Drought Tolerance in Cultivated and Wild Barley Genotypes: The Role of Root System Characteristics

M. Barati¹, M. M. Majidi^{1*} F. Pirnajmedin¹, A. Mirlohi¹, D. Sarfaraz¹, and A. Osivand¹

ABSTRACT

There are contrasting reports on the relationship between yield and drought tolerance of crops with root characteristics. This research aimed to study grain yield and rootrelated traits (at two depths) under optimal and drought stress conditions and assess the effect of root-related traits on grain yield and drought tolerance in cultivated barley (Hordeum vulgare ssp. vulgare) and wild barley (H. vulgare ssp. spontaneum). In this experiment, 30 barley genotypes were evaluated in pot culture experiment for root traits and in the field for grain yield and drought tolerance, in two consecutive years. The results indicated that the genotypes with high root dry weight, area, volume and length and root to shoot ratio at depth of 0-30 cm had also extensive root system at the depth of 30-60 cm. The root system size increased when the plants were exposed to drought stress, and the level of increase was higher in the deeper soil layer. The wild barley genotypes Hsp06, Hsp74 and Hsp79 had high averages of the root dry weight, area, volume, and length under both normal and water stress conditions. The results of farm experiment indicated that the cultivated barley genotypes mostly had higher yield potential; however, the wild barley genotypes had more yield stability under drought stress environment. The wild barley Hsp71 was identified with both high yield potential and stability under drought stress. Root dry weight and root to shoot ratio were negatively correlated with grain yield under no water stress condition. Under stress condition, root area, length, and volume were positively correlated with yield stability index. Results indicated that the vigorous root system is not necessarily related to higher grain yield in barley; however, higher yield stability under stress environment is highly related to root system extension.

Keywords: Relative species, Water stress, Root structure, Wild ancestors, Yield stability.

INTRODUCTION

Progress in plant breeding highly depends on the occurrence of desirable genetic variation for crop improvement and the availability of precise methods for the transfer of favorable genes and selection strategies (Abbasi *et al.*, 2014; Saeidnia *et al.*, 2017). Wild barley from Middle East has shown to be a rich source of genes for barley development (Ellis *et al.*, 2000). The genetic improvement for drought tolerance is essential for stable and adequate crop production in drought-prone areas. Comparing yield potential and yield stability, which are key objectives for plant breeders, previous studies focused mainly on shoot traits (Fang *et al.*, 2017) while root-related traits have been largely neglected by breeders due to the lack of high-throughput and non-destructive methods for studying root system architecture in the soil (Manschadi *et al.*, 2006; Den Herder *et al.*, 2010).

Root system is the major plant organ for water and nutrient acquisition, which influence plant growth and grain productivity (Ehdaie *et al.*, 2012; Palta and Yang, 2014). Extensive root systems enable plants to exploit the remaining soil water from the deeper layers. In previous studies on crops, relation between vigorous root system and above-ground

¹ Department of Agronomy and Plant Breeding, College of Agriculture, Isfahan University of Technology, Isfahan, Islamic Republic of Iran.

^{*}Corresponding author; e-mail: majidi@cc.iut.ac.ir



The present research aimed to: (1) Evaluate cultivated and wild barley germplasm for grain yield under optimal and drought stress conditions, (2) Study root system and development in different soil depths as affected by drought stress, and (3) Study the relation between root traits with grain yield and drought tolerance in barley.

MATERIALS AND METHODS

Plant Materials

In this study, a total of 30 genotypes including 23 genotypes of wild barley (*H. vulgare* ssp. *spontaneum*) and seven genotypes of cultivated barley (*H. vulgare* ssp. *vulgare*), including the cultivars "Steptoe" (drought tolerant) and "Morex" (drought susceptible), were used (Table 1). Seventeen accessions were provided by Leibniz-Institute of Plant Genetics and Crop Plant Research (IPK) gene bank, five from Isfahan Center for Agricultural Research, Iran, and eight were collected from west of Iran (Lorestan, Ilam, Kermanshah, Kordestan, and West Azarbaijan Provinces). Abbreviations and units of measurement for the measured characters are shown in Table 2

