Plant Knowledge Journal
ISSN: 2200-5390
EISSN: 2200-5404
4(1):13-24 (2015)

Southern Cross Publishing Group
AUSTRALIA

The impact of source limitations on yield formation, storage capacity and contribution of stem reserves to the growing grains of modern barley cultivars under post-anthesis water deficiency

Mandana Azhand[1], Mohsen Saeidi[1], Majid Abdoli[2*] and Maryam Khas-Amiri[1]

[1]Department of Agronomy and Plant Breeding, Campus of Agriculture and Natural Recourse, Razi University, Kermanshah, Iran
[2]Department of Agronomy and Plant Breeding, Faculty of Agriculture, Maragheh University, Maragheh, Iran

***Corresponding author: majid.abdoli64@yahoo.com; majid.abdoli64@gmail.com**

Abstract

Drought stress at grain filling is the prominent and inevitable characteristic of arid and semi-arid areas. The objectives of this research were to determine the effect of drought stress and the role of current of assimilates on grain filling, storage capacity and contribution of stem reserves to the growing grains. Therefore, an experiment was carried out in a split-plot factorial arranged in a randomized complete blocks design with three replications during 2010-2011 season cropping cycle in research farm of Razi University in Iran. The moisture regimes were well watered (non-water stress) and drought stressed (post-anthesis water deficiency with withholding of irrigation and continued until physiological maturity). The barley cultivars (*Hordeum vulgare* L.) including Aras, Afzal, Jonub, Reihan, Zarjo, Sararud, Sahra, Fajr-30, Karoun, Gorgan-4, Makuei and Nosrat, also the source manipulation treatments including control, defoliation of flag leaf, defoliation of all leaves except the flag leaf, de-awning and ear shaded were imposed at anthesis. The results showed that, grain yield (GY) was reduced by 20.7% under drought due to 9.8 and 15.3% reduction in thousand grain weight (TGW) and number of grains per spike (NGS), respectively. Under removing of assimilate sources, remobilization of stored material from the stem internodes was increased and these results suggest the compensatory role of different part of stem in preventing yield loss. Drought stress could not increase the remobilization efficiency (RE), but in terms of mentioned traits, there were significant differences between cultivars and different removing photosynthetic sources. Cultivars with longer internodes had greater amounts of photo-assimilates in different parts of the stem and also higher amount of remobilization to the growing grains than in comparison to cultivars with shorter internodes. In both well water and drought stress treatments, the amounts of remobilization from different parts of stem to the growing grains were similar, but under well watered condition due to higher photosynthesis rate compare to drought stress condition, GY was higher.

Keywords: barley; drought stress; grain growth; internode; remobilization.
Abbreviations: GY-grain yield; NGS-number of grains per spike; TGW-thousand grain weight; CO_2-carbon dioxide; RDM-remobilized dry matter; RE-remobilization efficiency; P_n-photosynthesis rate; WUE_p-photosynthetic water use efficiency.

Introduction

The grain filling of cereals depends on carbon from two sources: current assimilation and remobilization of reserves stored in the stem either pre- or post-anthesis (Wardlaw and Willenbrink, 1994). In the Mediterranean climate, during grain filling, occurrence of different biotic and abiotic stress factors such as water deficit decreases current photosynthesis (Blum et al., 1994; Brevedan and Egli, 2003). Under this condition demand rate for utilization of the stem accumulation increases and remobilization of stem reserves is an important supporting process that can largely compensate GY decrease (Palta et al., 1994). Most estimates of the contribution of stem reserves to grain filling are 20-30% of the final grain weight in non-stress conditions (Wardlaw and Willenbrink, 2000; Abdoli et al., 2014). Remobilization of such reserves to the grain is critical for GY if the plants are subjected to water stress (Palta et al., 1994). Tahmasebi (1998) concluded that remobilization of carbohydrates and nitrogen from the aerial organs of wheat and barley grains during filling stage was affected by water stress and remobilization of both elements decreased under in stress. The stress tolerance efficiency of cereals was dependent not only on the assimilation of stem reserves but also on the effective partitioning of these reserves to the grains (Kumar et al., 2006). Farhangi and Ghodsi (2011) reported that under terminal water stress condition, the percentage of storage material remobilization increased compared with the normal condition. There is real source-sink relationship between leaves and development of grains in wheat and barley because healthy grain formation depends upon the potential assimilation of CO_2 and accumulation of photosynthates during grain filling period (Li et al., 2006). Although the lower leaves also supply assimilates to grain, but the detachment of flag leaf considerably influenced the GY (Khaliq et al., 2008). Thus, the flag leaf is the primary source of assimilates for grain filling and GY due to its short distance from the spike and it also stays green for longer time than other leaves (Briggs and Aytenfisu, 1980; Khaliq et al., 2004). Moreover, Gelang et al. (2000) reported that leaf area duration was positive associated with grain weight and grain filling duration. Birsin (2005) reported that removal of flag leaf resulted approximately 13, 34 and 24% reduction in grain weight per spike, NGS and TGW, respectively and

2.8% increase in grain protein contents in both years. Also, removal of all leaves caused a reduction of NGS, TGW and grain weight per main spike by 17.2, 13.3 and 27.9%, respectively (Alam et al., 2008). Saeidi et al. (2012) reported that the photosynthesis of spike and leaves and carbohydrate remobilization from stem made significant contributions to the growing grains about 43, 25 and 32%, respectively. In wheat and barley, all parts of the ear, such as the awn, glume, lemma, palea, pericarp and even peduncle, are capable of photosynthetic CO_2 fixation, and a considerable portion of grain mass derives from the photosynthesis of these organs (Wang et al., 2001; Li et al., 2006; Maydup et al., 2010). Kriedemann (1996) reported that the contribution to assimilation made by ear photosynthesis ranged from 10 to 44%, depending on environmental conditions and genotypes. However, the mechanism of ear contribution to a higher yield is still not clear and remains to be further explored. The interpretation of source manipulation treatments must take into account compensatory mechanisms that may occur in the remaining photosynthetic tissues. There is evidence that when a photosynthetic source is detached, compensations in the remaining organs can occur (Chanishvili et al., 2005). Thus, photosynthetic rate is increased, compensating for the decrease of the photosynthetic area. Abdoli et al. (2014) reported that under removing of assimilate sources; remobilization of stored material from the stem internodes was increased. These results suggest the compensatory role of different part of stem in preventing yield loss. Improving the capacity of grain filling using stem reserves is one of the most important goals of barley and other small grains breeding under abiotic stress such as drought and heat, as well as biotic stress. However, there are genetic differences that affect various aspects of grain filling using stem reserves. This study was carried out to determine the amount of remobilization and translocation of stem reserves in some cultivars of barley under terminal drought stress.

Results and Discussion

Effect of drought stress on grain yield and agronomic traits

The analysis of variance (Table 2) indicated significant main effects for moisture regime, cultivar and source limitation for all the characters examined. The main effect of moisture regimes was significant for GY and its components. The averages of GY and TGW of different cultivars in well watered condition were 1.48 g/spike and 40.8 g respectively, while under drought stress these values significantly reduced to 1.17 g/spike and 36.8 g (Table 2). The GY, NGS and TGW were significantly affected by different barley cultivars. Therefor the maximum and minimum levels of GY and NGS were observed at Reihan and Sararud, respectively (Table 2). Genotypic variation for grain weight per spike was significant under both moisture regimes (Table 3). Under well watered treatment, Aras (1.00±0.18 g/spike) had the lowest and Reihan and Zarjo (1.71±0.36 and 1.68±0.24 g/spike, respectively) had the highest GY (Table 3). But, under post-anthesis drought stress, the lowest and highest significant reductions in GY were seen in Jounb (14.1%) and Sararud (26.4%), respectively. The findings from Shah and Paulsen (2003), when they imposed water deficit at different stages of grain growth separately, showed that significant reduction in GY production in these conditions may be result of reducing the production of photo-assimilates (source limitation) for grain filling, reducing the sink power to absorb of photo-assimilates and reducing the grain filling duration. GY, NGS and TGW were significantly reduced by 20.7, 15.3 and 9.8% due to post-anthesis drought stress, respectively (Table 2). Mirzaei et al. (2011) reported that the stress at grain filling stage is caused to reducing GY due to decreasing TGW. In grain filling stage, photosynthesis materials transferred to grain. Therefore, any deficit water stress in this stage induced thinning and small size of grain. Also, it is suggested that drought stress at grain filling stage decreases TGW (Nesmith and Ritchi, 1992). GY was highly correlated to NGS under well-watered ($r = 0.89$, $P < 0.01$) and droughted ($r = 0.87$, $P < 0.01$) conditions (Table 5).

