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PHENOTYPIC VARIATION IN WATERLOGGING STRESS TOLERANCE AMONG WHEAT CULTIVARS AND ITS WILD RELATIVES

IRFAN SADIQ[1]*, SYED TAHIR ABBAS SHAH[1], JAMSHAID HUSSAIN[2], ABDUL RAUF SIDDIQI[1] AND NAZIA BIBI[1]

[1]*Department of Biosciences, COMSATS University Islamabad, Park Road, Islamabad, 44000, Pakistan*
[2]*Department of Biotechnology, COMSATS University Islamabad, Abbottabad Campus, University Road, Abbottabad, Pakistan*
**Corresponding author's email: irfan_sadiq@comsats.edu.pk*

Abstract

Waterlogging is one of the limiting factors affecting global wheat yield including Pakistan. Its harmful effects on wheat crop depend on growth stage and type of cultivars. The main objectives of this study were to screen different wheat cultivars/accessions against waterlogging stress at imbibition stage and then at two leaf stage for those cultivars exhibiting tolerance at imbibition stage. In total one hundred and nineteen wheat cultivars/accessions were screened at imbibition/germination. These 119 cultivars/accessions were grown in Indian subcontinent during different time periods from early 20th century till present. Seeds after sowing were immediately exposed to waterlogging stress for 8 days. None of the cultivar/accession showed germination during eight days of stress. Waterlogging stress was terminated and kept for revival for one week under normal conditions. Sixteen cultivars/accessions showed revival (germination) in one week time. These 16 cultivars/accessions, along with three randomly selected cultivars, were further screened at two leaf stage against waterlogging stress for 16 days. These cultivars/accessions responded differently against waterlogging stress. Phenotypic traits like shoot length, shoot mass and root mass were recorded. Seven cultivars/accessions (010780, 010786, LYP-73, Lasani-2008, Punjab-76, Punjab-85 and Shakar-95) did not show significant changes in root mass, shoot mass and plant height under waterlogging stress and were considered tolerant at two leaf stage. This study helped use to find cultivars which showed tolerance at germination and two leaf stage against waterlogging stress.

Key words: Abiotic stress, *Aegilops*, Hypoxia, Waterlogging, *Triticum aestivum*, *Triticum turgidum*.

Introduction

Wheat growth is negatively affected by different kind of biotic and abiotic stresses (Akgun *et al*., 2011). Keeping in view food security, there is dire need to increase wheat production in order to feed growing population (Ahmad *et al.,* 2019). Waterlogging is one of the important abiotic stress which adversely affects wheat crop globally (Robertson *et al*., 2009). Among cultivated crops wheat is very sensitive to hypoxia (waterlogging) (Perata *et al*., 1996). In South and South East Asia, those regions where rice-wheat crop rotation is common are the most prone areas to waterlogging stress because puddled soil prepared for rice cultivation restricts water percolation from surface (Aslam *et al*., 1995). Globally, about 10% of the irrigated land is having waterlogging conditions (Yavas *et al*., 2012). In waterlogged soils, there is a decrease in oxygen supply to the plant roots because soil is fully saturated with water and oxygen diffusion in water is ten thousand times slower than air (Armstrong, 1980). This decrease in oxygen supply to the roots can leads to shift in metabolism of carbohydrates from aerobic to anaerobic metabolism which could be dangerous for plants because anaerobic metabolism yield lower number of ATP molecules compared to aerobic metabolism (Perata *et al*., 1996; Bailey-Serres & Voesenek, 2010). The lower production of energy can result in reduced root and shoot length, dry mass, photosynthesis and ultimately the crop yield (Collaku & Harrison, 2002; Parent *et al*., 2008). In roots, lower amount of ATP and damaged cellular membranes can lead to less uptake of nutrients ending up in nutrient deficiency not only in underground parts but also in aerial parts resulting in plant's death (Sauter, 2013). Apart from less energy production, waterlogging can also change the physico-chemical properties of soil by accumulation of carbon dioxide, manganese, ethylene and iron which are very lethal to plants (Boru *et al*., 2001; Bailey-Serres *et al*., 2012). In response to low oxygen stress, plants undergo different kinds of morphological and molecular changes (Sauter, 2013). Morphological changes include formation of adventitious roots and aerenchyma along with the changes at molecular level which include change in expression of different genes and proteins involved in different cellular pathways (Bailey-Serres & Voesenek, 2010; Sadiq *et al*., 2011).

