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Photosynthetic material remobilization and its contribution to barley yield

Abstract – The objective of this work was to evaluate the effect of seed rate, genetics, and environmental conditions on the remobilization of stored material from vegetative organs, as well as the contribution of this material to barley (*Hordeum vulgare*) grain yield. The experiment was carried out in a factorial randomized complete block design with four replicates, in the city of Gonbad Kavous, Iran, in 2016–2017 and 2017–2018 crop seasons. Two factors were evaluated: four seed rates (200, 300, 400, and 500 seed per square meters) and four barley genotypes ('Fardan', 'Khorram', 'Mahoor', and 'Sahra'). Material remobilization with an increasing seed rate per square meter contributed to barley grain yield, especially in the first year, when rainfall was lower. The highest and lowest contribution of remobilization to barley grain yield are related to the penultimate leaf and the flag leaf, respectively. In both years, 'Khorram' and 'Mahoor' genotypes show the highest and the lowest rates for reduction in grain yield, respectively, due to the increased seed rate per square meter.

Index terms: *Hordeum vulgare*, environmental conditions, flag leaf, peduncle.

Remobilização de material fotossintético e sua contribuição para a produtividade de cevada

Resumo – O objetivo deste trabalho foi avaliar o efeito da taxa de sementes, da genética e das condições ambientais sobre a remobilização de material armazenado de órgãos vegetativos, bem como a contribuição desse material para a produtividade de grãos de cevada (*Hordeum vulgare*). O experimento foi realizado em delineamento fatorial de blocos ao acaso, com quatro repetições, na cidade de Gonbad Kavous, Irã, nas safras de 2016–2017 e 2017–2018. Foram avaliados dois fatores: quatro taxas de sementes (200, 300, 400 e 500 sementes por metro quadrado) e quatro genótipos de cevada ('Fardan', 'Khorram', 'Mahoor' e 'Sahra'). A remobilização do material, com o aumento da proporção de sementes por metro quadrado, contribuiu para a produtividade de grãos de genótipos de cevada, principalmente no primeiro ano, quando a precipitação foi menor. A maior e a menor contribuição da remobilização para a produtividade de grãos de cevada estão relacionadas à penúltima folha e à folha-bandeira, respectivamente. Em ambos os anos, os genótipos 'Khorram' e 'Mahoor' apresentam a maior e a menor taxa de redução da produtividade de grãos, respectivamente, em razão do aumento da proporção de sementes por metro quadrado.

Termos para indexação: *Hordeum vulgare*, condições ambientais, folha-bandeira, pedúnculo.

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Introduction

Barley (*Hordeum vulgare* L.) is one of the most important cereals in Iran and in the world. In arid and semiarid regions of some developing countries, it is the only cereal and essential food source (Nuttall et al., 2017; Ahakpaz et al., 2021). The area under cultivation and production of barley in the world and Iran were 48 and 1.5 million hectares in 2018, respectively, and its production was 141.4 and 8.2 tons, respectively (FAO, 2019).

Seed rate is one of the main factors determining the ability of crops to gain resources and also the most important factor of crop management in barley yield, therefore, in sustainable production, the appropriate choice of seed rate is essential (Nandi et al., 2018). Because endosperm cell filling begins about two weeks after pollination, and so far strong sinks for photosynthetic material may have not been activated yet, the excess current photosynthetic material of the leaves accumulates in the stem (Ma et al., 2014). Then, in the later stages of growth, which usually begins 2–3 weeks after flowering, this excess is transferred to the seed; this process is called remobilization (Netanos & Koutroubas, 2002). In general, some sources are mentioned for the accumulation of minerals in the grain (carbon, nitrogen, etc.), which includes current leaf photosynthesis after pollination, remobilization of stored nonstructural materials in vegetative organs before pollination (Dordas, 2012), and spike photosynthesis after pollination (Azhand et al., 2015). In barley, current photosynthesis in green tissues (mainly flag leaves) and remobilization of stored material absorbed from sinks (mainly stems and leaves sheath) are carbon sources for grain filling (McIntyre et al., 2012; Biswal & Kohli, 2013).

In cereals, the flag leaf is the main source of carbohydrate production, and its contribution to photosynthetic products is 50 to 60% (Balkan et al., 2011), so that the removal of flag leaves in wheat genotypes results in a reduction of approximately 25% of grain weight per spike (Adams et al., 2018). The accumulation and remobilization of soluble stem carbohydrates determine physiological traits that strongly affect the yield potential in drought stress (Li et al., 2020). Thus, under drought stress conditions, the remobilization contribution can vary before and after pollination (Zhang et al., 2015). The remobilization contribution of accumulated material to spring barley grain yield before flowering was reported to be between 4% and 24% (Pržulj et al., 2014). The peduncle (the internode that connects to spike) and the penultimate leaf play a very important role in determining the grain yield (Scofield et al., 2009; Abdoli et al., 2016). In plants under severe stress, the lower internodes are more efficient at material remobilization than the upper internodes (Ma et al., 2014). In a study on barley, the authors found that with each unit increase of seed rate resulted in the increase of both the amount of storage material remobilization and the contribution of remobilization to grain yield (Soleimani Abiyat et al., 2015).