Effect of source limitation on grain yield and agronomic traits

As shown in Table 4, the interaction effect of cultivars and source limitation on the GY per main spike showed two remarkable results. The Zarjo showed the highest GY under the defoliation of all leaves except the flag leaf and ear shaded treatments, in addition to being the most stable cultivar amongst all the cultivars studied under optimum irrigation and the water deficit conditions (Table 3). On the other hand, the GY for the other cultivars, except for Sararud and Gorgan-4, decreased significantly under the source limitation. Barimavandi et al. (2010) reported that leaves defoliation had significantly effect on GY, rows number on cob, grains number on cob, grain dry weight and cob length in maize. Agronomic traits were reduced as defoliation increased and source restriction and control had the highest GY, TGW and NGS (Table 2). Removing of photosynthetic sources of assimilates reduced GY via grain weight reduction (Table 2). In this case the role of spike photosynthesis in grain filling (27.8%) was higher than the flag leaf (17.3%), lower leaves (24.1%) and awns (22.2%). Kriedemann (1996) and Abdoli et al. (2014) reported that the contribution to assimilation made by ear photosynthesis ranged from 10 to 44%, depending on environmental conditions and genotypes. Foulkes et al. (2007) reported that longer green flag leaf area duration was related with the ability to maintain yield under drought. However, in drought conditions optimum flag leaf area is important for optimum photosynthetic activity as more area causes more transpiration losses (Ali et al., 2009). For source treatments, GY and NGS were reduced significantly under well water and water deficit conditions (Fig. 1). The GY reduction percentage in shaded ear (24.3%) was higher than defoliated and de-awning under well water condition and also, the reduction percentage in shaded ear (32.4%) was higher than defoliated and de-awning under drought stress condition (Fig. 1). In this case, Maydup et al. (2010), Saeidi et al. (2012) and Abdoli et al. (2013) reported that role of photosynthesis spike on the GY is more than photosynthesis of leaves. Also, reduction in leaf area reduces resources for grain filling (Koptur et al., 1996). Ali et al. (2010) reported that flag leaf removal had less effect on yield and related components than awns detachment. Nonetheless the detachment of flag leaf + awns revealed greater effects than individual treatment.

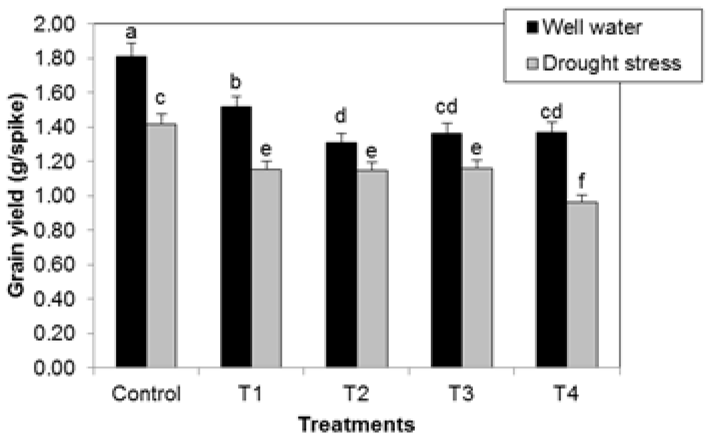
Grain growth and development

There were significant differences among the source limitation for rate and duration of linear grain growth per main spike and final grain yield per spike, and to some extent for length of the initial lag period under well-watered and

Table 1. Minimum and maximum of temperature and relative humidity also total precipitation during growing season.

Month	Average of temperature (°C)		Monthly total of precipitation (mm)	Average of relative humidity (%)	
	Minimum	Maximum		Minimum	Maximum
Oct.	10.6	30.3	1	13.2	46.4
Nov.	4.5	21.9	31	22.8	66.8
Dec.	-1.5	16.8	24	26.5	62.4
Jan.	-2.2	9.6	50	47.1	91.0
Feb.	-2.7	8.0	65	52.1	94.2
Mar.	0.6	15.4	21	28.1	82.0
Apr.	4.5	20.1	47	24.6	78.8
May.	9.5	23.6	128	33.6	87.4
Jun.	12.8	33.8	0	11.3	51.1
Jul.	17.1	38.5	0	6.6	32.1
Aug.	18.1	39.5	0	6.0	27.7
Sep.	13.8	34.6	0	7.8	32.0

Source: Meteorological Office, Iran.



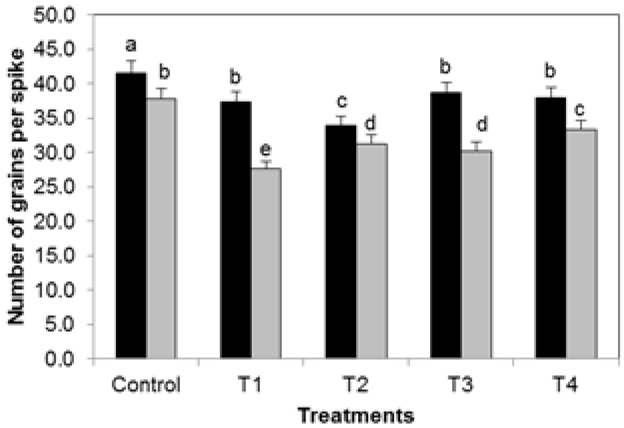


Fig 1. Mean comparison of interactions source limitation and moisture regime treatments on grain yield and number of grains per spike. Vertical bars above means are standard error (SE) of three replicates (n=3). Defoliation of flag leaf (T1), defoliation of all leaves except the flag leaf (T2), de-awning (T3) and ear shaded (T4). All the treatments in both experiments were imposed three-five days after anthesis. Shading of the ear (upper diagram) was made with a perforated aluminum foil. Means followed by the same letters in each column are not significantly different at 5% level, according to Duncan's Multiple Range Test.

under drought conditions (Fig. 2). The dry matter accumulation of grains from control plants followed a typical grain growth curve with a relatively long period in which the grain growth rate was constant (Fig. 2). Duration of linear growth, on average, was 21 days in well watered and 14 days in droughted conditions (Fig. 2). Under well watered and droughted conditions, only control treatment (no source limitation) showed higher rates of linear growth than the average, whereas those of defoliation of all leaves except the flag leaf and de-awning treatments had lower rates (Fig. 2).

Internode weight

Drought stress significantly reduced internode weight, which consequently reduced the weight of main stem (Fig. 3).

Table 2. Analysis of variance and means for grain yield (GY), number of grains per spike (NGS), thousand grain weight (TGW), remobilized dry matter and remobilization efficiency in barley cultivars as affected by source limitation and post-anthesis drought stress.

Treatments	GY (g/spike)	NGS	TGW (g)	Remobilized dry matter (mg)			Remobilization efficiency (%)		
				Peduncle	Penultimate	Lower internodes††	Peduncle	Penultimate	Lower internodes††
Moisture regimes (MR)									
Well water	1.48 a	37.9 a	40.8 a	81 a	73 a	149 a	29.2 a	29.1 a	33.7 a
Drought stress	1.17 b	32.1 b	36.8 b	76 a	67 a	123 a	30.3 a	29.3 a	33.0 a
Cultivars (C)									
Aras	0.92 e	29.1 d	36.3 d	58 fgh	92 a	129 d	30.3 c	40.1 a	33.2 cd
Afzal	1.45 b	36.7 bc	39.2 c	125 a	91 a	130 d	50.9 a	42.4 a	31.4 cde
Jonub	1.33 c	35.2 c	37.0 d	90 c	76 bc	97 f	37.9 b	38.5 a	39.1 b
Reihan	1.54 a	41.3 a	36.1 d	86 cd	69 cd	130 d	27.4 cd	24.5 c	24.4 f
Zarjo	1.57 a	37.2 b	42.4 b	101 b	67 de	159 c	27.8 cd	21.6 c	34.5 bcd
Sararud	0.92 e	21.8 e	45.2 a	91 c	78 b	111 e	39.5 b	33.8 b	48.1 a
Sahra	1.40 bc	36.4 bc	43.4 b	53 h	55 f	116 e	21.9 e	21.9 c	30.5 de
Fajr-30	1.39 bc	37.6 b	35.9 de	64 f	63 def	57 g	23.6 de	29.5 b	25.3 f
Karoun	1.41 bc	40.8 a	34.2 ef	55 gh	56 f	184 b	22.7 e	23.8 c	27.1 ef
Gorgan-4	1.06 d	23.0 e	46.8 a	63 fg	59 ef	152 c	23.6 de	22.7 c	36.1 bc
Makuei	1.45 b	40.6 a	33.6 f	75 e	55 f	136 d	23.8 de	20.9 c	24.7 f
Nosrat	1.43 b	40.0 a	35.5 de	80 de	79 b	227 a	27.6 cd	30.6 b	45.7 a
Source limitation (SL)									
Control	1.62 a	39.7 a	44.0 a	68 d	58 c	115 c	23.7 c	22.3 c	26.9 c
†T1	1.34 b	32.5 d	42.2 b	76 c	69 b	131 b	28.9 b	29.3 b	32.7 b
T2	1.23 c	32.6 d	37.7 c	83 ab	73 ab	146 a	33.3 a	32.1 ab	37.5 a
T3	1.26 c	34.4 c	37.8 c	79 bc	72 ab	140 a	30.0 b	29.3 b	34.1 b
T4	1.17 d	35.6 b	32.3 d	86 a	77 a	146 a	32.8 a	33.0 a	35.5 ab
MR	**	*	*	ns	ns	ns	ns	ns	ns
C	**	**	**	**	**	**	**	**	**
SL	**	**	**	**	**	**	**	**	**
MR×C	*	ns	ns	**	*	**	**	ns	**
MR×SL	**	**	ns	ns	ns	ns	ns	ns	ns
C×SL	**	**	**	**	**	**	**	**	**
MR×C×SL	ns	ns	ns	ns	ns	ns	ns	ns	ns
CV (%)	9.19	7.99	7.04	14.8	18.6	13.3	21.1	23.4	21.9

