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Research paper

Genetics of grain filling rate and remobilization of stem reserves in bread wheat under terminal drought stress

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Abstract
To determine the gene action and inheritance of grain filling rate and remobilization of stem reserves in bread wheat, a 6×6 half diallel was performed. The F_1 seeds along with parental varieties were evaluated under terminal drought stress at Islamic Azad University, Ardabil, Iran in 2018. Grain filling rate, effective grain filling period, remobilized dry matter, the contribution of remobilization in grain yield, remobilization efficiency of dry matter, carbohydrates remobilization efficiency, and specific weight of internodes were measured. Results showed the adequacy of the additive-dominance model in all of the characters except for the effective gain-filling period and contribution of remobilization in grain yield. The existence of partial dominance, complete dominance, and over-dominance was observed in control of the measured characters. Generally, broad sense heritability was high and ranged from 0.72 (carbohydrates remobilization efficiency) to 0.88 (grain filling rate). However, narrow sense heritability ranged from 0.17 (carbohydrates remobilization efficiency) to 0.66 (grain filling rate). Among the traits, grain filling rate had the highest narrow sense heritability (0.66) followed by the remobilized dry matter (0.46) and specific weight of internodes (0.44). There was also a positive relationship between dominance effects and the specific weight of internodes, where dominant alleles were favorable. Based on Griffing's method, Rasad, Konya2002, and Pishtaz had higher general combining ability (GCA) and consequently favorable alleles for the grain filling rate. However, for remobilization, Rasad and Konya2002 had higher GCA.

Keywords: diallel; drought stress, heritability, re-translocation; stem reserves

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Introduction

In arid and semi-arid environments, the decrease in rainfall and increase of evapotranspiration in the generative growth phase leads to deleterious effects on cereals, including wheat (Blum 1998). Grain filling in wheat occurs through current photosynthesis assimilation and re-translocation of stem reserves (Ehdaie *et al*. 2006). Accumulation of pre-anthesis assimilates, effective remobilization of stem reserves, and high grain filling rate are the main factors to achieve higher grain yield in wheat (Sanjari *et al*. 2011). According to Yang *et al*. (2001), pre-anthesis carbohydrate reserves of the stem in wheat contribute to 25 to 33% of the grain yield. Numerous studies indicated that drought stress resulted in leaf senescence and an increase in the re-translocation of stored reserves in cereals (e.g. Piaskowski *et al*. 2016; Nazir *et al*. 2021). Under drought stress conditions, remobilization of non-structural stored carbohydrates from the stem provides a greater proportion of grain weight and can be accounted for 70-92 percent of the kernel weight (Yang *et al*. 2001). So, proper remobilization and grain growth rate can be an appropriate way for the development of drought-tolerant varieties for arid regions (Blum 2011; Sanjari *et al*. 2011; Valdés *et al*. 2020).

The traits to be considered as selection criteria for improving varieties under drought stress must have a higher heritability than the grain yield and should be correlated with yield (Blum 2011). Ideally, measuring the secondary traits should be rapid, accurate, cheap, and preferably non-destructive (Tuberosa 2012).

The diallel cross provides useful information on the genetic control of crop characteristics. High grain growth rate and remobilization of stem reserves are regarded as drought tolerance indicators in wheat, but few studies have been carried out on their genetic basis (Gupta *et al*. 2011; Tatar *et al*. 2016; Li *et al*. 2020). The objective of this research was investigating the inheritance of grain filling rate and remobilization in wheat under terminal drought conditions.

Materials and Methods

Experimental design

Six wheat varieties (Table 1) were crossed in a half-diallel pattern. The F1 seeds with parental varieties were planted under terminal drought (rainfed) conditions in a randomized complete blocks design with three replicates at the Agricultural Research Station of Islamic Azad University, Ardabil, Iran in 2018-2019. Each plot consisted of four rows 1.5 meters in length, 20 cm apart with a plant density of 250 seeds per square meter. Drought stress was imposed using a rain exclusion shelter after anthesis. Before planting, 30 Kg of N ha^{-1} and 60 Kg of P_2O_5 ha^{-1} was applied to the soil.