Pot Experiment and Evaluation of Root System Characteristics

A pot experiment was conducted in factorial design arranged in a completely randomized block design with three replications. Thirty genotypes of barley were evaluated for root system characteristics at two separate depths (0-30 and 30-60 cm) under two levels of water treatments (control and drought stress). Five seeds of each genotype were planted in long Polyvinylchloride (PVC) tubes with 70 cm height and 16 cm diameter filled with a mixture of coarse river sand and silt loam soil (1:2 v/v) on March 2014. The plants were grown outdoors (daily temperatures of 18-28°C and 14 hours photoperiod). Ten days after emergence, three plants were kept in each tube. Four weeks after seedling emergence, the water stress treatments were started and continued for 45 days. The time of irrigation in the control treatment was determined based on soil water depletion in the root zone with maximum allowable depletion equal to 50% (Allen et al., 1998), as described by Pirnajmedin et al. (2015). Drought stress treatment received 50% of the water given to the control treatment. At the end of the treatment period, all plants in each PVC tube were cut manually from above ground level and shoot fresh weight was measured immediately. Shoot Dry Weight (SDW) was recorded after drying at 72°C for 48 hours. Then, the soil column was sliced into two sections (0-30 and 30-60 cm). The roots in each section were washed free of soil to measure Root Fresh Weight (RFW), promptly (Pirnajmedin et al., 2015). Then, the roots were scanned with a computer scanner and Cumulative Root Length (CRL) and Root Area (RA) were measured by GiA Roots software (Galkovskyi et al., 2012). Root Volume (RV)was measured as

Number ^a	Accession name	Origin	Name/Gene bank code
1	Hsp01	Cyprus	HOR 12752
2	Hsp02	United States of America	HOR 9771
3	Hsp05	Azerbaijan	HOR 10710
4	Hsp06	Tajikistan	HOR 10975
5	Hsp07	Israel	HOR 9470
6	Hsp08	Iran	HOR 2692
7	Hsp09	Turkmenistan	HOR 10037
8	Hsp13	Iran	HOR 2691
9	Hsp15	Libya	HOR 9721
10	Hsp16	Azerbaijan	HOR 4856
11	Hsp19	India	HOR 2514
12	Hsp21	Turkmenistan	HOR2695
13	Hsp33	Iran	HOR2686
14	Hsp45	Iran	HOR2685
15	Hsp47	Iran	HOR2684
16	Hsp70	Iran (Islamabad-e-Gharb)	-
17	Hsp71	Iran (Khoram Abad)	-
18	Hsp72	Iran (Ilam)	-
19	Hsp74	Iran (Urmia)	-
20	Hsp75	Iran (Poldokhtar)	-
21	Hsp78	Iran (Kermanshah)	-
22	Hsp79	Iran	-
23	Hsp80	Iran (Ivan)	-
24	Hvu603	United States of America	BCC906 (Morex)
25	Hvu605	United States of America	BCC934 (Steptoe)
26	Hvu651	Iran	Yousef
27	Hvu654	Iran	Reihan03
28	Hvu258	Iran (Zanjan)	-
29	Hvu659	Iran	-
30	Hvu663	Iran	-

Table 1. Information on wild and cultivated barley genotypes assessed for root characteristics and drought tolerance in pot and field experiments, respectively (2013-2014).

^a 1 to 23: Hordeum vulgare ssp spontaneum, 24-30: H. vulgare ssp vulgare.

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Character/Trait (Unit of measurement)	Abbreviation
Shoot Dry Weight (g)	SDW
Root Fresh Weight	RWW
Cumulative Root Length (cm)	CRL
Root Area (cm ²)	RA
Root Volume (cm ³)	RV
Root Dry Weight (g)	RDW
Root Shoot Ratio	RSR
Grain Yield per plot	GY
Stress Tolerance Index	STI
Yield Stability Index	YSI

recommended by Archimedes (Pirnajmedin *et al.* 2015). Root Dry Weight (RDW) and Root Shoot Ratio (RSR) were obtained after roots were dried in an oven at 70°C for 72 hours.

