Derleme

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Buğday Kök Sistemi, Genetiği ve Kök Özelliklerini Değerlendirme Metodolojisi: Derleme

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Özet

Buğday kök sisteminin topraktaki yatay ve dikey dağılımı, ortam şartlarına göre farklılık gösterir ve toplam kök kuru ağırlığının yaklaşık olarak %65'i toprağın 0-30 cm'sinde bulunur. Buğday kök gelişimi çiçeklenme döneminde maksimum sınırına ulaşır. Çiçeklenme döneminden sonra buğday kök gelişimi topraktaki su ve gübre miktarına bağlı olarak azalır veya durur. Kök özelliklerinin geliştirilmesi yönüyle yapılan seleksiyon marjinal alanlarda yetiştirilen buğday çeşitlerinin verim artışında önemli bir rol oynayabilir. Toprak profilinde kök büyümesi buğday genotipi, mevcut su, toprağın fiziksel ve kimyasal özellikleri, çevre şartları, gübreleme ve diğer canlı ve cansız faktörlere bağlıdır. Kök çalışmaları yoğun emek ve fazla zaman aldığından genelde araştırıcılar kök sistemleriyle çalışmaktan kaçınmaktadırlar. Bu yüzden buğday kök özelliklerinin genetiği hakkında çok az bilgi vardır ve kök sistemlerinin genetik gelişimi ıslah programlarının ortak hedefi olmamıştır. Sera ve arazi şartlarında seleksiyon çalışmasına uygun kök özelliklerini değerlendirmede birçok metot mevcuttur. İş gücü yoğunluğundan dolayı teknolojininde kullanıldığı ancak ilave masraf dezavantajına sahip modern teknikler geliştirilmiştir. Yeni çeşitlerin seleksiyonuyla ilgilenen ıslahçılar ve fizyolojistler agronomik verim ve kök büyümesinin geliştirilmesinde etkili olan buğday çeşitlerinin seleksiyonunda, kök analiz metodlarını artarak uygulamaya başlamalıdırlar.

Anahtar Kelimeler; *buğday, kök özellikleri, metotlar*

Wheat Root Systems, Genetics and Methodology for Evaluation of Root Characteristics: A Review

Abstract

The wheat root system varies considerably in vertical and horizontal distribution in soil depending on environmental conditions and approximately 65% of total root dry weight is in the 0 to 30 cm soil layer. Wheat root growth reaches maximum extension in the flowering stage. After flowering stage, root growth rates decrease or stop depending upon water and fertilizer availability. Selection for enhanced root traits may play a significant role in increasing yield of wheat varieties grown in marginal environments Root growth in the soil profile depends on conditions such as wheat genotype, available water, physical and chemical properties of soil, environmental condition, fertilization, and other biotic and abiotic factors. Researchers generally have avoided study of root systems because root research requires a lot of time and intensive labor. Thus little is known about the genetics of wheat root traits and genetic improvement of root systems is not a common objective of plant breeding programs. There are many methods available to select for improved root traits suitable for selection under greenhouse or field conditions. Additional modern techniques have been developed, that substitute technology for labor, but with the disadvantage of additional expense. Physiologists and breeders involved in the selection of new varieties should increasingly turn to root analysis methods to select for wheat varieties with enhanced root growth and agronomic yield.

Key Words: *wheat, root traits, methods*

Introduction

Cereal researchers have paid relatively little attention to root growth studies since such studies require a lot of time and intensive labor. However, root traits play an important role in the development of new varieties adapted to marginal environments. Three important areas relative to root growth are root ecology, physiology and genetics. Root ecological studies involve tests of soil bulk density, pH, moisture, and nutrient content. Physiological factors affecting root growth include cell division and water and nutrient intake from root to shoot. Genetic differences impacting root growth are those which influence root length, diameter, density, fresh and dry weight, shoot to root weight ratio, secondary root number, and root architecture and growth rates during different plant growth stages. This genetic variation affects resistant to drought, nutrient and water uptake, tolerance to elemental toxicity and lodging resistance.

