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Root Trait Characteristics and Genotypic Response in Wheat under Different Water Regimes

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Under limiting water resources, root system response of genotypes to soil-water conditions with enhanced shoot biomass holds the key for development of improved genotypes. Based on the hypothesis of root biomass contribution to higher yields under limiting conditions which might be attributed to the root system plasticity of genotypes, a set of thirty-four genotypes were evaluated under three moisture regimes in a pot experiment for root system traits. Total root dry matter had a positive association with total shoot dry matter (0.35). The identified genotypes showed greater yields and higher stress tolerance index (STI) in an independent field experiment. Root dry matter positively correlated with stress tolerance index on grain yields in both the years. The total variation was partitioned into principal components and GGE biplots were studied to identify the best performing genotypes under the three environments for root dry biomass and related traits. HD2932 appeared to be the winner genotype under different regimes. These results might be helpful in identifying donors for moisture stress tolerance that can be utilized in wheat breeding programmes for accelerated development of varieties with improved root systems.

Keywords: genotypic variation, root traits, water deficit, wheat

Introduction

Increasing food production with declining water availability for crop production is becoming major challenge throughout the world. Under changing climatic conditions, fluctuating trends of rains and irregular availability of irrigated water, the incidence of drought is going to increase significantly in major wheat producing areas of the world (Reynolds and Ortiz 2010), thereby posing a threat to wheat production stability. The effects are more pronounced in low yielding rainfed production systems. Wheat, one of the major staple food crops of India, is grown in varied climatic conditions. In central and peninsular India, wheat is mainly grown under restricted irrigation or rain fed condition. In the absence of canal irrigation, farmers irrigate their wheat crop with water stored in dug well

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during monsoon season or through deep bore well. In comparison to north-western plain zone of India, this region has not witnessed any significant yield gains. Under such circumstances, the development of drought tolerant varieties becomes imperative. Plants deploy number of strategies to combat stress including avoidance, escape, tolerance and recovery. Breeding for specific, sub-optimal environments needs detailed understanding of yield determining processes. Trait based breeding is more advantageous and complements the empirical breeding approaches for yield as it ensures sufficient genetic variation in the breeding populations (Wasson et al. 2012).

Most of the trait based selection strategies have regarded physiological traits as secondary selection criteria (Araus et al. 2002; Richards et al. 2010). Until recently, above ground traits largely because of ease in observation and selection have been exploited by the breeders for yield improvement both under optimum and stressed environment. Root based traits have not been exploited due to difficulty in observation, measurement, low heritabilities and variable expression (Tuberosa et al. 2002). Root system architecture is, however, very important in determining the crop productivity due to variable availability and accessibility of water and nutrients in the soil (Gregory et al. 2009). Plant canopies and root systems interact together for yield realization. Recent developments in screening techniques based on image analysis, and hydroponic, aeroponic and agar based systems (Gregory et al. 2009), had led to reliable screening in crops (Henry et al. 2011). Genotypic differences have been observed among wheat cultivars for root length density (Mian et al. 1994), root distribution, post-anthesis root growth (Ford et al. 2006), root angle and seminal root number (Manschadi et al. 2006, 2008), and partitioning of assimilate to deep roots (Lopes and Reynolds 2010). Ehdaie et al. (2012) observed the phenotypic plasticity response of root system on grain yields in wheat and its translocation lines under drought conditions and found positive correlations between root system components and grain yields. Genomic associations with quantitative trait loci for better root systems for higher productivity and water use efficiency have recently been reported in wheat (Sharma et al. 2011; Kadam et al. 2012).

Relevance of many root traits such as greater root length density, root surface area and root dry matter in improving water use-efficiency (Ehdaie et al. 2003; Liao et al. 2004) and availability of genetic variability for these and many other related root traits (Manschadi et al. 2006, 2008; Lopes and Reynolds 2010) have opened new opportunities for wheat improvement. Breeding programmes, however, are restrained due to non availability of information on many of these important root traits. Keeping this in view we tried to explore the genotypic diversity for root biomass and related root traits and correlate it with genotype performance under well watered and limited water condition.