The harmful effects of waterlogging vary from species to species as well as on genotypic differences within plant species (San Celedonio *et al*., 2014; Ghobadi *et al*., 2017). Among crops, wheat is considered waterlogging sensitive, however there are evidences of greater tolerance in some of the genotypes (Perata *et al*., 1996; Boru *et al*., 2001; Guglielminetti *et al*., 2001; Ghobadi & Ghobadi, 2010; Ghobadi *et al*., 2017). The difference in wheat tolerance to waterlogging stress can vary depending on growth stage, duration of waterlogging stress, growth conditions and soil type (Boru *et al*., 2001; Ghobadi *et al*., 2017). Germination stage is very sensitive to waterlogging stress and seeds fail to germinate if waterlogging stress is imposed immediately after sowing (Ghobadi *et al*., 2017). At germination stage enzymes involved in carbohydrate metabolism play important role in hypoxia tolerance (Guglielminetti *et al*., 2001). Rice is considered anoxia tolerant and can germinate even in complete absence of oxygen because of induction of amyolytic enzyme (Guglielminetti *et al*., 1995). Wheat is considered hypoxia/anoxia intolerant because under hypoxic conditions it fails to induce α-amylase resulting in decline of soluble sugar availability ultimately leading to decline in seed viability (Guglielminetti *et al*., 1995; Perata *et al*., 1996). Waterlogging can reduce the wheat yield by 32-94% if it stays for twenty days at pre-anthesis stage (San Celedonio *et al*., 2014).

The main objective of this study was to screen wheat cultivars/accessions against waterlogging to find suitable cultivar(s) which can better tolerate stress at early growth stages. The cultivars used in this study are the one which have been cultivated in different time periods from 1930 till 2011 in Indo-Pak region.

Materials and Methods

Plant material: To conduct this study 119 wheat cultivars and wild relatives which included different wheat species like Triticum aestivum, Triticum durum, Triticum compactum, Triticum spheroccum, Aegilops squarrosa, Aegilops triuncialis were acquired from "Wheat Program Pakistan" and Plant Genetic Resources Institute, National Agricultural Research Centre, Islamabad, Pakistan" (Supplementary Tables S1 and S2). These are the cultivars/accessions which have been grown for more than a century in Indian subcontinent.

Initial screening at germination stage: In first experiment, 119 cultivars/accessions were screened against waterlogging stress at imbibition/germination stage all experiments were conducted in controlled conditions at 20°C under 14 hours day and 10 hours night in growth room with light intensity of 300 µmol m^{-2} s^{-1} supplied by Led tube lights. Styrofoam cups (6 oz) were filled with equal amount of sand and one seed per cup was sown and irrigated with Hoagland solution (Hoagland & Arnon, 1950). Four biological replicates of each genotype for control and stress treatment were used.

Waterlogging was imposed for eight days immediately after sowing seeds at one inch depth. For waterlogging treatment Hoagland solution (Hoagland & Arnon, 1950) was kept one inch above soil surface in each cup to keep sand fully saturated with water whereas for control samples, a small hole was made at base of cups to drain extra water. After eight days waterlogging treatment was terminated by draining the water. Cups were kept for one week at 20°C under 14 hours day and 10 hours night in growth room with light intensity of 300 µmol m^{-2} s^{-1} supplied by Led tube lights for revival and were watered daily. Four biological replicates were used for every cultivar/accession.

Screening at two leaf stage: After the 1st round of screening, the sixteen cultivars/accessions showing revival after 8 days of waterlogging stress were selected for next round of screening at two leaf stage. Three randomly selected cultivars namely Soghat-90, Mairaj-2008 and 023813 which did not show tolerance at germination stage were also included to see how these cultivars responded to waterlogging stress at two leaf stage. These nineteen cultivars/accessions were used to investigate their response against waterlogging stress at two leaf stage. Seeds were sown as described in previous section. When plants reached at two leaf stage they were divided into control and treated groups. The cups kept for waterlogging stress were transferred to bigger cups and water level was kept one inch above soil surface. The control samples were irrigated daily with Hoagland solution. Waterlogging stress was terminated after sixteen days and different parameters were recorded from control and stressed plants. Four biological replicates for each cultivar/accession were used.