Table 1. List of wheat cultivars used as parents in the diallel cross

Parent	Cultivar	Rainfed/Irrigated	Pedigree	Origin
1	Rasad	Rainfed (semi-dwarf)	Fengkang/Sefid3	Iran
3	Konya2002	Rainfed (semi-dwarf)	Kanred/Tenmarg//P211-6/3/2183/CO65/LCR	Turkey
4	Sultan95	Rainfed (semi-dwarf)	AGRI/NAC	Turkey
2	Pishtaz	Irrigated (dwarf)	Alvand//Aldan/Yas58	Iran
5	Soissons	Irrigated (dwarf)	Jena/HN35	France
6	Seri82	Irrigated (dwarf)	KVZ/BUHO//KAL/BB	Mexica

Measuring remobilization characteristics

To determine the amount of remobilization of dry matter to grains, 25 uniform main tillers were labeled in each plot at anthesis. One week after anthesis, five tillers per plot were harvested at five-day intervals until physiological maturity. The harvested tillers were dried at 75 °C for 24 hours and then weighed. The amount of remobilization was measured by the formulas proposed by Ehdaei and Waines (1996) as follows:

$$\text{Mobilized dry matter} = \text{Post anthesis max weight} - \text{Post anthesis min weight}$$

$$\text{Contribution of mobilization in grain yield} = \frac{\text{Mobilized dry matter}}{\text{Grain dry weight}}$$

$$\text{Mobilization efficiency of dry matter} = \frac{\text{Mobilized dry matter}}{\text{Post anthesis maximum stem weight}}$$

$$\text{The specific weight of internodes(SWI)} = \frac{\text{Weight of internodes}}{\text{Length of internodes}}$$

$$\text{Carbohydrate mobilization Efficiency} = \frac{\text{Maximum SWI} - \text{SWI at maturity}}{(\text{Maximum SWIs}) \times 100}$$

Measuring grain filling rate and effective grain filling period

To measure the grain filling characters, seeds were picked up from the above-mentioned harvested tillers in each sampling time and dried for 48 hours at 80 °C. Grain number and dry weight were used to calculate the average grain weight. Grain filling rate was determined by fitting a bilinear model (Borrás and Otegui 2001; Borrás *et al.* 2004):

$$GW = \begin{cases} a + gfr(daa), & if \quad daa < P_m \\ a + gfr(P_m), & if \quad daa \geq P_m \end{cases}$$

where GW is the grain dry weight, a is the intercept, gfr is the slope of the grain weight calculating grain filling rate, daa is the days after anthesis, and pm is the physiological maturity. Effective grain filling duration (EGFD) was calculated from the following equation:

EGFD = Maximum grain weight (g)/ Grain filling rate (g day^{-1}).

Statistical analysis

The diallel analysis was done by the method developed by Hayman (1954) and also Griffing's Method II Model I (1956). The genetic components and genetic parameters of half diallel were estimated using formulas proposed by Singh and Singh (1984). T-test was used for determining the significance of genetic components. Broad sense heritability (Hb), narrow sense heritability (Hn), and average degree of dominance ($\overline{D}$), were estimated according to Mather and Jinks (1971). To evaluate the additive-dominant model goodness of fit, linear regression of Wr on Vr (H0: b = 1 vs. H1: b ≠ 1) and Wr-Vr analysis of variance were performed. Baker's variance ratio 2MSgca/(2MSgca+MSsca) was computed to determine the relative importance of additive and dominance genetic effects (Baker 1978). Combining ability was measured using SAS 9.2 software. Genetic components of Hayman's method was estimated by the Excel 2019 software. To fit the bilinear model for calculating grain filling rate, Proc NLIN DUD procedure was utilized in the SAS software.