Means within each column of each category followed by the different letters are significantly different (P < 0.05) according to Duncan test. ns, * and **: Non significant, significant at 5 % and 1 % levels of probability, respectively.†Defoliation of flag leaf (T1), defoliation of all leaves except the flag leaf (T2), de-awning (T3) and ear shaded (T4). All the treatments in both experiments were imposed three-five days after anthesis. Shading of the ear (upper diagram) was made with a perforated aluminum foil.††Internodes below penultimate.

The largest reduction was observed for peduncle followed by penultimate and the lower internodes. Significant variation was found among the source limitation for peduncle, penultimate and the lower internode dry weight (Fig. 3). We measured the decrease of stem (peduncle, penultimate and lower internodes) dry weight between anthesis and the end of grain filling (Fig. 3). Because respiration rate is negligible compared with remobilization (Cruz-Aguado et al., 2000), the change of stem dry weight is a good estimate of the amount of water-soluble carbohydrates translocation during grain filling (Ehdaie et al., 2008). Under well watered condition, peduncle maximum dry weight ranged from 263 mg for defoliation of flag leaf treatment to 300 mg for control treatment. Penultimate internode maximum weight varied from 238 mg for defoliation of all leaves except the flag leaf treatment to 264 mg for control treatment (no source limitation). The lower internodes, which consisted of 2 to 4 internodes, had much greater weight compared with each of the top internodes. Maximum dry weight of the lower internodes ranged from 389 mg for ear shaded treatment to 453 mg for defoliation of flag leaf treatment (Fig. 3). Under drought stressed condition, peduncle maximum weight ranged from 232 mg for defoliation of all leaves except the flag leaf treatment to 267 mg for control treatment. Penultimate internode maximum dry weight varied from 224 mg for control treatment to 241 mg for de-awning treatment. Maximum dry weight of the lower internodes ranged from 374 mg for ear shaded treatment to 398 mg for de-awning treatment (Fig. 3). Barimavandi et al. (2010) reported that leaf defoliation intensity and leaf position affected total dry matter. Maximum weight of the lower internodes, on average, was reached 7 days post-anthesis, whereas those of peduncle and penultimate internode were reached 14 days after anthesis (Fig. 3). After attaining their maximum dry weight, internode weights were progressively decreased over time until maturity. GY was highly correlated to peduncle maximum weight under well-watered ($r = 0.66$, $P < 0.01$) and droughted ($r = 0.71$, $P < 0.05$) conditions. Also, GY was highly correlated to maximum dry weight of the lower internodes under well-watered ($r = 0.44$, $P < 0.05$) and droughted ($r = 0.43$, $P < 0.05$) conditions (Table 5).

Internode length

In order to determinate the effect of post-anthesis drought stress on plants length and genetic variation between cultivars in terms of this traits, average length of all cultivars in both conditions were compared. Post-anthesis drought stress had no significant effect on internodes and total length (data not shown). There were tremendous variations for internodes

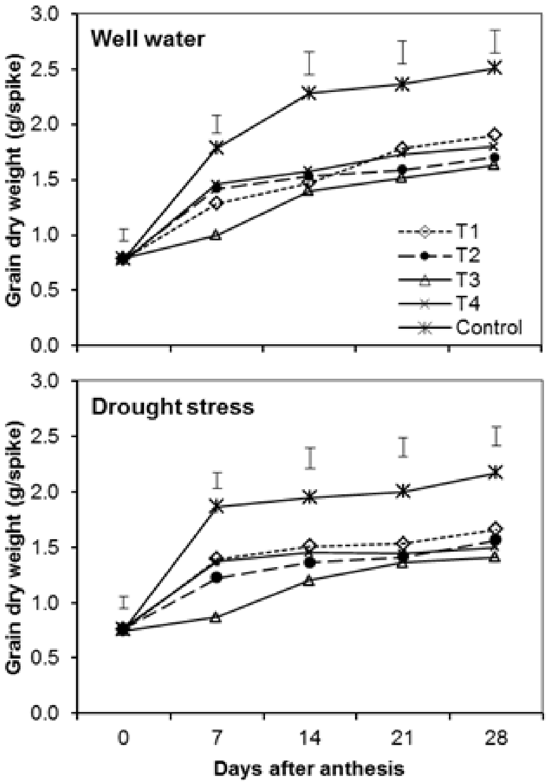


Fig 2. Post-anthesis changes in grain yield in main spike of source limitation treatments along with the means under well watered and droughted field conditions. I: Standard error (SE) of three replicates (n=3). Defoliation of flag leaf (T1), defoliation of all leaves except the flag leaf (T2), de-awning (T3) and ear shaded (T4). All the treatments in both experiments were imposed three-five days after anthesis. Shading of the ear (upper diagram) was made with a perforated aluminum foil.

length among the cultivars, therefor Zarjo had the longest stem (87.5 cm) and Jonub lower stem length (52.6 cm) (Fig. 4). Zarjo had the largest peduncle (38.1 cm), Zarjo and Gorgan-4 the largest penultimate (21.4 and 21 cm, respectively) and Karoun (41.0 cm) the largest lower internodes length (Fig. 4). In contrast, Afzal had the shortest peduncle (19.8 cm) and Jonub the largest penultimate (12.6 cm) length and also Jonub and Fajr-30 the shortest lower internodes length (17.8 and 17 cm, respectively). Such differences between mentioned traits in different wheat cultivars also reported by Moragues et al. (2006), Ehdaie et al. (2008), Sabet et al. (2009), Abdoli et al. (2013) and etc.
Contribution of each component of the stem (peduncle, penultimate and lower internodes) in forming of stem length was different. In tall cultivars such as Zarjo, Makuei and Karoun (the tallest), the peduncle made up 37.7 to 46% of stem length. The penultimate internode in Zarjo, Makuei and Karoun made up only 24.4%, 19.4% and 22.4% and the lower internodes made up 32.1%, 42.9% and 50.3% of the main stem length respectively (Fig. 4). The present findings seem to be consistent with Ehdaie et al. (2006 a) which found these result in other wheat cultivars. Stem length was highly correlated to maximum dry weight of peduncle, penultimate and lower internodes under well-watered (r = 0.51, 0.75 and 0.71, respectively in $P < 0.01$) and droughted (r = 0.53, 0.69 and 0.68, respectively in $P < 0.01$) conditions (Table 5).

Remobilized dry matter

Drought stress could not increase the remobilized dry matter (RDM) and remobilization efficiency (RE), but in terms of mentioned traits, there were significant differences between cultivars and different removing photosynthetic sources (Table 2). In both well watered and drought stress treatments, the amounts of remobilization from different parts of stem to the growing grains were similar. Under well watered condition due to higher photosynthesis rate compare to drought stress condition, GY was higher. It has been demonstrated that under certain and suitable conditions, the stem reserve accumulation can become the main source of adequate carbohydrate storage before the grain filling period, depending on the plant traits improved at the pre-anthesis (Yang et al., 2001; Plaut et al., 2004). Under removing of assimilate sources, remobilization of stored material from the stem internodes was increased (Table 2 and 4). These results suggest the compensatory role of different part of stem in preventing yield loss. Post-anthesis drought stress decreased RDM of peduncle in all cultivars except of Aras, Sahra and Fajr-30, in addition decreased RDM of penultimate in all cultivars except of Jonub, Reihan and Zarjo and also post-anthesis drought stress decreased RDM of lower internodes in all cultivars except of Aras, Afzal and Fajr-30 (Table 3). Cultivars with longer internodes had greater amounts of photo-assimilates in different parts of the stem and also higher amount of remobilization to the growing grains than in comparison to cultivars with shorter internodes (Fig. 4 and Table 3). Several studies have been reported that the contribution of stem remobilization in GY formation depends on genotypes and water regimes and ranges from 10% to 50% (Plaut et al., 2004; Ehdaie et al., 2008). Genotypic variation in main stem reserve accumulation and mobilization for the genotypes used here were reported in detail elsewhere

Table 3. Mean comparison of interactions between barley cultivars and moisture regime treatments on grain yield, remobilized dry matter and remobilization efficiency.