Morphology, Ecology and Physiology of Wheat Root

The two types of cereal roots are termed primary and secondary roots (Fig. 1 and Fig. 2). The primary or

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seminal root emerges from the scutellar and epiblast nodes of the embryonic hypocotyl of the germinating caryopsis. Secondary roots which may also be termed adventitious, nodal or crown roots subsequently develop at the coleoptilar nodes at the base of the apical culm and tillers. The number of primary root in cereals generally ranges from five to seven but sometimes may reach ten. In wheat the number of seminal roots is under genetic control and ranges from three to six and from 1-14% of the entire root system. Primary roots penetrate deeper into the soil than secondary roots. Secondary roots begin to develop only at the first foliar node, when the fourth main stem leaf appears (Manske and Vlek, 2002).

The number of adventitious roots is mostly related to tiller number (Reynolds et al., 2001).

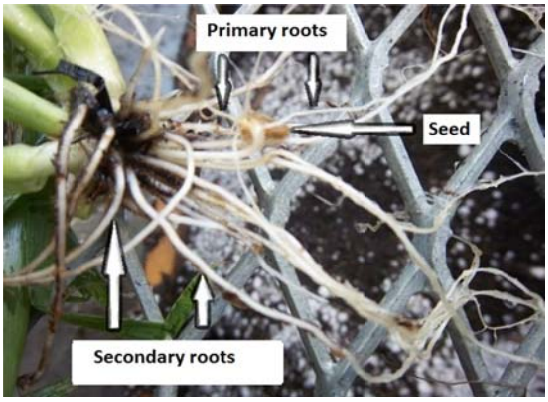

Fig.1. Primary and secondary roots at the booting stage of spring wheat (Akman and Bruckner, 2011).

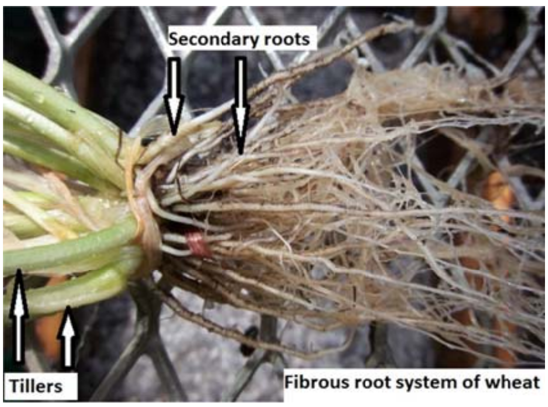

Fig.2. Secondary roots after flowering stage (GS 70) of Yellowstone winter wheat variety (Akman and Bruckner, 2011).

Wheat root growth in organic soil at the flowering stage is shown in Fig. 10 and Fig.11. In the organic soil, winter wheat root length at the tillering stage was about 49 cm (Fig. 12), while spring wheat root length at the booting stage was about 90 cm (Fig. 13).

The roots of wheat usually spread horizontally between 30 and 60 cm and may be abundant at soil depths of more than 100 cm, with some reaching beyond 200 cm (Reynolds et al., 2001). Winter wheat reaches depths of 2.2 m, twice that of spring wheat (Kristensen et al., 2009). Under wet regimes, roots have greater horizontal development; while under moisture deficit conditions in the upper soil layer (0.45 m), roots invade lower horizons and have a greater vertical distribution (Mishra et al., 1999). Approximately 65% of wheat roots total dry weight is in the top 30 cm (Gregory et al., 1978).

Winter wheat roots reach maximum extension at the flowering growth stage (Martinez et al., 2008; Efetha 2011). Wheat root growth slows or ceases after anthesis; however, this pattern may vary as a function of soil water content and N status. Root growth after anthesis may compete with grain for C and N, or play a major role in N translocation to the grain (Munoz-Romero et al., 2010).

