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RESEARCH

Persistent Indifference of Emmer Wheats Grain Yield and Physiological Functions to Nitrogen Supply: Evidence from Two Irrigation Regimes and Dryland Conditions

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Abstract

Scientific data on emmer wheat's response to N and water supplies is scarce. Two field experiments were conducted on a group of five emmer wheat landraces (Joneghan, Zarneh, Singerd, Shahrekord, Khoygan), a durum, and a bread wheat genotype. In the first experiment, the genotypes were subjected to 30 (N-limited) and 100 kg N ha^{-1} (N-supplied) at non-stress and drought stress conditions. In the second experiment, responses of these genotypes to the mentioned N supplies were studied under dryland and dryland + terminal complementary irrigation conditions. Water deprivation (being either due to the imposed drought stress or the dryland condition) led to decreases in chlorophyll concentration, maximum quantum efficiency of photosystem II, relative water content, grains/spike, spikes/plant, 1000-grains weight, grain yield, plant above-ground dry mass, and N use efficiency of the examined wheat genotypes. However, emmer wheat genotypes tended to vary less in response to water supply at least in terms of a majority of the traits, including grain yield (28–30% vs 40–58% drought-induced decreases for emmer and improved wheats, respectively) and above-ground dry mass (12–17% vs 23–40% drought-induced decreases for emmer and improved wheats, respectively). Increase in N supply led to decreases in grains/spike, spikes/plant, 1000-grains weight, and grain yield of the emmer wheats, despite increases in these grain yield attributes and grain yield of the durum and bread wheats. Results were indicative of greater protein content (15.7 vs 12.4% for non-stressed emmer and improved wheats, respectively) but a smaller grain yield (2985 vs 7275 kg ha^{-1} for non-stressed emmer and improved wheats, respectively), harvest index, and N use efficiency in the emmer wheats, compared to the durum and bread wheats, across different N and water supplies. Our findings were novel in that the emmer wheat was found more sustained across different water availabilities and no responsive to N levels that are beneficial to the durum and bread wheats.

Keywords Tetraploid wheat · Drought · Hulled wheats · Landraces · Fertilizer · Dryland

Abbreviations

ANOVA	Analysis of variances
Cars	Carotenoids
Chl	Chlorophyll
dryland + CI	Dryland + complementary irrigation
HI	Harvest index
LSD	Least significant difference
F_v/F_m	Maximal quantum efficiency of PSII
N	Nitrogen
NIR	Near infrared spectroscopy
NUE	N use efficiency
RCBD	Randomized complete block design
SDM	Plant above-ground dry mass

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Introduction

Threefold increase in N fertilizer application for crop production in the present century (Kant et al., 2011) and the increasing threat of an escalated occurrence and magnitude of adverse and extreme agro-climatic events in the upcoming decades (Tosti et al., 2016) are anticipated. Furthermore, lack of sufficient water for irrigation along with environmental concerns around environmental pollution due to excessive use of N-containing fertilizers have added fuel to the quest for drought tolerant crop species and sustainable food production systems characterized by minimal N use. Today's organic farming systems are operating with the handicap of using improved cultivars better fitted to these high-input systems. Organic farming in low rainfall regions (< 300 mm/annum) necessitates cultivars adapted to low levels of N inputs (Murphy et al., 2007).

The genus *Triticum* consists species from three ploidy levels, i.e. di-, tetra- and hexaploid. Emmer wheats are hulled tetraploid wheats and are probably amongst the earliest domesticated plants (Arzani, 2011). These rather ancient wheats were gradually replaced from 2 to 5 millennia ago and then forced to marginal areas during recent centuries due, mainly, to the development of free-threshing improved wheat cultivars (D'Antuono and Bravi, 1995). Domesticated emmer wheat (*T. turgidum* ssp. *dicoccum*) has played a chief role as staple food crop of the ancient nations in the Old World for centuries (Arzani, 2011). Emmer is a ancient domesticated relative of the durum wheat that its hulled grain yield may exceed yield of improved wheat cultivars if planted under less-favorable conditions (Stallknecht et al., 1996). It is rather discouraging that no many farmers, nowadays, rely on emmer wheat any more to the extent that this species is facing extinction and/or at least genetic erosion. It is fortunate that man-oriented selection and breeding has led to increased crop productivity but at the same time it is unfortunate that over the course of breeding certain valuable alleles have been left behind. Local hulled wheat landraces of central Zagros in Iran are believed to be tetraploid emmer that contain AABB genome, as postulated in a previous publication (Sheibanirad et al., 2014). They are truly primitive, as they have most probably never been subject to modern breeding programs. The landrace farmers have kept them mainly because they are satisfied with their grain quality and suitability for homemade products, rather than with grain yield per se. But these wheats are matter of interest also because they are alternative cereals and bring about diversity to the field. Furthermore, these landraces could be qualified candidates for organic farming and health food products. Even though insufficient nitrogen (N) levels are generally known to impose serious suppressions to the photosynthetic functions and, subsequently, plant dry mass and grain yield of improved varieties of many crop plants, some reports indicate that this generalization may not be valid with less-developed ancient landraces of some staple crops (Pourazari et al., 2015).

Considering the possession of a considerable genetic diversity, resistance to low input cultural conditions and usefulness in organic farming and achieving health food products, ancient wheats are valuable assets needing scientific exploration. The present work was designed and implemented to shed light on the response of emmer wheat landraces of central Iran to N fertilizer and water supply and to ascertain quality and sustainability advantages of these wheats compared to bread and durum wheats. The main aim of the present work was to assess the emmer wheat landraces as a potential source for enhancing agronomic attributes of bread and durum wheat cultivars with minimal reliance on N and water supplies.

Materials and Methods

Experiment 1: Agronomic and Physiological Attributes of Emmer Wheats in Response to N and Water Supplies

Plant Material and Experiment Set-up

This experiment was conducted as two separate 3-replicates of factorial combination at the Lavark Research Farm of the Isfahan University of Technology, Isfahan (32° 32′ N, 51° 23′ E, 1630 m above the mean sea level, 14.5 °C mean annual temperature and 140 mm mean annual precipitation), central Iran in 2015. This region is characterized by an arid climate and the soil was a Fine Loam Typical Haplargid with N = 0.078%, P = 61 mg kg^{-1}, K = 882 mg kg^{-1}, pH = 7.1, EC = 2.1 dS m^{-1}, bulk density = 1.34 g cm^{-3}, and OC = 0.57%. Irrigation after 30–40% depletion of soil water of the field capacity was considered as non-stress and irrigation after 60–70% depletion of soil water of the field capacity was chosen as drought stress conditions, respectively. Previous studies (Askari & Ehsanzadeh, 2015) in the same experimental field had found that these levels of soil moisture depletion are appropriate for implementing non-stress and drought stress irrigation regimes on different crops. Depletion of soil moisture at a 60 cm depth was monitored using a TDRinstrument (TDR Trase System, Model 6050XI; Soil Moisture, Santa Barbara, CA). The two irrigation regimes were considered as two environments and, hence, the collected data can be subjected to a combined analysis of variances. A factorial combination of seven wheat genotypes, i.e. five emmer wheats (Joneghan, Zarneh, Singerd, Shahrekord, Khoygan), and two improved wheats (including Yavaroos free-threshing tetraploid durum wheat cultivar and Roushan free-threshing hexaploid bread wheat cultivar) along with two levels of soil-applied N fertilizer were evaluated in each of irrigation regimes (i.e. environments). The two levels of applied N were 30 kg ha^{-1} of N (N-limited) and 100 kg ha^{-1} of N (N-supplied) in the form of urea (46% N), where the first half of each level was applied at the seeding and the second half was top-dressed at the stem elongation. The top-dressed half of the urea fertilizer was applied immediately before irrigation, to assure that it is dissolved into the soil moisture. Seeds of the wheat genotypes were sown 3–5 cm deep in a 2 × 4 m plot in each replication in first week of November 2015, where each plot consisted of 10 rows spaced 20 cm apart. Seeding rate was set to nearly 400 seeds m^{-2} in all experimental units. In order to assure uniform plant emergence and seedling establishment, all experimental units were irrigated uniformly twice, one immediately after sowing and the other at third week of November 2015. Plants were allowed to over-winter and undergo tillering throughout November 2015 to February 2016. With the exception of application of a 2, 4-D herbicide to control the broad-leaved weeds, weeding was done manually throughout the experiment. Irrigation regimes were applied from early March to mid-June 2016. In order to carry out the above irrigation regimes, a moisture release curve was developed for the soil of the experimental field (Fig. 1) and calculation of the available soil water and volume of irrigation water (V_{irrg}) were done based on Eqs. (1) and (2) (Allen et al., 1998) according to the details provided by Kiani et al. (2016) and Yousefzadeh Najafabadi and Ehsanzadeh (2017).