Materials and Methods

Plant material and pot experimental design

The material consists of thirty-four wheat genotypes including five parents of international mapping populations received from CIMMYT under Generation Challenge Program, 26 commercially released cultivars in India and 3 germplasm lines used in wheat breeding program (Table S1*). The international parents and Indian elite lines were known for their performance under moisture stress conditions with respect to morpho-physiological traits and were chosen as representative set for root traits screening under the present study.

The experiment was laid out under natural conditions in pots with three water regimes, each in two replications during 2011–12. Four plants of each genotype were planted in a plastic pot of size (29.5 × 15.5 cm) filled with 16 kg of soil. In the treatment with full irrigation (WW), pots were watered as and when required to maintain the moisture at field capacity (32% volumetric moisture content). In the other two treatments, water stress was created by restricting the water supply to 30 and 70 per cent of field capacity. Field capacity was calculated at the beginning of the experiment by filling the pots with known weights of 1sand: 1clay mixture saturated with water and kept overnight for draining. Field capacity was calculated as the percentage of the difference of this constant weight and the soil fresh weight. Water stressed conditions were created after four weeks by holding the moisture content to 30% (WS30) and 70% (WS70) less than the field capacity by weighing the pots after every three days and bringing the pots to the desired moisture content level.

Measurements

Physiological parameters and the data on total number of tillers were recorded for each treatment after eight weeks of sowing. After ten weeks of sowing, plants were gently uprooted by loosening the soil with water. The roots and shoots were separated, roots were washed under running water to remove traces of soil and submerged in water trays to minimize overlaps. Images of root were scanned using WINRHIZO pro software (Regent Instruments Inc., Quebec city, Canada). Images were then analyzed for root parameters such as total root length, root volume, root surface area and average root diameter. Root dry biomass was observed after imaging was done. Roots and shoots were oven dried at 65°C for 48 hours and weighed.

Field experimental design

The field experiment was laid out with two replications in α lattice design under rainfed and irrigated conditions each. Under rainfed conditions, conserved moisture was used for sowing of the experiments. In irrigated conditions, one pre-sown irrigation was provided alongwith first irrigation at crown root stage (at 20–25 DAS), second irrigation at tillering stage (40–45 DAS), third irrigation at node formation stage (60–65 DAS), fourth irrigation at flowering stage (80–85 DAS), fifth irrigation at milk stage (100–105 DAS) and sixth irrigation at grain filling stage (115–120 DAS). The thirty-four genotypes used in the pot experiment were planted with 2 rows of 6 m at 30 cm apart. The fertilizer dose for the rainfed experiments were 60:40:20 NPK and for irrigated experiments the dose was 150: 80:60 NPK. The nitrogen was supplied in form of Urea, phosphorus as Di Ammonium Phosphate and potash was given in form of Murate of Potash. The weeds were controlled

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* Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

by spraying post emergence weedicide Sulfasulfuron at the rate of 13.3 g per acre. Data was recorded for yield under both irrigation regimes and the stress tolerance index (STI) on grain yield data was determined during 2011–12 and 2012–13 crop season.

Data analysis

The measurements were taken on an average of four plants per genotype in the pot experiment. Data on all the traits were analyzed separately and the differences among the treatments were determined using LSD at $p = 0.05$ for each trait. Pearson correlations were used to determine the relationships between root and shoot traits. The stress tolerance index (STI) on grain yield data was characterized for each genotype to assess their relative performance in different water regimes using the generalized formula as explained by Fernandez (1992). The data was subjected to analysis of variance (ANOVA) and GGE biplot [genotype main effect (G) and genotype by environment interaction (GE)] to determine the effects of genotype in different environments using GENSTAT software (VSN International Ltd, Hemel Hempstead, UK), version 14. The GGE biplot is a graphical tool which analyzes the two sources of variation, genotypes and environments in data. The GGE biplot was plotted from the two principal component (PC) scores of the genotypes and the environments data. The polygon was drawn on genotypes located farthest away from the biplot origin in various directions such that all genotypes are contained in it to identify the best genotype in that sector.

