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# Root biomass and genotypic response in bread wheat (*Triticum aestivum* L.) under well-watered and drought field conditions

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## ABSTRACT

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**An optimum root system in wheat might enhance water and nutrient uptake under drought-prone environments without depleting soil moisture, thus improving grain yield. Two experiments were carried out at the University of California, Riverside, under well-watered and droughted field conditions; receiving 412 and 268 mm of water and rain, respectively. Five recombinant inbred lines with root biomass ranging from 1.175 to 7.850 g plant$^{-1}$ plus a check parent variety, Yecora Rojo, with root biomass of 1.820 g plant$^{-1}$ were used. Phenological, morphological and agronomic characters were measured. Covariate analysis between grain yield (GY) with number of days from sowing to anthesis (DTA) and to physiological maturity (DTM), grain filling period (GFP), and plant height (PH) were not significant under both irrigation regimes indicating GY was not confounded with these traits. The main effect of irrigation on DTM, GFP, PH, number of tillers (NT) and spikes (NS) per 50 cm, thousand grain weight (TGW), GY, and shoot biomass (SB) was either significant or highly significant, but not on days to anthesis (DTA), number of grains per spike (NGS), and harvest index (HI). The main effect of genotype on the traits measured was highly significant. The effect of genotype × irrigation interaction was relatively low. The mild drought before anthesis and severe drought after anthesis reduced DTM by 5%, GFP by 10%, NS per 50 cm by 24.6%, and TGW by 11% which resulted in 25% and 27% reduction in GY and SB, respectively. Stress tolerance index (STI) of the genotypes calculated based on GY ranged from 0.52 to 0.88. A quadratic pattern of relationship was observed between root biomass measured under well-watered (soil water-holding capacity) glasshouse conditions with GY measured under well-watered ($R^2$ = 0.62) and droughted field conditions ($R^2$ = 0.93). The relationship between root biomass and STI also followed a quadratic pattern ($R^2$ = 0.60). According to the quadratic equations, GY under well-watered and droughted field conditions maximized at 5.806 and 4.575 t ha$^{-1}$ when root biomass was 1.630 and 3.975 g plant$^{-1}$, respectively, and STI was highest when root biomass was 3.500 g plant$^{-1}$. These results indicated that wheat lines with vigorous root system might be better adapted to drought-prone environments. However, over-sized root biomass might reduce grain yield under both well-watered and drought conditions.**

**Keywords: bread wheat, correlation coefficient, root system, optimum root biomass, stress tolerance index**

## INTRODUCTION

Drought is the most important environmental factor limiting bread wheat production worldwide. About 37% of areas allocated to wheat cultivation are in semi-arid or arid environments where intermittent and/or terminal drought occurs. In these areas, because of limited and unpredictable rainfall, grain yield is reduced significantly and it fluctuates annually, which results in instability in grain yield (Gallagher *et al.*, 1975; Dhanda *et al.*, 2004; Ehdaie *et al.*, 2008).

Drought tolerance in a crop plant is manifested by many different genes influencing phenological, morphological, and physiological traits during plant growth and life cycle (Araus *et al.*, 2003a; Araus *et al.*, 2003b; Reynolds *et al.*, 2007). Thus, genetic improvement for drought tolerance in crop plants, including bread wheat, has not been significant.

There is renewed interest in root research and in identification of root system traits in wheat that might be involved in expression of drought tolerance. Genotypic variation for root characteristics and their functional implications for water uptake and yield increase under water-deficit conditions have been reported for many crops (O'Toole and Oyanagi, 1987).

In wheat, the root traits that may contribute to drought tolerance include depth of rooting (Hurd 1974), root elongation rate (O'Brien, 1979), xylem vessel diameter (Richards and Passioura, 1989), root distribution at depth (Hurd, 1968; O'Brein, 1979; Manske and Vlek, 2002), angle and number of seminal roots (Nakamoto and Oyanagi, 1994; Manschadi *et al.*, 2008), root to shoot dry matter ratio (Siddique *et al.*, 1990), and root partitioning of assimilates to shallow and/or deep roots in response to drought (Ehdaie *et al.*, 2012). However, Palta *et al.* (2011) concluded that individual root traits do not adequately describe a root system size that might be optimum for water uptake under drought conditions.

Blum (2009) concluded that enhancement of biomass production and grain yield stability under drought stress can be achieved primarily by maximizing soil water uptake. The largest part of the available soil moisture should be diverted toward stomatal transpiration during the grain-filling period. He defined this system as crop 'effective water use'. An effective means of achieving satisfactory grain production under terminal drought stress is soil moisture capture by a vigorous deep root system (Kirkegaard *et al.*, 2007; Blum, 2009).

A shallow root system might also be important to capture soil moisture during occasional late spring rainstorms when only the top layers of soil are replenished with moisture during early grain filling (Ehdaie *et al.*, 2012). Based on a modeling technique, it was estimated that each additional millimeter of water extracted by the root system during grain filling might generate an extra 55 kg ha$^{-1}$ of grain in Australian dry environments (Manschadi *et al.*, 2006). Furthermore, a vigorous shallow root system is required for absorption of nutrients that are mostly concentrated in the upper layers of soil (Manske and Vlek, 2002).

Relatively little effort has been devoted to the selection of desirable root traits or root biomass in cereal breeding programs, mainly due to lack of appropriate screening techniques to evaluate large numbers of plants in the field. Also, the heterogeneity of field soil along with significant genotype × environment interactions results in unreliable evaluation. Therefore, different procedures and techniques were developed for measuring root traits, mostly during early growth of wheat plants (see review by Gregory *et al.*, 2009).

Hurd (1968) used glass columns and Liao *et al.* (2006) and Manschadi *et al.* (2008) used glass boxes to measure variation for root architectural traits. Mian et al. (1993) used hydroponic culture to characterize root growth and to measure root traits in several wheat genotypes. Ehdaie *et al.* (2003) quantified root biomass of several wheat genotypes at maturity using pot culture to measure the relationship between root biomass and grain yield under well-watered and drought conditions.

A sand-tube culture was developed and used by Ehdaie and Waines (2006) to identify a segment of the short arm of chromosome 1 of rye (*Secale cereale* L.) affecting root traits in isolines of wheat-rye translocations. The same procedure was used to determine the effect of root system size on water-nutrient uptake in several wheat genotypes (Ehdaie *et al.*, 2010). Watt *et al.* (2013) used a paper-roll technique to screen a large number of wheat genotypes for seedling roots. However, crop plants grown in artificial media or in non-field environments may not represent the root system of plants grown under field conditions.

A number of studies have reported on the association of root system traits with grain yields measured either under controlled conditions or in the field. Hurd (1968) noted that wheat lines with deep root density evaluated in glass boxes had higher grain yield in water-limited field plots than lines with low root density. Ehdaie *et al.* (2003) reported wheat-rye (1RS) translocated isolines with increased root biomass evaluated in a glasshouse had significant positive correlations with grain yield under both well-watered and drought stressed pot conditions. Also, they reported a significant positive correlation between root biomass and grain yield measured in well-watered field conditions, but not under drought conditions. Placido *et al.* (2013) found that a wheat-agropyron translocated line with greater root biomass had improved water stress adaptation compared with a control genotype. Ehdaie *et al.* (2014), using a large set of spring bread wheat recombinant inbred lines (RILs), found significant positive correlation coefficients between grain yield and root biomass and its components evaluated under well-watered glasshouse conditions.