Results

The goodness of fit test for adequacy of the additive-dominant model is shown in Table 2. For all traits, Wr-Vr mean squares of the crosses (treatment source of variation) were non-significant indicating the adequacy of the additive-dominant model. However, in the case of effective grain filling duration and contribution of remobilization to grain yield, the linear regression slope was not significantly higher than 0 and the simple additive-dominant model failed to fit (Table 2). Genetic parameters for Hayman's method are presented in Table 3. The D component (additive effect) was significant for all of the estimated characters, showing the existence of additive effects in the control of the characteristics under study. Generally, the significant D component in Hayman's method was confirmed by the

Table 2. The additive-dominance goodness of fit for the evaluated characters

Character	Heterogeneity of Wr-Vr		t-test of β	
	$MS_{Treatment}$	MS_E	H_0: β= 0	H_0: β= 1
Grain filling rate	0.051	0.025	0.66*± 0.270	0.66 ± 0.270
Effective grain filling duration	2.77	4.51	0.228 ± 0.314	0.228 * ± 0.314
Remobilized dry matter	4.21	8.91	1.14*± 0.259	1.14 ± 0.259
Contribution of remobilization in grain yield	823.4	743.2	0.613 ± 0.498	0.613 ± 0.498
Remobilization efficiency of dry matter	129.3	758.4	1.17** ± 0.183	1.17 ± 0.183
Carbohydrates remobilization Efficiency	257.2	610.7	0.806* ± 0.21	0.806 ± 0.21
Specific weight of internodes	5.59	5.31	1.05* ± 0.139	1.05 ± 0.139

*, **: Significant at the 5 and 1 percent probability levels, respectively

Table 3. Estimates of genetic parameters in the half- diallel design of wheat

Parameter	Grain filling rate	Remobilized dry matter	Remobilization efficiency of dry matter	Carbohydrates remobilization efficiency	The specific weight of internodes
D	0.152* ± 0.011	0.105* ± 0.034	61.6** ± 2.57	60.3** ± 3.06	20.5** ± 1.17
H1	0.089 ± 0.29	0.17 ± 0.087	145.8** ± 6.5	169.7** ± 7.8	22.02** ± 2.98
H2	0.077 ± 0.26	0.12 ± 0.078	104.1** ± 5.8	122.5** ± 6.9	17.8** ± 2.66
F	0.050 ± 0.28	0.078 ± 0.085	71.6** ± 6.3	88.3** ± 7.47	15.6** ± 2.87
d	0.76	1.27	1.53	1.67	1.03
H2/4H1	0.215	0.173	0.178	0.180	0.20
Hn	0.66	0.46	0.30	0.17	0.44
Hb	0.884	0.803	0.79	0.72	0.85
rYr (Wr+Vr)	-0.38	-0.35	0.098	-0.38	0.74*
$\overline{F}_1 - \overline{P}$ (%)	0.037	0.04	3.2	4.6	-2.16

*, **: Significant at the 5 and 1 percent probability levels, respectively; D: Additive variance component, H1: Uncorrected dominance variances, H2: Corrected dominance variances, F: Additive-dominance covariance, d: Average degree of dominance, Hn: Narrow-sense heritability, Hb: Broad sense heritability, rYr (Wr+Vr): Relationship between the dominance and favorability of alleles,: $\overline{F}_1 - \overline{P}$: Average heterosis

significant GCA mean squares in Grifting's method (Table 4).

Uncorrected and corrected dominance variances (H_1 and H_2, respectively) were significant only for the remobilization efficiency of dry matter, carbohydrates remobilization efficiency, and specific weight of internodes, demonstrating the importance of dominant gene effects governing these traits. Nevertheless, specific combining ability (SCA) mean squares (equivalent to dominant variance) were significant only for the specific weight of internodes in the Grifting's method. Possible different results in the two methods have been pointed out by Singh and Singh (1984). The F parameter estimates were significant except for the grain filling rate and remobilized dry matter. Significant and positive F values indicate that dominant alleles have higher frequency among the parents. The ratio of negative and positive alleles (H2/4H1) was lower than 0.25 in all cases, showing the existence of asymmetry in the distribution of the negative and positive alleles in the parents. This is proven by H_1 being greater than H_2 and means that some parents are superior to other parents. The average degree of dominance (d) was smaller than 1 for the grain filling rate (d= 0.76) indicating the partial dominance of the genes in governing this trait. d was close to 1 for the specific weight of internodes. However, d was greater than 1 for the remaining characteristics, implicating the existence of over dominance in some loci. The contribution of partial dominance, complete dominance, and over-dominance was acknowledged by the intercept of Wr on Vr graphs (Figures 1 to 5).