Field Experiment and Evaluation of Grain Yield

The experiment was performed on a silty clay loam soil at Isfahan University of Technology Research Farm (32° 30' N, 51° 20' E), Isfahan, Iran. The mean annual temperature and precipitation were 14.5°C and 140 mm, respectively. The experiment consisted of 4 environments which were created by the combination of two water environments (normal and stress), and two years (2012-2013 and 2013-2014). A completely randomized block design with 30 genotypes and three replications was used in each environment. The seeds of all genotypes were planted in the farm on mid-November. Each plot contained six 1.5 m rows, with 20 cm spacing between the rows and 2 cm spacing between the plants in each row. All of the plots (in both normal and drought stress treatment) were irrigated normally from the sowing date until the beginning of stem elongation. After that, for applying drought stress in drought stress treatment, the irrigation was totally stopped. For the control environment, irrigation was applied when 50% of the total available water was depleted from the root zone (Allen et al., 1998). Soil samples were taken to determine the gravimetric soil-water content. Three samples were taken at the depths of 0-20, 20-40, and 40-60 cm for control and drought stress environments, respectively. Samples were collected every day between two irrigations. The Irrigation depth (I) was determined according to the following equation:

I= [(FC- θ)/100] D×B

Where, FC is soil gravimetric moisture percent at Field Capacity, θ is soil gravimetric moisture percent at irrigating time, D is the root zone depth (cm)., and B is the soil Bulk density at root zone (1.4 g cm^3) . Water was delivered from a pumping station *via* PE pipe and the water volumes applied were measured with a volumetric counter.

After physiological ripening of each plot, plants were removed from 3 cm above the ground, dried at 70°C for 48 h. Then, the grains were separated and the Grain Yield per plot (GY) was measured. Stress Tolerance Index (STI) (Fernandez, 1993) and Yield Stability Index (YSI) (Bouslama and Schapaugh, 1984) were calculated as the following formulae:

YSI= Ysi/Yci

 $STI = (Ysi \times Yci)/(Ymc)^2$

Where, Ysi and Yci are the Yield of the i^{th} genotype under stress and control conditions, respectively. Ymc is the mean Yield of all genotypes in control condition.

Statistical Analysis

The data were submitted to Excel software and the descriptive statistics including minimum, maximum, and means were obtained. Normality test was done before subjecting data for Analysis Of Variance (ANOVA) to determine differences among water treatments, soil depths and genotypes for each trait using procedure GLM of SAS (SAS Institute, 2001). Least Significant Differences (LSD) test (P< 0.05) was used for mean comparisons. Correlation analysis (Pearson coefficients), cluster analysis, and preparing biplots were performed using **Statgraphics** centurion XVI (www.statgraphics.com).

RESULTS

Root Traits

The results of analysis of variance for root traits are presented in Table S1. The main effects of water treatment and genotype were significant for all of the traits. The main effect of depth was significant for all of the traits, with the exception of RDW and RSR. Interactions of water treatment×depth and water treatment×genotype were significant for all of the measured traits. Depth×genotype and water treatment×depth×genotype were only significant for RDW (Table S1).

The averages of root-related traits were calculated for all barley genotypes in each water treatment, separately (Figures 1 and S1; Table S2). Under control condition, the highest average of RDW and RSR was obtained for Hsp06 (Table S2). The highest average of RA, CRL, and RV was observed for Hsp79. Under the stress condition, the highest averages of RDW and RSR were observed for Hsp05. The genotype Hsp16 had the highest averages of RA and RV. The highest average of CRL was

observed for Hsp79. Some wild barley genotypes including Hsp06, Hsp74, and Hsp79 had high averages of the traits RDW, RV, RA, RSR and CRL under both water treatments (Table S2). The lowest averages of the RDW, RV, CRL, RA and RSR under both conditions were observed in some cultivated barley genotypes, especially Hvu258 (Table S2). The comparison of the mean RDW for genotypes under control and stress condition revealed that the average RDW for each genotype increased from the control to the stress conditions; however, the rate of increase varied among the genotypes (Figure 1-a). Similar results were observed for the other root traits such as RA, CRL, RV, and RSR (Figure S1; Table S2).







Figure 2. Mean comparison of water treatment×depth for root dry weight (a) and root area (b). Means of water treatment×depth for the two groups of genotypes, the first group with strong root system and the second group with poor root system for the traits root dry weight (c) and root area (d). The columns for the depth 0-30 and 30-60 cm are shown with dark green and light green, respectively. The columns with the same letter do not have significant difference according to the LSD test at the 5% level of probability (in the parts a and b). The unit for root dry weight and root area is g and cm², respectively.

The averages of root traits for the genotypes

were also calculated at each depth, separately, and the results are organized in Figures 1-b and S2. The results of RDW indicated that the genotypes with high RDW in depth 0-30 cm had also high values for root traits in the depth 30-60 cm (Figure 1-b). Similar results were observed for other traits RA, RV, CRL, and RSR (Figure S2).