Palta *et al.* (2011) questioned the importance of large root biomass in adapting wheat to dry environments. They examined the relationship between root system size and its functional implication for water capture. Using data from glasshouse and field experiments, Palta *et al.* (2011) concluded that the usefulness of a large and vigorous root system in increasing wheat yield under water-limited conditions might be greater in environments where crops rely largely on seasonal rainfall, such as Mediterranean-type environments. In environments where crops are reliant on stored soil moisture, a large root system may increase the risk of depleting soil water before completion of grain filling.

Despite the importance of greater root biomass in bread wheat as an adaptive root system trait under drought conditions, information about optimum size or a range of root biomass in bread wheat that improves grain yield under drought is scarce. The main objectives of this study are: to (i) evaluate a set of recombinant inbred lines (RILs) of bread wheat with diverse root biomass under well-watered and droughted field conditions, (ii) quantify drought tolerance of different RILs for grain yield and its components, (iii) determine the relationship between root biomass measured in a glasshouse with grain yield and drought tolerance measured in the field, and (iv) estimate optimum root biomass for maximum grain yield under well-watered and droughted field conditions.

## MATERIALS AND METHODS

### Plant materials

A population of RILs was produced by single-seed decent from crossing Iran #49 (a tall late landrace collected at Allary, 30° 56′, 61° 39′, alt. 530 m, average rainfall of 50 mm, in Sistan & Baluchistan, southeast Iran, with large root system) (Moghaddam *et al.*, 1997) and Yecora Rojo (a modern Mexican derived, two-gene dwarf cultivar with small root system) grown in Southern California for more than 45 years.

In a previous study (Ehdaie, 1995), dry root biomass of Iran #49 was 6.43 and 5.63 g plant$^{-1}$ under well-watered and droughted pot conditions compared with 2.00 and 1.60 g plant$^{-1}$ for Yecora Rojo, respectively. When these two genotypes were evaluated in a sand-tube experiment under well-watered conditions, shallow dry root weight (roots between 0 – 30 cm), deep root weight (roots below 30 cm), and root biomass of Iran #49 was 5.3, 4.5, and 9.8 g plant$^{-1}$ compared with 1.3, 0.5, and 1.8 g plant$^{-1}$ for Yecora Rojo, respectively (Ehdaie *et al.*, 2014). Also, the two genotypes were different for number of days from sowing to anthesis, and to maturity, plant height, number of spikes plant$^{-1}$, grain weight, grain yield plant$^{-1}$, shoot biomass plant$^{-1}$, and harvest index (HI).

Of the 104 RILs evaluated in the sand-tube experiment under well-watered (sand water-holding capacity) conditions (Ehdaie et al. 2014), five inbred lines, #8, #57, #115, #122, and #136, were chosen to represent a set of genotypes with diverse dry root weight, but with small variation for days from sowing to anthesis and to maturity and plant height (Table 1). Yecora Rojo was also included as the standard check in this study. These genotypes were planted in the field to determine the relationship between root biomass measured in the glasshouse with grain yield and drought tolerance index measured in the field.

**Table 1.** Mean values for root biomass (RB), shallow root weight (SRW), deep root weight (DRW), the ratio of DRW to SRW, number of days from sowing to anthesis (DTA) and to maturity (DTM), grain- filling period (GFP), and plant height (PH), of the bread wheat RILs and the check variety (Yecora Rojo, YR) measured under well-watered conditions in a sand-tube glasshouse experiment in Riverside in 2013 used in this study (Ehdaie *et al.*, 2014).

| RILs/ | RB | SRW | DRW | DRW/ | DTA | DTM | GFP | PH |
|---|---|---|---|---|---|---|---|---|
| Genotype | | (g plant$^{-1}$) | | SRW | | (days) | | (cm) |
| YR | 1.820 | 1.280 | 0.590 | 0.42 | 71 | 113 | 42 | 60 |
| #8 | 1.535 | 1.165 | 0.370 | 0.32 | 67 | 119 | 52 | 81 |
| #57 | 7.850 | 4.890 | 2.960 | 0.61 | 86 | 119 | 33 | 77 |
| #115 | 1.525 | 0.985 | 0.540 | 0.55 | 66 | 117 | 51 | 83 |
| #122 | 3.975 | 2.035 | 1.940 | 0.95 | 74 | 120 | 46 | 72 |
| #136 | 1.175 | 0.695 | 0.480 | 0.69 | 64 | 117 | 53 | 78 |

### Field experiments

Two field experiments were planted on 25-26 Jan. 2014 on a sandy loam soil at the Riverside Farm of the University of California Experiment Station, Riverside, California. The five RILs and Yecora Rojo were used in each experiment. One of the experiments was irrigated with sprinklers as needed to minimize water shortage until plants reached physiological maturity. Irrigation was reduced in the other experiment after sowing to develop a mild drought during plant growth until anthesis, then irrigation was terminated when plants in 50% of the plots reached anthesis.

The well-watered experiment, hereafter called the ‘wet’ experiment, received 270 mm of water including rain between sowing and days to boot stage (58 days after sowing), 10 mm between boot stage and heading (65 days after sowing), 33 mm between heading and anthesis (74 days after sowing), and 99 mm between anthesis and maturity (128 days after sowing). The second experiment, hereafter called the ‘dry’ experiment, received 240 mm, 6 mm, 12.3 mm, and 10mm of irrigation water and rain during these stages of plant growth, respectively. Thus, plants in the wet and dry experiments received a total of 412 mm and 268 mm of water, respectively.

A randomized complete block design with six replicates was used in each experiment. Each plot consisted of four rows, 6 m in length. Inter-row spacing was 10 cm and interplant spacing was 5 cm. The land was fallowed the previous year and 50 kg ha$^{-1}$ $NH_4NO_3$, 40 kg ha$^{-1}$ $P_2O_5$, and 30 kg ha$^{-1}$ $K_2O$ was added to the soil before planting. Monthly total precipitation during the experiments from February to March 2014 was from 29.2 to 0.00 mm. Maximum, minimum, and average air temperature ranged from 21.3 to 28.3 °C, from 8.5 to 13.8 °C, and from 14.3 to 20.8 °C, respectively. Maximum, minimum, and average air relative humidity varied from 72 to 65%, from 31 to 26%, and from 51 to 48%, respectively.

### Measured traits

Plants were harvested at physiological maturity between June 5 and 12. Before harvesting, the two outer rows were removed and 50 cm of each end of the two middle rows discarded to eliminate border effects. Two 50-cm lengths of the two middle rows were used to count the number of tillers and effective spikes at maturity. Plant height from soil surface to the tip of spikes, excluding awns, was recorded on five randomly chosen plants in each plot. Five randomly chosen spikes were collected from each plot to determine the number of grains spike$^{-1}$.

Four phenological periods, namely days from sowing to booting, to heading, to anthesis, and to physiological maturity were recorded. These phenological periods were determined when in each plot 50% of the plants showed booting, when 50% of spikes partially emerged from flag leaf sheath, when 50% of plants had extruded anthers, and when 50% of spikes lost their green color, respectively. Grain filling period was calculated from the difference between number of days from sowing to maturity and number of days to anthesis.

Aboveground biomass including spikes was harvested by hand from the soil surface in each plot and put in a drier at 65 °C for a week before measuring shoot dry weight for each plot. After weighing, spikes were cut and mechanically threshed to determine grain yield. Thousand grain weight was measured for each plot and harvest index was calculated from the ratio of grain yield to aboveground dry matter.