Moisture regimes	Cultivars	Grain yield (g/spike)	Remobilized dry matter (mg)			Remobilization efficiency (%)	
			Peduncle	Penultimate	Lower internodes†	Peduncle	Lower internodes†
Well water	Aras	1.00±0.18 gh	51±19 lm	97±21 a	113±24 hij	26.0±12.2 d	28.2±6.7 fghi
	Afzal	1.61±0.32 ab	130±20 a	96±26 a	127±26 efgh	50.0±8.6 a	28.8±7.2 fghi
	Jonub	1.44±0.16 cd	92±14 de	74±17 cde	103±12 ijk	37.7±8.0 c	40.2±4.0 bcd
	Reihan	1.71±0.36 a	94±13 de	68±13 defgh	147±28 d	28.3±4.8 d	26.7±5.9 ghij
	Zarjo	1.68±0.24 a	107±23 b	62±17 efghi	177±28 c	28.1±6.6 d	37.1±5.8 de
	Sararud	1.06±0.12 g	105±10 bc	87±16 ab	125±22 fgh	43.8±6.6 b	46.0±7.2 ab
	Sahra	1.59±0.16 ab	47±12 m	59±14 fghij	128±26 efgh	17.6±6.0 e	32.0±7.1 efgh
	Fajr-30	1.54±0.28 bc	60±16 jkl	65±15 defgh	49±25 m	22.2±6.8 de	24.3±11.4 ij
	Karoun	1.60±0.33 ab	57±15 jklm	56±16 ghij	252±28 a	21.9±9.5 de	35.0±6.1 def
	Gorgan-4	1.22±0.17 f	65±17 ijk	62±12 efghi	165±17 c	23.2±7.0 de	35.4±5.7 def
	Makuei	1.65±0.28 ab	84±14 efg	63±12 efghi	137±26 def	24.8±5.4 d	23.5±5.8 ij
	Nosrat	1.62±0.24 ab	87±16 def	88±15 ab	260±42 a	27.1±7.6 d	47.0±9.4 ab
Drought stress	Aras	0.85±0.21 ij	66±21 ij	86±16 abc	145±28 de	34.6±11.8 c	38.3±10.2 cde
	Afzal	1.28±0.35 ef	121±16 a	85±22 abc	133±36 defg	51.8±7.5 a	33.9±11.6 defg
	Jonub	1.23±0.26 f	87±16 def	78±21 bcd	92±18 k	38.1±9.4 c	37.9±9.6 cde
	Reihan	1.37±0.28 de	79±18 fgh	70±14 def	113±23 hij	26.5±7.0 d	22.0±3.3 ij
	Zarjo	1.45±0.14 cd	96±18 cd	71±14 def	141±24 def	27.4±6.6 d	31.9±8.7 efgh
	Sararud	0.78±0.14 j	76±21 fghi	69±16 defg	96±15 jk	35.3±9.9 c	50.2±11.5 a
	Sahra	1.20±0.14 f	59±13 jkl	51±11 ij	104±25 ijk	26.3±8.0 d	29.0±9.5 fghi
	Fajr-30	1.25±0.27 f	68±12 hij	62±13 efghi	66±26 l	25.1±7.3 d	26.2±10.5 hij
	Karoun	1.22±0.21 f	54±14 klm	55±13 hij	116±19 ghi	23.4±9.0 de	19.3±5.2 j
	Gorgan-4	0.91±0.15 hi	61±17 jkl	55±10 hij	138±21 def	24.0±7.5 d	36.9±9.1 de
	Makuei	1.26±0.23 ef	66±19 ij	47±9 j	135±27 def	22.7±9.4 de	25.8±7.5 hij
	Nosrat	1.23±0.16 f	73±14 ghi	70±24 def	193±45 b	28.1±8.9 d	44.4±14.2 abc

Means followed by the same letters in each column are not significantly different at 5% level, according to Duncan's Multiple Range Test. Mean ± standard deviation (SD).
†Internodes below penultimate.

(Ehdaie et al., 2006 a,b). Moreover, Saeidi et al. (2012) reported that the water deficiency caused more remobilization of soluble sugars in peduncle and penultimate internodes of resistant cultivars. It was reported that dry matter remobilization to grains is strongly and positively related to sink capacity than source strength (Blum et al., 1994). The interaction effect of cultivar and source limitation with cultivar (Table 4) on the RDM showed that the RDM of peduncle, penultimate and lower internodes increased considerably with the application of source limitation at the post-anthesis for all the cultivars studied. However, the RDM of lower internodes value surprisingly decreased in the Fajr-30 and Gorgan-4 barley cultivars under the ear shaded treatment compared to the other cultivars. Dry matter mobilized of lower internodes in droughted conditions was significantly correlated with the lower internodes maximum dry weight ($r = 0.46$, $P < 0.01$). Also, positive correlations were found between mobilized dry matter of lower internodes and maximum weight for penultimate and lower internodes ($r = 0.54$ and $r = 0.81$, $P < 0.01$, respectively) in well watered conditions (Table 5). The important and considerable role of plant source and sink in the remobilization of the pre-anthesis assimilates to grain is well known and documented and thus an investigation on the effective parameters for improving their capacity during different plant growth and developmental stages can help to increase remobilized carbohydrates (Blum, 1998; Kuhbauch and Thome, 1989). According to Table 2, comparing the effect of source limitation on dry matter of remobilization from stem internodes was significant in 1% level. In our work, GY per spike was partially maintained even when the photosynthetic source was severely reduced (for instance, in defoliated treatments), reinforcing the importance of retranslation of post-anthesis assimilates (Table 2 and 4). The maximum remobilization dry matter from stem internodes was related to defoliation of all leaves except the flag leaf and ear shaded and also the minimum amount was seen in control treatment. Saeidi et al. (2012) reported that the photosynthesis inhibition treatments caused more remobilization of soluble sugars in peduncle and penultimate internodes of resistant cultivars. Also, Janmohammadi et al. (2010) reported that defoliation increased the photosynthesis rate (P_n), photosynthetic water use efficiency (WUE_p) and dry matter remobilization from stem.

Remobilization efficiency

Genotypic variation for remobilization efficiency (RE) of peduncle and lower internodes was significant under both moisture regimes (Table 3). Under well watered treatment, Sahra (17.6%) had the lowest and Afzal and Sararud (50.0% and 43.8%, respectively) had the highest RE of peduncle (Table 3). Also, under post-anthesis drought stress, Makuei (22.7%) had the lowest and Afzal and Jounb (51.8% and 38.1%, respectively) had the highest RE of peduncle (Table 3). The stress tolerance efficiency of cereals was dependent not only on the assimilation of stem reserves but also on the effective partitioning of these reserves to the grains (Kumar et al., 2006). RE of lower internodes ranged from 23.5 (Makuei) to 47% (Nosrat) under well-watered and from 19.3 (Karoun) to 50.2% (Sararud) under droughted conditions. Post-anthesis drought stress decreased RE of lower internodes in all cultivars except of Jonub, Reihan, Zarjo, Sahra, Karoun and Nosrat (Table 3).