The objective of this work was to evaluate the effect of seed rate, genetics (genotypes), and environmental conditions (intraspecific competition and drought) on the storage material remobilization and the contribution of material remobilization to barley grain yield.

Materials and Methods

The experiment was carried out in the research farm of Gonbad-Kavous University (37°16'N, 55°12'E), Gonbad Kavous, Iran, during the 2016–2017 and 2017–2018 crop years. A comparison of meteorological data of the experimental periods and 10-year long-term show that minimum average temperature was 5.7°C and 7°C for the experimental periods of 2016–2017 and 2017–2018, respectively, which was less in the first year and a little more in the second year than 10-year long-term statistics (6.9°C). Average maximum temperature of the experimental periods in 2016–2017 and 2017–2018 was 18.4°C and 19°C, respectively, that in both years was more than the average of 10-year long-term statistics (17.9°C). Rainfall in the experimental periods of 2016–2017 and 2017–2018 was 238.8 and 271.5 mm (Figure 1 A). Additionally, in most months of the second year, the relative humidity was higher than in the first year. In both years, the amount of radiation followed a similar trend and was nearly identical, but the amount of radiation in the second year, in February, March, and April was less than in the first year, due to cloudier days (Figure 1 B).

The experiment was carried out in a randomized complete block design as a factorial, with four replicates, under rainfed conditions, without nutrient limitations, and as pest, disease, and weed control. The cultivar factor consisted of four cultivars 'Fardan' (two rows), 'Khorram' (two rows), 'Mahoor' (two-row) and 'Sahra' (six rows), and the seed rate factor consisted of four seed quantities (200, 300, 400 and 500 seed m^{-2}). The studied traits included material remobilization and its contribution to grain yield, from flag leaf, penultimate leaf, peduncle (first internode), penultimate (second internode), and grain yield.

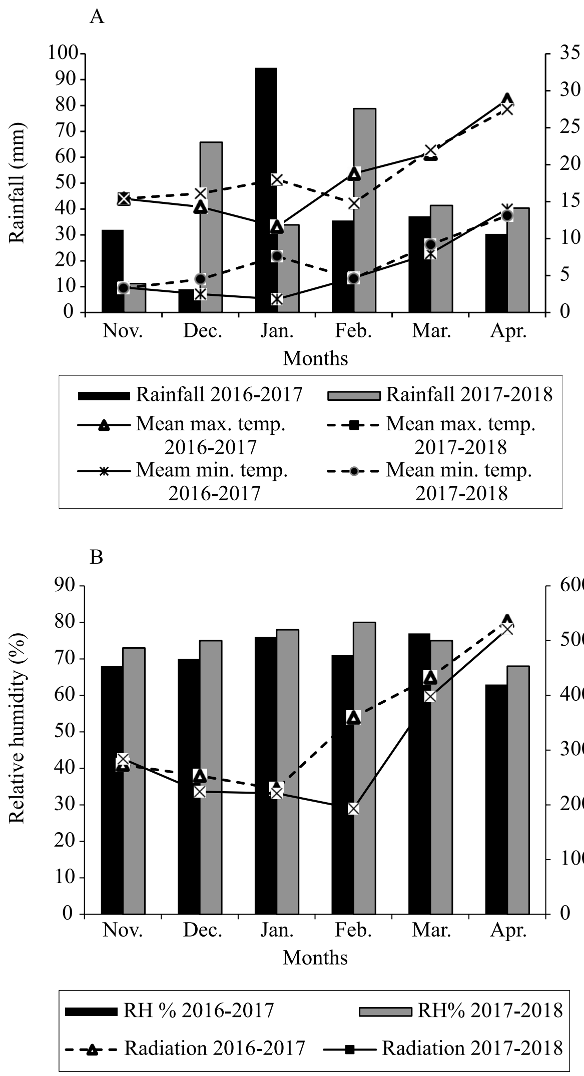

Figure 1. Monthly meteorological data of the experimental area 2016-2017 and 2017-2018 crop seasons: A, rainfall and temperature; and B, radiation and relative humidity. Gonbad Kavous, Iran.