Shoot length of control and treated plants was measured before the onset of treatment and after the termination of the stress. It was measured from soil surface till the tip of the longest leaf. After sixteen days, the waterlogged and control plants were removed from cups, the roots were cleaned with tap water to remove excess sand and were dried with paper towels. Post-treatment shoot length was measured from crown till tip of the longest leaf. Fresh weight of roots and shoots of control and stressed plants were taken with the help of weighing balance. To determine dry weight, roots and shoots were kept in oven at 80°C for 72 hours. Four independent biological replicates for control and waterlogged plants were used in this study.

Statistical analysis

Data obtained in this study was analyzed by using XLSTAT software (version 2016.4). The statistical significant difference between cultivars and treatment was determined using ANOVA at $p \leq 0.05$. Means of measured traits among wheat cultivars/accessions and treatment were compared by Fisher LSD test ($p \leq 0.05$).

Results

Screening at germination stage: After eight days of waterlogging stress none of the tested 119 cultivars/accessions showed growth. The waterlogged cups were drained after eight days and kept under aerated conditions for one week to see if seeds are still viable after eight days of waterlogging stress. Out of 119 tested cultivars/accessions only sixteen were germinated (Table 1). Among these sixteen there were two Triticum aestivum landraces accessions (010780, 010786) and one Triticum turgidum landrace accession (023886). Interestingly, none of the Aegilops showed tolerance against waterlogging stress. These 16 cultivars/accessions showed germination in minimum two replicates.

Phenotypic changes at two leaf stage: The sixteen cultivars/accessions which showed revival after eight days of waterlogging stress at imbibition/germination stage, along with three randomly selected cultivars namely Soghat-90, Mairaj-2008 and 023813, which did not show revival at germination stage were selected to evaluate their response against waterlogging stress at two leaf stage. The plants were subjected to waterlogging stress when they reached at two leaf stage as described in material and methods section. After 16 days of waterlogging stress, most of the cultivars/accessions did not show statistically significant difference in shoot biomass, root biomass, plant height as compared to control plants. One of the cultivars Rohtas-90 showed significant reduction in plant height during waterlogging stress (Fig. 1). The cultivars/accessions 010800, 023886 and Punjab-96 showed significant reduction in shoot fresh weight while cultivars 010800, 023886, Kaghan-93, Marwat-J-01 and Punjab-96 showed significant reduction in shoot dry weight as compared to control (Fig. 2A, 2B).

In case of root biomass, cultivars 010800, 023886, Kaghan-93, Kohinoor-83, Punjab-81 and Punjab-96 showed significant reduction in fresh root biomass while cultivars Kaghan-93, Kohinoor-83, Punjab-81 and Saleem-2000 showed reduction in dry root mass (Fig. 3A, 3B).

Few other cultivars namely Lasani-2008, Punjab-85, 010780, Shakar-95, 010786, Punjab-76, LYP-73, 023813, Soghat-90 and Mairaj-2008 did not show any statistically significant difference in any of the studied parameters (Fig. 1, 2, 3). All the cultivars/accessions which showed significant reduction in different parameters under waterlogging stress belonged to *Triticum aestivum* except for accession 023886 which belonged to *Triticum turgidum.*

Table S1. Name of wheat (*Triticum aestivum*) cultivars obtained from wheat program Pakistan along with year of release/cultivation.