Root hairs emerge from the zone of root elongation and have a diameter of 0.003-0.007 mm, a length of 3-13 mm, a normal life-span of a few days and function to absorb nutrients and water. The number, size, length, and life span of root hairs are important in determining the surface area of wheat roots (Manske and Vlek, 2002) and can play a significant role in P acquisition, especially in low-P soils (Gahoonia et al., 1997; Manske and Vlek, 2002). Root mass, length and straightness are reduced in layered or compacted soil (Wilhelm and Mielk, 1998). Compacted soil prevents deep growth in soil of wheat roots and may negatively affect agronomic traits such as plant height, tiller number per plant, and possibly grain yield. Increased tillage depth and decreased field traffic can be employed to decrease soil compaction and thus increase rooting depth (Wilhelm and Mielk, 1998).

Large root systems of wheat contribute to water and nitrogen uptake early in the season, and provide additional water for grain filling. In environments where crops are reliant on stored soil water, an early vigorous root system increases the risk of depleting soil water before completion of grain filling. Maximum rooting depth, distribution of root system, root length density, rate of root descent, number of axes or total root dry weight can all be taken as indication of root system size. A deep, wide-spreading and much-branched root system is essential in the design of drought-tolerant crops, however a small root system can provide benefits in water-limited situations through improved water use efficiency (Palta et al., 2011).

A well-developed wheat root system can recover more water from greater soil depths and will therefore tend to adjust water balance between topsoil and bottom soil. Liu and Li (2005) reported that drought stress may result in a larger root system, which increases absorption of water from the soil. Under water deficit, total root growth is reduced in the top 30 cm, although the root system continues to grow deeper in the soil profile between 30 and 60 cm, and water uptake in deeper layers may be increased. However, limited soil water can restrict photosynthetic rates and overall plant and root growth rates depending on plant growth period, duration and severity. Water deficit reduces root growth in the top 30 cm of soil while water uptake from the 30 and 60 cm zone is increased. Therefore, a crop subjected to early vegetative period water deficit could compensate for root growth reductions during subsequent re-watering, but mid-season (terminal spikelet to anthesis) water deficits are more severe and permanent (Asseng et al., 1998). Wheat genetic traits affect the distribution of seminal and adventitious roots in soil and can affect plant response to water stress. For example, Manske and Vlek (2002) reported that drought-tolerant semi-dwarf bread wheat varieties have more roots in the deep soil whereas the non-tolerant varieties form fewer roots in the deeper layers.

Crop species, cultural application (especially water supply, nutrients) (Asseng et al., 1998) and soil chemical and physical characteristics, all influence the root distribution in the soil profile (Kuhlmann and Baumgartel, 1991).

Excess soil water and water logging has been shown to decrease root growth through reduction in oxygen concentration and increase in carbon dioxide concentration in the root zone. Root-zone CO_2 enrichment at ambient O_2 had no significant effects on shoot growth, but reduced root growth in wheat genotypes (Huang et al., 1997).

Wheat Genes Impacting Root Growth

Today >70% of modern wheat cultivars are semi-dwarf. Mutations in the *Rht* genes located on wheat chromosome group 4 reduce coleoptile length and leaf elongation rates (Ellis et al., 2004). In northwest Europe, two semi-dwarfing alleles are widely used: *Rht-B1b* (formerly Rht1) and *Rht-D1b* (formerly *Rht2*) located on chromosome 4B or 4D, respectively, both cause a reduced response to gibberellic acids and a semi-dwarf phenotype. *Rht8* is the third dwarfing gene in wheat associated with decreased plant height. Effects of the *Rht* alleles on the wheat root system have been studied extensively but results of these studies are variable and inconclusive (Wojciechowski et al., 2009).

Subbiah et al. (1968) reported that semi-dwarf wheat varieties have a shorter root system with decreased water uptake under dryland conditions. However, Wojciechowski et al. (2009) reported there were no significant differences in root length between semi-dwarf and isogenic control lines in gel chamber, soil-filled column, and field experiments. They also showed root characterization was heavily influenced by experimental methodology and environment.