$$ASW = \left(\theta_{FC} - \theta_{PWP}\right) \times Bd \times V \tag{1}$$

where θ_{FC} is the gravimetric soil–water content (%) at field capacity, θ_{PWP} is the gravimetric soil–water content (%) at permanent wilting point, Bd is the bulk density of the soil (g cm^{-3}) and V is the volume of soil layer in the root zone (m^3).

$$V_{irrg} = (ASW \times f)/E_a \tag{2}$$

where f is the fraction of available soil water (ASW) depletion (30–40 and 60–70%) from the root zone and E_a is the percent of irrigation efficiency.

A volumetric counter was used for controlled delivering of water from a pumping station to plots of each irrigation level via polyethylene pipe. Drip-tapes (Tiran Fitting Polymer Co., Tiran, Isfahan, Iran) of 16 mm diameter, working pressure of 2.1 bars, containing drippers that were spaced 15 cm apart were installed alongside each other row of planting. Flow rate for each dripper was maintained at 1.3 L h^{-1}. Drip-tape spacing was 0.40 m, the access tubes were installed at a distance of 5–10 cm from the drip-tape. Irrigation started as soon as either 30–40% or 60–70% of the total ASW was depleted in the root zone, for non-stress and drought stress irrigation regimes, respectively. The irrigation depth for the both non-stress and drought levels of irrigation regime was calculated based on the amount of water required to replenish soil water depletion to the field capacity point. The non-stress and drought stress irrigation regimes received 13 and 8 irrigations, respectively, throughout the growing season. In each of the irrigation events the two irrigation regimes received an equal amount of water, i.e. 0.055 m^3/m^2. In other words, each experimental unit (i.e. an 8 m^2 plot) was irrigated with 0.44 m^3 of water in each irrigation event.

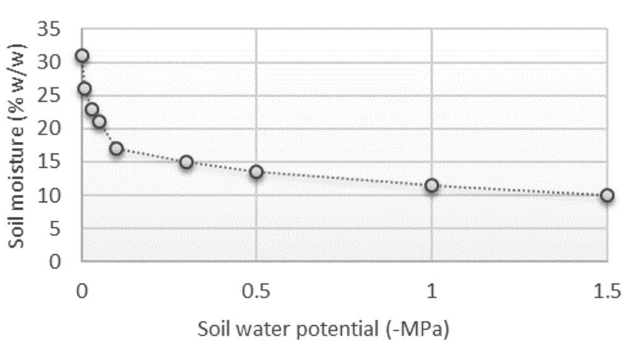

Fig. 1 Soil moisture curve for Experiment 1, conducted at Isfahan

Leaf Relative Water Content and Proline Concentration Measurements

Relative water content (RWC) was measured on leaf sections obtained from the second fully developed upper leaves taken between 09:00 and 10:00 a.m., 6 weeks after applying the irrigation treatments. The leaf sections were quickly sealed in plastic bags and fresh masses were determined immediately after excision. The samples were kept in distilled water in test tubes for 5 h at room temperature (nearly 20−23 °C) and under the low light conditions of laboratory to estimate the turgid masses. Dry masses were measured after drying the leaf samples in an oven for 48 h at 70 °C. The RWC was calculated using the Eq. (3) (Smart & Bingham, 1974):

$$RWC(\%) = \left[(Fresh\,Mass - Dry\,Mass) / (Turgid\,Mass - Dry\,Mass)\right] \times 100 \tag{3}$$

For measuring proline concentration, the samples were taken from fully matured leaves between 09:00 to 10:00 a.m., 6 weeks after applying the irrigation treatments and then were stored at −20 °C. Total proline content was extracted using the method of Bates et al. (1973). For this purpose, leaf samples (0.5 g) were homogenized in 10 mL of 3% aqueous sulfosalicylic acid and the homogenate was filtered through filter paper. Then, 2 mL of the filtered extract was reacted with 2 mL of acid ninhydrin and 2 mL of glacial acetic acid in a test tube for 1 h at 100 °C and the reaction was terminated by placing the tube on an ice bath. The reaction mixture was extracted in 4 mL of toluene and vortexed. The chromophore containing toluene was aspirated from the aqueous phase, warmed to room temperature, and the absorbance was read at 520 nm using a spectrophotometer (U-1800 UV/VIS, Hitachi, Japan). Toluene was used as a blank for the spectrophotometric measurements. Proline concentration was determined using the calibration curve and expressed as μmole proline g^{-1} DM.

Grain Yield and Yield Attributes Measurements

Plant height, spikes/plant, and grains/spike of 5 random plants from each experimental unit (i.e., subplot) were measured at physiological maturity. The harvested plants were air-dried for 10 days to determine their 1000-grains weights. Grains/m^2 was calculated by the multiplication of spikes/m^2 and grains/spike. Grain yield was determined from samples taken from the central 1.0 m^2 part of each plot. Harvest index (HI) was determined using air-dried whole plant samples (i.e., above-ground parts) and the ratio of grain yield to the above-ground dry mass (SDM) was reported in percent. SDM was determined at physiological maturity (i.e. late June 2016) using samples harvested from two 0.5 m-long sections of the second and third rows of each plot. The samples were dried at 68 °C for 72 h, weighed and expressed as g m^{-2}. The N use efficiency for grain (NUE_{grain}) and above-ground dry mass (NUE_{SDM}) were calculated by dividing grain yield and SDM, respectively, to N applied to each m^2 of the experimental plot.

Measurement of grain protein concentration was carried out by near infrared spectroscopy (NIR). Grain samples from each experimental unit were dry milled to a flour of less than 80 meshes in a Cyclone mill (Tecator Inc., Boulder, CO). The NIR reflectance spectra of the flour samples were collected over 500–2400 nm spectral region with a Perten Inframatic 8620 (Perten Inc., Sweden) spectrometer equipped with PbS and Silicon detectors, as detailed by Sabzalian et al. (2014).