The soil classification is silty clay loam. The land was prepared by plowing and disking, in the autumn of each year (November). The use of chemical fertilizers based on soil test results (Table 1) included: 50 kg ha^{-1} P_2O_5 from triple superphosphate source, and 75 kg ha^{-1} N from urea source. Before the last disking, all phosphate and one third of urea fertilizer were added to the soil as a base, and the rest of urea fertilizer was added by hand spraying in two stages of tillering and stemming. Sown was performed by hand in each experimental plot, in eight planting lines of 4 m length and 20 cm row spacing. The distance between replicates was 1 m, and the distance between plots was 60 cm. Seed were provided by the Golestan Agricultural and Natural Resources Research and Education Center. In both experimental years, weed control was carried out chemically, using pinoxaden and triasulforon + dicamba herbicides with 1.3 L ha^{-1} and 165 g ha^{-1} at the tillering stage of barley (Zadoks=21), according with Zadocks et al. (1974). To control barley diseases (spot blotch and barley stripe), iprodione+ carbendazim were used (in a ratio of two per thousand) in two stages: at the second node emergence in the stem (Zadoks=32), and at booting stage (Zadoks=45). To control Lema larvae, mospilan (at a dose of 300 g ha^{-1}) was used in the heading stage (Zadoks=55). The experiment was carried out in rainfed conditions.

In order to investigate the rate of storage material remobilization in flag leaves and penultimate leaf, peduncle (first internode), and penultimate (second internode), and the remobilization contribution to grain yield, five days after pollination, 5 plants were sampled from each plot and the flag leaf, penultimate leaf, peduncle and penultimate of main stem were placed separately in the oven, at 75°C for 48 hours, and their dry weight was recorded. Then, in the

Table 1. Physical and chemical soil properties at 0–30 cm soil depth in the experimental site, in Gonbad Kavous, Iran.

Year	OC (%)	TNV (%)	pH	EC (ds m^{-1})	Total N (%)	P_{ava} (ppm)	K_{ava} (ppm)	Clay (g kg^{-1})	Silt (g kg^{-1})	Sand (g kg^{-1})
2016–2017	1.29	9.5	7.5	0.94	0.13	9.2	807	180	700	120
2017–2018	0.68	9.8	7.9	1.19	0.12	13.4	356	150	640	210

OC, organic carbon; TNV, total neutralizing value; EC, electrical conductivity; P_{ava}, available phosphorus; K_{ava}, available potassium.

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physiological maturation stage, after separating the main stem seed, the above-mentioned operation was repeated. Calculations were conducted using the following equations (Dordas, 2012): Photosynthetic remobilization of each organ (g m^{-2}) = maximum dry weight after pollination - maximum dry weight after pollination and Material remobilization contribution in yield = (photosynthetic material remobilization / grain yield) ×100.

The traits were analyzed using the SAS, version 9.4, software (SAS Institute Inc., Cary, NC, USA). Because this investigation was carried out during two growing seasons, Levene's homogeneity test was conducted and it was significant, explaining why each season was evaluated separately. Moreover, since the treatments were cultivar (qualitative) and seed density (quantitative), for each trait at the cultivar level, regression was obtained from seed density and means were compared using the upper and lower limits of the 95% confidence interval.

Results and Discussion

The analysis of variance results in two years of experiment showed that the storage material remobilization and the contribution of material remobilization from studied organs to grain yield were affected by the simple effects of seed rate, cultivar, and the interaction of them at 1% probability (Table 2). The significance of interaction effects of seed rate on cultivar for the studied traits may indicate a different or identical response of barley genotypes to seed rate, therefore, regression analysis and a simple linear equation (y=a+bx) were used to better justify the relationships.

Barley grain yield of the studied genotypes was affected by simple factor effects of cultivar and density, and their interactions at 1% probability (Table 3). Therefore, the regression analysis was used to further investigation of these effects and the relationships between them and grain yield, since the simple linear regression equation showed the best fit from the data and it was able to justify these relationships to a large extent, according to the coefficients of determination. The results showed that in all barley cultivars, grain yield decreased for each unit of seed consumption increased, in both years, but it was different in two years, as in the first year it was less than the second year (Table 3).

Table 2. Analysis of variance of the remobilization and tthe contribution of remobilization to grain yield of barley (*Hordeum vulgare*) genotypes, at different seed rates (200, 300, 400, and 500 seed m^{-2}), in the 2016–2017 and 2017–2018 crop seasons, in Gonbad Kavous, Iran.