Under the control condition, mean RDW was significantly higher under depth of 0-30 cm in comparison to depth of 30-60 cm (Figure 2-a). The averages of RDW under stressed environment were extremely higher than the control condition in both depths (Figure 2-a), however, the level of increase was much higher in the 30-60 cm depth (Figure 2-a). Exactly similar result was observed for RSR (Figure S3C). Regarding the other root traits including RA (Figure 2-b), RV, and CRL (Figures S3a and b, respectively), similar results were also observed, but the difference between the two depths was not significant under control condition.

Cluster analysis with root traits separated the barley genotypes into three groups (Figure S4). The first group included 11 wild barley

genotypes with high root dry weight, area, length, and volume under both water treatments and, therefore, was named "strong root system". The second group consisted of 8 genotypes including two cultivated and six wild genotypes, had low root-related traits at both water treatments, and was labeled as "weak root system". The remaining 11 genotypes were categorized in the third group with "moderate root system" (Figure S4). The averages of RDW and RA for the genotypes within the first and second above-mentioned groups were calculated and the results are presented in Figures 2-c and -d. By comparison of the data of these two groups of genotypes, three interesting results become obvious: (1) In both groups, the mean traits increased from the control to the drought stress condition in both depths, (2) The level of increase was more in depth 30-60 cm, and (3) The level of increase was higher in the first group, the genotypes with "strong root system". These results can be obtained while comparing the scan of roots for a genotype with strong root system i.e. Hsp05, and a genotype with poor root system, i.e. Hsp45 (Figure 3). Similar results were obtained for



Figure 3. Scanned root profile for a genotype with strong root system, Hsp05 and a genotype with poor root system, Hsp45, evaluated in pot experiment.

other root traits i.e. RV, CRL and RSR (results are not shown).

Grain Yield and Tolerance Indices

Analysis of variance of grain yield and tolerance indices revealed a significant effect of year on grain yield under control and drought stress conditions, and on yield stability index (Table S3). Effects of genotype and genotype×year were significant for grain yield and both indices (Table S3).

Regarding the means of genotypes calculated for grain yield and drought tolerance indices (Table S4), the six-rowed barley cultivars Hvu654, Hvu659, and Hvu651 had higher GY under control conditions, and genotypes Hsp71, Hvu654, and Hvu605 had higher GY under drought stress condition. The genotype Hvu258 had lower grain yield under both control and drought stress conditions (Table S4). The highest and the lowest STI were observed in genotypes Hvu654 and Hvu258, respectively. The highest and the lowest YSI were observed for the genotypes Hsp71 and Hsp45, respectively (Table S4).

Relation between Results of the Two Experiments

In order to investigate relation between results of the two experiments, correlation analysis was performed among root-related traits evaluated in pot experiment, grain yield, and tolerance indices obtained from farm experiment (Table 3). Pearson rank correlation coefficients were used for correlation between traits from different environments. In both control and drought stress conditions, the traits RDW, RA, RV and RSR had high positive correlation to each other (Table 3). Based on the Pearson correlation coefficients rank obtained between GY and all of the root-related traits, only RDW had a weak but negative significant correlation with grain yield, under the control condition. Under drought stress condition, the Pearson rank correlation between root related traits with grain yield and STI were not significant, however, positive and significant correlation was observed between RA, CRL, and RV with Yield Stability Index (YSI).

DISCUSSION

The root system is taking care of indispensable plant functions such as uptake of nutrients and water, anchorage in the substrate, and interaction with symbiotic organisms (Den Herder et al., 2010). In this study, high genetic diversity was observed for the root traits under both control and drought stress conditions within cultivated barley and its wild progenitor (Figure 1). This high genetic variation is the starting point of breeding programs and provides the possibility of selecting parents for genetic studies as well as breeding programs. In this regards, the genotypes with vigorous root system (high root dry weight, area, volume and length) such as Hsp06, Hsp74 and Hsp79 were identified for further studies. Manju (2019) reported promising sources for drought tolerance in cultivated and wild species germplasm of barley based on root architecture. Similar results were observed in the study on Oryza species, where some accessions from 0. rufipogon, О. longistaminata, O. officinalis and 0. latifolia showed approximately 2-2.5 times longer root length and number than the indica rice elite cultivar (Neelam et al., 2018). Their results indicated potentiality of selected wild species germplasm for conferring drought tolerance to the elite cultivars.