Statistical Analysis

The data collected from the separate experiments in each irrigation regime were subjected to combined analysis of variance using Statistical Analysis Software (*SAS Institute Inc., Version 9.1,* Cary, North Carolina, USA). Orthogonal contrasts were conducted for comparing the emmer group of five tetraploid wheats (i.e. Joneghan, Zarneh, Singerd, Shahrekord, Khoygan) against the improved group of two free-threshing wheats, i.e. Roushan genotype of hexaploid bread wheat and Yavaroos genotype of tetraploid durum wheat. Interacting effects of these two groups of wheat with irrigation and N regimes were also examined. For those statistical tests, where the F-tests were significant, mean comparisons were conducted using LSD test at 0.05 level of probability. In analysis of variance, replication was considered as random and irrigation, N and genotype were considered as fixed effects. While mean squares for replication within irrigation (nested) were used as denominators for conducting F-test for irrigation regime, the mean squares of experimental residuals (experimental errors) were used as denominators for carrying out the F-tests for N, genotype, and their interactions.

Experiment 2: Agronomic and Physiological Attributes of Emmer Wheats in Response to N Supply and Dryland Condition

Experiment Location, Set-up, and Lay-out and Wheat Genotypes

This experiment was conducted as two separate 3-replicates of factorial combination at the research farm of Aligudarz's Department of Agriculture, Aligudarz (33° 28′ N, 49° 41′ E, 2072 m above the mean sea level, 12.5 °C mean annual temperature and 387 mm mean annual precipitation), Lorestan, in central-west of Iran in 2018. This region is characterized by a semiarid climate. The soil characteristics were: N = 0.09%, P = 7.4 mg kg^{-1}, K = 571 mg kg^{-1}, pH = 7.6, EC = 1.6 dS m^{-1}, texture = sandy loam, bulk density = 1.8, and OC = 0.93%. It had been fallowed for two years and was ploughed, disc-harrowed and leveled before seeding. In the experiment, the irrigation regimes encompassing dryland (no irrigation) and dryland + complementary irrigation (dryland + CI: dryland supplied with two terminal irrigation events at grain filling stage) were considered as two environments and, hence, the collected data can be subjected to a combined analysis of variances. A factorial combination of seven wheat genotypes, i.e. five emmer wheats (Joneghan, Zarneh, Singerd, Shahrekord, Khoygan), and two improved wheats (including Yavaroos free-threshing tetraploid durum wheat cultivar and Roushan free-threshing hexaploid bread wheat cultivar) along with two levels of soil-applied N fertilizer were evaluated in each of irrigation regimes (i.e. environments). Healthy seeds of the wheat genotypes were sown 3–5 cm deep in 2 × 4 m plots in mid-November 2018, where each plot consisted of 10 rows spaced 20 cm apart. Seeding rate was set to nearly 300 seeds m^{-2} in all experimental units. Plants were emerged, over-wintered and underwent tillering throughout late-November 2018 to early-March 2019. A 2, 4-D herbicide was applied at a two L ha^{-1} equivalent to control the broad-leaved weeds throughout the late-tillering stage and then, the narrow-leaved weeds were controlled manually. Two complementary irrigations were applied from mid-May to mid-June 2019. In order to carry out the above irrigations, watering with 10% of the total irrigation water that would had been applied throughout the growing season (i.e. approximately 5000 m^3/ha) in an irrigated-wheat crop in this region was targeted. A volumetric counter was used for controlled delivering of tap water to plots of the dryland + CI part of the experiment via polyethylene pipe. Each of these plots received a 200 L volume of irrigation water at each of the two irrigation events, i.e. 400 L/plot for the two irrigation events.

Leaf Chlorophyll Concentration, Chlorophyll Fluorescence, and Relative Water Content Measurements

Chlorophyll (Chl) and carotenoids (Cars) measurements were carried out using the procedure of Lichtenthaler and Wellburn (1994) that has been explained in Abdehpour and Ehsanzadeh (2019) using the samples of 0.1 g of mature flag leaves at early grain filling. A 80% acetone solution was used to extract the Chl pigments with the help of centrifuging at 5000 rpm for 15 min. Absorbencies of the extracts were measured by the spectrophotometer at 663 and 470 nm for Chl a and Cars, respectively. Maximal quantum efficiency of PSII (F_v/F_m) was assessed at grain filling stage using healthy flag leaves. To accomplish this, two measurements per plot were carried out between 11:00 and 13:00 h on the flag leaves, which had been dark-adapted for approximately 20 min using a portable Chl fluorometer (*Opti-Sciences, Inc.,* Hudson, NH, USA) and a mean of the two measurements was used for each plot.

RWC was measured according to the details given in Sect. 2.1.2.

Plant Height, Dry Mass, Grain Yield, and Yield Attributes Measurements, and Statistical Analysis

Alike Experiment 1 (Sect. 2.1.3), these measurements were made at physiological maturity stage before harvesting. Ten randomly-chosen plants per plot were used to measure spikes/plant, grains/spike, and 1000-grains weight on mid-July 2019. Grain yield was measured based on harvesting an area of 1 m^2 in the central rows of each plot. SDM and HI were determined according to the procedures given in Sect. 2.1.3. Since the Yavaroos durum wheat was invaded and damaged by the birds at grain dough stage, no valid data were obtained for the grain yield and hence for SDM and HI of this genotype.

Statistical analyses were conducted according to Sect. 2.1.4.

Results

Experiment 1: Agronomic and Physiological Attributes of Emmer Wheats in Response to N and Water Supplies

All studied traits were significantly affected by either irrigation, N and/or genotype (Table 1). Furthermore, the two groups of emmer and improved wheats differed in terms of all examined attributes, with the exception of SDM. In the meantime, all of the examined attributes were significantly affected by at least two of the interactions, i.e. irrigation × N, irrigation × genotype, irrigation × wheat group, N × genotype, and N × wheat group. Albeit spikes/m^2 must be exempted from the above generalization, as it was not affected by any of the latter interactions. HI was only affected by the interaction of irrigation × N. The trait of spikes/m^2 in the emmer group of wheats was greater than the improved wheats. HI of the emmer wheats was substantially smaller than the improved wheats, 17.5% vs. 43.5%. As for the remaining traits, the interactions effects were statistically significant, only the means for the interactions of wheat groups with N and irrigation will be explained herein.

Proline concentration in the drought-stressed plants of the improved group of wheat was increased in comparison to non-stressed plants, but that of the emmer wheats did not modify significantly (Table 2). Traits of RWC, 1000-grains weight, grains/spike, grains/m^2, grain yield and SDM, NUE_{grain} and NUE_{SDM} in both groups of wheat were depressed when subjected to drought. However, the extent of the depressions was more notable in the improved group of wheats.

Grains/spike, grains/m^2, grain yield, SDM, proline concentration, RWC, plant height, and NUE_{grain} responded to N supply in a group-specific manner (Table 3). While grains/spike, grain yield and SDM in the emmer group of wheats were decreased, however, these traits were increased substantially in improved group of wheat, when treated with sufficient amount of N. While proline concentration of emmer wheats tended to decrease, that of the improved wheats tended to increase in response to N supply. Furthermore, RWC and plant height of emmer wheats did not altered in response to N, but these traits in improved wheats were decreased and increased, respectively. Trait of NUE_{grain} in both groups of wheat was decreased due to N supply but the extent of decrease was greater in the improved group.