Numerous other genes have been found to impact shoot and root growth. In addition to the impact of *Rht* mutations upon root growth, genes located on wheat chromosome 7B impact root growth with the early flowering allele associated with decreased root growth (Sharma and Lafever, 1992). Flowering earlier or avoiding excess later growth are two strategies to avoid drought stress. Duggan et al. (2005) reported that genetic variation linked to the tiller inhibition (*Tin*) gene increased root to shoot ratios and lead to reduced final tiller number. It was concluded that the *tin* gene might be advantageous under terminal drought. Genotypes that are productive in acid soils typically exhibit aluminum toxicity tolerance and have long primary roots which may enable them to be more drought tolerant. Sensitivity to aluminum is controlled by one single recessive gene that also controls root length and selection for aluminum tolerance could be used to improve both root length and drought stress (Sharma and Lafever, 1992). A survey conducted with the *SuT4* and *SuT5* wheat carbohydrate transporter genes found the highest expression levels in salt tolerant cultivars under salt stress (Charkazi et al., 2010).

Several wheat-rye translocation segments incorporated into wheat varieties confer tolerance to biotic and abiotic (drought) stress conditions. More than 16 wheat-rye translocations are available with the *1AL.1RS* and *1BL.1RS* translocations the most well-known. The *1RS* chromosome translocations have been reported to increase grain yield and agronomic performance in both optimum and reduced irrigation conditions. This advantage is attributed to high grain yield, above-ground biomass yield at maturity, grains/spike, 1000-grain weight and test weight (Villareal et al., 1995). Inherent differences in root morphology and anatomy of different *1RS* (short arm of chromosome 1 of rye) translocation lines may be advantageous compared to normal bread wheat under stress conditions. An increase in grain yield among *1RS* wheats has been found to be positively correlated with higher root biomass. Wheat varieties containing the *1RS* translocations have increased root biomass and grain yield under irrigated field conditions (Figure 3, Sharma et al., 2010a). Additive and epistatic effects have been detected for different traits of root length and root weight in *1RS* wheat. Epistatic interactions have been further partitioned into inter-genomic (wheat and rye alleles) and intra-genomic (rye–rye or wheat–wheat alleles) interactions affecting various root traits. (Sharma et al., 2010b). A survey of 111 bread and 26 durum Turkish wheat varieties registered from 1931 to 2006 found that only 2.9% had a wheat-rye translocation, which is much lower than that of other countries (Yediay, 2009).

Fig.3. Roots of different container grown wheat genotypes with different *1RS* translocations in spring bread wheat 'Pavon 76' background harvested 45 d after germination (Sharma et al., 2010a).

Primary root growth is controlled quantitatively and is at least partially recessive. This implies that selection for strong root growth in early generations would be effective (Camargo and Ferreira Filho, 2005). Additional genetic diversity for root traits may be useful to increase plant growth under water stress. Radiation induced mutants have been found to differ to various degrees from the parent variety in root anatomy (Cabrera et al., 2004). The characterization of mutations within genes known to impact root development in other plant systems may prove useful in two ways. The first would be in testing the role of candidate genes in wheat root development and the second would be in creating allelic variation useful in wheat varietal development.

Root Genes Identified in Model Plants

A survey of *KNAT* gene root-specific expression in the model plant *Arabidopsis thaliana* indicated that the individual *KNAT* genes might play distinct developmental roles (Truernit and Haseloff, 2007). In *A. thaliana*, composition of *CULLIN3* (*CUL3*)-based E3 ligases, which are essential enzymes in both metazoans and plants, regulates primary root growth by a novel ethylene-dependent pathway. In particular, *CUL3* knockdown inhibits primary root growth by reducing root meristem size and cell number. This phenotype is suppressed by ethylene-insensitive or resistant mutations (Thomann et al., 2009). *TaSnRK2.8* is involved in response to PEG, NaCl and cold stresses, and possibly participates in ABA dependent signal transduction pathways. Over expression of the *TaSnRK2.8* in *A. thaliana* results in enhanced tolerance to abiotic stress, longer primary roots, increased chlorophyll, and enhanced PSII activity (Zhang et al., 2010).