The Hb values were mostly high and ranged

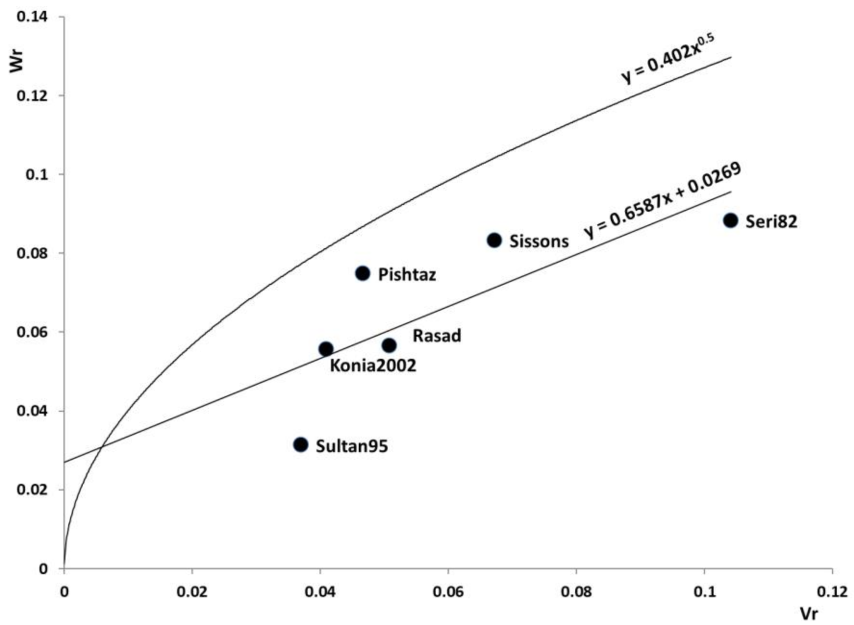

Figure 1. Regression of Wr on Vr and distribution of parents for the grain filling rate in wheat

from 0.72 for the carbohydrate remobilization efficiency to 0.88 for the grain filling rate. Among the traits, the grain filling rate had the highest Hn (0.66), followed by the remobilized dry matter (Hn= 0.46) and the specific weight of internodes (Hn= 0.44). The observed differences between the broad and narrow sense heritability reflect the existence of dominance in the control of the traits under study. The correlation between the order of dominance and parental means "rYr(Wr+Vr)" which shows the relationship between the dominance and favorability of alleles, was significant and positive for the specific weight of internodes (Table 3), indicating that dominant alleles decrease the specific weight of internodes. Based on the distance of each parent from the origin of Wr-Vr graph, it was observed that for the grain filling rate, the semi-dwarf parents (Sultan95, Konia 2002, Rasad) had higher concentrations of the dominant alleles and the dwarf parents (Seri82, Sissons) had higher concentration of the recessive alleles. Pishtaz was in an intermediate situation. For most of the remobilization traits (except for the specific weight of internodes), Konia2002 showed a higher concentrations of the dominant alleles, Pishtaz had a higher concentration of the recessive