Supplying different wheats with 100 kg ha^{-1} of N led to increase in plant height and 1000-grains weight. Though, it led to decreases in these traits in the stressed plants and did not lead to notable changes in grain yield and HI of non-stressed plants (Table 6). NUE_{grain} and NUE_{SDM} of both stressed and non-stressed plants were decreased when subjected to 100 kg N ha^{-1}, but the amount of decrease was more notable in the non-stressed plants.

Experiment 2: Agronomic and Physiological Attributes of Emmer Wheats in Response to N Supply and Dryland Condition

Alike Experiment 1, water condition, N supply, genotype, and wheat group affected a great majority of the traits (data not shown). Since nearly all of the examined traits were affected by at least one of the first order interactions,

Table 1 A synopsis of combined analysis of variances over two irrigation regimes (mean squares) for plant height, relative water content (RWC), proline concentration, 1000-grains weight (1000-grains), grains/spike, spikes/m^2, grains/m^2, grain yield (GY), above-ground dry mass (SDM), nitrogen use efficiency of grain (NUE_{grain}), nitrogen use efficiency of SDM (NUE_{SDM}), harvest index (HI), and grain protein concentration of emmer and improved wheats in Experiment 1 (conducted at Isfahan, central Iran)

Trait	DF	Height	RWC	Proline	1000-grains	Grains/spike	Spikes/m^2	Grain/m^2 (×10^5)	GY(×10^5)
Replication	2	35.68	3037	27.01	0.58	42.38	3447.58	186.98	5.53
Irrigation(Ir)	1	10,058.67**	783.75**	273.97**	343.6**	336**	0.29^{ns}	573.12**	422.75**
Replication (Ir)	4	35.68	30.37	27.01	0.58	42.38	3447.58	186.98	5.53
Nitrogen(N)	1	242.76**	41.9^{ns}	5.35^{ns}	1.51^{ns}	17.19^{ns}	8102.67**	149.41**	48.15**
Genotype(G)	6	1646.18**	229.75**	96.68**	383.25**	3192.63**	30,895.01**	3620.24**	305.78**
Emmer vs. improved	1	7094.01**	71.25^{ns}	402.77**	2200.48**	18,990.51**	106,672.8**	19,833.29**	1801.35**
Emmer vs. Yavaroos	1	9576.96**	238.13*	94.36**	1417.8**	11,133.34**	129,504.4**	7843.46**	904.95**
Emmer vs. Roushan	1	948.35**	802.35**	438.56**	1156.09**	11,022.4**	19,330.67**	16,017.22**	1207.50**
Ir×N	1	1243.55**	31.05^{ns}	31.41^{ns}	14.34**	15.42^{ns}	0.96^{ns}	42.80^{ns}	29.33*
Ir×G	6	52.38*	138.84**	45.9**	39.37**	33.08**	0.29^{ns}	50.04**	33.57**
Ir×Group	1	56.52^{ns}	515.46**	70.55*	197.31**	145.83**	0.68^{ns}	164.45**	188.45**
N×G	6	22.85^{ns}	148.51**	40.45*	0.31**	64.99**	0.28^{ns}	118.85**	30.05**
N×Group	1	96.62*	247.97*	55.19^{ns}	1.25^{ns}	262.97**	0.0048^{ns}	547.17**	77.77**
Ir×N×G	6	72.38**	112.03*	41.47*	11.05**	6.28^{ns}	0.57^{ns}	12.58^{ns}	24.28**
Error	52	21.12	42.66	14.95	0.67	8.53	1.64	14.18	5.90

Trait	DF	SDM(×10^5)	NUE_{grain}	NUE_{SDM}	HI	Protein
Replication	2	40.80	821.45	11,267.5	19.97	0.42
Irrigation(Ir)	1	2352.70**	14,615.39**	99,074.56**	101.81^{ns}	14.25**
Replication (Ir)	4	40.80	821.45	11,267.5	19.97	0.42
Nitrogen(N)	1	10.92^{ns}	178,020.1**	2,342,843**	497.83**	6.25**
Genotype(G)	6	116.87^{ns}	119,223.32**	8426.85^{ns}	1795.23**	27.46**
Emmer vs. improved	1	165.62^{ns}	66,699.54**	19,097.81^{ns}	10,443.45**	162.8**
Emmer vs. Yavaroos	1	125.81^{ns}	24,834.94**	20,269.5^{ns}	5234.6**	84.97**
Emmer vs. Roushan	1	71.26^{ns}	56,127.06**	4723.13^{ns}	7014.42**	105.51**
Ir×N	1	0.027^{ns}	1501.42*	26,211.445*	383.34**	0.21^{ns}
Ir×G	6	224.25*	1459.19**	15,335.66*	23.36^{ns}	0.22^{ns}
Ir×Group	1	278.05^{ns}	5816.01**	57,052.66**	46.97^{ns}	1.08**
N×G	6	118.18^{ns}	2732.43**	7640.42^{ns}	81.26*	0.14^{ns}
N×group	1	131.57^{ns}	9246.86**	22,568.92^{ns}	4.51^{ns}	0.6080*
Ir×N×G	6	340.09**	1149.55**	16,983.42**	310.05**	0.07^{ns}
Error	52	102.48	357.42	5703.11	35.29	0.12

*, **Indicating significant at 0.05 and 0.01 levels of probability, respectively. ns: non-significant. Since combined analyses of variances over two irrigation regimes were conducted, Replication (Ir) was employed as a denominator for the F-test of the Irrigation effect

i.e. irrigation × N, irrigation × genotype, irrigation × wheat group, N × genotype, or N × wheat group, no emphasize is given to the comparison of the main effects.

Chl concentration, F_v/F_m, and RWC of all wheat genotypes of two ploidy groups were suppressed under the dryland condition, compared to dryland + CI condition (Table 4). The magnitude of the suppressions differed among genotypes; Chl concentration and, consequently, F_v/F_m of the emmer group of wheats suffered more from dryland condition, compared to the durum and bread improved wheats. Averaged over the two moisture conditions, improved wheats out-numbered the emmer wheats in terms of Chl concentration. But, RWC of the improved wheats was greater than the emmer wheats under dryland + CI and a reversed tendency was observed under dryland condition. Cars concentration of the examined genotypes of emmer and improved wheats was decreased when grown under dryland condition but the extent of the decreases differed among certain genotypes. Unlike the above-mentioned physiological traits, RWC of the improved durum and bread wheats was suppressed more notably than those of the emmer wheats. Plant height and SDM of both improved bread wheat and emmer wheats were

Table 2 Mean comparisons of genotype × irrigation and wheat group × irrigation interaction effects for plant height, relative water content (RWC), proline concentration, 1000-grains weight (1000-grains), grains/spike, grains/m^2, grain yield, above-ground dry mass (SDM), nitrogen use efficiency of grain (NUE_{grain}), nitrogen use efficiency of SDM (NUE_{SDM}), and grain protein concentration of emmer and improved wheats in Experiment 1 (conducted at Isfahan, central Iran)