### Statistical analysis

Analysis of variance was performed for each character for both wet and dry experiments. Data from the wet and dry experiments were combined and the combined ANOVA was performed for each character (Steele *et al.*, 1997). Covariate analysis was performed between grain yield and number of days to anthesis and to maturity, and plant height to determine the impact of these characters on grain yield. Associations among characters were examined by correlation analysis. Relationship between root biomass and other characters was determined by regression analysis (Steele *et al.*, 1997).

A stress tolerance index (STI) was used to characterize relative response of each genotype to stressed field conditions (Fernandez, 1992). The index was calculated from genotype means using the generalized formula:

$$\mathrm{STI} = (Y_P/\bar{Y}_P)(Y_S/\bar{Y}_S)(\bar{Y}_S/\bar{Y}_P) = (Y_P)(Y_S)/(\bar{Y}_P)^2$$

where $Y_p$ and $Y_s$ are the grain yield of a given genotype in non-stressed (yield potential) and stressed environment, respectively, and $\bar{Y}_P$ and $\bar{Y}_S$ are mean yield in none stressed and stressed environments, respectively. Therefore, STI is a function of relative grain performance of a genotype in non-stressed $(Y_P/\bar{Y}_P)$ and stressed $(Y_S/\bar{Y}_S)$ environments, and the stress intensity ($\overline{Y}_S/\overline{Y}_P$). Greater values of STI for a genotype indicate greater stress tolerance and grain yield potential.

## RESULTS

The covariate analysis of grain yield with number of days to anthesis and to maturity, and plant height under wet and dry field conditions were not significant (Table 2). Genotype accounted for 79% of total sum of squares followed by plant height (11%), number of days to maturity (11%) and number of days to anthesis (6%) under well-watered field experiment. Under drought field conditions, genotype accounted for 90% of total sum of squares followed by days to maturity (6%), plant height (4%), and days to anthesis (0.0%) (Table 2).

**Table 2.** Covariate analysis of grain yield with number of days to anthesis (DTA) and to maturity (DTM), and plant height (PH) for the bread wheat genotypes evaluated under well-watered and droughted field conditions in Riverside in 2014

| | | Well-watered | | Droughted | |
|---|---|---|---|---|---|
| Source of variation | Degrees of freedom | Sum of squares | % of total | Sum of squares | % of total |
| Genotype | 5 | 68504$^{**}$ | 79 | 38505 | 90 |
| DTA | 1 | 5416 | 6 | 26 | 0 |
| DTM | 1 | 3667 | 4 | 2163 | 6 |
| PH | 1 | 9447 | 11 | 1293 | 4 |
| Error | 22 | 82662 | | 101483 | |

$^{**}$: Significant at the $P < 0.01$.

The combined ANOVA (Table 3) indicated highly significant main effects for irrigation regime on days to maturity, grain filling period, thousand grain weight, grain yield, and shoot biomass, and significant effect on plant height, and number of tillers and spikes per 50 cm. Highly significant main effects for genotypes were observed on all of the characters examined (Table 3). Genotype × irrigation interaction (GE) was significant for days to anthesis and to maturity, grain filling period, grain yield, shoot biomass either at the P = 0.05 or P = 0.01, and for harvest index at P = 0.10 (Table 3).

**Table 3.** The combined ANOVA for number of days to anthesis (DTA) and to maturity (DTM), grain-filling period (GFP), plant height (PH), number of tillers (NT) and spikes (NS), number of grains per spike (NGS), thousand grain weight (TGW), grain yield (GY), shoot biomass (SB), and harvest index (HI) of the bread wheat genotypes measured under well-watered and droughted field conditions in Riverside in 2014

| | Sum of squares | | | % Total sum of squares | | |
|---|---|---|---|---|---|---|
| Traits | Irrigation (E) | Genotype (G) | G × E | E | G | G × E |
| DTA (day) | 23.4 | 1234.8$^{**}$ | 20.9* | 1.8 | 96.0 | 1.5 |
| DTM (day) | 910.2$^{**}$ | 1919.4$^{**}$ | 65.4** | 31.4 | 66.3 | 2.2 |
| GFP (day) | 642.0$^{**}$ | 332.2$^{**}$ | 77.6* | 61.0 | 31.6 | 7.4 |
| PH (cm) | 1153.6$^{*}$ | 7684.5$^{**}$ | 117.1 | 12.9 | 85.8 | 1.3 |
| NT (50 cm$^{-1}$) | 1088.9$^{*}$ | 740.4$^{**}$ | 175.8 | 54.3 | 36.9 | 8.8 |
| NS (50 cm$^{-1}$) | 1406.3$^{*}$ | 355.7$^{*}$ | 172.5 | 72.7 | 18.4 | 8.9 |
| NGS (no.) | 7.7 | 1764.6$^{**}$ | 106.2 | 0.5 | 93.9 | 5.6 |
| TGW (g) | 325.3$^{**}$ | 669.9$^{**}$ | 47.7 | 31.2 | 64.2 | 4.6 |
| GY (t ha$^{-1}$) | 33.3$^{**}$ | 13.2$^{**}$ | 7.3** | 62.8 | 24.5 | 13.5 |
| SB (t ha$^{-1}$) | 280.7$^{**}$ | 146.3$^{**}$ | 64.3* | 57.1 | 29.8 | 13.1 |
| HI (%) | 2.5 | 1717.5$^{**}$ | 266.1+ | 0.1 | 86.5 | 13.4 |

$^{+}$, $^{*}$ and $^{**}$: Significant at the $P < 0.10$, $P < 0.05$, and $P < 0.01$, respectively.

The irrigation impact was much stronger than genotype and GE for grain filling period, number of tillers and spikes per 50 cm, grain yield, and shoot biomass accounting for 61.0, 54.3, 72.7, 62.8, and 57.1% of the total sum of squares, respectively (Table 3). The genotype impact was stronger than irrigation regime and GE for days to anthesis and to maturity, plant height, number of grains per spike, thousand grain weight, and harvest index accounting for 96.0, 66.3, 85.8, 93.9, 64.2, and 86.5%, respectively (Table 3). The impact of GE was relatively low, although GE effects were significant for days to anthesis and to maturity, grain filling period, grain yield, shoot biomass, and harvest index (Table 3).

Mean values for different characters examined under wet and dry field conditions are shown in Table 4. Yecora Rojo and #57 were the earliest and latest to reach anthesis and maturity, respectively, under both irrigation regimes. Grain filling period was similar for #8, #115, and #122, but longer than Yecora Rojo, #57, and #136 under wet field conditions. In dry field conditions, #8, #57, #115, and #122 showed similar grain filling period, but longer than Yecora Rojo and #136. Plant height was the shortest for Yecora Rojo (69 cm) and the tallest for #57 (101 cm) in wet field conditions. Plant height ranged from 61 cm (Yecora Rojo) to 88 cm (#57 and #115) under dry field conditions (Table 4).