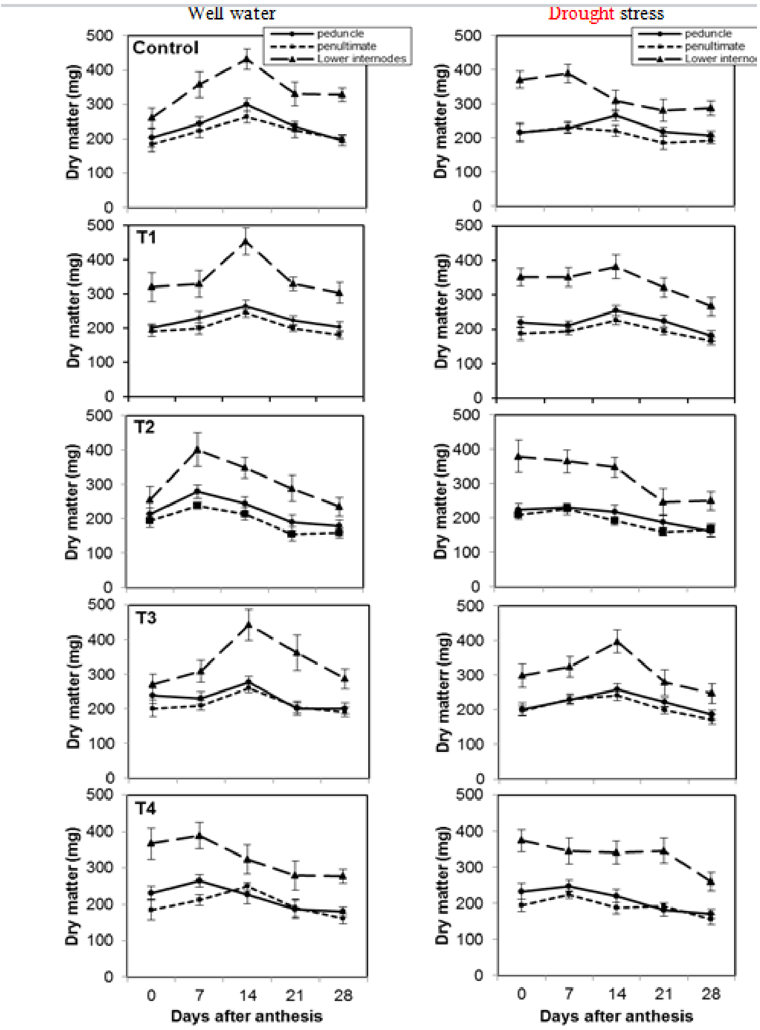


Fig 3. Dry weight changes of peduncle, penultimate and lower internodes during grain filling of source limitation treatments under well water and post-anthesis drought stress. Defoliation of flag leaf (T1), defoliation of all leaves except the flag leaf (T2), de-awning (T3) and ear shaded (T4). Bars represent means ± standard error (SE).

Materials and Methods

Plant material and treatments

The present study was conducted during 2010-2011 season cropping cycle in the field research of Razi University in Kermanshah state in the west of Iran (47° 9′ E and 34° 21′ N), 1319 meters above sea level. The research was conducted on a field where the previous crop was a corn. The soil is a clay loam (36.1% clay and 30.7% silt) and the experiment was laid out in a split plot factorial design arranged in a randomized complete blocks with three replications. Factors evaluated were moisture regimes (two levels), barley cultivars (twelve levels) and source limitation (five levels). Moisture regimes as the main-plot factor included: irrigation in all stages of plant growth and post-anthesis drought stress with withholding of irrigation. Tested cultivars were different improved barley cultivars included: Aras, Afzal, Jonub, Reihan, Zarjo, Sararud, Sahra, Fajr-30, Karoun, Gorgan-4, Makuei and Nosrat and also, source limitation treatments including: control, defoliation of flag leaf, defoliation of all leaves except the flag leaf, de-awning and ear shaded as sub-plot were considered. Shading of the ear (upper diagram) was made with a perforated aluminum foil. In order to prevent the accumulation of ethylene and to allow for convective heat flux, several holes were made in the aluminum foil covers (Maydup et al., 2010). Date of anthesis was determined from middle rows in each plot when 50% of the spikes had extruded anthers (Ehdaie et al., 2006 a). Each plot included 6 rows 20 cm apart, 3 meter long, 3 and 1 meter distances were taken between test plots and replicates, respectively. Seeds were sown at a density of 400 seeds m^{-2} on 12th October 2010. Humidity and moderate temperatures during the crop season is presented in Table 1.

Internode weight and remobilization content

In each plot, 30 to 40 main tillers from the two middle rows next to the guard rows were tagged as spikes emerged from the flag leaf sheaths. Three main tillers were harvested at random at anthesis and at seven days intervals after anthesis until maturity. The main tillers were harvested from the soil surface. After each harvest, leaf blades were removed and main tillers were immediately dried in a forced-air drier at 70 ^{o}C for 48 h. Then, each main tiller was divided into spike and stem; then leaf sheaths were removed from the stem. Each stem was divided into three segments, namely peduncle (first internode below the spike including the distal node), penultimate internode (the internode below the peduncle

Table 4. Mean comparison of interactions between barley cultivars and source limitation treatments on agronomic traits, remobilized dry matter and remobilization efficiency.

Treatments	Aras	Afzal	Jonub	Reihan	Zarjo	Sararud	Sahra	Fajr-30	Karoun	Gorgan-4	Makuei	Nosrat
Grain yield (g/spike)												
Control	1.15±0.22 n-t	1.90±0.24 ab	1.60±0.04 d-f	2.01±0.32 a	1.86±0.29 ab	1.05±0.23 r-w	1.57±0.26 d-g	1.86±0.23 ab	1.73±0.36 b-d	1.21±0.20 m-s	1.81±0.25 bc	1.63±0.38 c-f
†T1	1.02±0.13 s-w	1.60±0.19 d-f	1.46±0.19 e-l	1.50±0.22 e-j	1.50±0.18 e-j	0.94±0.19 u-x	1.33±0.37 i-n	1.33±0.21i-n	1.44±0.22 f-l	0.98±0.39 t-x	1.52±0.19 e-i	1.44±0.38 f-l
T2	0.94±0.01 u-x	1.52±0.08 e-i	1.11±0.15 o-u	1.35±0.17 i-n	1.51±0.14 e-i	0.85±0.14 w-y	1.36±0.16 h-n	1.21±0.07 m-s	1.16±0.05 m-t	1.01±0.07 s-w	1.46±0.37 e-l	1.28±0.19 l-p
T3	0.72±0.07 y	1.15±0.18 n-t	1.27±0.19 l-q	1.66±0.22 c-e	1.50±0.07 e-j	0.89±0.14 v-y	1.35±0.10 i-n	1.26±0.24 l-q	1.56±0.36 d-h	1.04±0.13 r-w	1.27±0.13 l-q	1.49±0.17 e-k
T4	0.79±0.18 xy	1.07±0.34 q-v	1.23±0.24 m-r	1.20±0.26 m-s	1.45±0.19 f-l	0.86±0.26 w-y	1.37±0.33 g-m	1.30±0.22 j-o	1.17±0.23 m-t	1.09±0.22 p-v	1.20±0.31 m-s	1.29±0.20 k-p
Number of grains per spike												
Control	33.0±0.8 l-p	42.8±1.8 c-f	39.3±2.6 e-j	47.3±2.0 ab	41.1±3.5 c-h	26.0±2.9 r-u	42.1±8.7 c-g	42.8±2.8 c-f	47.5±3.9 a	25.3±1.3 s-v	44.7±2.7 a-c	44.4±3.5 a-d
T1	26.4±6.2 q-u	35.7±5.5 i-l	36.2±5.6 i-l	41.2±6.1 c-h	34.4±5.6 k-o	21.2±5.8 v-x	30.7±7.1 n-q	33.0±4.5 l-p	36.7±4.2 h-l	19.4±7.5 x	36.5±5.4 h-l	38.4±8.0 f-k
T2	28.7±0.1 p-s	37.3±5.0 h-l	28.0±2.8 q-t	34.4±4.5 k-o	38.3±4.1 f-k	20.2±0.8 wx	30.8±5.5 n-q	34.8±0.5 j-n	36.1±2.0 i-l	23.0±1.5 u-x	42.9±2.9 b-f	37.1±0.3 h-l
T3	26.5±3.0 q-u	29.9±6.4 o-r	37.3±5.1 h-l	43.8±6.5 a-e	37.2±3.5 h-l	19.3±4.0 x	37.1±3.9 h-l	38.3±6.8 f-k	43.8±6.2 a-e	23.4±7.5 u-x	36.6±8.3 h-l	40.2±4.4 c-i
T4	30.9±5.9 m-q	37.6±5.3 g-l	35.4±1.9 i-m	39.9±4.5 d-i	34.8±3.4 j-n	22.1±2.2 u-x	41.2±2.8 c-h	39.4±3.7 e-j	40.0±5.8 c-i	24.1±0.7 t-w	42.3±1.5 c-g	40.0±4.5 c-i
Thousand grain weight (g)												
Control	42.6±3.3 e-l	46.4±2.2 b-e	40.6±2.6 h-n	41.4±2.6 g-n	46.1±2.1 b-f	51.7±1.4 a	48.2±7.6 a-d	39.6±5.2 i-p	38.6±2.6 j-q	51.2±4.4 a	41.2±2.6 g-n	40.4±6.2 h-n
T1	40.5±0.7 h-n	41.7±1.8 f-m	40.1±1.2 i-n	38.1±1.2 l-q	45.0±3.2 c-h	49.5±2.6 ab	43.1±3.3 e-j	41.3±4.9 g-n	37.3±4.4 m-r	48.8±4.3 a-c	42.9±4.1 e-k	37.9±1.6 l-r
T2	37.5±3.8 m-r	38.6±2.1 j-q	38.0±6.7 l-r	34.4±3.2 q-v	40.0±4.2 i-n	42.4±3.1 e-l	46.9±1.9 b-e	34.5±1.2 q-v	32.2±2.9 t-x	44.1±4.1 d-i	29.3±5.5 w-z	35.0±3.6 p-v
T3	35.3±3.4 o-u	36.7±3.2 n-t	32.2±2.3 t-x	38.2±1.2 k-q	41.3±2.0 g-n	45.7±2.9 b-g	41.3±0.7 g-n	33.4±2.6 r-w	37.5±7.8 m-r	43.5±6.9 e-i	31.4±2.9 u-x	37.0±2.9 m-s
T4	25.4±2.2 z	32.6±4.9 s-x	34.3±3.4 q-v	28.4±5.4 x-z	39.8±1.4 i-o	36.7±3.1 n-t	37.6±3.8 m-r	30.7±3.0 v-y	25.5±1.9 z	46.3±3.2 b-e	23.3±1.1 z	27.0±0.6 yz
Remobilized dry matter of peduncle (mg)												
Control	42±8 v-x	130±11ab	73±19 j-r	74±14 j-q	79±7 g-o	74±26 j-q	41±9 wx	55±10 q-x	54±9 q-x	41±9 wx	72±20 k-r	79±6 g-o
T1	48±20 u-x	108±16 cd	101±4 c-f	84±11 f-n	114±16 bc	92±17 d-k	55±18 q-x	58±13 p-x	50±10 t-x	59±14 o-x	75±17 i-p	70±12 m-s
T2	60±28 o-w	134±9 a	98±7 c-g	84±24 f-n	94±7 d-i	97±19 c-h	52±7 s-x	79±13 g-o	72±15 k-r	83±11 f-n	53±13 r-x	96±16 c-h
T3	66±15 n-u	128±29 ab	81±10 g-n	85±11 e-n	93±8 d-j	102±11 c-f	69±8 m-t	73±6 j-r	40±6 x	71±8 l-s	84±4 f-n	65±13 n-u
T4	77±17 h-p	127±14 ab	96±9 c-h	104±13 c-e	128±19 ab	88±31 e-m	48±12 u-x	55±13 q-x	61±9 o-v	59±8 o-x	93±9 d-j	91±8 d-l
Remobilized dry matter of penultimate (mg)												
Control	65±13 f-m	80±25 b-i	58±11 i-m	62±9 g-m	51±13 k-m	66±11 f-m	47±6 m	54±9 k-m	54±10 k-m	50±10 lm	53±12 k-m	64±13 f-m
T1	86±12 b-f	110±17 a	67±12 f-m	72±13 e-l	70±11 f-m	70±16 f-m	68±14 f-m	57±14 j-m	50±13 lm	57±8 j-m	59±16 h-m	68±16 f-m
T2	99±8 a-c	78±17 b-j	93±13 a-e	60±11 h-m	56±13 j-m	81±10 b-h	56±13 j-m	77±10 c-j	72±8 e-l	59±10 h-m	53±18 k-m	98±13 a-c
T3	98±10 a-c	85±19 b-f	83±19 b-g	64±7 f-m	74±12 d-k	96±12 a-d	58±9 i-m	64±14 f-m	48±13 m	69±10 f-m	54±9 k-m	67±23 f-m
T4	111±15 a	100±33 ab	80±19 b-i	86±11 b-f	83±11 b-g	81±28 b-h	48±15 m	65±11 f-m	57±15 j-m	60±15 h-m	56±16 j-m	98±13 a-c