Source of variation	DF	Mean square								
		FLR	PLR	PR	PNR	FLRC	PLRC	PRC	PNRC	GY
2016–2017 crop season										
Block	2	1.78^{ns}	12.38^{ns}	4.29^{ns}	5.86^{ns}	0.15^{ns}	0.59^{ns}	0.26^{ns}	0.04^{ns}	2097.93^{ns}
Seed rate (D)	3	187.81**	1424.91**	561.33**	561.33**	9.89**	82.16**	253.69**	237.4**	1081.81**
Cultivar (C)	3	24.96**	69.25**	131.21**	1733.67**	40.26**	54.87**	496.99**	395.52**	13885.5**
D×C	9	100.65**	253.59**	1049.48**	1423.9**	20.0**	89.54**	368.41**	306.17**	6683.96**
Error	30	32.62	116.73	705.97	547.53	3.69	15.95	53.59	33.59	66020.22
CV (%)		17.44	14.5	14.49	12.32	16.87	15.39	11.35	8.77	10.81
2017–2018 crop season										
Block	2	1.87^{ns}	30.52**	15.65^{ns}	16.47^{ns}	0.26^{ns}	1.93*	1.33^{ns}	2.2^{ns}	2770.14^{ns}
Seed rate (D)	3	568.72**	730.49**	2022.25**	4440.04**	12.37**	13.79**	78.34**	78.86**	31963.31**
Cultivar (C)	3	621.67**	556.31**	682.78**	110.08**	8.83**	19.23**	149.79**	115.0**	27879.85**
D×C	9	362.96**	311.84**	1501.03**	3429.54**	14.24**	26.93**	136.51**	288.9**	12293.68**
Error	30	52.08	58.7	93.481	215.61	4.11	7.65	11.79	21.34	99180.89
CV (%)		13.1	9.5	11.51	15.58	14.01	12.31	13.7	17.24	11.81

*, **Significant at 5% and 1% probability, respectively. ^{ns}Nonsignificant. DF, degree of freedom; FLR, remobilization from the flag leaf (g m^{-2}); PLR, remobilization from the penultimate leaf (g m^{-2}); PR, remobilization from the peduncle (g m^{-2}); PNR, remobilization from the penultimate (g m^{-2}); FLRC, contribution of remobilization from the flag leaf to grain yield (%); PLRC, contribution of remobilization from penultimate leaf to grain yield (%); PRC, contribution of remobilization from the peduncle to grain yield (%); PNRC, contribution of remobilization from penultimate to grain yield (%); GY, grain yield (g m^{-2}).

In both years, 'Khorram' and 'Mahoor' genotypes had the highest and lowest rate of grain yield reduction, respectively, because of the increase of seed rate m^{-2}. In the first year, there was no significant difference between genotypes; while the results were different in the second year, and a significant difference was observed only between 'Khorram' and the other genotypes; thus, the genotypes were divided into two distinct groups (Table 3).

The linear relationship between the material remobilization from flag leaves and seed rate in m^2 was positive and significant. This equation with the determination coefficient of 91–72% and 90–98%, in the first and second years, respectively, was able to justify the relationship between this trait and the seed rate consumption, very good (Table 3). In other words, with the increasing of each unit of seed m^{-2}, the material remobilization rate from flag leaf increased between 0.015 to 0.033 and 0.021 to 0.036 g m^{-2}, in the first and the second crop year, respectively. Significant differences were observed between the studied genotypes in both years. 'Khorram', in the first year, and 'Sahra', in the second year, were the best cultivars for material remobilization rate from flag leaf.

The study of the relationship between the material remobilization contribution from flag leaf to grain yield, with the amount of seed consumed m^{-2} showed that in both years, a significant difference occurred between treatments (Table 3). The regression line slope was positive in both years. The contribution of material remobilization from flag leaf to grain yield with 0.012% of increase for each seed unit consumption m^{-2} was the highest in 'Sahra', but had no significant difference for 'Khorram' cultivar. The lowest value was recorded for 'Mahoor' with 0.001% m^{-2}, but the behavior of the genotypes in the second year was different from that of the first year, as 'Fardan', with 0.007%, had the highest increase, and 'Mahoor' and 'Sahra' genotypes, with 0.003%, had the lowest increase rate in material remobilization and contribution to grain yield, due to the increase of each seed unit used m^{-2} (Table 3).

The linear regression equation was able to justify the relationships between the material remobilization from penultimate leaf and seed rate m^{-2} with the determination coefficient above 84%, in both years of experiment. The slope of this line was positive for both years, and the rate of this line for the increase of each seed unit consumption m^{-2} was from 0.042 to 0.062 and from 0.036 to 0.57 g m^{-2}, for the first and the second crop year, respectively. There was no significant difference between treatments in the first year; however, in the second year, some treatments showed significant differences. The material remobilization from the penultimate leaf showed the most increase for 'Khorram' and 'Mahor' (in the first and second year, respectively), and the least increase for 'Sahra' in both years (Table 3).