In this study, the root system size (root dry weight, area, volume, and length) increased when the plants were exposed to drought stress. Regarding the incensement of root system size under drought stress condition in this study, three interesting results were observed. The first one is that the rootsystem size increased in all of the genotypes

including under drought stress, the genotypes with vigorous root system size and the ones with weak root characteristics. Second, root-system size increased in both soil depths; however, the level of increase was much higher in the deep layer (30-60 cm). This increment enhances root system distribution at deeper soil layers during drought stress and hence contributes to better water absorption (Serraj et al., 2004; Farre and Faci, 2009). Increased root length at deeper soil layers during drought stress has also been reported in other species and is thus considered as an important adaptation mechanism to improve the efficiency of plant water uptake (Pirnajmedin et al., 2015 and 2017; Gallardo et al., 1996). In another study, tolerant corn genotypes presented a greater root system, mainly of fine roots, and greater proportions of aerenchyma (Souza et al., 2016). Another study on wheat demonstrated that greater root mass and root length density in subsoil layers, with enhanced access to subsoil water after anthesis, contributes to high grain yield when soil water is scarce (Fang et al., 2017). In an experiment on barley, root dry mass production was reduced under severe water deficit and there was no root growth in deeper soil layers (Sahnoune et al., 2004). In another experiment, total root length decreased with decreasing soil water content (Soda et al., 2010). However, it highly depends on the method, as well as the developmental stage in which drought stress has been imposed.

The third interesting result was that drought stress increased the root traits including RDW, RA, RV, CRL, and RSR. On the other hand, correlation coefficients among these traits were positive in both moisture environments. This means that selection based on one of these traits will cause an increase of the other ones. Therefore, RDW, the trait which is easier to measure, seems to be a favorable index to select for better root system characteristic. Here, genotypes with high RSR should keep root contact with larger root volume to maintain cell turgor and to survive during drought period and/or meet vegetative growth demand for nutrients. Increased root to shoot ratio during drought stress has also been reported as a drought avoidance mechanism (Guo *et al.*, 2002; Karcher *et al.*, 2008).

The results obtained from evaluation of grain yield and drought tolerance of the barley and wild barley genotypes aimed at an index for identification of the highyielding genotypes, as well as the genotypes with high Stress Tolerance Index (STI) and Yield Stability Index (YSI). These are two most important groups of indices that are used for identification of drought tolerance. The first group, including STI, considers the grain yield potential, meaning that the genotypes with higher grain yield under both stress and non-stress conditions will have the higher STI (such as the genotypes Hvu654, Hvu605, and Hsp71) (Fernandez, 1993). Selection based on the other group of indices. such as YSI, will aim at identification of the genotypes that have more stability under the drought stressed conditions, regardless of their yield potential (such as genotypes Hsp71, Hsp08 and Hsp74) (Bouslama and Schapaugh, 1984). We strongly recommend the second group of the indices, when the low-yielding wild genotypes are compared with the highyielding elite cultivars. However, the genotypes with high value of both of these indices are the most suitable to choose (such as Hsp71) (Fang et al., 2017).

There are contrasting reports on the value of the root system characteristic under drought stress for grain yield. One argument is that a relatively large root system is essential for crops grown in drought areas to absorb more soil water and relief drought stress (Palta *et al.*, 2011; Ehdaie *et al.*, 2012). This result was observed in the study of Tomar *et al.* (2016) in a trial carried out in PVC pipes. They found that higher root biomass possessed higher aboveground biomass compared to small rooted plants. In their study, the water and nutrient absorption was increased with higher root biomass, leading to increased yield. However, an alternative view is that since the roots are a major sink for assimilates, reducing root mass increases the availability of assimilates for aboveground parts including grain yield (Song et al., 2009; Fang et al., 2017). In an experiment, for example, Zhu and Zhang (2013) argued that a small root system could have a positive effect on wheat grain yield in water-limited situations. Nagy et al. (2018) found negative correlation between root dry mass and grain yield under drought stressed conditions. The glasshouse experiment was carried out in pots, so the larger root system was not a benefit for plants, because there was no deeper soil layer to find extra water. Other researchers have mentioned that wheat genotypes with a large topsoil root system should be able to capture soil moisture from the topsoil during occasional spring rainfall and use it for grain filling (Palta et al., 2011; Ehdaie et al., 2012). Soda et al. (2010) reported a weak but positive correlation between tiller number and root length on barley. They also observed a notable change in the root-shoot ratio only after a 15-day stress cycle. The results of this study indicated that, under control conditions, there was a weak negative significant correlation between RDW and RSR with grain yield. This indicates that under optimum conditions, an increase in root system will cause a decrease in the grain vield indicating that under no stress condition, the plant does not need a vigorous root system for high grain yield, maybe because of the availability of water in the soil. This observation maybe because the high yielding cultivated barley genotypes have lower values for root characteristics compared to the wild barley genotypes. On the other hand, under stressed conditions, neither positive nor negative correlation was observed between grain yield and drought tolerance. The reason for the unexpected difference between the results of the two experiments could be due to the difference in drought stress levels imposed in the two experiments, as well as the difference between the model of root growth and development in the polyethylene tubes and the soil in the field.