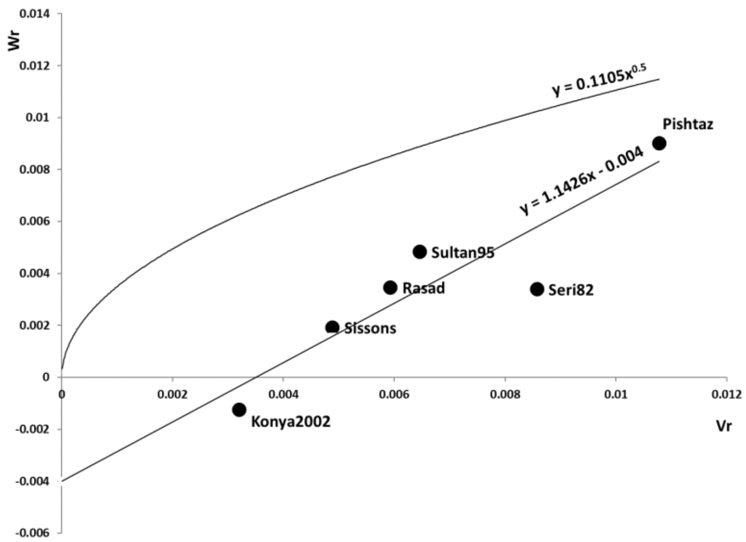

Figure 2. Regression of Wr on Vr and distribution of parents for the remobilized dry matter in wheat

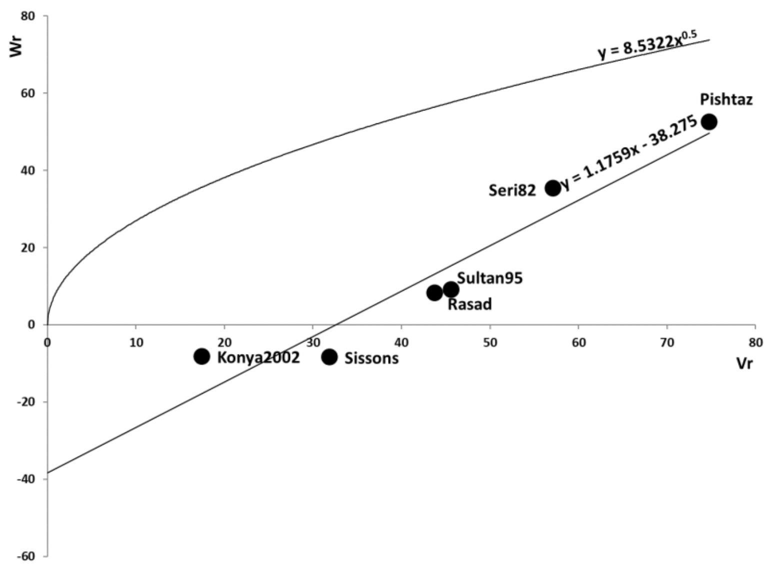

Figure 3. Regression of Wr on Vr and distribution of parents for the remobilization efficiency of the dry matter in wheat

alleles, and the remaining parents were at the intermediate conditions. However, in the case of the specific weight of internodes, Sultan 95 and Konya2002 had higher concentrations of dominant and recessive alleles respectively (Figures 1 to 5).

Based on GCA effects (Table 5), Rasad and Konya2002 had favorable alleles for the grain filling rate. Interestingly, Rasad and Konia2002 also had favorable alleles for the remobilization characters, suggesting that selection for remobilization can lead to a better grain filling rate. In temperate cereals, grain filling under end-season drought stress is mainly supplied by stem reserves (Borrell *et al*. 1993). A longer stem and a higher

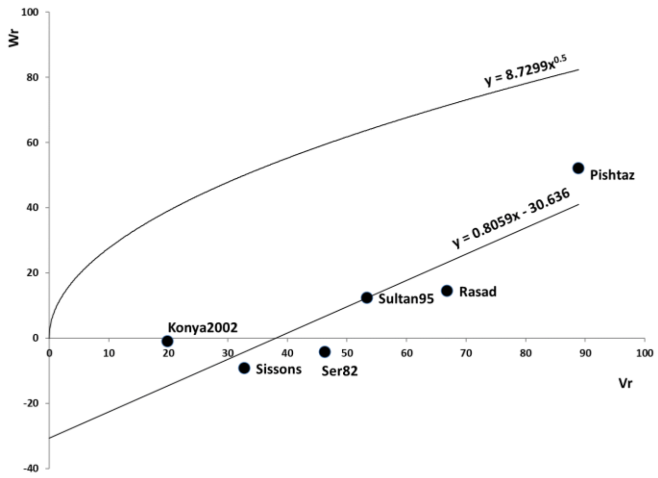

Figure 4. Regression of Wr on Vr and distribution of parents for the carbohydrates remobilization efficiency in wheat