The contribution of material remobilization from penultimate leaf to grain yield was between 0.01 to 0.02 for the increase of each seed unit consumption m^{-2}, in the first year as the highest and lowest rates were related to 'Khorram' and 'Sahra', respectively. In the second year, there was still an increasing trend in this trait, but with less slope, as different genotypes were in the range from 0.003 to 0.013%. The highest and lowest contribution of material remobilization to grain yield were obtained from 'Khorram' and 'Sahra' genotypes, in both years (Table 3).

The linear regression slope from the fitting of the material remobilization trait from peduncle with seed rate m^{-2} was positive and showed a high determination coefficient. The regression line coefficient that indicates the material remobilization rate for increase of seed unit m^{-2} was between 0.086 to 0.015 g m^{-2}, in the first year, and between 0.045 to 0.099 g m^{-2}, in the second year. The highest and the lowest rate of increase were related to 'Mahoor' and 'Sahra' genotypes, in the first year, respectively, and to 'Khorram' and 'Fardan' genotypes, in the second year (Table 3).

The determination coefficient of the linear relationship of material remobilization contribution from peduncle to barley genotypes grain yield, with seed consumption rate m^{-2}, was high in both years, being from 73 to 93% in the first year, and from 80 to 98% in the second year, which can justify the relationship between this trait and the amount of seed consumed m^{-2}. The slope of this line was between 0.021 and 0.062% and 0.008 to 0.023%, for the first and second year, respectively, which indicates the increase of the contribution of remobilization from the peduncle to grain yield per unit increase of seed rate m^{-2}. In the first year, the highest and lowest values were obtained from 'Mahoor' and 'Fardan' genotypes, respectively, while in the second year such values were observed in 'Khorram' and 'Fardan' genotypes, respectively. In

Table 3. Equation coefficients (y= a+bx) of the remobilization and the contribution of remobilization to grain yield of barley (*Hordeum vulgare*) genotypes, at different seed rates (200, 300, 400, and 500 seed m^{-2}), in the 2016–2017 and 2017–2018 crop seasons, in Gonbad Kavous, Iran.

Year	Cultivar	Character	n	a ± se	b ± se	R²
2016–2017	Fardan	Yield	4	420±44	-0.24±0.12	0.84*
	Khorram		4	498±75	-0.44±0.2	0.85*
	Mahoor		4	443±37	-0.14±0.1	0.75*
	Sahra		4	401±13	-0.15±0.03	0.94*
	Fardan	Remobilization from the flag leaf	4	-3.41±1.58	0.019±0.004	0.90**
	Khorram		4	-3.4±2.96	0.033±0.008	0.90**
	Mahoor		4	0.7±0.78	0.009±0.002	0.91**
	Sahra		4	2.32±0.6	0.015±0.001	0.98**
	Fardan	Contribution of remobilization from the flag leaf to grain yield	4	-0.79±0.45	0.006±0.001	0.91**
	Khorram		4	0.33±0.64	0.008±0.00	0.91**
	Mahoor		4	1.66±0.25	0.001±0.00	0.72**
	Sahra		4	-0.16±1.59	0.012±0.004	0.80**
	Fardan	Remobilization from the penultimate leaf	4	-3.11±2.02	0.045±0.005	0.97**
	Khorram		4	-2.65±4.01	0.049±0.01	0.91**
	Mahoor		4	-7.01±6.78	0.062±0.018	0.85**
	Sahra		4	-4.92±3.05	0.042±0.008	0.93**
	Fardan	Contribution of remobilization from penultimate leaf to grain yield	4	-0.92±0.96	0.017±0.002	0.96**
	Khorram		4	-1.58±1.51	0.02±0.004	0.92**
	Mahoor		4	1.48±1.63	0.017±0.004	0.88**
	Sahra		4	1.34±0.98	0.01±0.002	0.88**
2017–2018	Fardan	Yield	4	429±52	-0.15±0.14	0.69*
	Khorram		4	699±59	-0.77±0.16	0.96*
	Mahoor		4	502±44	-0.15±0.12	0.73*
	Sahra		4	449±12	-0.17±0.03	0.96*
	Fardan	Remobilization from the flag leaf	4	-3.09±2.84	0.034±0.007	0.91**
	Khorram		4	-1.61±1.55	0.029±0.004	0.96**
	Mahoor		4	-2.7±2.42	0.021±0.006	0.84**
	Sahra		4	0.23±2.05	0.036±0.005	0.96**
	Fardan	Contribution of remobilization from the flag leaf to grain yield	4	0.82±0.22	0.007±0.00	0.98**
	Khorram		4	1.12±0.32	0.006±0.00	0.96**
	Mahoor		4	0.46±0.75	0.003±0.002	0.60**
	Sahra		4	2±0.16	0.003±0.00	0.90**
	Fardan	Remobilization from the penultimate leaf	4	-3.7±5.24	0.046±0.014	0.84**
	Khorram		4	-6.45±2.63	0.057±0.007	0.97**
	Mahoor		4	-6.47±2.2	0.043±0.006	0.96**
	Sahra		4	1.14±1.1	0.036±0.003	0.99**
	Fardan	Contribution of remobilization from the penultimate leaf to grain yield	4	2.38±0.9	0.005±0.002	0.69**
	Khorram		4	0.87±1.37	0.013±0.004	0.86**
	Mahoor		4	0.56±0.84	0.007±0.002	0.84**
	Sahra		4	2.05±0.25	0.003±0.00	0.92**

Continuation...