**Table 4.** Mean values for number of days to anthesis (DTA) and to maturity (DTM), grain-filling period (GFP), plant height (PH), number of spikes per 50 cm (NS), number of grain per spikes (NGS), thousand grain weight (TGW), grain yield (GY), shoot biomass (SB), and harvest index (HI) for the genotypes evaluated under well-watered and droughted field conditions in Riverside in 2014

| Treatment/ genotype | DTA[a] (d) | DTM (d) | GFP (d) | PH (cm) | NS (50 cm$^{-1}$) | NGS (no.) | TGW (g) | GY (t ha$^{-1}$) | SB (t ha$^{-1}$) | HI % |
|---|---|---|---|---|---|---|---|---|---|---|
| Well-watered | | | | | | | | | | |
| Yecora Rojo | 72c | 128d | 56b | 69e | 34.6ab | 43.4a | 33.2c | 5.994a | 13.698b | 43.9a |
| #8 | 73c | 134b | 62a | 85c | 36.7ab | 33.1c | 37.7b | 5.928a | 13.742b | 43.7a |
| #57 | 82a | 137a | 55b | 101a | 40.8a | 36.6bc | 34.1c | 4.375c | 17.913a | 25.7d |
| #115 | 72c | 132c | 60a | 95b | 32.b | 27.5d | 42.1a | 4.953bc | 13.139b | 37.7b |
| #122 | 77b | 137a | 60a | 77d | 41.3a | 41.5ab | 37.8b | 5.694ab | 18.143a | 32.1c |
| #136 | 69d | 125c | 56b | 90c | 37.6ab | 37.5c | 38.4b | 6.271a | 15.730ab | 40.0ab |
| Mean[b] | 74A | 132A | 58A | 86A | 37.8A | 36.6A | 37.A | 5.536A | 15.394A | 37.2A |
| Droughted | | | | | | | | | | |
| Yecora Rojo | 70d | 118d | 48b | 61d | 25.8c | 42.2a | 27.7c | 3.703b | 8.642b | 43.2a |
| #8 | 73c | 126c | 54a | 80b | 28.8abc | 36.6b | 32.1b | 4.554a | 12.039a | 37.6ab |
| #57 | 80a | 134a | 53a | 88a | 26.7bc | 36.0b | 30.8bc | 3.665b | 11.844a | 30.9c |
| #115 | 73c | 126c | 53a | 88a | 32.3bc | 25.9c | 37.7a | 4.379ab | 12.074a | 36.3bc |
| #122 | 76b | 130b | 54a | 69c | 30.3ab | 36.9b | 36.6a | 4.546a | 12.719a | 35.8bc |
| #136 | 68e | 117d | 49b | 82b | 32.7a | 38.1b | 32.8b | 4.209ab | 11.356a | 37.0bc |
| Mean | 73A | 125B | 52B | 78A | 28.5B | 36.0A | 33.0B | 4.176B | 11.446B | 36.8A |

[a] In each section, means followed by at least one letter in common, within a column, are not significantly different at the $P < 0.05$ according to LSD test.

[b] Means followed by the same capital letter, within a column, are not significantly different at the $P < 0.05$ according to LSD test

Number of spikes per 50 cm was the highest for #57 (40.8) and the lowest for #115 (32.9) under wet field conditions. Under dry field conditions, it was the highest for #136 (32.7) and the lowest for Yecora Rojo (25.8). Number of grains per spike was the highest in Yecora Rojo (43.4) and the lowest in #115 (27.5) under wet field conditions. The same genotypes also showed the highest and the lowest number of grains per spike under dry field conditions; 42.2 and 25.9, respectively. Thousand grain weight was the highest in #115 and the lowest in Yecora Rojo under wet, 42.1 and 33.2 g and also under dry field conditions; 37.7 and 27.7 g, respectively (Table 4).

Mean grain yield ranged from 6.271 t ha$^{-1}$ (#136) to 4.375 t ha$^{-1}$ (#57) in wet and from 4.554 t ha$^{-1}$ (#8) `to 3.703 t ha$^{-1}$ (Yecora Rojo) in dry field conditions (Table 4). The highest shoot biomass was produced by #122 (18.143 t ha$^{-1}$) and the lowest by #115 (13.139 t ha$^{-1}$) in wet and by #122 (12.719 t ha$^{-1}$) and by #136 (11.356 t ha$^{-1}$) in dry field conditions. Yecora Rojo and #57 had the highest and the lowest harvest index, 43.9 and 25.7%, in wet and also in dry field conditions, 43.2 and 30.9%, respectively (Table 4).

Stress tolerance indices for grain yield and its primary components are shown in in Table 5. Stress tolerance index for number of spikes per 50 cm was high for #122 (0.89), intermediate for #136 (0.78), #115 (0.76), #57 (0.76), and #8 (0.74), but low for Yecora Rojo (0.65). Yecora Rojo had the highest STI (1.37) for number of grains per spike followed by #122 (1.14), #136 (1.07), #57 (0.98), and #8 (0.90). The STI values for thousand grain weight was relatively high for #115 (1.15) and #122 (1.00), medium for #136 (0.91), #8 (0.87), and #57 (0.87), but low for Yecora Rojo (0.66). Genotypes #8, #136, and #122 had relatively high STI values for grain yield, (0.88), (0.86), and (0.84), followed by #155 and Yecora Rojo with medium STI values, (0.71) and (0.67), respectively, while #57 showed the lowest STI value, (0.52) (Table 5).

**Table 5.** Stress tolerance indices based on number of spikes per 50 cm (NS), number of grains per spike (NGS), thousand grain weight (TGW), grain yield for bread wheat genotypes evaluated under well-watered and droughted field conditions in Riverside in 2014

| | Stress tolerance index (STI)[a] | | | |
|---|---|---|---|---|
| Genotype | No. of spikes per 50 cm | No. of grains per spike | Thousand grain weight | Grain yield |
| Yecora Rojo | 0.65 | 1.37 | 0.66 | 0.67 |
| #8 | 0.74 | 0.90 | 0.87 | 0.88 |
| #57 | 0.76 | 0.98 | 0.76 | 0.52 |
| #115 | 0.76 | 0.53 | 1.15 | 0.71 |
| #122 | 0.89 | 1.14 | 1.00 | 0.84 |
| #136 | 0.78 | 1.07 | 0.91 | 0.86 |

[a] $\mathrm{STI} = (Y_p / \overline{Y}_p)(Y_s / \overline{Y}_s)(\overline{Y}_s / \overline{Y}_p) = (Y_p)(Y_s) / (\overline{Y}_p)^2$ , where $Y_p$ and $Y_s$ are mean of a genotype for a trait in non-stressed and stressed environment and, $\overline{Y}_p$ and $\overline{Y}_s$ are overall mean, averaged over the genotypes, of a trait in non-stressed and stressed environments, respectively. Greater values of STI for a genotype indicate greater stress tolerance.

Root biomass measured in the glasshouse under wet conditions (Ehdaie *et al.*, 2014) was negatively correlated with grain yield measured in wet, r = -0.59 and dry, r = -0.48, field conditions. These correlation coefficients were not statistically significant due to a small number of degrees of freedom, df = 4. However, these negative correlations between grain yield and root biomass were misleading if the pattern of relationship between the two traits had not been exploited.

The pattern of relationship between root biomass and grain yield in wet and dry field conditions followed a quadratic trend with $R^2 = 0.62$ and $R^2 = 0.41$, respectively (Fig. 1a and b). When the standard check variety, Yecora Rojo was excluded from the pattern analysis in dry conditions, the value of $R^2$ increased from 0.41 to 0.93 (Fig. 1c). The pattern of relationship between root biomass and STI measured based on grain yield was also quadratic with $R^2 = 0.60$ (Fig. 1d).

## DISCUSSION

An important issue in wheat breeding programs is to what extent and how root system traits measured in non-field media, such as in pots or tubes in glasshouse or in hydroponic cultures, are associated with traits measured under field conditions. Mian *et al.* (1994), using bread wheat genotypes, reported significant positive correlation between root weight measured in hydroponic culture with root length density measured in varying field conditions.