In conclusion, in the pot experiment, drought stress increased root weight, size, and length in all of the genotypes, as well as in both surface and deep soil layers; however, the level of increase was much higher in the deeper layer (30-60 cm). In the farm experiment, the genotypes from cultivated barley showed higher grain yield, meaning their higher yield potential. However, some genotypes from wild barley had higher yield stability under drought stressed condition. Comparison of the results of the two experiments indicated that the higher grain yield under optimum and even drought stress condition was not necessarily dependent on the extensive root system; however, there was a high correlation between yield stability under drought stress environment and extensive root size, weight, and area.

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تحمل به خشکی در ژنوتیپهای جو زراعی و وحشی: نقش خصوصیات سیستم ریشهای

م. براتی، م. م. مجیدی، ف. پیرنجم الدین، آ. میرلوحی، د. سرفراز، ا. اوسیوند

چکیدہ

گزارش های متناقضی در زمینه ارتباط بین عملکرد و تحمل به خشکی با ساختار ریشه در گیاهان زراعی وجود دارد. پژوهش حاضر با هدف بررسی عملکرد دانه و صفات ریشهای (در دو عمق) تحت شرایط مطلوب و تنش خشکی و همچنین بررسی اثر صفات ریشهای بر عملکرد دانه و تحمل به خشکی در ژنوتیپهای جو زراعی (Hordeum vulgare ssp. vulgare) و وحشی (.vulgare ssp در ژنوتیپهای جو زراعی (Hordeum vulgare ssp. vulgare) و وحشی (. spontaneum) انجام شد. در این مطالعه، ۳۰ ژنوتیپ از نظر صفات ریشهای در آزمایش گلدانی و از نظر صفت عملکرد دانه و تحمل به خشکی در مزرعه طی دو سال متوالی ارزیابی شدند. نتایج نشان داد که ژنوتیپهای دارای وزن خشک، سطح، حجم و طول ریشه و نسبت ریشه به اندام هوایی بیشتر در



عمق ۳۰- سانتی متر از سیستم ریشه ای گسترده ای در عمق دوم (۶۰- ۳۰ سانتی متر) نیز برخوردار بودند. در این مطالعه تنش خشکی منجر به افزایش گسترش سیستم ریشه ای بویژه در اعماق پایین گردید. در هر دو محیط رطوبتی، ژنوتیپ های جو وحشی، Hsp06 و Hsp77 دارای بیشترین مقدار میانگین وزن خشک، سطح، حجم و طول ریشه بودند. نتایج آزمایش مزرعه ای نشان داد که تحت شرایط تنش خشکی اغلب ژنوتیپ های زراعی دارای پتانسیل عملکرد بیشتر، در حالیکه ژنوتیپ های وحشی دارای پایداری عملکرد بالاتری بودند. در شرایط تنش خشکی، ژنوتیپ جو وحشی 14sp71 به عنوان ژنوتیپ ای با پتانسیل عملکرد و پایداری بالا شناخته شد. در شرایط شاهد صفات وزن خشکی سطح، نسبت ریشه به اندام هوایی با عملکرد دانه همبستگی منفی داشتند. تحت شرایط تنش خشکی سطح، عملکرد دانه در جو الزاما ناشی از گسترش سیستم ریشه ای نمی باشد، گرچه افزایش پایداری عملکرد تحت شرایط تنش نمان داد که افزایش میستم ریشه ای نمی باشد، گرچه افزایش پایداری عملکرد