Table 4. Continued

Treatments	Aras	Afzal	Jonub	Reihan	Zarjo	Sararud	Sahra	Fajr-30	Karoun	Gorgan-4	Makuei	Nosrat
Remobilized dry matter of lower internodes (mg)												
Control	95±17.0 s-v	102±18 q-v	89±24 uv	118±28 m-u	138±30 i-p	93±20 t-v	81±15 vw	41±16 xy	163±74 f-i	141±26 i-o	122±19 l-t	201±40 b-d
†T1	125±32 l-s	108±18 p-v	95±12 s-v	113±15 o-u	152±17 g-l	115±32 n-u	132±11 j-q	62±20 wx	181±66 d-g	166±18 f-i	110±14 o-v	218±44 b
T2	127±32 k-r	128±22 k-r	99±14 r-v	146±22 h-n	151±24 g-l	111±13 o-v	129±11 l-r	93±17 t-v	210±98 b-c	165±13 f-i	126±16 l-s	266±15 a
T3	148±15 h-m	168±14 e-i	101±16 q-v	117±30 m-u	195±28 b-e	110±23 o-v	116±27 n-u	62±15 wx	173±81 d-h	148±24 h-m	160±9 f-j	183±52 c-f
T4	151±23 g-l	146±27 h-n	103±14 q-v	157±37 f-k	160±35 f-j	124±27 l-t	124±36 l-t	31±8.0 y	195±82 b-e	138±27 i-p	164±14 f-i	266±68 a
Remobilization efficiency of peduncle (%)												
Control	20.0±3.5 s-w	50.9±8.0 ab	29.7±6.0 i-t	22.0±4.7 n-w	22.0±5.2 n-w	27.4±8.4 j-u	15.1±6.1 w	18.5±3.7 u-w	18.1±6.2 u-w	15.4±4.8 w	20.5±4.7 r-w	24.7±3.5 k-w
T1	22.7±9.8 m-w	45.6±11 a-e	44.4±6.7 a-e	28.4±5.5 j-u	31.3±6.8 g-r	42.8±7.3 b-f	24.2±9.5 l-w	21.0±7.7 p-w	19.0±7.5 t-w	23.3±7.0 l-w	21.7±7.2 o-w	23.3±5.5 l-w
T2	32.9±17 f-n	54.2±8.8 a	41.8±9.0 b-g	27.1±6.6 j-v	24.8±5.6 k-w	46.2±5.6 a-d	20.9±7.2 q-w	32.0±7.4 g-p	35.4±5.8 e-k	31.8±5.8 g-q	16.1±6.1 vw	37.1±7.0 d-j
T3	35.3±9.7 e-k	53.5±8.0 a	32.0±6.0 g-p	26.5±2.4 j-v	27.2±1.9 j-u	41.1±2.9 b-g	30.1±6.3 h-s	27.1±1.7 j-v	14.7±2.7 w	25.0±3.1 k-w	28.2±4.7 j-u	19.2±3.0 s-w
T4	40.6±9.6 b-h	50.6±3.8 a-c	41.6±5.0 b-g	33.1±6.0 f-m	33.7±5.9 f-l	40.2±10 c-i	19.4±6.2 s-w	19.7±2.3 s-w	26.4±3.1 j-v	22.5±4.3 m-w	32.4±2.3 f-o	33.8±2.8 f-l
Remobilization efficiency of penultimate (%)												
Control	26.9±6.4 g-o	33.1±14 d-k	26.1±6.0 h-o	19.9±4.4 l-o	15.9±6.5 o	25.4±1.8 h-o	16.9±1.8 o	22.6±5.4 i-o	21.7±5.2 i-o	18.7±3.7 m-o	18.7±4.1 m-o	21.5±8.3 j-o
T1	40.7±1.6 a-f	51.9±6.5 a	32.0±1.8 d-l	27.1±4.4 g-o	22.2±2.9 i-o	31.7±2.4 d-l	30.4±3.0 e-m	24.6±3.1 i-o	21.0±3.2 l-o	22.7±1.3 i-o	22.0±2.9 i-o	25.1±2.7 i-o
T2	40.7±2.9 a-f	36.9±7.9 d-h	50.9±6.0 ab	20.7±5.3 l-o	17.6±4.2 no	38.3±3.4 c-g	21.4±4.1 j-o	39.9±3.8 b-f	33.4±2.1 d-j	24.0±5.3 i-o	19.3±5.9 m-o	42.2±5.6 a-e
T3	43.4±4.4 a-d	40.8±8.9 a-f	42.1±13 a-e	21.3±3.8 k-o	24.5±6.6 i-o	40.7±5.6 a-f	22.0±5.3 i-o	30.6±8.3 e-m	18.9±8.1 m-o	25.0±4.2 i-o	21.0±1.8 l-o	21.7±6.2 i-o
T4	48.8±7.0 a-c	49.5±17 a-c	41.5±11 a-e	33.6±9.1 d-i	27.7±9.6 g-o	33.1±10 d-k	18.7±8.3 m-o	29.6±8.9 f-n	24.2±8.7 i-o	23.2±8.4 i-o	23.4±7.8 i-o	42.7±11 a-d
Remobilization efficiency of lower internodes (%)												
Control	23.8±5.6 k-r	23.5±6.1 k-r	33.6±9.0 f-n	22.1±3.8 m-r	28.0±4.5 i-q	35.7±8.1 e-l	19.6±5.2 o-r	17.1±5.3 qr	23.8±9.6 k-r	36.3±9.4 e-k	21.1±6.6 n-r	38.4±12 d-j
T1	31.7±11 f-p	26.1±7.0 j-q	38.5±3.0 d-j	21.3±3.7 n-r	35.7±3.6 e-l	43.4±7.0 d-f	37.2±3.7 e-j	27.3±4.8 i-q	26.7±7.6 i-q	43.1±5.9 d-f	19.3±1.6 p-r	42.5±9.6 d-g
T2	33.3±13 f-n	29.9±8.2 g-p	41.4±8.6 d-h	26.7±4.4 i-q	32.2±7.0 f-o	64.2±27 a	33.3±5.9 f-n	41.3±5.9 d-h	32.1±13 f-p	37.4±8.8 e-j	23.1±7.3 l-r	54.9±9.6 a-c
T3	38.5±5.7 d-j	39.2±4.7 d-i	38.1±6.7 d-j	22.1±4.4 m-r	42.3±5.1 d-g	46.9±3.2 b-e	31.6±5.8 f-p	27.5±2.5 i-q	24.2±9.8 k-r	33.9±4.2 f-n	28.0±2.2 i-q	37.2±7.1 e-j
T4	39.0±7.3 d-j	38.1±13 d-j	43.9±6.4 c-f	29.7±5.8 g-q	34.4±11 e-m	50.4±8.8 b-d	31.0±9.9 f-p	13.4±2.2 r	29.0±11 h-q	30.0±2.7 g-p	31.8±5.8 f-p	55.6±8.6 ab