S. No.	Cultivar name	Year of Release	S. No.	Cultivar name	Year of Release
1.	C518	1933	50	Marvi-200	2000
2.	C591	1934	51	Haider-2000	2000
3.	SA-42	1942	52	Iqbal-2000	2000
4.	C217	1944	53	Bhawalpur-2000	2000
5.	C271	1957	54	Marwat-j-01	2001
6.	C273	1957	55	Wafaq-01	2001
7.	Dirik	1958	56	GA-2002	2002
8.	Mexipak-65	1965	57	AS-2002	2002
9.	Chenab-70	1970	58	Bakkhr-2002	2002
10.	Yeccora-70	1970	59	SH-2003	2003
11.	Barani-70	1970	60	Manthar	2003
12.	Nuri-70	1970	61	Pirsabak-04	2004
13.	B-silver-71	1971	62	Pirsabak-05	2005
14.	Sandal-73	1973	63	Imdad-2005	2005
15.	Pari-73	1973	64	Shafaq-2006	2006
16.	LYP-73	1973	65	Sussui-06	2006
17.	Sa-75	1975	66	Sehar-06	2006
18.	Wl-711	1975	67	Farid-2006	2006
19.	Lu-26	1976	68	Kirman-2006	2006
20.	Punjab-76	1976	69	Khber-87	1987
21.	Sonalika	1978	70	Rawal-87	1987
22.	Zarghoon-79	1979	71	Shalimar-88	1988
23.	Bwp-79	1979	72	Pasban-90	1990
24.	Pak-81	1981	73	Rohtas-90	1990
25.	Punjab-81	1981	74	Soghat-90	1990
26.	Sarhad-82	1982	75	Anmol-91	1991
27.	3.Jau-83	1983	76	Pirsabak-91	1991
28.	Kohinoor-83	1983	77	Inqalab-91	1991
29.	Barani-83	1983	78	Sarab-92	1992
30.	Fsd-83	1983	79	Zardana	1993
31.	Fsd-85	1985	80	Kaghan-93	1993
32.	Punjab-85	1985	81	Bakhtawar-94	1994
33.	Sarsabaz-86	1986	82	Parwaz-94	1994
34.	Sutlag-86	1986	83	Shakar-95	1995
35.	Kohisar-95	1995	84	Skd-1	2006
36.	Punjab-96	1996	85	Chakwal-50	2008
37.	Tatara	1996	86	Mairaj-2008	2008
38.	Suleman 96	1996	87	Lasani-2008	2008
39.	Soorab-96	1996	88	Fsd-08	2008
40.	Nowshera-96	1996	89	NARC-09	2009
41.	Kohistan-97	1997	90	Punjab-2011	2011
42.	Chakwal-97	1997	91	AARI-2011	2011
43.	Zarlashta-97	1997	92	Millat-011	2011
44.	Bwr-97	1997	93	Pothwar	Not Known
45.	MH-97	1997	94	Drawer	Not Known
46.	Margala-99	1999	95	Deman	Not Known
47.	Chenab-2000	2000	96	Kiran	Not Known
48.	Saleem-2000	2000	97	Barsat	Not Known
49.	Auqab-2000	2000			

Table S2. Accessions obtained from Plant Genetic Resources Institute, National agricultural research Centre, Islamabad, Pakistan.

S. No.	Accession No.	Species name	S. No.	Accession No.	Species name
1.	000105	*Aegilops squarrosa*	12	023886	*Triticum turgidum*
2.	000106	*Aegilops squarrosa*	13	023887	*Triticum turgidum*
3.	000141	*Aegilops triuncialis*	14	023888	*Triticum turgidum*
4.	019027	*Triticum spheroccum*	15	023813	*Triticum turgidum*
5.	012961	*Triticum compactum*	16	010741	*Triticum aestivum*
6.	012986	*Triticum durum*	17	010746	*Triticum aestivum*
7.	012991	*Triticum durum*	18	010780	*Triticum aestivum*
8.	012996	*Triticum durum*	19	010781	*Triticum aestivum*
9.	013001	*Triticum durum*	20	010786	*Triticum aestivum*
10.	013006	*Triticum durum*	21	010790	*Triticum aestivum*
11.	013011	*Triticum durum*	22	010800	*Triticum aestivum*

Table 1. List of wheat cultivars/accessions showed regrowth during seven days of revival period after eight days of waterlogging stress at germination/imbibition stage.

S. No.	Name of cultivar /Accession	Species name
1.	Punjab-81	*Triticum aestivum*
2.	Marwat-J-01	*Triticum aestivum*
3.	Kohinoor-83	*Triticum aestivum*
4.	Lasani-2008	*Triticum aestivum*
5.	Kaghan-93	*Triticum aestivum*
6.	Punjab-85	*Triticum aestivum*
7.	Saleem-2000	*Triticum aestivum*
8.	Shakar-95	*Triticum aestivum*
9.	010786	*Triticum aestivum*
10.	Punjab-76	*Triticum aestivum*
11.	Punjab-96	*Triticum aestivum*
12.	010800	*Triticum aestivum*
13.	Rohtas 90	*Triticum aestivum*
14.	LYP-73	*Triticum aestivum*
15.	010780	*Triticum aestivum*
16.	023886	*Triticum turgidum*

Discussion

Waterlogging negatively affects plant growth and grain production in wheat and the extent of yield loss depends on cultivars, duration of waterlogging and growth stage at which plants are exposed to waterlogging stress (Cannell *et al*., 1980; Amri *et al*., 2014; San Celedonio *et al*., 2014; Sheikh *et al*., 2014; Ghobadi *et al*., 2017). Waterlogging stress at early growth stages is dangerous for wheat plants, especially at germination stage and it can lead to reduction in grain yield or complete death of plants (Cannell *et al*., 1980; Herzog *et al*., 2016; Ghobadi *et al*., 2017). It is important to screen available germplasm against waterlogging stress to find suitable tolerant cultivars which can better perform at early growth stages.