Genotype	Irrigation regime	Height (cm)	RWC (%)	Proline (µmoles g^{-1})	1000-grains (g)	Grains/spike	Grains/m^2	Grain yield (kg ha^{-1})	SDM (kg ha^{-1})	NUE_{grain} (kg kg^{-1})	NUE_{SDM} (kg kg^{-1})	Grain protein (%)
Goneghan	Control	122.5	78.0	5.88	32.0	25.3	11,949.2	3076.7	14,033.3	67.7	311.7	16.1
	Drought	95.0	77.0	12.39	31.4	21.0	9901.8	2223.3	13,866.7^{b}	56.2	279.8	16.7
Shahrekord	Control	118.0	70.8	10.75	31.48	27.5	13,785.8	3362.7	15,671.7	79.8	360.9	15.6
	Drought	95.8	74.7	11.54	32.3	23.3	11,709.8	2024.8	12,233.3	48.8	240.6	16.4
Zarneh	Control	118.1	76.8	10.45	30.6	20.7	9351.7	2516.7	17,083.3	60.9	363.3	15.7
	Drought	100.5	74.2	14.11	28.6	20.3	9181.3	1902.0	14,436.7	44.7	323.3	16.4
Khoygan	Control	118.3	80.2	13.73	33.1	21.7	9329.2	3080.7	15,450.0	72.8	332.2	15.7
	Drought	97.6	73.2	11.45	28.3	21.7	9389.3	2281.0	14,433.3	55.6	346.6	16.3
Singerd	Control	123.8	79.3	10.69	30.8	24.7	10,412.5	2888.0	17,333.3	62.6	344.4	15.6
	Drought	97.1	71.1	14.27	28.8	21.8	9184.3	2395.0	15,233.3	59.1	343.7	16.3
Yavaroos	Control	85.9	86.3	9.61	46.7	60.0	20,564.2	7083.3	17,253.3	145.5	345.6	12.6
	Drought	69.5	74.6	19.59	39.0	52.3	17,987.5	4083.3	10,458.3	75.8	213.7	13.7
Roushan	Control	110.0	74.7	16.63	46.7	60.3	24,838.3	7466.7	17,766.7	153.6	388.1	12.2
	Drought	87.8	58.5	19.67	36.6	51.7	21,312.5	4633.3	10,500.0	117.9	217.8	13.5
LSD(0.05)		5.3	7.6	4.48	0.9	3.4	1380.0	890.5	3709.0	21.9	87.5	0.4
Emmer wheat	Control	120.1	77.0	10.3	32.0	24.0	10,965.7	2984.9	15,914.3	68.8	342.5	15.7
	Drought	97.2	74.1	12.8	29.9	21.6	9873.3	2165.2	14,040.7	52.9	306.8	16.4
Improved wheat	Control	98.0	80.5	13.1	46.7	60.2	22,701.3	7275.0	17,510.0	149.6	366.8	12.4
	Drought	78.7	66.5	19.6	37.8	52.0	19,650.0	4358.3	10,479.2	96.9	215.7	13.6
LSD(0.05)		3.1	4.5	2.63	0.6	2.0	815.6	530.1	2192.2	12.9	51.7	0.2

LSD least significant difference at 0.05 level of probability

Table 3 Mean comparisons of genotype × N and wheat group × N interaction effects for plant height, relative water content (RWC), proline concentration, 1000-grains weight (1000-grains), grains/spike, grains/m^2, grain yield, harvest index (HI), N use efficiency of grain (NUE_{grain}), and grain protein concentration of emmer and improved wheats in Experiment 1 (conducted at Isfahan, central Iran)

Genotype	Applied nitrogen (kg ha^{-1})	Height (cm)	RWC (%)	Proline (µmoles g^{-1})	1000-grains (g)	Grains/spike	Grains/m^2	Grain yield (kg ha^{-1})	HI (%)	NUE_{grain} (kg kg^{-1})	Protein (%)
Joneghan	30	107.4	80.0	8.57	31.7	24.5	11,314.3	3040.0	21.5	101.3	16.3
	100	110.1	76.1	9.70	31.7	21.8	10,536.7	2260.0	18.2	22.6	16.5
Shahrekord	30	106.3	62.2	10.00	32.9	26.6	13,124.7	3204.1	24.2	106.8	15.7
	100	107.6	79.3	12.29	32.9	24.1	12,371.0	2183.3	15.9	21.8	16.3
Zarneh	30	108.7	79.9	12.46	29.7	19.6	8696.0	2634.7	17.0	87.8	15.8
	100	109.9	75.0	12.11	29.5	21.3	9837.0	1784.0	12.4	17.8	16.3
Khoygan	30	108.8	76.9	15.88	30.6	21.1	9355.3	3204.7	20.0	106.8	15.8
	100	110.5	76.6	9.30	30.8	21.1	9363.2	2157.0	16.0	21.6	16.2
Singerd	30	110.1	77.8	14.55	29.5	24.3	10,050.7	2951.3	19.1	98.6	15.7
	100	110.7	72.7	10.40	30.0	22.1	9546.2	2331.7	13.6	23.3	16.2
Yavaroos	30	75.1	82.7	14.51	42.5[a]	51.0	16,969.7	4700.0	38.5	156.7	12.8
	100	80.3	78.2	14.69	43.2	61.0	21,582.0	6466.7	42.9	64.7	13.6
Roushan	30	94.8	71.2	16.18	41.0	54.0	21,985.8	5650.0	50.6	215.0	12.4
	100	103.1	62.0	20.12	42.0	57.0	24,165.0	6450.0	37.9	56.5	13.2
LSD(0.05)		3.1	7.6	4.48	0.9	3.4	1380.0	890.5	6.9	21.9	0.4
Emmer wheat	30	120.1	75.2	12.29	30.9	23.5	10,508.2	3007.0	20.4	100.2	15.9
	100	97.2	75.9	10.76	31.0	21.1	10,330.8	2143.2	15.2	21.4	16.3
Improved wheat	30	98.0	76.9	15.35	41.9	52.8	19,477.8	5575.0	44.5	185.8	12.6
	100	78.7	70.1	17.40	42.6	59.3	22,873.1	6058.3	40.4	60.6	13.4
LSD(0.05)		3.1	4.5	2.63	0.6	2.0	815.6	530.1	4.1	12.9	0.2

LSD least significant difference at 0.05 level of probability

Table 4 Mean comparisons of genotype × irrigation and wheat group × irrigation interaction effects for chlorophyll a (Chl) and carotenoids (Cars) concentration, maximum efficiency of photosystem II (F_v/F_m), relative water content (RWC), plant height, grains/spike, 1000-grains weight (1000-grains), grain yield, above-ground dry mass (SDM), and harvest index (HI) of emmer and improved wheats grown under dryland or dryland + complementary irrigation (dryland + CI) in Experiment 2 (conducted at Aligudarz, central-west of Iran)