†Defoliation of flag leaf (T1), defoliation of all leaves except the flag leaf (T2), de-awning (T3) and ear shaded (T4). All the treatments in both experiments were imposed three-five days after anthesis. Shading of the ear (upper diagram) was made with a perforated aluminum foil.Means followed by the same letters in each column are not significantly different at 5% level, according to Duncan's Multiple Range Test. Mean ± standard deviation (SD).Mark dashes between the letters (-), represents other letters between them and is sorted alphabetically.

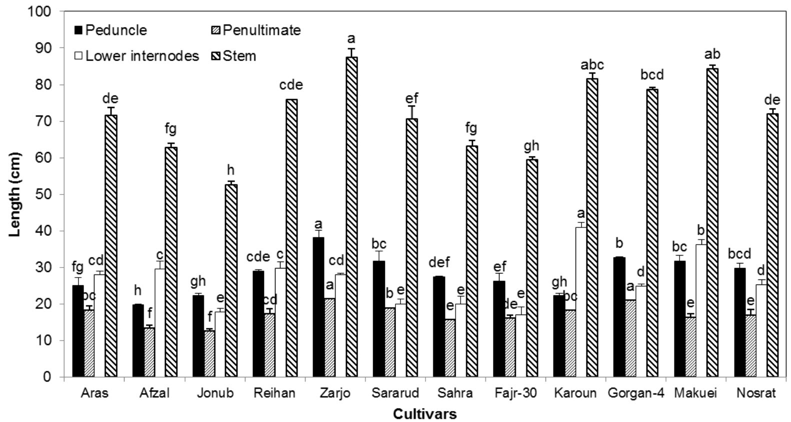


Fig 4. Length (cm) of peduncle, penultimate, lower internodes and stem in different barley cultivars. Means followed by the same letters in each column are not significantly different at 5% level, according to Duncan's Multiple Range Test. Vertical bars above means are standard error (SE).

Table 5. Correlation coefficients grain yield, remobilized dry matter and remobilization efficiency in barley cultivars under water and drought stress after anthesis.

Traits	Condition	GY	NGS	TGW	Mped	Mpen	Moth	RDMped	RDMpen	RDMoth	REped	REpen	REoth
NGS	Well water	0.89**	1										
	Drought	0.87**	1										
TGW	Well water	-0.39	-0.68**	1									
	Drought	-0.35	-0.73**	1									
Mped	Well water	0.66**	0.42*	-0.13	1								
	Drought	0.71*	0.48*	-0.03	1								
Mpen	Well water	0.37	0.22	0.12	0.74**	1							
	Drought	0.42*	0.20	0.22	0.80**	1							
Moth	Well water	0.44*	0.49*	-0.31	0.43*	0.56**	1						
	Drought	0.43*	0.56**	-0.43*	0.37	0.49*	1						
RDMped	Well water	0.24	0.01	-0.24	0.30	0.15	-0.06	1					
	Drought	0.35	0.13	0.15	0.19	-0.03	-0.16	1					
RDMpen	Well water	-0.41*	-0.31	-0.07	-0.43*	-0.28	-0.25	0.38	1				
	Drought	-0.08	-0.12	0.01	-0.21	-0.20	-0.26	0.56**	1				
RDMoth	Well water	0.28	0.27	-0.12	0.35	0.54**	0.81**	0.02	-0.11	1			
	Drought	0.01	0.07	-0.03	0.14	0.36	0.46*	0.07	0.17	1			
REped	Well water	-0.17	-0.29	0.11	-0.28	-0.29	-0.31	0.83**	0.61**	-0.18	1		
	Drought	-0.09	-0.14	0.12	-0.40*	-0.51	-0.36	0.82**	0.35**	-0.01	1		
REpen	Well water	-0.44*	-0.30	-0.11	-0.64**	-0.67**	-0.45*	0.27	0.90**	-0.34	0.63**	1	
	Drought	-0.23	-0.17	-0.09	-0.51*	-0.62**	-0.46*	0.49*	0.88**	-0.04	0.76**	1	
REoth	Well water	-0.27	-0.35	0.32	-0.03	0.16	-0.07	0.24	0.20	0.50*	0.29	0.05	1
	Drought	-0.56**	-0.60**	0.44*	-0.36	-0.29	-0.61**	0.19	0.43*	0.37	0.39	0.49*	1
Lplant	Well water	0.14	0.06	-0.04	0.51*	0.75**	0.71**	-0.03	-0.24	0.51*	-0.33	-0.53**	-0.12
	Drought	0.11	0.04	0.13	0.53**	0.69**	0.68**	-0.15	-0.32	0.45*	-0.46*	-0.25	-0.24

Grain yield (GY), Number of grains per spike (NGS), Thousand grain weight (TGW), Maximum dry weight of peduncle (Mped), penultimate (Mpen) and lower internodes (Moth), Remobilized dry matter of peduncle (RDMped), penultimate (RDMpen) and lower internodes (RDMoth), Remobilization efficiency of peduncle (REped), penultimate (REpen) and lower internodes (REoth), Length of plant (Lplant). * and **: significant at 5 % and 1 % levels of probability, respectively.

including the distal node) and the lower internodes. The weight of each segment was measured. The magnitude of mobilized reserves in each internode segment was determined based on post-anthesis changes in internode dry weight (Ehdaie et al., 2006 a, b). Remobilization efficiency of dry matter in each internode segment was estimated by the proportion (%) of mobilized dry matter relative to post-anthesis maximum weight of that segment (Ehdaie et al., 2006 a). An approximate standard deviation for mobilization efficiency was determined by assuming the numerator and denominator are independent. In this case, the estimates will be conservative since the numerator (amount of mobilized dry matter) and the denominator (post-anthesis maximum weight) are positively correlated.

Grain yield and agronomy traits

At economical maturity, grain weight spike, number of grains per spike, thousand grain weight and plant height in each treatment in 20 plants randomly selected and measurements were calculated.

Statistical analysis

Statistical analyses were performed using EXCEL software (ver. 10) and SAS software (ver. 9.0). Mean comparisons were also performed using Duncan test at % 5 level (Steel et al., 1997). Figures were generated by using EXCEL software (ver. 10).

Conclusions

These findings further support the idea that increasing of carbohydrates remobilization from different part of stem does not necessarily increase grain yield production or grain yield stability under variable environments. Higher values of carbohydrates remobilization from different parts of stem that were coincident with lower grain yield in this research showed that may be more respiratory losses of remobilized carbohydrates or more movement of remobilized carbohydrates to the alternative sinks such as young developing tillers and roots in such cultivars may be the main reasons for these results. So, we should be followed barley cultivars with remobilization of the greater amount of carbohydrates from different part of stems to the growing grains. These cultivars have advantages for the various environmental conditions.

Acknowledgements

The authors would like to thank their colleagues in Agricultural and Natural Resource, university of Razi, Kermanshah, Iran.

References

Abdoli M, Saeidi M, Jalali-Honarmand S, Kazemi-Gavar H, Heidari A, Hashemzade H (2013) The role of current photosynthesis on grain yield formation, some agronomic characteristics and germination traits in two bread wheat cultivars under terminal drought stress condition. Int J Agri Crop Sci. 5(14): 1585-1594.