Table 3. Continuation...

Year	Cultivar	Character	n	a ± se	b ± se	R^2
2016–2017	Fardan	Remobilization from the peduncle	4	-1.48±1.12	0.093±0.003	0.99**
	Khorram		4	3.54±3.89	0.1±0.01	0.98**
	Mahoor		4	-13.43±11.32	0.15±0.031	0.92**
	Sahra		4	2.59±6.45	0.086±0.017	0.92**
	Fardan	Contribution of remobilization from the peduncle to grain yield	4	5.63±2.79	0.021±0.007	0.79**
	Khorram		4	4.89±5.27	0.033±0.014	0.73**
	Mahoor		4	1.01±4.51	0.062±0.012	0.93**
	Sahra		4	6.89±3.67	0.028±0.01	0.79**
	Fardan	Remobilization from the penultimate	4	-0.32±6.58	0.096±0.018	0.93**
	Khorram		4	-13.35±4.34	0.124±0.012	0.98**
	Mahoor		4	-11.65±7.21	0.613±0.02	0.96**
	Sahra		4	1.53±4.93	0.069±0.013	0.93**
	Fardan	Contribution of remobilization from the penultimate to grain yield	4	6.14±1.15	0.023±0.003	0.96**
	Khorram		4	-1.56±2.02	0.044±0.005	0.97**
	Mahoor		4	-2.14±2.71	0.064±0.007	0.97**
	Sahra		4	5.85±4.23	0.023±0.011	0.67**
2017–2018	Fardan	Remobilization from the peduncle	4	-3.94±7.62	0.045±0.021	0.70**
	Khorram		4	-11.92±8.38	0.099±0.022	0.90**
	Mahoor		4	-10.66±6.49	0.083±0.018	0.92**
	Sahra		4	-12.43±7.77	0.078±0.021	0.87**
	Fardan	Contribution of remobilization from the peduncle to grain yield	4	0.64±0.5	0.008±0.001	0.95**
	Khorram		4	0.68±0.74	0.023±0.002	0.98**
	Mahoor		4	1.38±1.82	0.014±0.005	0.80**
	Sahra		4	-0.66±0.42	0.012±0.001	0.98**
	Fardan	Remobilization from the penultimate	4	-16.13±8.88	0.107±0.024	0.91**
	Khorram		4	-24.45±6.7	0.127±0.018	0.96**
	Mahoor		4	-10.59±4.68	0.096±0.013	0.97**
	Sahra		4	-16.5±5.78	0.098±0.016	0.95**
	Fardan	Contribution of remobilization from the penultimate to grain yield	4	-0.1±1.44	0.02±0.004	0.93**
	Khorram		4	-5.13±2.5	0.037±0.007	0.94**
	Mahoor		4	5.29±1.46	0.01±0.004	0.75**
	Sahra		4	-0.31±0.23	0.011±0.00	0.99**

*, ** Significant at 5% and 1% probability, respectively; n, number of samples; a and b, intercept and slope in the linear regression, respectively; R^2, coefficient of determination.

both years, no significant differences were observed between most genotypes (Table 3).

The distribution diagram of storage material remobilization data from the penultimate and its contribution to grain yield for seed rate m^{-2} showed a linear relationship with a positive slope, and the determination coefficients obtained for this equation were above 91% in both years. The remobilization rate of material from penultimate was between 0.069 and 0.136%, and between 0.096 to 0.127% g m^{-2} per unit increase in seed rate m^{-2} in the first and second years, respectively. In the first year, the highest and lowest remobilization rates belonged to 'Mahoor' and 'Sahra' genotypes, respectively; however, in the second year, the highest and lowest remobilization rates were observed in 'Khorram' and 'Mahoor' genotypes, No significant differences were observed between genotypes (Table 3).

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The equation slope for material remobilization contribution from the penultimate in grain yield per unit increase of seed rate m^{-2} was between 0.023 and 0.064% in the first year, and between 0.01 and 0.037% in the second year. In the first year, the highest increase rate was related to 'Khorram', and the lowest one was related to 'Sahra'. In the second year, 'Khorram' and 'Mahoor' genotypes had the highest and lowest increase rate, respectively. In both experimental years, the response of genotypes to seed rate was similar, and there was no significant difference between most of them (Table 3).