In maize, a relationship between seminal root traits measured in hydroponic culture and root lodging in the field has been reported (Landi *et al.*, 1998; Sanguineti, 1998). Landi *et al.* (2002) reported a significant association between seminal root traits in hydroponic culture and root pulling resistance in maize under field conditions. Tuberosa *et al.* (2002), using a maize mapping population, reported a noticeable overlap of QTLs for seminal root traits in hydroponic culture with QTLs for grain yield under well-watered and water-deficit field conditions. These observations support our assumption that root biomass produced by the genotypes in sand-tube culture under wet glasshouse conditions would be similar in size and ranking under field conditions. This assumption might hold as root biomass shows plasticity under different environmental conditions (Ehdaie *et al.*, 2012). In wheat, a major problem in determining the relationship between root biomass measured under glasshouse conditions and grain yield evaluated under field conditions has been small genotypic variation in root biomass. The subset of RILs chosen to conduct this study represented a wide range for root biomass, but with relatively narrow variation for days to anthesis and to maturity, grain filling period, and plant height (Table 1). It was intended to reduce variation for these phenological and morphological characters in order to avoid the confounding effects of these characters on the expression of grain yield (Lopes and Reynolds, 2010).

Root biomass in wheat is an integrated function of number of seminal and nodal roots with their branching, total root length, root density, and root diameter. Thus, root biomass is a measure of the overall root system (Ehdaie *et al.*, 2010). Significant positive correlations were reported between root biomass and its components in wheat (Løes and Gahoonia, 2004; Ehdaie, 1995; Jain *et al.*, 2014).

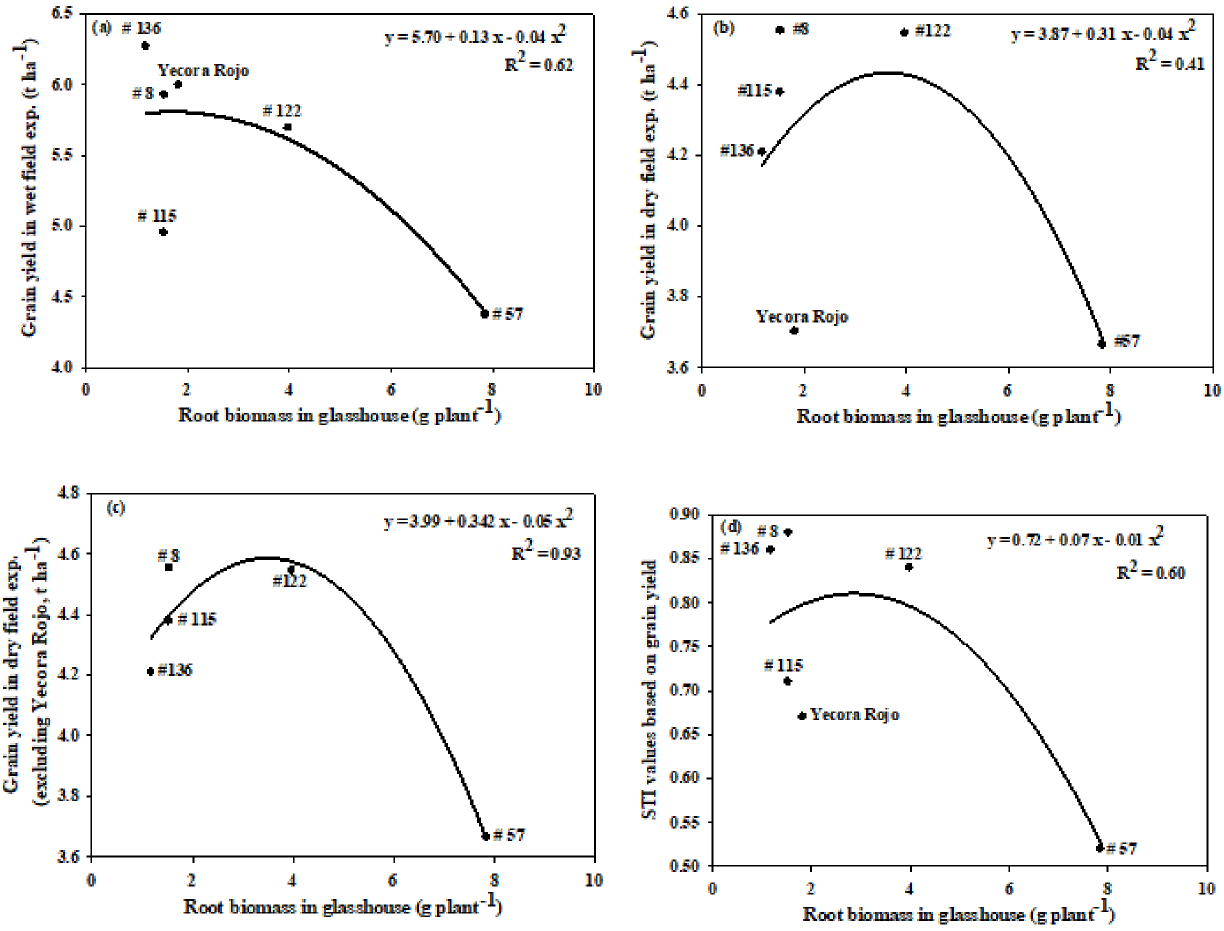

Fig. 1. Quadratic relationships between root biomass measured in glasshouse and grain yield evaluated under well-watered (a) and droughted field conditions with check variety Yecora Rojo (b) and excluding Yecora Rojo (c), and with stress tolerance indices (STI) (d) using five recombinant inbred lines of bread wheat. The second degree equation and coefficient of determination (R2) are included for each quadratic pattern

The covariate analysis between grain yield and the phenological characters and plant height (Table 2) indicated that grain yield was not confounded by the effects of these characters. Since grain filling period was a function of number of days to anthesis and to maturity, its effect was not confounding the grain yield variation observed in the field.

The mild drought imposed during plant growth until anthesis and the severe drought after anthesis had a significant negative effect on some of the characters, whereas the main effect of genotype was significant for all the characters measured (Table 3). Genotype × irrigation interaction (GE) was relatively small compared to the main effects of genotype and irrigation. Examination of GE for days to anthesis and to maturity, grain filling period, thousand grain weight, grain yield, shoot biomass, and harvest index observed in the field indicated that all genotypes had greater mean values under wet than in dry field conditions (non-crossover interaction). Therefore, the significance of GE for these characters was due to inconsistency of relative performance of the genotypes at the two water regimes. The non-crossover interaction was the reason for smaller effect of GE compared with the main effects of genotype and irrigation.

Drought, on average, significantly reduced number of days to maturity by 5%, grain filling period by 10%, number of spikes per 50 cm by 24.6%, and thousand grain weight by 11%. Therefore, the 25% reduction in grain yield observed under drought was mainly due to reduction in number of effective spikes per 50 cm and to some extent due to thousand grain weight and grain filling period (Table 4). Drought, on average, reduced shoot biomass by 27%, whereas it did not reduce harvest index, indicating that under drought grain yield and shoot biomass were proportionally reduced.

Reduction in shoot biomass under drought was mainly due to reduction in number of spikes per 50 cm and grain yield since plant height that is one of components of shoot biomass was similar in wet and dry field conditions.