Wheat root analysis methods

Several methods exist to study the root system of plants grown under greenhouse or field conditions. The minirhizotron (root periscope) is a modern technique to measure root systems in situ. Glass or acrylic minirhizotron tubes are inserted between rows of plants at a defined angle. Cameras and computers are used to analyze root systems quantitatively (Fig. 4). Minirhizotron methods have been successively used in several field crops, vegetables, and trees to evaluate root systems. Romero et al. (2010) reported that after wheat emergence, minirhizotron tubes were installed on a permanent basis until harvest at the center of each plot on the sowing line, 45° off vertical (Fig. 5). A minirhizotron that shows root growth and size parameters is one of the best techniques available for obtaining root system data (Hendricks et al., 2006). However, the minirhizotron technique underestimates root length in the upper soil layers and overestimates root length in the deeper soil layers when compared to the soil core method (Romero et al., 2010). Another disadvantage of this technique is its higher expense.

Fig.4. Equipment for root study using the minirhizotron method (Chen, 2011).

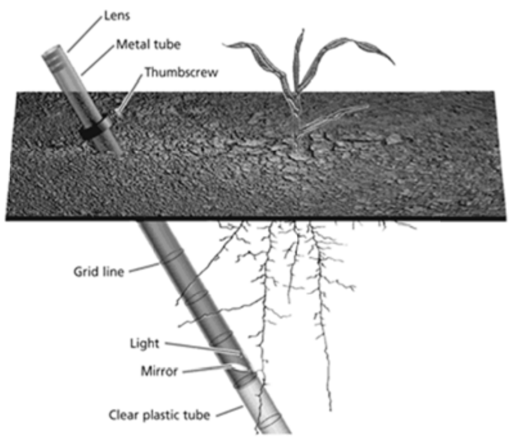

Fig.5. A minirhizotron installed near an oat seedling for root research (Taiz and Zeiger, 2010).

The electrical capacitance method can be used to measure root volume and root length density. This method is based on measuring the electrical capacitance of an equivalent parallel resistance-capacitance circuit formed by the interface between soil-water and the plant root surface (Fig. 6). This method facilitates root studies without intensive labor such as root washing and counting. The major disadvantage of this method is that it is not able to measure spatial distribution of roots within the soil (Reynolds et al., 2001).

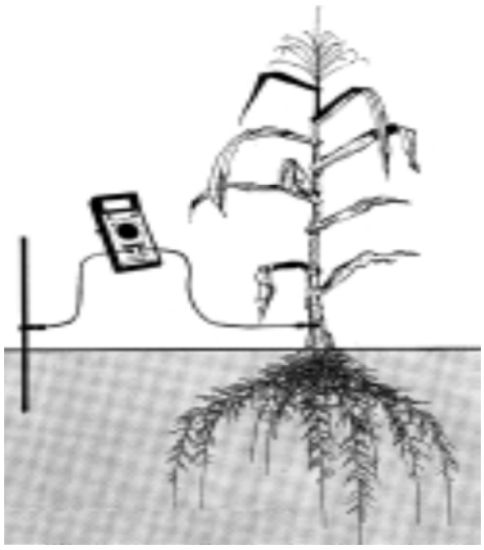

Fig.6. Electrical capacitance measurement of root size in a maize plant (Reynolds et al., 2001).

The mesh bag method can be used to evaluate root growth under field conditions. Mesh bags filled with root-free soil replace soil from holes of defined width and depth. A plant is established in the mesh bag and allowed to grow for a pre-determined period. Mesh bags are retrieved and roots washed carefully to determine root parameters (Fabiao et al., 1985).