The results showed that the response of grain yield to the increase of seed consumption was a downward trend and, for all treatments, which was observed at different rates in both years. The rate of grain yield decrease was lower in the first year than in the second year, which can be attributed to good climatic conditions until the beginning of the reproductive stage, and also to the longer vegetative period in the first year. Such conditions led to an increased storage capacity of photosynthetic materials in the vegetative organs, and to a further remobilization of these materials to seed, consequently leading to a lower rate of grain yield reduction. Increasing the storage capacity of photosynthetic materials and the potential of material remobilization from vegetative organs to seed, under conditions of increased seed consumption, is a supportive process to moderate the reduction of grain yield (Akbari et al., 2010).

The linear regression coefficients of grain yield showed that 'Khorram' and 'Mahoor' genotypes had the highest and lowest rate of decrease of grain yield for increasing seed rate m^{-2}, in both years, respectively. The mean comparison of grain yield in the density treatments showed that 'Mahoor' was less sensitive to the increase of seed consumption; and its grain yield decreased at a slower rate than the other genotypes, in both years. The resistance of 'Mahoor' grain yield to increasing seed rates can be attributed to this cultivar high storage potential of photosynthetic materials, and also to the remobilization of these materials from the studied organs to the grain, under terminal drought stress conditions. The high rate of grain yield decrease with increasing seed consumption in 'Khorram', despite the high rate of remobilization of these materials from the studied organs, can be attributed to other reasons, such as the low storage capacity and remobilization of photosynthetic materials from other vegetative organs, low activity of sinks in more absorption of photosynthetic materials, or reduced current photosynthesis due to interspecific competition (Pourhadian & Zahedi, 2012).

In the first year of experiment, the material remobilization trait from flag leaves showed an extensive variety in the studied genotypes, and significant differences were observed between them, as the highest and lowest rate of material remobilization from flag leaves were observed for 'Khorram' and 'Mahoor', respectively. However, in the second year, there was no significant differences between the genotypes, and the reason for such behavior could be the genetic diversity of genotypes for dry matter storage capacity and potential for remobilization of material to grain. The low potential of remobilization from the flag leaf of 'Mahoor', in both years, can also be due to the smaller flag leaf and, consequently, the lower cross section of the phloem than that of the other genotypes. In an evaluation of the yield response of some wheat genotypes to flag leaf removal, the authors observed that genotypes with larger leaf area faced a wider shortage of photosynthetic materials, in the absence of the flag leaf (Noori et al., 2014). With the increasing seed rate m^{-2}, the material remobilization from the flag leaf also had an upward trend, in both years. It seems that with increasing seed rate and leaf area index, inter-plant competition has intensified, which has led to accelerate the process of leaf chlorosis, reduced current photosynthesis, and more dependence of seed on the remobilization of stored material in leaves and stems (Pourhadian & Zahedi, 2012).

The fitting of material remobilization data from the penultimate leaf and the contribution of these materials to grain yield for seed rate, in both years, had a positive slope, as the seed rate m^{-2} increased, the amount of material remobilization from the penultimate leaf and the contribution of these materials to grain yield also increased. It seems that high amounts of seed rate, increased shading, excessive respiration, and lack of light cause a rapid yellowing of lower leaves, reduce the current photosynthesis, leading to an increased dependence of seed on the storage materials in the leaves and stem. In order to increase the plant density, the material remobilization rate of stored materials from the vegetative organs toward seed also increases. The increasing contribution of remobilization from penultimate leaf to grain yield can partially prevent the grain yield reduction, since such contribution follows a reduction of current photosynthesis, as a supportive process (Akbari et al., 2010).

The process of change in the material remobilization rate and its contribution from the peduncle and penultimate in the studied genotypes showed that a significant part of the grain dry matter can be supplied from the source of photosynthetic materials that are temporarily accumulated in different parts of the plant. In both years of the experiment, with the increase of seed consumption m^{-2}, the upward trend of the material remobilization and its contribution from the peduncle and penultimate was quite obvious. The response of the genotypes to seed consumption rate was completely different, in two years. In this regard, Bagherikia et al. (2017) found that some parameters – such as plant type, cultivar, leaf aging rate, amount of material storage in the stem, sink power, and the amount of carbohydrate reserves in the stem before pollination and using the capacity of stem length reserves – are genetic factors influencing the diversity of genotypes under stress conditions for the remobilization of stem soluble carbohydrates during grain filling.