The STI values calculated for each genotype based on grain yield components and grain yield were a measure of pre-anthesis stress tolerance (number of spikes per 50 cm), post-anthesis stress tolerance (number of grains per spike and thousand grain weight) and overall stress tolerance (grain yield) (Bruckner and Frohberg, 1987; Ehdaie *et al.*, 1988). The genotypes examined exhibited different patterns for pre- and post-anthesis tolerance to drought stress (Table 5). The STI values for Yecora Rojo were the lowest for number of spikes per 50 cm and thousand kernel weight which resulted in low STI value for its grain yield (0.67). Therefore, Yecora Rojo was sensitive to drought with regards to number of spikes per 50 cm and thousand grain weight, but not for number of grains per spike.

Ehdaie *et al.* (2003) also reported a relatively low STI for Yecora Rojo based on grain yield. The STI values for #8 were relatively intermediate for the three components of grain yield and its overall STI value based on grain yield was the highest (0.88). The STI value of #57 based on grain yield was the lowest (0.52) which appeared to be due to production of high and intermediate number of tillers and spikes in wet and dry field conditions, respectively (Table 4). This genotype had the highest root biomass (7.850 g plant$^{-1}$) in the glasshouse and the lowest grain yield in wet (4.375 t ha$^{-1}$) and in dry (3.665 t ha$^{-1}$) field conditions (Table 4).

It appeared that competition for assimilates to produce an extensive root system along with production of a larger number of tillers and spikes on the one hand and assimilates needed to fill the grains on the other hand, as measured by thousand grain weight, resulted in lower grain yield in #57 under both irrigation regimes. Therefore, an over-sized root system, as observed in #57, was not advantageous in maintaining or improving grain yield under wet and dry field conditions. Genotype #115 had intermediate, low, and high drought tolerance for number of spikes per 50 cm, number of grains per spike and thousand grain weight, respectively, and as a result had medium drought tolerance for grain yield (0.71). The STI values for #122 and #136 were relatively high for the three components of grain yield indicating their pre-and post-anthesis drought tolerance and as a result both lines had high overall drought tolerance for grain yield as evidenced by their STI values, 0.84 and 0.86, respectively (Table 5).

Among the three genotypes with high and similar STI based on grain yield, namely #8, #122, and #136, the last genotype (#136) showed the highest reduction (33%) in grain yield under dry field conditions followed by #8 (23%), and #122 (20%). Considering the overall grain yield performance and the STI values, it appeared that line #122 possessed greater agronomic characteristics than the other genotypes examined. It should be noted that #122 was the only genotype that allocated similar amount of assimilates for production of deep root weight (1.940 g plant$^{-1}$) and shallow root weight (2.035 g plant$^{-1}$) (Table 1). This genotype had the second largest deep root biomass. Lopes and Reynolds (2010) reported that greater deep root biomass was associated with cooler canopies and increased grain yield under drought in wheat.

The quadratic relationship between root biomass and grain yield under wet field conditions (Fig. 1a) indicated that grain yield was relatively high when root biomass ranged between 1.175 to 3.975 g plant$^{-1}$, with the exception of #115. Variation in root biomass in the present study could explain 62% of variation observed in grain yield under wet field conditions. Therefore, the relatively low grain yield of #115 under wet conditions could be due to relatively low number of spikes per 50 cm and low number of grains per spike in this genotype (Table 4). As root biomass per plant increased beyond 3.975 g plant$^{-1}$ grain yield gradually reduced followed with significant reduction under wet field conditions (Fig. 1a and Table 4). Maheepala *et al.* (2015) also reported root biomass greater than 5.05 g plant$^{-1}$ significantly reduced grain yield under both wet and dry field conditions.

According to the second-degree prediction equation in Fig 1a, grain yield, on average, was maximized under wet field conditions when root biomass was 1.630 g plant$^{-1}$. The quadratic relationship between root biomass and grain yield under dry field conditions (Fig. 1 c) was more pronounced ($R^2$ = 0.93%) than that under wet field conditions ($R^2$ = 0.62%). The trend in this relationship was similar to the trend observed between root biomass and grain yield under wet field conditions. However, according to the second-degree prediction equation in Fig. 1c, grain yield, on average, maximized under dry field conditions when root biomass was 3.420 g plant$^{-1}$. Therefore, greater root biomass was required to maximize grain yield under dry than under wet field conditions. If the genotypic variation in root biomass is substantial, as in the present study, a quadratic relationship between root biomass and grain yield is expected. However, the optimum root biomass to maximize grain yield might change depending on target environments.

The STI values based on grain yield, which is a function of drought intensity and grain yield performance of the genotypes under wet (yield potential) and dry field conditions, also had a quadratic relationship with root biomass (Fig.1 d). Variation in root biomass could explain 60% of variation observed in STI based on grain yield. The low STI values of Yecora Rojo and #115 might be attributable to their pre- and/or post-anthesis sensitivity to drought stress. According to the second-degree prediction equation in Fig. 1d, STI value based on grain yield maximized, on average, at root biomass 3.500 g plant$^{-1}$. It was not coincidence that both grain yield under drought and STI value based on grain yield were maximized at similar root biomass, 3.420 and 3.500 g plant$^{-1}$, respectively. It appeared that drought tolerance was influenced more by grain yield under drought than potential yield. These observations signify the importance of a separate breeding program for drought tolerance in wheat.

In contrast to our results with regard to the relationship between root biomass measured in glasshouse and grain yield evaluated in the field, Jain et al. (2014) reported a linear positive correlation coefficient between root biomass and grain yield and between root biomass and STI based on grain yield. These differences in results are mainly due to the range in root biomass of the genotypes used and/or the stage of plant growth when roots were measured. In the study by Jain *et al.* (2014) root biomass was measured in glasshouse 10 weeks after sowing during early plant growth, and root biomass ranged from 0.457 to 0.978 g plant$^{-1}$, whereas in our study root biomass was measured at maturity and it varied from 1.175 to 7.850 g plant$^{-1}$. Watt et al. (2013) and Ehdaie *et al.* (2014) reported that in wheat, root biomass measured at early stages of plant growth might not be correlated or be only weakly correlated with root biomass measured at maturity.

Among the physiological characters, the amount of water uptake by the roots and transpiration efficiency along with dry matter partitioning efficiency (harvest index) have large impacts on grain yield, especially under drought conditions (Passioura, 1977). Ehdaie (1995) observed that the amount of water uptake by wheat genotypes was significantly and positively correlated with root biomass under both well-watered (r = 0.87) and droughted (r = 0.83) glasshouse conditions. Izzi *et al.* (2008) reported significant correlations, ranging from r = 0.79 to r = 0.95, between root biomass in bread wheat and the ability to extract water from the soil under varying field conditions. Palta *et al.* (2011) concluded that a large root system (root biomass) contributes to increasing the capture of water and nutrients early in the season, and facilitates the capture of additional water for grain filling where wheat crops rely largely on seasonal rainfall. In contrast, Inagaki *et al.* (2010), using synthetic-derived bread wheat genotypes, reported unexpectedly less water uptake ability for a genotype with a greater root biomass than those with smaller root biomass.

In the present study, the amount of water uptake and transpiration efficiency was not measured. However, it is speculated that genotypes #8 with relatively small root biomass (1.535 g plant$^{-1}$) had low water uptake ability, but possessed high transpiration efficiency, thus it produced high grain yield under drought field conditions (4.554 t ha$^{-1}$). In contrast, genotype #122 with medium root biomass (3.975 g plant$^{-1}$) had optimum water uptake ability during pre- and post anthesis period without depleting soil moisture, thus it produced high grain yield under drought (4.546 t ha$^{-1}$). The harvest index of #8 and #122 were similar under drought field conditions, 37.6 and 35.8%, respectively. However, the optimum root biomass (3.500 g plant$^{-1}$) to maximize drought tolerance was closer to root biomass of #122 than to #8.