In physiological point of view waterlogging tolerance can be defined as survival or maintaining good growth under waterlogged conditions in comparison to normal conditions (aerobic) (Setter & Waters, 2003). There is no information about large scale screening of Pakistani wheat germplasm against waterlogging stress at germination stage to find out cultivars which can better tolerate waterlogging stress at this important growth stage which is more prone to waterlogging in rice-wheat cropping system in South and South-East Asia. Rainfall at early growing stages can damage wheat crop grown in these cropping systems.

Wild relatives of crops are important source of genes involved in biotic and abiotic stress tolerance (Dwivedi *et al*., 2008). It is important to explore wild relatives of crops against different biotic and abiotic stresses. In this study, wild relatives of wheat (*Aegilops*) along with available wheat cultivars and landraces were screened against waterlogging stress. In present study, only 14% of the total tested cultivars/accessions could show revival after 8 days of stress while rest failed to revive during one week of revival period. In past, similar kind of study was performed on Australian wheat cultivars against waterlogging stress at germination stage where the survival rate was 68% after 4 days of waterlogging stress (Setter & Waters, 2003). The lower rate of survival could be due to prolonged waterlogging stress compare to that in previous study. Prolonged waterlogging stress can lead to extreme deficiency of oxygen and increase in other gases like ethylene, carbon dioxide, toxins in soil which are harmful for plant growth (Setter & Waters, 2003). The survival of cultivars/accessions under eight days of waterlogging stress showed genotypic differences within wheat cultivars/accessions where some can adopt themselves under unfavorable conditions possibly by activating defense mechanisms. This might be linked with maintaining amylase activity during the period of waterlogging stress and upon arrival of favorable conditions it activates and helps in breakdown of starch important for seed germination. The cultivars which failed to germinate in revival period might not able to maintain amylase activity because of waterlogging stress and hence failed to revive. Similar kind of genotypic differences were found in other studies in barley against waterlogging stress at germination stage (Takeda & Fukuyama, 1986; Bertholdsson, 2013).