Genotype	Irrigation regime	Chl (mg g^{-1})	Cars (mg g^{-1})	F_v/F_m	RWC (%)	Height (cm)	Grains/spike	1000-grains (g)	Grain yield† (kg ha^{-1})	SDM† (kg ha^{-1})	HI† (%)
Joneghan	dryland + CI	1.97	0.46	0.78	79.2	76.7	23.5	22.8	1519.0	7136.9	21.8
	Dryland	1.78	0.46	0.75	76.5	75.5	22.3	16.8	1118.4	5564.9	20.4
Shahrekord	dryland + CI	2.02	0.48	0.79	77.7	80.5	21.6	20.6	1437.0	7205.6	19.2
	Dryland	1.68	0.42	0.74	74.5	75.4	20.7	19.1	1048.2	5859.5	17.9
Zarneh	dryland + CI	1.58	0.54	0.80	76.9	76.5	22.0	20.6	1466.2	7220.8	20.3
	Dryland	1.29	0.52	0.72	74.6	72.2	19.3	15.9	959.2	6963.5	12.5f
Khoygan	dryland + CI	1.92	0.49	0.79	67.5	72.5	21.0	22.6	1948.3	7712.9	25.6
	Dryland	1.61	0.46	0.73	58.4	71.5	20.3	15.4	1205.5	5575.1	22.2
Singerd	dryland + CI	1.94	0.53	0.79	74.9	73.4	22.0	19.6	1253.5	7058.8	17.6
	Dryland	1.74	0.50	0.72	70.2	72.6	18.4	14.6	905.5	5939.1	15.3
Yavaroos	dryland + CI	2.51	0.58	0.75	86.7	64.2	33.4	40.0	–	–	–
	Dryland	2.27	0.55	0.74	72.3	62.1	16.3	29.2	–	–	–
Roushan	dryland + CI	2.64	0.60	0.79	82.6	78.2	38.5	44.2	2935.2	8128.2	36.3
	Dryland	2.27	0.55	0.74	69.3	77.3	28.2	27.5	1222.5	7334.1	17.2
LSD(0.05)		0.06	0.02	0.09	3.4	2.4	4.1	5.7	181.7	1506	–
Emmer wheat	Dryland + CI	1.89	0.50	0.79	76.6	76.0	22.0	21.2	1524.0	7266.7	21.1
	Dryland	1.62	0.47	0.72	71.5	73.6	20.2	16.2	1047.4	6040.4	18.9
Improved wheat	Dryland + CI	2.58	0.59	0.76	84.6	71.3	35.9	42.0	2935.2	8128.2	36.3
	Dryland	2.27	0.55	0.74	70.7	69.7	22.2	28.2	1222.9	7334.1	17.2
LSD(0.05)		0.05	0.02	0.02	3.0	2.3	3.6	4.9	157.3	1304	5.9

LSD Least significant difference at 0.05 level of probability

† Since the Yavaroos durum wheat was invaded and damaged by the birds at grain dough stage, no valid data were obtained for the grain yield and hence SDM and HI of this genotype

decreased in dryland condition, compared to dryland + CI condition. Some differences were observed in the extent of decreases in different genotypes, leading to the significant interaction. While emmer wheats were generally taller than the improved wheats under both moisture conditions, the opposite was the case for SDM. Grain yield components (i.e. grains/spike and 1000-grains weight) and, hence, grain yield and HI of all examined genotypes of emmer and improved wheats were adversely affected by dryland condition, but negative impact of the dryland condition was more notable for the improved durum and bread wheat genotypes. These attributes were greater in the improved wheats, in general, and under dryland + CI condition, in particular. Emmer wheat genotypes tended to maintain, at least in part, the grain yield and its attributes under dryland condition.

In spite of the notable tendency of the emmer and improved wheats to maintain Chl and Cars concentrations, F_v/F_m, and RWC across the two N supply conditions, increase in the N supply led to contrasting responses of emmer and improved wheats in terms of grains/spike, 1000-grains weight, and grain yield, giving rise to crossover interactions (Table 5). The latter attributes in the improved durum and bread wheats were enhanced by an increase in N supply, but the reverse was true in the emmer wheats. Nonetheless, plant height and SDM (only in Roushan improved bread wheat) of the examined emmer and improved wheat genotypes were increased with the increase in N supply, leading to notable decrease in their HI, in general, and the emmer wheats, in particular.

Chl and Cars concentrations and 1000-grains weight were increased with increase in the N supply under both dryland and dryland + CI conditions (Table 6). Plant height and grain yield were positively affected by the N supply under dryland + CI condition, but the opposite was true under dryland condition. HI was suppressed due to increase in the N supply under both dryland and dryland + CI conditions, but the suppression was more notable under dryland condition.

Table 5 Mean comparisons of genotype × N and wheat group × N interaction effects for chlorophyll a (Chl) and carotenoids (Cars) concentration, maximum efficiency of photosystem II (F_v/F_m), relative water content (RWC), plant height, grains/spike, 1000-grains weight (1000-grains), grain yield, above-ground dry mass (SDM), and harvest index (HI) of emmer and improved wheats in Experiment 2 (conducted at Aligudarz, central-west of Iran)

Genotype	Applied nitrogen (kg ha^{-1})	Chl (mg g^{-1})	Cars (mg g^{-1})	F_v/F_m	RWC (%)	Height (cm)	Grains/spike	1000-grains (g)	Grain yield† (kg ha^{-1})	SDM† (kg ha^{-1})	HI† (%)
Joneghan	30	1.8	0.45	0.77	77.4	73.7	25.0	21.4	1474.6	5605.2	26.8
	100	1.9	0.48	0.77	78.3	74.4	20.8	18.3	1162.9	7396.6	14.9
Shahrekord	30	1.2	0.44	0.76	78.2	74.4	23.0	20.3	1380.4	6537.8	21.1
	100	1.8	0.47	0.78	74.0	74.7	19.3	19.4	1105.0	6527.2	17.0
Zarneh	30	1.4	0.52	0.77	76.0	73.7	21.4	18.6	1338.2	6669.2	20.1
	100	1.5	0.55	0.77	75.5	73.9	20.5	18.0	1087.1	7515.2	14.6
Khoygan	30	1.7	0.46	0.77	64.2	71.9	26.3	18.9	1748.2	5704.4	30.5
	100	1.8	0.50	0.76	61.8	72.9	20.0	18.8	1401.1	7552.9	19.3
Singerd	30	1.8	0.50	0.75	72.6	74.6	20.3	17.5	1217.9	6247.2	18.0
	100	1.9	0.54	0.77	72.4	75.5	20.2	16.8	941.2	6749.7	15.6
Yavaroos	30	2.3	0.56	0.74	81.4	69.0	24.2	32.3	–	–	–
	100	2.5	0.59	0.75	77.6	71.4	25.9	37.0	–	–	–
Roushan	30	2.4	0.56	0.77	77.7	68.9	32.3	29.7	2017.9	6712.7	31.0
	100	2.5	0.60	0.77	74.0	71.5	34.4	41.9	2140.2	8749.7	25.9
LSD(0.05)		0.02	0.06	0.09	3.4	2.4	4.1	5.7	181.7	1506	–
Emmer wheat	30	1.7	0.47	0.76	73.7	73.6	22.2	19.4	1431.9	6152.8	23.7b
	100	1.8	0.51	0.77	72.4	74.3	20.2	18.3	1139.5	7154.2	14.1a
Improved wheat	30	2.4	0.56	0.76	79.5	69.0	28.3	31.0	2017.9	6712.7	31.0d
	100	2.5	0.59	0.76	75.9	71.5	29.3	39.4	2140.2	8749.7	25.9c
LSD(0.05)		0.05	0.02	0.02	3.0	2.3	3.6	4.9	157.3	1304	5.9

LSD least significant difference at 0.05 level of probability

†Since the Yavaroos durum wheat was invaded and damaged by the birds at grain dough stage, no valid data were obtained for the grain yield and hence SDM and HI of this genotype