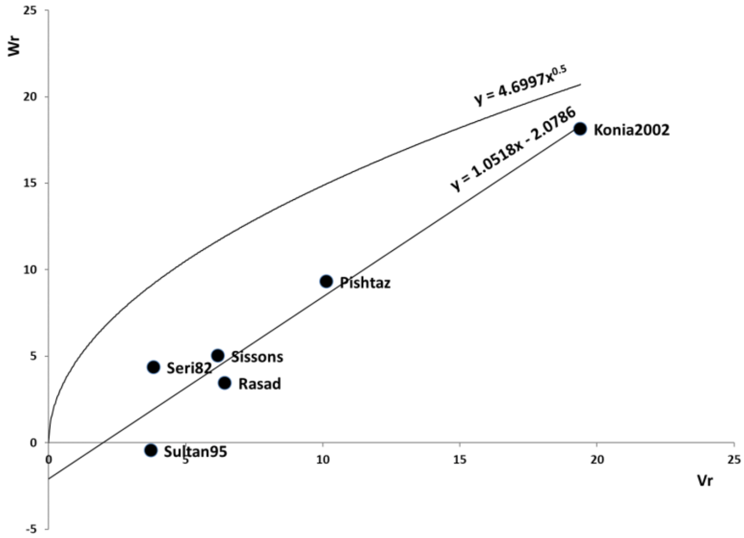

Figure 5. Regression of Wr on Vr and distribution of parents for the specific weight of internodes

Table 4. Analysis of variance of the general and specific combining ability for the evaluated traits in wheat

Source of variation	df	Grain filling rate	Remobilized dry matter	Remobilization efficiency of dry matter	Carbohydrates remobilization efficiency	The specific weight of internodes
GCA	5	0.465**	0.265**	100.87*	61.77	46.93**
SCA	15	0.038	0.068	59.99	63.73	10.74**
Error	40	0.030	0.051	33.46	47.75	3.07
Baker's Ratio			88.6%	77.1%	65.9%	89.7%

*, **: Significant at the 5 and 1 percent probability levels, respectively; GCA: General combining ability, SCA: Specific combining ability

Table 5. General combining ability (GCA) effects of the parents for the evaluated characters in wheat

Parent	Character				
	Grain filling rate	Remobilized dry matter	Remobilization efficiency of dry matter	Carbohydrates remobilization efficiency	The specific weight of internodes
Rasad	0.210	0.060	4.00	3.13	-2.32
Konya2002	0.177	0.031	0.654	-0.454	2.63
Sultan95	-0.157	-0.049	-3.39	-2. 82	0.236
Pishtaz	0.056	-0.015	-0.368	-0.596	-1.37
Soissons	-0.165	-0.31	-1.67	0.975	0.212
Seri82	-0.121	0.005	0.785	-0.227	0.613
SE for gcai	0.0015	0.0003	1.74	2.48	0.160
SE for gcai-gcaj	0.0037	0.0006	4.18	5.97	0.384

maximum specific weight of the stem increases the storage capacity of stem reserves (Blum *et al.* 1997). However, the Rht1 and Rht2 dwarfing genes of wheat reduces the reserve storage by reduction of the plant height (Borrell *et al.* 1993), which may be the reason for the relatively lower GCA of the dwarf Parents Pishtaz and Soissons compared to the semi-dwarf Rasad and Konia2002.

Discussion

Based on the results, it was inferred that the additive-dominance model can adequately fit most of the characters. In the study of Li *et al*. (2020) both additive and epistatic genetic effects played a significant role in phenotypic variations of the stem water-soluble carbohydrates. In the study of Nazir *et al.* (2021) in wheat, both the SCA and GCA effects were significant for the remobilization of stem reserves.

Generally, the traits had high Hb, indicating that most of the variation among the genotypes is genetic and not environmental. Nazir *et al.* (2021) also found high Hn for the remobilization of dry matter in a half-diallel cross in wheat. However, moderate heritability of 0.51–0.72 was observed for the remobilization of stem reserves in the study by Li *et al*. (2020).

