inheritance of root traits in wheat, and the identification of genes to genetically engineer specific root characteristics (see also Chapter 17 by Bucher in this volume), in the near future.

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