Table 6 Mean comparisons of irrigation × N interaction effect for plant height, 1000-grains weight (1000-grains), grain yield, N use efficiency of grain (NUE_{grain}), N use efficiency of grain (NUE_{SDM}), and harvest index (HI) of emmer and improved wheats in Experiment 1 (conducted at Isfahan, central Iran) and plant height, 1000-grains weight (1000-grains), grain yield, harvest index (HI), chlorophyll a (Chl) and carotenoids (Cars) concentration of emmer and improved wheats in Experiment 2 (conducted at Aligudarz, central-west of Iran)

Irrigation regime	Applied nitrogen (kg ha^{-1})	Height (cm)	1000-grains (g)	Grain yield (kg ha^{-1})	HI† (%)	NUE_{grain} (kg kg^{-1})	NUE_{SDM} (kg kg^{-1})
Experiment 2 (conducted at Isfahan, central Iran)							
Control	30	108.2	35.6	4263.2	26.2	142.1	534.1
	100	119.3	36.7	4158.1	25.6	41.6	164.8
Drought	30	94.0	32.4	3218.1	28.3	107.3	430.1
	100	89.8	31.9	2365.5	19.2	23.7	131.4
LSD (0.05)		2.8	0.5	476.5	3.7	11.6	46.5
		Height (cm)	1000-grains (g)	Grain yield (kg ha^{-1})	HI† (%)	Chl (mg g^{-1})	Cars (mg g^{-1})
Experiment 3 (conducted at Aligudarz, central-west of Iran)							
Dryland + CI	30	70.2	34.8	2561.1	40.2	2.0	0.58
	100	74.0	49.2	3309.4	39.4	2.2	0.62
Dryland	30	71.4	27.2	1474.7	24.7	1.8	0.54
	100	69.7	29.6	971.0	17.3	1.9	0.57
LSD (0.05)		2.4	5.2	168.2	–	0.06	0.02

dryland + CI dryland + complementary irrigation, *LSD* least significant difference at 0.05 level of probability

†Since the Yavaroos durum wheat was invaded and damaged by the birds at grain dough stage, no valid data were obtained for the grain yield and hence SDM and HI of this genotype

Discussion

Emmer Wheats Primitiveness Reconfirmed

Modern wheat cultivars have been bred for production under chemical-intensive agriculture systems. The drawback of such systems lies in the fact that a high proportion of environmental footprint goes to the mineral fertilizers (Bavec et al., 2011). These high-yielding cultivars have also been defined for particular environmental conditions at the expense of under-utilizing the landraces. However, having experienced all kinds of modifications in climatic conditions of past millennia, wheat landraces are precious genetic resources for meeting the challenges of today's agriculture (Morgounov et al., 2016) and adopting alternative farming systems. From the results of the two field experiments certain core findings on emmer wheat landraces of central Iran are worthy of being highlighted. The first core finding was that the emmer wheats possess an array of traits characteristic to the primitiveness. Tall culms, a great number of infertile tillers, poor spikes bearing a small number of spikelets and scanty grains (data not shown) distinct these wheats from the improved wheats. A great number of non-reproductive tillers could be positive from the stand point of contributing to assimilate accumulation and hence SDM, but it could be negative from the angle that they are competitors for assimilates that otherwise are allocated to reproductive organs (Moragues et al., 2006a). It is unfortunate that potentially valuable traits have been overshadowed by the primitiveness, leading to the present abandoned status of these valuable resources.

Emmer Wheats Invest Nothing much Photoassimilates into the Grain

The second core finding was that these primitive wheats fail to allocate a notable amount of photoassimilates to the reproductive organs. An extended vegetative growth coupled to a shortened grain filling duration, reflected in a 30-days period between anthesis to physiological maturity of emmer wheats (versus 42-days in the improved wheats) was remarkable (data not shown). Low grain yields along with HI of only 15–22% under irrigation conditions of Experiment 1 (conducted at Isfahan, central Iran) (Tables 2, 3) and 14–24% under dryland conditions of Experiment 2 (conducted at Aligudarz, central-west of Iran) (Table 4) in emmer wheats could be seen as evidence for lack of man-oriented selection pressure towards sufficient assimilates allocation to the reproductive organs of these primitive wheats. It is clear that a tendency for a substantially smaller HI in the emmer wheats was driven by, among others, a great number of taller infertile tillers per plant. Our results were in agreement with those of Bavec et al. (2011), where they describe the hulled hexaploid spelt wheat as a lower yielding species compared to bread wheat. Data obtained in the present study agree also to those of Longin et al. (2016), where they found that emmer wheats's grain yield was 55% smaller than the bread wheat. Allocation of smaller portions of photoassimilates to reproductive organs and hence smaller HI's in the less improved taller landraces of durum wheat, compared to semi-dwarf modern cultivars, has been emphasized in the literature (Moragues et al., 2006b). We did not measure stored carbohydrate remobilization, but it has been argued that a higher HI might be related to partitioning of a greater proportion of dry matter to easily remobilizing soluble carbohydrates (Moragues et al., 2006a). The pattern and mechanism of photoassimilates allocation, partitioning, and remobilization of these landraces merits further studies.

Emmer Wheats Tend to Maintain Physiological Functions and Grain Yield Across Different Water Availabilities

The third core finding of the present work was a tendency in the emmer wheats to maintain RWC, proline concentration, SDM and yield components such as spikes/m^2, grains/spike, grains/m^2, 1000-grains weight, and hence grain yield, despite the serious water deprivation imposed in Experiment 1 (conducted at Isfahan, central Iran) and Experiment 2 (conducted at Aligudarz, central-west of Iran) (Table 4). Leaf RWC and water potential are the most widely used measures for representing the water status of a plant (Askari & Ehsanzadeh, 2015). Thus, RWC and water potential are expected to decline in subsequent to the tissue water loss, as it has been the case with the emmer and improved wheats used in our study. Maintaining a higher RWC is, hence, regarded as a reliable criterion for discriminating drought-tolerant plants from the drought-sensitive ones. A sustained capacity in the water-deprived emmer wheat plants to maintain RWC, i.e. across diverse water availabilities (Tables 4 and 6), is an interesting finding of the present work at least from the stand point of our endeavor for exploring drought-tolerant genetic resources. Prevalence of proline among osmolytes that are accumulated in the course of drought and salt stresses has been accepted as an evidence for its pivotal role in adaptive measures of plants of different species (Porcel & Ruiz-Lozano, 2004). Even though proline concentration in the stressed plants of both groups of emmer and improved wheats was increased, but the amount of increase in the emmer wheats was not statistically significant. A tendency of these ancient wheats to maintain RWC and proline concentration in the presence of drought (Table 4) might be interpreted as an evidence for their drought tolerance. We did not attempt measuring root characteristics of these little-known wheats, but the results of a recent study (Abdehpour & Ehsanzadeh, 2019) revealed greater root length and volume for these wheats. We surmise that possession of a deep and extensive root system may have enabled these wheats to obtain sufficient amount of water and hence to avoid water limitation at an extent that lowers cell water and necessitates energetically expensive osmolytes synthesis and accumulation.

Despite the tendency of emmer wheats to maintain (i.e. at least in part) the foregone physiological and agronomic attributes, the Chl concentration and, hence, F_V/F_M of the dryland-grown emmer wheat plants tended to decrease more notably, compared to the improved wheats (Table 4). This could be taken as an evidence for a graver dryland-induced damage to the photosynthetic pigments and, hence, chloroplast's electron transport system of the emmer, compared to the improved wheats. While many environmental stresses may lead to an enhanced Chl degradation, species and varietal differences in the magnitude of the degradation process are expected. Drought not only accelerates Chl degradation, but it also aggravates photoinhibition of the electron transport system, leading to a decreased F_v/F_m (Thomas & Turner, 2001). Unlike the other physiological, growth and grain yield attributes, light absorbing and electron transport components of photosynthesis of emmer wheats appeared to be more vulnerable, compared to the improved wheats, at least against the dryland-induced water limitation.