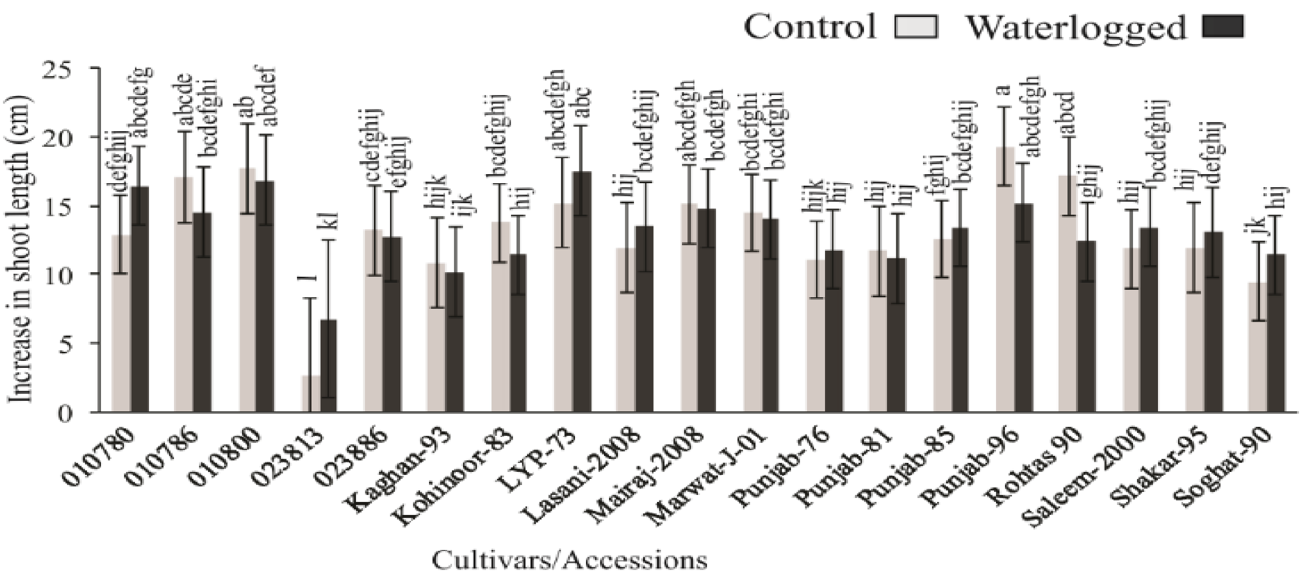

Fig. 1. Increase in height of shoots from start of stress day till end of stress treatment. Bars in columns represent ± SD (n=4). Means with different letters indicate significance difference according to the Fisher LSD test ($p \leq 0.05$).