The container or PVC tube method can be used in the greenhouse or under field conditions to study plant root growth by establishing plants in nylon mesh encased by a PVC tube. Using this method, root growth is limited to a predetermined soil volume. After a predetermined growth period roots are by removing the nylon bag without breaking the PVC tubes and washed (Fig. 7). Like the mesh bag method, this method is labor intensive but can be used for many root parameters such as dry weight, root to shoot ratio, secondary root number, length (if taller containers used) and diameter. Under field conditions, the PVC tubes are inserted into holes in the soil and then filled with soil.

The core break method is a rapid and simple method of observing and recording the presence of roots as a function of depth (Fig. 8). A cylindrical auger is rotated clockwise with a crank handle and soil cores are extracted from soil to allow measurements of root length density (cm root length/cm^3 soil) (Smit et al., 2000; Reynolds et al., 2001).

Fig.7. Root research using the PVC tube method (Ehdaie, 2008 unpublished).

Fig.8. (a) Root auger for obtaining soil cores; (b) breaking a 10-cm long soil core to count the roots at the breakage faces (Reynolds et al., 2001).

Other less commonly used root growth measurement methods are the monolith (Fig. 9), root angle, radioactive and non-radioactive tracer, trench profile, profile or glass wall, excavation, split-root technique, hydroponic, aeroponic and agar-plate system methods (Böhm, 1979; Bennie et al., 1987; Atwell, 1989; Kücke et al., 1995; Ghedira et al., 2009; Chen et al., 2011).

Fig.9. Root box with extracted root-soil monolith together with wheat shoots (Reynolds et al., 2001).

Fig.10. Appearance of the root system in organic soil (Peat 70% and Perlite 30%) at the flowering stage of Scholar spring wheat (Akman and Bruckner, 2011).

Root separation and drying

The root media has major effects on plant shoot and root growth. It provides anchorage, nutrients, available water and gas exchange between atmosphere and roots. Mixing of soil, organic matter such as peat moss, compost, manure, coconut coir, rice hull, and other components such as vermiculite, perlite, calcined clay, sand, and polystyrene foam to provide drainage and aeration have been used for rooting media (Kessler, 2011). Research investigating effects of growing medium on rooting of six barley genotypes showed that plants grown in soil and nutrient solution had longer lateral roots than those grown in sand and perlite (Wahbi and Gregory, 1989). However, wheat roots can also be studied in sand cultures with Hoagland's solution which ensures an adequate nutrient supply (Champoux et al., 1995; Waines and Ehdaie, 2007; Sharma et al., 2010b). In general, sand is easier to wash from root systems than soil based media.

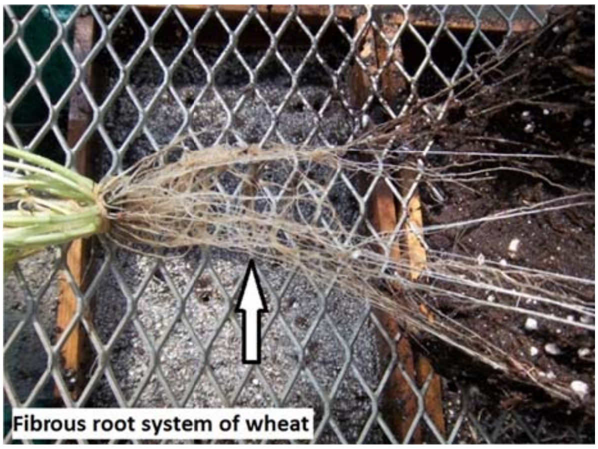

Fig.11. Appearance from washing roots of Yellowstone winter wheat after flowering stage (GS 70). (Akman and Bruckner, 2011).