Results

Pot experiment

Moisture stress significantly affected most of the traits under this study. The phenotypic differences between well-watered and water deficit conditions are exhibited in Table 1. The mean values for most of the traits were significantly different among the three environments (LSD, $p = 0.05$). Water deficit caused a huge reduction in shoot dry matter, root dry matter thereby leading to significant decrease in total dry matter. A twofold decrease was observed for the mean total dry matter of genotypes in WS70 environment compared to well-watered environment. Averaged over the three environments shoot dry matter was positively and significantly correlated to total dry matter of the genotypes (Table 2). Root dry matter also exhibited significant correlation with total dry matter, root length, root/shoot ratio, root length density and other root parameters ($p < 0.05$) in water limited environments. The total shoot dry matter and root dry matter showed a positive association and seems to be the best traits for discriminating genotypes under limiting conditions.

The combined analysis of variance among the studied traits under the three water regimes was undertaken (Table 3). The environment impact was much stronger than genotype and genotype × environment for root dry matter, shoot dry matter, root/shoot dry matter ratio, and total number of tillers accounting for 43.1%, 85.2%, 72.2% and 48.0% of the total sum of squares, respectively. The genotype variability was significant at $p < 0.001$ for all the traits except shoot dry matter that showed significant variance at $p < 0.1$ (Table 3).

Table 1. Genotype means for shoot and root parameters measured under watered and water deficit conditions among 34 wheat genotypes

Trait	Control	WS30	WS70	LSD (p = 0.05)	Overall mean
Tiller number	5.6 ± 0.25	4.92 ± 0.10	2.96 ± 0.14	0.576	4.49 ± 0.11
Shoot dry matter (g)	14.21 ± 0.31	8.59 ± 0.23	5.13 ± 0.18	0.76	9.31 ± 0.40
Root dry matter (g)	0.978 ± 0.05	0.685 ± 0.03	0.457 ± 0.03	0.11	0.7 ± 0.03
Root/shoot dry matter ratio	0.07 ± 0.007	0.08 ± 0.004	0.09 ± 0.003	0.01	0.08 ± 0.005
Total root length (m)	98.62 ± 5.54	80.40 ± 3.5	63.32 ± 4.0	12.4	80.78 ± 2.9
Total root surface area (cm^2)	974 ± 56.8	730 ± 38.8	570.8 ± 44.8	133.2	759 ± 31.7
Root average diameter (mm)	0.31 ± 0.007	0.28 ± 0.004	0.27 ± 0.004	0.01	0.29 ± 0.003
Root volume (cm^3)	7.8 ± 0.50	5.35 ± 0.31	4.17 ± 0.42	1.2	5.78 ± 0.21
Total dry biomass (g)	15.19 ± 0.32	9.27 ± 0.22	5.58 ± 0.19	0.78	10.02 ± 0.42

Table 2. Correlation coefficients among various traits under different water regimes

Traits	Control		WS30		WS70	
	Shoot dry biomass	Root dry biomass	Shoot dry biomass	Root dry biomass	Shoot dry biomass	Root dry biomass
Number of tillers	0.125	0.085	–0.011	0.27	0.154	0.426**
Root/shoot dry biomass ratio	–0.374*	0.9**	–0.107	0.902**	0.017	–0.39**
Root length	0.08	0.7**	0.277	0.896**	0.36*	0.89**
Root average diameter	–0.18	0.711**	0.266	0.84**	0.15	0.62**
Total dry biomass	0.98**	0.166	0.981**	0.458**	0.988**	0.492**
Shoot dry biomass	1	0.02	1	0.266	1	0.35*
Stress tolerance index on grain yield in 2011–12	–	–	–	–	0.116	0.33*
Stress tolerance index on grain yield in 2012–13	–	–	–	–	0.05	0.35*

* and ** significant at 5% and 1% level of probability, respectively

Table 3. Genotype by environment interaction analysis for various root and shoot traits