There existed a tremendous amount of variation for root biomass and other root traits in a population of RILs in bread wheat (Ehdaie *et al.*, 2014). Kashiwagi *et al.* (2015) reported the existence of substantial genotypic variation for root water uptake efficiency. Conventional selection for root biomass among a large number of plants, such as an $F_2$ population, a population of RILs, or a population of doubled haploids, is very difficult if not impossible. Using molecular markers to locate QTLs affecting root traits might be effective in manipulating the root system through MAS procedures in wheat. Canopy temperature measured by infrared thermometry under drought conditions offers the possibility of screening a large number of wheat genotypes in the field for root system (Blum *et al.*, 1989; Reynolds *et al.*, 1998). The water uptake ability and transpiration efficiency of the genotypes examined in this study should be assessed in a future investigation.

In conclusion, the relationship between root biomass measured in glasshouse and grain yield evaluated under both well-watered and droughted field conditions followed a quadratic pattern. Accordingly, as root biomass increased grain yield also increased under well-watered conditions until it peaked at 5.806 t ha$^{-1}$ at root biomass 1.630 g plant$^{-1}$. As root biomass further increased, grain yield decreased gradually then followed a sharp decrease. A similar relationship between root biomass and grain yield was observed under droughted field conditions where grain yield peaked at 4.575 t ha$^{-1}$ at root biomass 3.975 g plant$^{-1}$. The relationship between root biomass and grain yield was more pronounced under drought than under well-watered field conditions.

The genotypes examined demonstrated different responses to drought with regards to primary components of grain yield. Root biomass and drought tolerance, calculated based on grain yield, also showed a quadratic relationship. Drought tolerance was highest at root biomass 3.500 g plant$^{-1}$. These observations signified the importance of a separate breeding program for developing wheat genotypes adapted to drought-prone environments as also suggested by Jain *et al.* (2014). Since there exists a highly significant negative correlation between root biomass and harvest index (Ehdaie *et al.,* 2014), simultaneous selection should be practiced for these two characters in wheat breeding programs.

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## REFERENCES

Araus, J. L., Bort, J., Sterduto, P., Villegas, D. and Royo, C. 2003a. Breeding cereals for Mediterranean conditions: ecophysiological clues for biotechnology application. Ann. Appli. Biol. 142: 129-141. DOI: 10.1111/j.1744-7348.2003.tb00238.x

Araus, J. L., Villegas, D., Aparrico N., García del Moral, L. F., El-Hani, S., Rharrabti, Y., Ferrio, J. P. and Royo C. 2003b. Environmental factors determining carbon isotope discrimination and yield in durum wheat under Mediterranean conditions. Crop Sci. 43: 170-180. DOI: 10.2135/cropsci2003.1700

Blum, A. 2009. Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. Field Crops Res. 112: 119-123. DOI: 10.1016/j.fcr.2009.03.009

Blum, A., Shpiler, L., Golan, G. and Mayer, J. 1989. Yield stability and canopy temperature of wheat genotypes under drought-stress. Field Crops Res. 22: 289-296. DOI: 10.1016/0378-4290(89)90028-2

Bruckner, P. L. and Frohberg, R. C. 1987. Stress tolerance and adaptation in spring wheat. Crop Sci. 27: 31-36. DOI: 10.2135/cropsci1987.0011183X002700010008x

Dhanda, S. S., Seti, G. S. and Behl, R. K. 2004. Indices of drought tolerance in wheat genotypes at early stages of plant growth. J. Agron. Crop Sci. 190: 6-12. DOI: 10.1111/j.1439-37X.2004.00592.x

Ehdaie, B. 1995. Variation in water-use efficiency and its components in wheat: II. Pot and field experiments. Crop Sci. 35: 1617-1626. DOI: 10.2135/cropsci1995.0011183X003500060017x

Ehdaie, B., Alloush, G. A. and Waines, J. G. 2008. Genotypic variation in linear rate of grain growth and contribution of stem reserves to grain yield in wheat. Field Crops Res. 106: 34-43. DOI: 10.1016/j.fcr.2007.10.012

Ehdaie, B., Layne, A. P. and Waines, J. G. 2012. Root system plasticity to drought influences grain yield in bread wheat. Euphytica 186: 219-232. DOI: 10.1007/s10681-011-0585-9

Ehdaie, B., Maheepala, D. C., Bektaş, H. and Waines, J. G. 2014. Phenotyping and genetic analysis of root and shoot traits of recombinant inbred lines of bread wheat under well-watered conditions. J. Crop Improv. 28: 834-851. DOI: 10.1080/15427528.2014.948107

Ehdaie, B., Merhaut, D. J., Ahmadian, S., Hoops, A. C., Khuong, T., Layne, A. P. and Waines, J. G. 2010. Root system size influences water-nutrient uptake and nitrate leaching potential in wheat. J. Agron. Crop Sci. 196: 455-466. DOI: 10.1111/j.1439-037X.2010.00433.x

Ehdaie, B. and Waines, J. G. 2006. Determination of a chromosome segment influencing rooting ability in wheat-rye 1BS-1RS recombinant lines. J. Genet. Breed. 60: 71-76.

Ehdaie, B., Waines, J. G. and Hall, A. E. 1988. Differential responses of landrace and improved spring wheat genotypes to stress environments. Crop Sci. 28: 838-842. DOI: 10.2135/cropsci1988.0011183X002800050024x

Ehdaie, B., Whitkus, R. W. and Waines, J. G. 2003. Root biomass, water-use efficiency, and performance of wheat-rye translocations of chromosomes 1 and 2 in spring bread wheat 'Pavon'. Crop Sci. 43: 710-717. DOI: 10.2135/cropsci2003.0710

Fernandez, G. C. J. 1992. Effective selection criteria for assessing plant stress tolerance. pp. 257-270. In: Adaptation of Food Crops to Temperature and Water Stress: Proceeding of an International Symposium, Taiwan, 13-10 August 1992. DOI: 10.22001/wvc.72511

Gallagher, J. N., Biscoe, P. V. and Scott, R. K. 1975. Barley and its environment. V. Stability and grain weight. J. Appl. Ecol. 12: 319-336. DOI: 10.2307/2401735

Gregory, P. J., Bengough, A. G., Grinev, D., Schmidt, S., Thomas, W. T. B., Wojciechowski, T. and Young, I. M. 2009. Root phenomics of crops: opportunities and challenges. Funct. Plant Biol. 36: 922-929. DOI: 10.1071/FP09150

Hurd, E. A. 1968. Growth of roots of seven varieties of spring wheat at high and low moisture levels. Agron. J. 60: 201-205. DOI: 10.2134/agronj1968.00021962006000020018x

Hurd, E. A. 1974. Phenotype and drought tolerance in wheat. Agric. Meteorol. 14: 39-55. DOI: 10.1016/B978-0-444-41273-7.50010-6

Inagaki, M. N., Mori, M. and Nachit, M. M. 2010. Yield comparison for synthetic-derived bread wheat genotypes with different water uptake ability under increasing water deficits. Cereal Res. Commun. 38: 497-505. DOI: 10.1556/CRC.38.2010.4.6