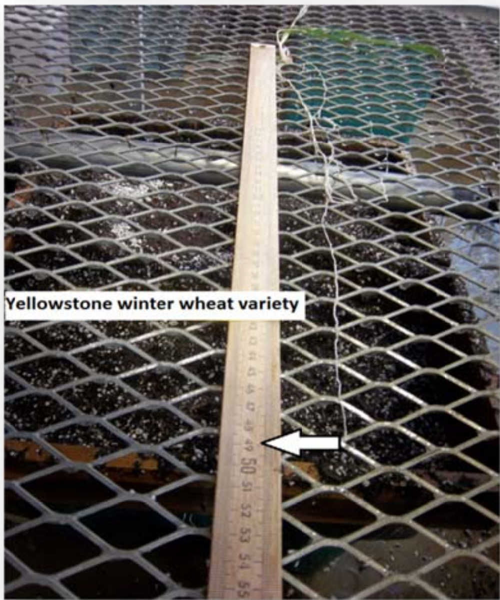

Fig.12. Root length of Yellowstone winter wheat at the tillering stage (Akman and Bruckner, 2011).

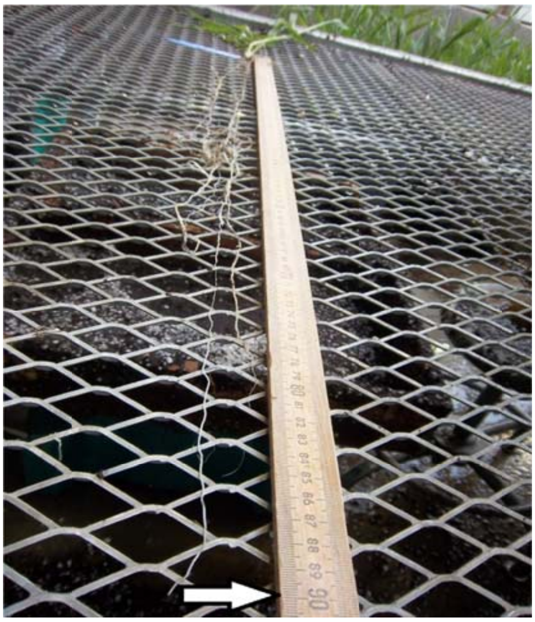

Fig.13. Root length of Scholar spring wheat at the booting stage (Akman and Bruckner, 2011).

Roots are easily separated when they are pre-soaked overnight in water prior to washing. Both manual and automatic washing machines can be used to separate roots from soil. A root-washing machine can be more effective than washing by hand when there are high sample volumes or if samples contain larger soil amounts. However, manual washing is simpler, more accurate, and inexpensive. After washing, organic debris must be removed by tweezers. Roots are then cut into 1-2 cm segments and placed in water prior to determining fresh weight. Washed and cleaned roots may be stored in a solution of 50% alcohol in a refrigerator (Reynolds et al., 2001). Root and shoot dry weights are recorded after drying at 55^{o}-70°C for 48-72 hours (Danneels et al., 1994; Halter et al., 1997; Mahmood et al., 2001; Rehman and Iqbal, 2010; Nasr et al., 2011). Drying temperatures above 70°C may lead to substantial root breakage (Reynolds et al., 2001).

Conclusion

Researchers who choose to study wheat root traits should be aware that it is labor intensive and time-consuming. Because of this, many breeding programs have not traditionally measured root parameters. Evaluation of root traits is very important to wheat adaptation affecting traits such as drought tolerance, toxicity to elements, diseases, lodging and waterlogging. A genotype that has tolerance to stress in one environment may not perform well in another season or environment. Therefore target environment and patterns of rainfall and water stress should be considered when determining root traits for selection and breeding.

Many root measurement methods have been utilized to assess wheat roots under various greenhouse and field conditions. Each technique has some advantages and selection of technique depends on resources and the objectives of the study. The best technique might be that which is easy to use in both the greenhouse and field and that does not require sophisticated equipment.

For selection of improved wheat varieties, wheat breeders should incorporate selection for root traits to improve plant growth and development.

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Ehdaie, B., 2008. Photograph showing root study by the PVC method in the greenhouse at University of California, Riverside, USA. Used with permission of author.

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