Trait	Sum of squares			% Total sum of squares		
	Genotype	Environment	GXE	Genotype	Environment	GXE
Root dry biomass (g)	4.23	4.64	1.88**	39.3	43.1	17.4
Shoot dry biomass (g)	102.2	1430.05	144.6	6.0	85.2	8.6
Root surface area (cm^2)	5412036	2809547	2169313**	52.0	27.0	20.8
Total root length (m)	4335890.96	2118775.66	2340983.84**	49.2	24.0	26.6
Root volume (cm^3)	453.5	232.7	177.8**	52.4	26.9	20.5
Root average diameter (mm)	0.07	0.02	0.036**	53.9	15.3	27.8
Root/shoot dry biomass ratio	0.055	0.258	0.043**	15.4	72.2	12.0
Tiller number	80.6	131.2	61.1**	29.5	48.0	22.3

** $p < 0.001$

The contribution of genotype was relatively higher for physiological traits such as chlorophyll content, membrane thermo stability index and root traits as total root length, root volume, root surface area and root average diameter (Table 3).

Field experiment

The root dry matter observed in the pot experiment was correlated with stress tolerance index (STI) based on grain yield data from field experiment under well watered and rainfed conditions during the year 2011–12 and 2012–13. Grain yield significantly decreased for all the genotypes in rainfed compared to the irrigated plots. Root biomass and its component traits had positive correlations with grain yield under drought. Root biomass was not observed in the field experiment in our study but we correlated the pot experiment data with the STI on grain yields obtained under field experiment. Genotypes HD2987, DBW17, HD3016, HD3086, HD2932, HD3043, GW366 and WBLL$/Nursit had Stress tolerance index of 0.8–0.95 in both the years (Table S1). The greater values of STI indicate greater tolerance to moisture stress and were higher for genotypes with higher root dry biomass as revealed by the significant positive correlation in both the years.

Genotype performance under three environments in pot experiment

The data matrix variation was partitioned into principal components, the first two of which explained >85% variation among the data. The acute angle of the environment vectors indicated that WW and mild stress environment (WS30) were positively related to each other. For all the root related traits the well watered and high water deficit environment (WS70) was independent of each other. All the measured root traits grouped together indicating strong correlation among them. Total dry biomass was significantly associated with both root and shoot dry matter. Genotypes were ranked and compared for each trait individually across the three environments. Genotypes HD2932 (G24), HD2687 (G23), DBW17 (G2) and HD3016 (G6) being closer to the axis and having shortest vector were better and stable genotypes for most of the root traits. WBLL$/Nursit (G32) and Raj3765 (G26), on the other hand, observed greater mean performance but less stable due to their large vectors to the AEC axis for some of the root traits. In all HD2932 was found not only to suffer less for root dry matter, root volume and root length under moisture stress condition but also responds well to irrigation. An ideal genotype having higher mean, better stability and responsiveness to better environment is represented by a circle with an arrow pointing towards it. Genotypes HD2932 (G24), DBW17 (G2), HD2687 (G23), HD3016 (G6) and WBLL$/Nursit (G32) were the ideal genotypes and were present in the center of concentric circles in Figure 1.

Figure 2 shows the polygon view of genotypes for root dry matter. All the three environments were represented in single sector for root dry matter. The vertex genotypes for root dry matter includes HD2932 (G24), HD3016 (G6), Raj 3765 (G26), WBLL$/Nursit (G32), NIAW34 (G27), GW322 (G3) and Halna (G9). The last two genotypes on the vertex were the least performers for root dry matter as being present on the left side of the biplot axis. On the basis of their consistent presence in the stress environment sector, the winner genotypes for the water deficit environment for the root traits were found to be HD2932, and HD3016.