Izzi, G., Farahani, H. J., Bruggeman, A. and Oweis, T. Y. 2008. In-season wheat root growth and soil water extraction in the Mediterranean environment of northern Syria. Agri. Water Manage. 95: 259-270. DOI: 10.1016/j.agwat.2007.10.008

Jain, N., Singh, G. P., Yadav, R., Pandey, R., Ramya, P., Shine, M. B., Pandey, V. C., Rai, N., Jha, J. and Prabhu, K. V, 2014. Root trait characteristics and genotypic response in wheat under different water regimes. Cereal Res. Commun. 42: 426-438. DOI: 10.1556/CRC.42.2014.3.6

Kashiwagi, J., Morito, Y., Jitsuyama, Y., An, P., Inoue, T. and Inagaki, M. 2015. Effects of root water uptake efficiency on soil water utilization in wheat (*Triticum aestivum* L.) under severe drought environments. J. Agro. Crop Sci. 201 (3):161-172. DOI: 10.1111/Jan. 12092

Kirkegaard, J. A., Lilley, M., Howe, N. G. and Graham, J. M. 2007. Impact of subsoil water use on wheat yield. Aust. J. Agric. Res. 58: 303-315. DOI: 10.1071/AR06285

Landi, P., Albrecht, B., Giuliani, M. M. and Sanguineti, M. S. 1998. Seedling characteristics in hydroponic culture and field performance of maize genotypes with different resistance to root lodging. Maydica 43: 111-116.

Landi, P., Sanguineti, M. C., Darrah, L., Giuliani, M., Salvi, S. and Tuberosa, R. 2002, Detection of QTLs for vertical root pulling resistance in maize and overlaps with QTLs for root traits in hydroponics and for grain yield at different water regimes. Maydica 47: 233-243.

Liao, M., Palta, J. A. and Fillery I. R. P. 2006. Root characteristics of vigorous wheat improve early nitrogen uptake. Aust. J. Agric. Res. 57: 1097-1107. DOI: 10.1071/AR05439

Løes, A. K. and Gahoonia, T. S. 2004. Genetic variation in specific root length in Scandinavian wheat and barley accessions. Euphytica 137: 243-249. DOI: 10.1023/B:EUPH.0000041587.02009.2e

Lopes, M. S. and Reynolds, M. P. 2010. Partitioning of assimilates to deeper roots is associated with cooler canopies and increases yield under drought in wheat. Funct. Plant Biol. 37: 147-156. DOI: 10.1071/FP09121

Maheepala, D. C., Ehdaie, B. and Waines, J. G. 2015. Yield performance of wheat isolines with different dosages of short arm of rye chromosome 1. J. Agron. Crop Sci. 21: 152-160. DOI: 10.1111/jac.12077

Manschadi, A. M., Christopher, J., de Voil, P. and Hammer, G. H. 2006. The role of root architectural traits in adaptation of wheat to water-limited environment. Funct. Plant Biol. 33: 823-837. DOI: 10.1071/FP06055

Manschadi, A. M., Hammer, G. H., Christopher, J. T. and de Voil, P. 2008. Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.). Plant Soil 303: 115-129. DOI: 10.1007/s11104-007-9492-1

Manske, G. G. B. and Vlek, P. L. G. 2002. Root architecture - wheat as a model plant. pp. 249-259. In: Y. Waisel, and A. Eshel (eds.) Plant Roots: The Hidden Half, Marcel Dekker, Inc., New York. DOI: 10.1201/9780203909423.ch15

Mian, M. A. R., Nafziger, E. D., Kolb, F. L. and Teyker, R. H. 1993. Root growth of wheat genotypes in hydroponic culture and in greenhouse under different soil moisture regimes. Crop Sci. 33: 283-286. DOI: 10.2135/cropsci1993.0011183X003300020014x

Mian, M. A. R., Nafziger, E. D., Kolb, F. L. and Teyker, R. H. 1994. Root size and distribution of field-grown wheat genotypes. Crop Sci. 34: 810-812. DOI: 10.2135/cropsci1994.0011183X003400030037x

Moghaddam, M., Ehdaie, B. and Waines, J. G. 1997. Genetic variation and interrelationships of agronomic characters in landraces of bread wheat from southeastern Iran. Euphytica 95: 361-369.

Nakamoto, T. and Oyanagi, A. 1994. The direction of growth of seminal roots of *Triticum aestivum* L. and experimental modification thereof. Ann. Bot. 73: 363-367. DOI: 10.1006/anbo.1994.1045

O’Brien, L. 1979. Genetic variability of root growth in wheat (*Triticum aestivum* L.). Aust. J. Agric. Res. 30: 587-595.

O’Tool, J. C. and Oyanagi, W. L. 1987. Genotypic variation in crop plant root systems. Adv. Agron. 41: 91-145. DOI: 10.1016/S0065-2113(08)60803-2

Palta, J. A., Chen, X., Milroy, S. P., Rebetzke, G. J., Dreccer, M. F. and Watt, M. 2011. Large root systems: are they useful in adapting wheat to dry environments? Funct. Plant Biol. 38: 347-354. DOI: 10.1071/FP11031

Passioura, J. B. 1977. Grain yield, harvest index, and water use of wheat. J. Aust. Inst. Agric. Sci. 43: 117-120.

Placido, D. F., Campbell, M. T., Folsome, J. J., Cui, X., Kruger, G. R., Baenziger, P. S. and Walia, H. 2013. Introgression of novel traits from a wild wheat relative improves drought adaptation. Plant Physiol. 161: 1806-1819. DOI: 10.1104/pp.113.214262

Reynolds, M. P., Singh, R. P., Ibrahim, A., Ageeb, O. A. A., Larqué-Saavedra, A.and Quick, J. S. 1998. Evaluating physiological traits to complement empirical selection for wheat in warm environments. Euphytica 100: 85-94.

Reynolds, M. P., Saint, Pierre C., Saad, R. S. I., Vargas, M. and Condon, A. G. 2007. Evaluating potential genetic gains in wheat associated with stress-adaptive trait expression in elite genetic resources under drought and heat stress. Crop Sci. 47: 172-189.
DOI: 10.2135/cropsci2007.10.0022IPBS

Richards, R. A. and Passioura, J. B. 1989. A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. Aust. J. Agric. Res. 40: 943-950.

Sanguineti, M. C., Giuliani, M. M., Govi, G., Tuberosa, R. and Landi, P. 1998. Root and shoot traits of maize inbred lines grown in the field and in hydroponic culture and their relationships with root lodging. Maydica 43: 211-216.

Siddique, K. H. M., Belford, R. K. and Tennant, D. 1990. Root: shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. Plant Soil 121: 89-98.

Steel, R. G. D., Torrie, J. H. and Dickey, D. A. 1997. Principles and procedures of statistics: a biometrical approach. McGraw-Hill, New York, NY, USA. 666 pp.

Tuberosa, R., Sanguineti, M. C., Landi, P., Giuliani, M. M., Salvi, S. and Conti, S. 2002. Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QLTs for grain yield in the field at two water regimes. Plant Mol. Biol. 48: 697-712. DOI: 10.1023/A:1014897607670

Watt, M., Moosavi, S., Cunningham, S. C., Kirkegaard, J. A., Rebetzke, G. J. and Richards, R. A. 2013. A rapid, controlled-environment seedling root screen for wheat correlates well with deep rooting depth at vegetative, but not reproductive, stages at two field sites. Ann. Bot. 112: 447-455. DOI: 10.1093/aob/mct122.