Abdoli M, Saeidi M, Jalali-Honarmand S, Mansourifar S, Ghobadi ME (2014) Evaluation of effect water deficiency and source limitation at the post anthesis on grain yield and remobilization of dry matter in bread wheat cultivars. Environ Stress Crop Sci. 7(2): 137-154.

Abdoli M, Saeidi M, Jalali-Honarmand S, Mansourifar S, Ghobadi ME (2013) Effect of post-anthesis water deficiency on storage capacity and contribution of stem reserves to the growing grains of wheat cultivars. Plant Knowledge J. 2(3): 99-107.

Alam MS, Rahman AHMM, Nesa MN, Khan SK, Siddquie NA (2008) Effect of source and/or sink restriction on the grain yield in wheat. J Appl Sci Res. 4(3): 258-261.

Ali MA, Hussain M, Khan MI, Ali Z, Zulkiffal M, Anwar J, Sabir W, Zeeshan M (2010) Source-sink relationship between photosynthetic organs and grain yield attributes during grain filling stage in spring wheat (*Triticum aestivum*). Int J Agric Biol. 12: 509-515.

Ali MA, Niaz S, Abbas A, Sabirv W, Jabran K (2009) Genetic diversity and assessment of drought tolerant sorghum landraces based on morph-physiological traits at different growth stages. Plant Omics. 2: 214-227.

Barimavandi AR, Sedaghathoor S, Ansari R (2010) Effect of different defoliation treatments on yield and yield components in maize (*Zea mays* L.) cultivar of S.C704. Aust J Crop Sci. 4(1): 9-15.

Birsin MA (2005) Effects of removal of some photosynthetic structures on some yield components in wheat. Tarim Bill Dergi. 11(4): 364-367.

Blum A (1998) Improving wheat grain filling under stress by stem reserve mobilization. Euphytica. 100: 77-83.

Blum A, Sinmena J, Mayer G, Shpiler L (1994) Stem reserve mobilization supports wheat grain filling under heat stress. Aust J Plant Physiol. 21: 771-781.

Brevedan RE, Egli DB (2003) Short periods of water stress during seed filling, leaf senescence and yield of soybean. Crop Sci. 43: 2083-2088.

Briggs KG, Aytenfisu A (1980) Relationship between morphological characters above the flag leaf node and grain yield in spring wheat. Crop Sci. 20: 350-354.

Chanishvili G, Badridze S, Barblishvili TF, Dolidze MD (2005) Defoliation, photosynthetic rates, and assimilates transport in grapevine plants. Russ J Plant Physiol. 52: 448-453.

Cruz-Aguado JA, Rodés R, Pérez IP, Dorado M (2000) Morphological characteristics and yield components associated with accumulation and loss of dry mass in the internodes of wheat. Field Crops Res. 66: 129-139.

Ehdaie B, Alloush GA, Madore MA, Waines JG (2006 a) Genotypic variation for stem reserves and mobilization in wheat I. Post anthesis changes in internode dry matter. Crop Sci. 46: 735-746.

Ehdaie B, Alloush GA, Madore MA, Waines JG (2006 b) Genotypic variation for stem reserves and mobilization in wheat: II. Post anthesis changes in internode water-soluble carbohydrate. Crop Sci. 46: 2093-2103.

Ehdaie B, Alloush GA, Waines JG (2008) Genotypic variation in linear rate of grain growth and contribution of stem reserves to grain yield in wheat. Field Crops Res. 106: 34-43.

Farhangi S, Ghodsi M (2011) The contribution of remobilization of storage materials in wheat yield as affected by potassium iodide (KI). Int J Plant Physiol Biochem. 3(3): 60-63.

Foulkes MJ, Sylvester-Bradley R, Weightman R, Snape JW (2007) Identifying physiological traits associated with improved drought resistance in winter wheat. Field Crops Res. 103: 11-24.

Gelang J, Pleijel H, Sild E, Danielsson H, Younis S, Selldén G (2000) Rate and duration of grain filling in relation to flag leaf senescence and grain yield in spring wheat

(*Triticum aestivum* L.) exposed to different concentrations of ozone. Plant Physiol. 110: 366-375.

Janmohammadi M, Ahmadi A, Pustini K (2010) Effect of leaf area reduction and nitrogen application on stomatal characteristics of flag leaf and grain yield of wheat under deficit irrigation. Elec J Crop Prod. 3(4): 177-194.

Khaliq I, Irshad A, Ahsan M (2008) Awns and flag leaf contribution towards grain yield in spring wheat (*Triticum aestivum* L.). Cer Res Commun. 36: 65-76.

Khaliq I, Parveen N, Chowdhry MA (2004) Correlation and path coefficient analyses in bread wheat. Int J Agric Biol. 6: 633-635.

Koptur S, Smith CL, Lawton JH (1996) Effects of artificial defoliation on reproductive allocation in the common vetch *Vicia sativa* (fabaceae; papilionoideae). Amer J Bot. 83(7): 886-889.

Kriedemann P (1996) The photosynthetic activity of the wheat ear. Ann Bot. 30: 349-363.

Kuhbauch W, Thome U (1989) Nonstructural carbohydrates of wheat stems as influenced by sinksource manipulations. Plant Physiol. 134: 243-250.

Kumar R, Sarawgi AK, Ramos C, Amarante ST, Ismail AM, Wade LJ (2006) Partitioning of dry matter during drought stress in rainfed lowland rice. Field Crops Res. 98(1): 1-11.

Li X, Wang H, Li H, Zhang L, Teng N, Lin Q, Wang J, Kuang T, Li Z, Li B, Zhang A, Lin J (2006) Awns play a dominant role in carbohydrate production during the grain-filling stages in wheat (*Triticum aestivum*). Plant Physiol. 127: 701-709.

Maydup ML, Antonietta M, Guiamet JJ, Graciano C, López JR, Tambussi EA (2010) The contribution of ear photosynthesis to grain filling in bread wheat (*Triticum aestivum* L.). Field Crops Res. 119: 48-58.

Mirzaei A, Naseri R, Soleimani R (2011) Response of different growth stages of wheat to moisture tension in a semiarid land. World Appl Sci J. 12(1): 83-89.

Moragues M, García-Moral LF, Moralejo M, Royo C (2006) Yield formation strategies of durum wheat landraces with distinct pattern of dispersal within the Mediterranean basin. II. Biomass production and allocation. Field Crop Res. 95: 182-193.

Nesmith DS, Ritchi JT (1992) Short and long term response of corn to a pre-anthesis soil water deficit. Agron J. 84: 107-113.

Palta JA, Kobata T, Turner NC, Fillery IR (1994) Remobilization of carbon and nitrogen in wheat as influenced by post-anthesis water deficits. Crop Sci. 34: 118-124.

Plaut Z, Butow BJ, Blumenthal CS, Wrigley CW (2004) Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. Field Crops Res. 86: 185-198.

Sabet M, Aynehband A, Moezzi A (2009) Genotype and N rates effect on dry matter accumulation and mobilization in wheat (*Triticum aestivum* L.) in sub-tropical conditions. Bulg J Agric Sci. 15: 514-527.

Saeidi M, Moradi F, Jalali-Honarmand S (2012) The effect of post anthesis source limitation treatments on wheat cultivars under water deficit. Aust J Crop Sci. 6(7): 1179-1187.

Shah NH, Paulsen GM (2003) Interaction of drought and high temperature on photosynthesis and grain-filling of wheat. Plant Soil J. 257: 219-226.

Steel RGD, Torrie JH, Dicky DA (1997) Principles and procedures of Statistics, A biometrical approach. 3rd edn. McGraw Hill, Inc. Book Co. N.Y. (USA). pp. 352-358.

Tahmasebi SZ (1998) A review on the dry matter remobilization and protein in wheat and barley cultivars under water stress conditions. 5th Iranian Crop Science Congress, Karaj, pp. 122-123.

Wang ZM, Wei AL, Zheng DM (2001) Photosynthetic characteristics of non-leaf organs of winter wheat cultivars differing in ear type and their relationship with grain mass per ear. Photosy. 39: 239-244.

Wardlaw IF, Willenbrink J (1994) Carbohydrate storage and mobilization by the culm of wheat between heading and grain maturity: the relation to sucrose synthase and sucrose-phosphate synthase. Aust J Plant Physiol. 21; 255-271.

Wardlaw IF, Willenbrink J (2000) Mobilization of fructan reserves and changes in enzymes activities in wheat stems correlate with water stress during kernel filling. New Phytol. 148: 413-422.

Yang JC, Zhang JH, Wang ZQ, Zhu QS (2001) Activities of starch hydrolytic enzymes and sucrose-phosphate synthase in the stems of rice subjected to water stress during grain filling. J Exp Bot. 52: 2169-2179.