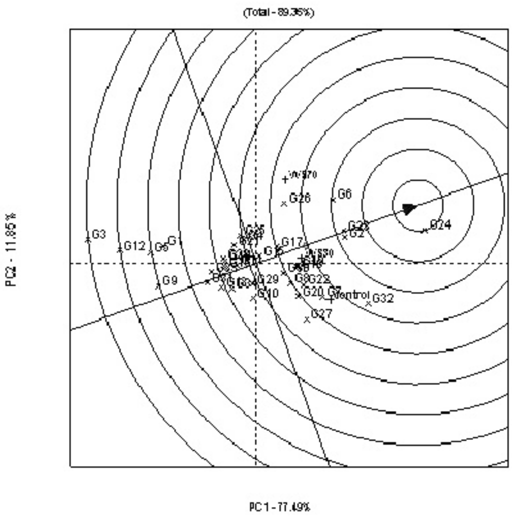

Figure 1. Biplot for root dry biomass across three environments

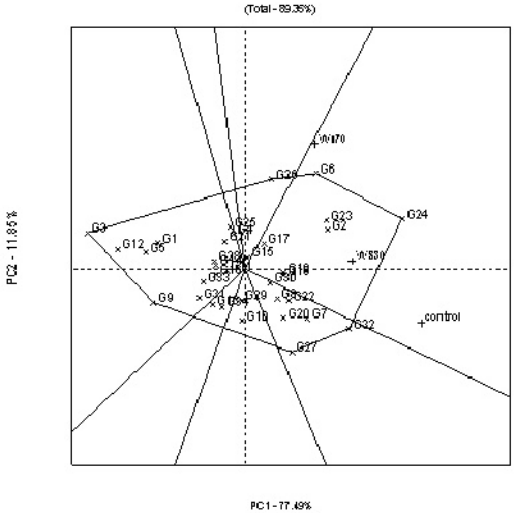

Figure 2. Polygon view in the biplot for root dry biomass across three environments

Discussion

Yield realization by a particular genotype under variable environmental condition is cumulative effect of various physiological processes happening in above ground parts of the plant as well as moisture and nutrient extracting capacity of its root system. In the breeding endeavors for better plant type throughout the world, root system was less explored due to difficulty in observation, and measurement of these traits. The impact of selection for above ground parts, on the other hand can be very well visualized through success of green revolution during later half of the 20th century. However, the success of green revolution was mainly confined to irrigated ecosystem (Joshi 1999) and it is now increasingly being realized that to make similar impact under water limiting condition, selection for root traits are imperative. Manschadi et al. (2008) have reported genotypic differences in water limiting environments due to contrasting root systems. The study emphasized on possible exploitation of root architectural traits in breeding for improved cultivars. Waines and Ehdaie (2007) also reported that root characters may be integrated in to components of yield analysis in wheat. Ehdaie et al. (2012) observed that genotypes with increased root biomass had higher grain yields under terminal drought due to the greater root system plasticity in response to drought. Our studies corroborates with these hypothesis that the genotypic variability on the basis of their root system response to well watered and water deficit conditions can be used to identify superior genotypes with high yield potential.

Pot experiment

Water stress had a severe impact on physiological and root attributes in wheat genotypes. Shoot dry matter observed lower genotypic contribution in comparison to GE interactions. The larger GXE effect for shoot dry matter indicates there might be differential response of genotypes for yield performance among well watered and deficit conditions. According to Blum (2005), shoot reserves have strong implication for yield realization due to higher translocation of assimilates to the grain under drought stress condition and therefore, in order to develop moisture stress adaptive genotype, we can indirectly select for yield by improving these traits. The presence of strong GE interaction for these moisture stress adaptive traits signifies the importance of a separate breeding programme for drought tolerance. Recently, Kadam et al. (2012) identified that drought-responsive shoot and root traits colocalize on same genomic regions. Chromosome 4B in wheat harbors QTLs for grain yield under drought, harvest index and root biomass, lateral root length, total root length and root tip number for seminal roots at seedling stage (Ren et al. 2011; Kadam et al. 2012). Consistent genomic region associations for shoot and root traits for drought response will further improve the breeding efficiency. Genotypic differences were more apparent in the combined analysis for different traits in our study. The root traits showed highly significant differences among genotypes for the three environments. The positive correlation between shoot and root dry matter indicates that they can be selected by breeders for ultimately enhancing the yields in stress conditions. Both the traits, shoot and root dry matter were highly associated with total dry matter that may culminate into greater yields and harvest index. The genotype having higher biomass realization under drought condition leads to higher translocation of assimilates from vegetative stage to the grain during anthesis and grain-filling period (Kandic et al. 2009).