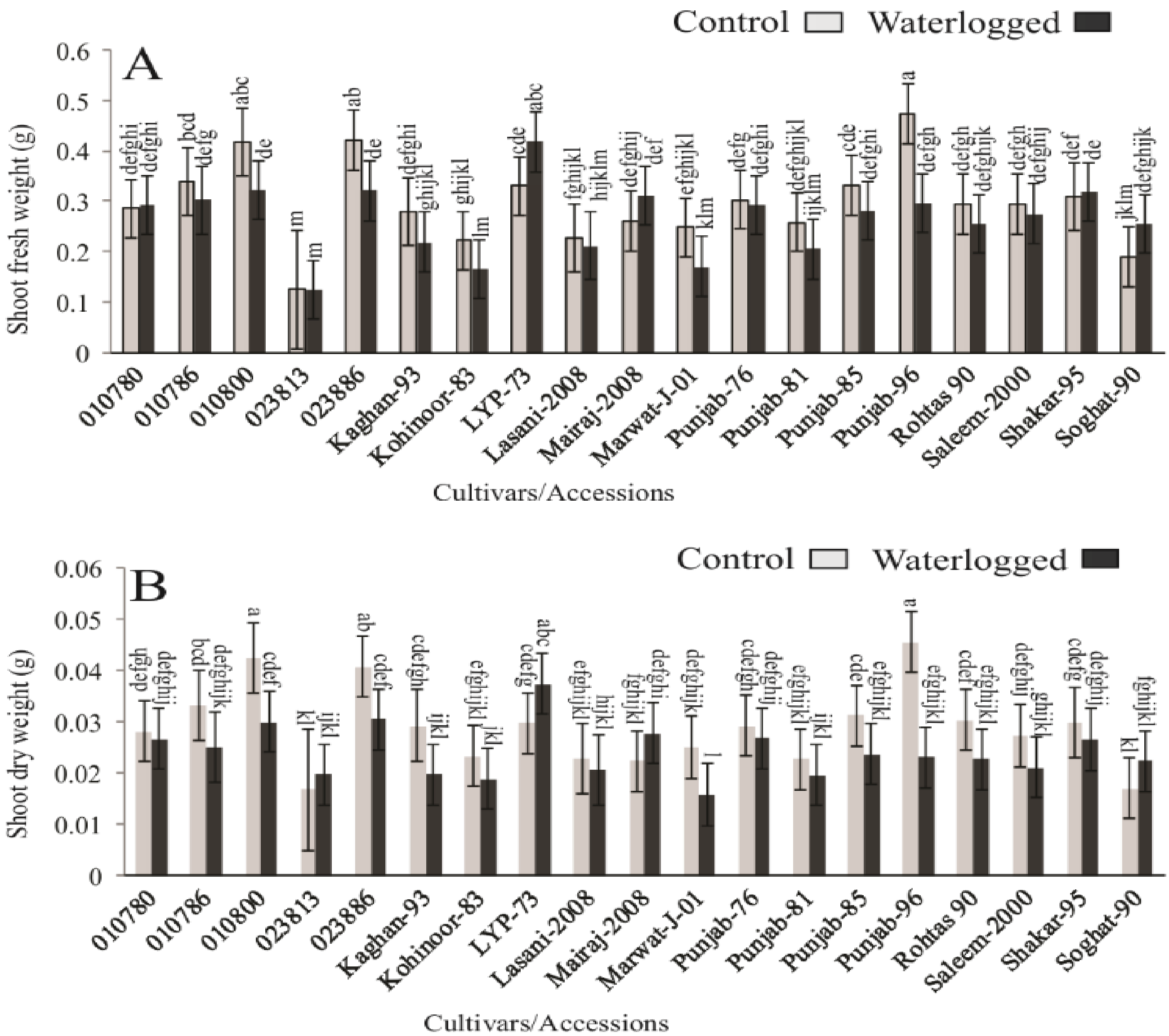

Fig. 2. Change in shoot biomass after sixteen days of waterlogging stress A) Fresh shoot weight B) dry shoot weight. Bars in columns represent ±SD (n=4). Means with different letters indicate significance difference according to the Fisher LSD test ($p \leq 0.05$).

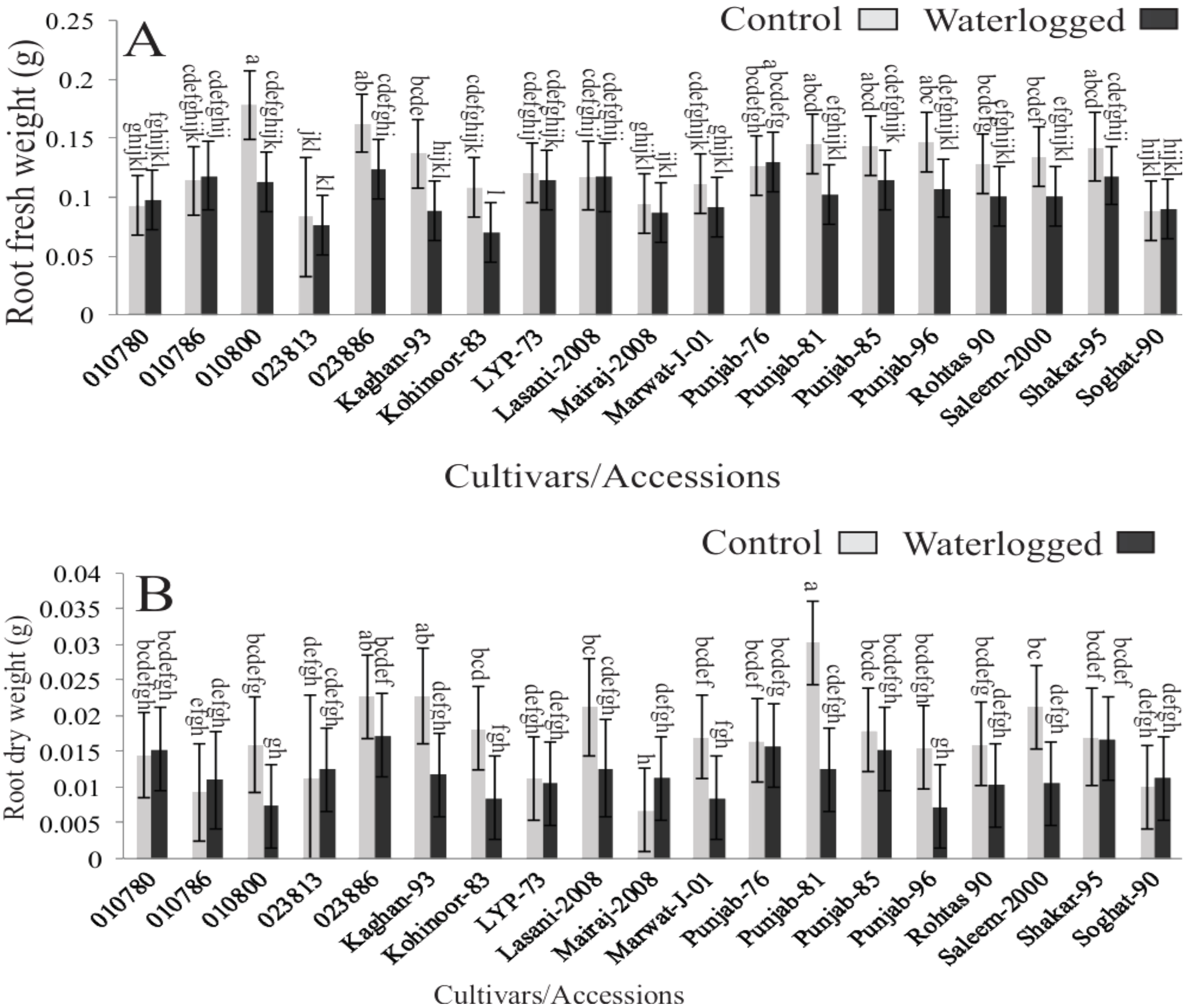

Fig. 3. Change in root biomass after sixteen days of waterlogging stress A) Fresh root weight B) dry root weight. Bars in columns represent ±SD (n=4). Means with different letters indicate significance difference according to the Fisher LSD test ($p \leq 0.05$).