There is a difference between the leaves for the dry matter remobilization, since the flag leaf transfers photosynthetic material to the spike quickly, while the transfer rate of photosynthetic material from the penultimate leaf is only one-third of the transfer rate from the flag leaf and it keeps about 90% of these materials, then transferring them to the spike. The results of the present study are completely similar to those of the two-year research by Mohammadi Gonbad (2016) on wheat. The evaluation of the two-year results of these traits showed that the increase of their rates in genotypes for increasing seed consumption was higher in the first year than in the second year. This different behavior of barley genotypes can be attributed to their genetic characteristics and their potential for storing photosynthetic material in the stem, as well as their remobilization ability to sink (grain) under special environmental conditions of each year.

The rate of material remobilization and the remobilization contribution to grain yield from three organs (peduncle, penultimate leaf, and flag leaf), in two years of experiment, showed that their rate in the peduncle was higher than that of the penultimate leaf, and their rate in the penultimate leaf was higher than that of the flag leaf. Besides, in both years, the rate of the material remobilization and its contribution to grain yield from the penultimate was higher than that of the peduncle. This difference in carbohydrate store was largely predictable. In this regard, Mhrpyan et al. (2012) believe that the high rate of dry matter remobilization from the peduncle could be due to this organ proximity to seed, so that the remobilization of storage materials to the grain is done with more speed and less energy. Abdoli et al. (2016) reported that the peduncle continues to grow longitudinally, increasing its weight after pollination, so it can be a good source of photosynthetic material when in excess of plant needs. Asseng et al. (2016) reported that the peduncle did not store carbohydrates until after pollination and until it was fully grown, therefore, its sugar reserves are less than that of the penultimate. Mphande et al. (2016) also reported that the most changes occurred in the storage of wheat stalks from the penultimate, in their studies.

The comparison of material remobilization contribution from flag leaf, penultimate leaf, peduncle, and penultimate in grain yield, in the two years of experiment, also showed that in the first year it was higher than that in the second year.

This result could be attributed in part to the different climatic conditions in the two years of experiment. Rainfall in the experimental periods of 2016–2017 and 2017–2018 was 238.8 and 271.5 mm, respectively. Although rainfall was lower in the first year of experiment than in the second one, its distribution was more appropriate, especially for barley reproductive stage and grain filling period, so that, in the first year, the average daily temperature before the pollination stage was lower than that of the second year, and the vegetative growth phase was longer. However, in the first year, plants received more photosynthetically active radiation than in the second year; therefore, the environmental conditions for photosynthetic material production and more material accumulation in storage organs (stem and leaf sheath) were better in the first year. Total rainfall in both years was much less than that in the 10-year long-term statistics (347.6 mm), which represents the occurrence of drought periods during the growth season, and seed dependence on the photosynthetic material remobilization, especially in the first year (Figure 1). Consequently, in the first year, there was enough opportunity to accumulate and store photosynthetic material in the sheath of leaves and stems, and the plant was able to store more dry matter and transfer it to seed. Minerals transferred and stored in vegetative organs such as stem and leaf sheath, during the slow growth stage of seed, due to the lack of strong sinks, are transferred to filling seed during the linear growth stage of seed (Bagherikia et al., 2017).

One of the most important physiological traits at the source and sink level that play a key role in the formation and maintenance of resource and sink power, under different environmental conditions, is the leaf area index and its durability; in small grain cereals; the flag leaf photosynthesis, especially when other leaves are aging, plays an important role in grain filling and its yield (Gregersen et al., 2014; Borrill et al., 2015). The results of the present study are quite similar to the findings by Soleimani Abiyat et al. (2015).

The factors that can change the amount of transferred dry matter include climatic conditions, soil type, cultivar, and crop management, according to Dordas (2012). It seems that, in the first year, as a result of low average daily temperature, the number of days required to for plants to go through the vegetative stage was greater than those in the second year; therefore, the genotypes had more chance to accumulate and store materials in the stem and, then, remobilize them to seed. The results of the present study corroborate the findings on wheat by Ardalani et al. (2014).

Azhand et al. (2015) observed that the remobilization rate of the stem is controlled by sink size, genotype, and environment. Pourhadian & Zahedi (2012) also considered the remobilization potential of stored materials as one of the desirable physiological indicators, the amount of which depends on various factors, such as seed rate and row spacing.

Conclusions

1. The material remobilization with increasing seed rate m^{-2} contributes to grain yield of barley (*Hordeum vulgare*) genotypes, especially in the first crop year because the rainfall in the first year was lower than the second year.

2. Linear regression coefficients of grain yield show that 'Khorram' and 'Mahoor' genotypes show the highest and lowest rate of decrease of grain yield for increasing seed rate m^{-2}, in both years, respectively.

3. The highest and lowest contribution of the remobilization in barley grain yield are related to penultimate leaf and flag leaf, respectively.

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