Environment-driven variations in yield components and, hence, grain yield and SDM is expectedly common in crop plants. Grain yield sensitivity to environmental changes (i.e. coarse regulation) is mainly attributed to grains/m^2 (Marti & Slafer, 2014). Grain size (i.e. 1000-grains weight) is thought to have the smallest plasticity (Slafer et al., 2014), but this attribute still is known to be variable enough to be able to potentiate minor changes and hence fine-tuning of grain yield, at least in cereal crop plants. In the present work, drought-associated decreases in grains/spike, grains/m^2, and 1000-grains weight of the improved wheats were in the range of 15–20% (data not shown) and those of emmer wheats were confined to the 6–10% range in the Experiment 1 (conducted at Isfahan, central Iran). Even though these decreases were more notable in the Experiment 2 (conducted at Aligudarz, central-west of Iran), drought-associated decreases in emmer wheats were consistently smaller than the improved wheats (Tables 2, 4). When wheat is subject to a continuous drought, all grain yield components suffer from the stress (Ozturk & Aydin, 2004). The marked decrease in 1000-grains weight of the improved group of wheats in the present study stems from the fact that the water deprivation in both Experiment 1 (conducted at Isfahan, central Iran) and Experiment 2 (conducted at Aligudarz, central-west of Iran) was aggravated throughout stem elongation to post-anthesis and physiological maturity. While the notion of fine and coarse-tuning of grain yield by 1000-grains weight and grains/m^2, respectively, does not seem to be holding completely true with the examined wheat genotypes, but the extent of depressions in yield components, grain yield and SDM conform, more or less, to the literature. Compatible to our finding, number of spikes in bread wheat (Lyudmila et al., 2009) and number of umbels and grains/umbel in fennel (Askari & Ehsanzadeh, 2015) were decreased as a result of drought stress, indicating that the stress-induced decrease in this yield component is general across different plant species. The 12–17% decreases in the SDM of emmer, in contrary to 23–40% decreases of this attribute in drought-stricken improved wheats, concomitant to 28–30% and 40–58% decreases in grain yield of these two groups of wheat, respectively, are further indications of a strikingly greater tolerance of these ancient wheats to water deprivation, at least within the set of genotypes examined in the present work.

Another finding was the superiority of emmer wheats in terms of some quality attributes, reflected mainly in the grain protein concentration (Table 4). A greater protein concentration of emmer, compared to bread wheat (Longin et al., 2016; Peleg et al., 2008), and drought-associated improvement in grain protein concentration at the expense of carbohydrate synthesis and accumulation (Ozturk & Aydin, 2004) have been reported in the literature. N supply is known to improve wheat grain protein concentration (Mahjourimajd et al., 2016) and it did not come as a surprise that protein concentration of N-supplied plants was encouraged.

Emmer Wheats Non-Responsiveness to Nitrogen Supply

The fourth and probably the most appealing core finding of this study, at least from the environmental and ecological stand points, was a consistent tendency in emmer wheats to turn away from N supply under different environmental conditions of Experiment 1 (conducted at Isfahan, central Iran) and Experiment 2 (conducted at Aligudarz, central-west of Iran), exemplified in reductions in grain yield when exposed to a sufficient amount of N fertilizer (Tables 3 and 5). Modern genotypes of different plant species are bred to exploit resources to meet the goal of increasing quantity and quality of yield and hence they are input-responsive (Ghaouti & Link, 2009). It must be noted that N uptake efficiency in bread wheat cultivars have increased over the course of breeding, leading to increases in NUE of modern cultivars (Muurinen et al., 2006). This reasoning alone may suffice to justify the twofold NUE values in the improved wheats, compared to emmer ones in the present work. In view of the rather negative consequences that N application imposes to the emmer wheat SDM and particularly its grain yield, it is tempting to suggest that this ancient wheat is a valuable asset for organic agricultural production systems. We propose that adopting such less-improved genetic resources is potent to lower the environmental burden caused by fertilizer-responsive improved cultivars. Albeit, applicability and suitability of the examined landraces to organic farming systems warrants further studies.

A Diminished Benefit from Nitrogen Supply Under Low Water Availabilities

Maximal utilization of water and N, by plant, is associated to the availability of each of these resources; WUE is normally enhanced with N supply and NUE decreases with aggravating drought stress, irrespective of level of available N (Pan et al., 2011). Increase in N supply was more beneficial to NUE, grain yield, and certain physiological functions of different wheats in the present study, when they were grown at the absence of drought and dryland conditions (Table 6). Durum wheat grain yield and grain N concentration are known to increase but NUE decreases with increase in N fertilization (Liang et al., 2014) and our data are in line with this established fact, irrespective of wheat type. N use efficiencies have been ranging from 35 kg grain kg^{-1} N in N inefficient to 48 kg grain kg^{-1} N in N-efficient barley genotypes (Anbessa et al., 2009). With increase in water and N supplies, canola was more efficient at accumulating grain biomass per unit grain N and accumulating grain N per unit of available N (Maaz et al., 2016). Our results are, generally, in line with the above reports. Albeit, discrepancies in the amounts of NUE reported in the literature and found in the present study are a reflection of differences in the method of calculating of NUE, whether or not taking into account the background soil N, plant species, and genotype.

According to the foregone discussions, the examined emmer wheats possess several characteristics of interest to those researchers that are seeking to take advantage of promising traits of the abandoned relatives of wheat to tackle the question of ever-increasing reliance on inputs to agricultural of food production. One important finding of the present study was the reconfirmation of primitiveness of the emmer wheats. Another important finding was the maintained superior grain protein concentration of these primitive wheats, despite the failure to allocate a notable amount of photoassimilates to the reproductive organs and, hence, grain yield. The most striking and hence novel finding was a tendency in the emmer wheats to maintain physiological functions, yield components and hence grain yield, despite the serious water and N deprivation.

Conclusions

The low-yielding emmer wheat plants underwent minimal modifications in agronomic traits, grain yield and SDM, despite variations in water and N supplies. Unlike a more or less similar trend of increasing response of SDM, grain yield and NUE to water availability, the two groups of wheat contrasted in response of SDM, grain yield, and in a lesser extent NUE to N supply. The novel finding of the present study was, perhaps, where N-supplied emmer wheat plants had lower grain and SDM relative to N-deprived plants while the reverse was true in the improved wheats. Precise nature of the negative response of emmer wheats to N is not settled at the mechanistic level and, hence, may be taken to manifest a unique characteristic of these little-known wheats needing further studies. Since N supplement is not beneficial to the emmer wheat and supplying crop plants with N fertilizers is costly, in both monetary and environmental standpoints, it seems reasonable if this asset wheat be taken into account as an alternative crop for organic and health food production with minimal ecological footprint.

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Author contributions PE designed the experiments, supervised the research work, and prepared the manuscript. MV conducted the Experiment 1 and collected and analyzed the data. VR conducted the Experiment 2 and collected and analyzed the data.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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