The two leaf growth stage in wheat is also prone to waterlogging stress and prolonged waterlogging stress after two weeks of sowing can lead to greater reduction in grain yield (Watson *et al*., 1976). The data obtained from shoot length, shoot and root biomass showed different response of wheat accessions/cultivars against 16 days of waterlogging stress at two leaf stage. Marwat-J-01, 023886, Punjab-96 and 010800 showed significant reduction in shoot dry mass in waterlogging plants compare to control plants (Fig. 2B). Punjab-81, Kohinoor-83 and Saleem-2000 showed significant reduction in dry root mass with change in shoot mass under waterlogging conditions (Fig. 3B). This contrasting behavior in cultivars with respect to reduction in shoot biomass without change in root biomass and vice versa indicate that these cultivars utilize energy resources differently under waterlogging conditions. It is possible that some cultivars utilized energy sources to sustain shoot biomass while others used available energy source to conserve root biomass. There is a possibility that the cultivars/accessions which showed reduction in shoot length, shoot biomass and root biomass might be linked to another kind of tolerance mechanism at vegetative stage where plants under low oxygen stress grow slowly and save energy to utilize it upon arrival of favorable conditions (Bailey-Serres & Voesenek, 2008). A study conducted by Setter & Waters (2003) showed that wheat cultivars previously identified as waterlogging tolerant performed better under waterlogging stress and showed double shoot growth compared to intolerant wheat cultivar but upon recovery they could not perform in the same way and their shoot growth declined till 7% compare to control plants during recovery period.

Eleven cultivars/accessions, which included 010780, 010786, 023813, LYP-73, Lasani-2008, Mairaj-2008, Punjab-76, Punjab-85, Shakar-95 and Soghat-90 showed no significant changes in any of the tested parameter under waterlogged conditions compared to control (Figs. 1, 2, 3). No significant change in any tested trait could lead to hypothesis that these cultivars had tolerance mechanisms which helped them to maintain plant growth under stress conditions like control plants. This could lead to conclusion that there might be no change in grain yield in these cultivars if they are exposed to waterlogging stress at two leaf stage for sixteen days. A strong correlation has been observed between maintaining biomass and yield under waterlogging stress (San Celedonio *et al*., 2014). However further experiments are required to prove this hypothesis. Waterlogging results in decrease in root and shoot biomass which is directly linked with reduction in grain yield (Robertson *et al*., 2009; San Celedonio *et al*., 2014). In previous studies it was found that tolerant varieties showed less reduction in shoot height, root and shoot biomass compared to susceptible ones (Singh *et al*., 2017).

Three of the cultivars Soghat-90, Mairaj-2008 and 023813 which were unable to tolerate waterlogging stress at germination stage showed tolerance at two leaf stage (Figs. 1, 2, 3). This shows that different kind of defense mechanisms are involved in waterlogging stress tolerance at different growth stages. These cultivars might lack defense mechanism involved at germination stage.

In a previous study it is known that waterlogging at early stages can delay tillering in stressed plants compare to non-stressed (Robertson *et al*., 2009). However, in our study we did not find any significant difference in leaf development between stressed and non-stressed plants of tested accessions (unpublished data).

Conclusion

Waterlogging can be harmful for wheat if they are exposed to this stress at early growth stage. In this study only 14% of the cultivars/accessions could show regrowth after 8 days of waterlogging stress at germination stage. Seven cultivars/accessions 010780, 010786, LYP-73, Lasani-2008, Punjab-76, Punjab-85 and Shakar-95 showed tolerance against waterlogging stress at germination and two leaf stage. These cultivars showed revival after eight days of waterlogging stress at imbibition/germination stage and exhibited no change in different growth parameters like root mass, shoot mass and plant height when exposed to waterlogging stress at two leaf stage. These cultivars are ideal candidates to grow them in areas where wheat is more prone to waterlogging stress at early growth stages.

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