Field experiment

Phenotypic plasticity of roots influences the response of genotypes to drought conditions (Ehdaie et al. 2012). Root biomass and its component traits had positive correlations with grain yield under drought. Ehdaie et al. (2003) observed that increased root biomass in 1RS translocation lines in the glass house experiments might have contributed to the overall higher grain yields obtained in field conditions. The results of field experiments in our study also corroborates with Ehdaie et al. (2003). We observed greater stress tolerance index on grain yields for the genotypes that had increased root dry matter under the pot conditions. Significant positive correlations were obtained between STI on grain yields and root dry matter. Sharma et al. (2011) detected genomic regions for greater rooting ability in wheat on 1RS chromosome arm. They identified four regions for all the QTLs of root traits that were responsible for inter-genomic and intra-genomic interactions. The tendency of 1RS translocation lines to produce more root biomass was also revealed in some of our genotypes in this study. The genotypes HD3016, Raj 3765, DBW 17 that performed well under moisture stress environments are 1RS translocation lines and were confirmed by the molecular marker analysis. Yield being a complex trait, selection based on yield alone under drought condition does not lead to yield improvement. However, the selection based on root dry matter coupled with above ground traits like shoot dry matter particularly under high drought stress condition will improve the selection efficiency.

Genotype performance under three environments in pot experiment

We also studied the GGE biplot analysis to identify genotypes on the basis of their superior performance in water deficit conditions. The three environments well watered, mild water deficit and severe water deficit environments were analyzed on the basis of the mean performance of genotypes for various root traits. Yan and Tinker (2006) reported that equal length of environment vectors represent their discriminating abilities among environments. The shorter length of the environment vector suggested that it provided little or no information about the genotypic differences. The similar observation is obtained for the environment WS30 in our study where short vector showed less discrimination among the genotypes for root traits.

The AEC (average environment coordination) view facilitates the comparison of genotypes on the basis of their mean performance and stability across environments (Yan and Tinker 2006). Farshadfar et al. (2012) analyzed GGE biplots to identify stable genotypes with high yield performance under rainfed and irrigated conditions in wheat-barley disomic addition lines. Recently, Hamidou et al. (2013) also observed significant GXE interactions under combined drought and heat stress and selected genotypes with superior performance using GGE biplots in groundnut. In our study, the genotypes HD2932 (G24), DBW17 (G2) and HD3016 (G6) were closest to AEC axis for most of the root traits. These genotypes were exceptional under deficit conditions and thus can be used as potential donors for enhancing root characteristics in the breeding material. These genotypes were close to the ideal genotype in terms of their performance. The polygon or “which-won-where” view further classifies the genotypes on the basis of their performance in selected environments. The vertex genotypes on this polygon are the best or poorest performers in the environments as they are farthest from the origin of the biplot. The genotypes that are located on the vertex are the winners for the environments lying in that sector (Yan and Tinker 2006). The genotype HD2932 was the most stable in normal and moisture stress environments for root dry matter, root volume and was a consistent performer. The variety HD2932 during its testing phase in All India Coordinated Programme was found to out yield the checks in three geographically different zones, namely North Eastern Plain Zone, Central Zone and Peninsular zone under late sown condition. Present study corroborates those results and high environmental resilience in this variety largely comes through better adaptive root traits. Similarly, HD3016 was found to out yield all national checks for water stressed environments. Large scale testing is therefore required for identification of such genotypes, however, observation on root traits in highly stressed and well-watered environment along with data on above-ground traits like shoot dry matter, harvest index and yield could also give similar result and can economize the breeding process.

The analysis indicates that significant genotypic variation exists for root traits under water-limiting conditions. The root systems are relatively less explored for their role in crop improvement. Breeders might be indirectly selecting for root traits while selecting for above-ground traits. In future, the identification of genotypes based on root traits may offer potential gains in yield under water limited environments, although latter is a combination of expression of different agronomic and physiological stress-adaptive traits. Our study implicates the importance of root system characteristics in understanding genotypic variability for higher yield potential under water limited conditions. The genotypes identified in this study can be used as donors for moisture stress tolerance in the breeding programs.

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at http://www.akademiai.com/content/120427/

Electronic Supplementary *Table S1*. Shoot, root and total dry biomass under mild and severe stress conditions for various traits in pot conditions and stress tolerance index on grain yield of the genotypes under field conditions