The magnitude of the average degree of dominance showed that for the grain filling rate, additive effects have greater importance, however for the remobilization of stem reserves dominant effects were more important. Nazir *et al.* (2021) reported that dominant effects have greater importance in the control of the contribution of post-anthesis assimilates, translocation of dry matter, and translocation efficiency percentage in wheat. Since the grain filling rate was governed by additive effects, the evaluation of genotypes can be performed at early inbreeding generations. However, the remobilization traits were governed almost by dominant effects and the evaluation of genotypes must be performed after decreasing the frequency of heterozygote loci within families at advanced generations. In the case of remobilization traits, despite the high Baker's ratio (as an indicator of the stronger role of additive effects), the degree of average dominance was also high. Therefore, it can be argued that d was overestimated probably due to the failure of the independent distribution of alleles in the parents. It is necessary to mention that, Baker's ratio also can be overestimated as general combining ability variance may contain some part of dominance variance (Singh and Singh 1984).

The narrow sense heritability of the grain filling rate was high. However, it was generally low for the remobilization traits, except for the remobilized dry matter and the specific weight of internodes with intermediate Hn. According to Tuberosa (2012), most of the characteristics that determine the performance of crop plants under water stress usually have low to intermediate inheritance. This takes down our ability to analyze their genetic basis exactly and, importantly, decreases the genetic gain of phenotypic selection.

Based on the findings of this study, low heterosis was estimated in all of the traits, which is a common feature in the self-pollinating crop plants. Results also showed a significant relationship between dominance and desirability of alleles only for the specific weight of internodes ($rYr_{(}Wr+Vr_{)}$=0.74*). This positive and significant correlation indicates that dominant alleles are decreasing alleles. Consequently, parents with more dominant alleles for this trait will have lower specific weight of the internodes and possibly will have higher general combining ability. Regarding the importance of grain filling rate and stem reserves remobilization in breeding programs for drought tolerance (Blum 2011; Valdés *et al*. 2020), and acceptable narrow sense heritability, (especially for the grain filling rate, the specific weight of internodes and the remobilized dry matter), these traits are recommended as potential candidates for selection in the breeding programs for drought tolerance. Due to the ease of measurement (no need for multiple sampling), and significant correlations with the remobilized stem dry matter (Ehdaie *et al*. 2006) and with grain yield (Shakiba *et al*. 1996), the specific weight of internodes (at physiological maturity) can be recommended as a high throughput selection criterion for improving the drought tolerance of the wheat crop. However, the grain filling duration was governed by the epistatic effects and has been reported to be more sensitive to environmental fluctuations than the grain filling rate (Royo *et al*. 2000). Lack of relationship between the duration of grain filling and grain yield also was reported in wheat (Sanjari *et al*. 2011) and it seems that this trait can't be considered as a favorable selection criterion to improve the drought tolerance of wheat. Finally, based on GCA effects, the semi-dwarf parents (i.e., Rasad and Konya2002) had favorable alleles for the grain filling rate and remobilization traits, suggesting that selection for higher remobilization can lead to better grain filling rate. Additionally, these parents may produce offspring with better remobilization under terminal drought conditions.

Conflict of interest

The authors declare that there is not any conflict of interest regarding the publication of this manuscript.

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ژنتیک سرعت پر شدن دانه و انتقال مجدد ذخایر ساقه در گندم نان تحت تنش خشکی انتهایی

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چکیده

به منظور تعیین نحوه عمل ژن و وراثت پذیری سرعت پر شدن دانه و انتقال مجدد ذخایر ساقه در گندم نان، یک تلاقی دی آلل ۶ × ۶ یک‌طرفه انجام شد. بذور F_1 حاصل به همراه والدین تحت تنش خشکی انتهایی در سال ۱۳۹۷ در دانشگاه آزاد اسلامی اردبیل مورد ارزیابی قرار گرفتند. سرعت پر شدن دانه، دوره موثر پر شدن دانه، انتقال مجدد مواد ذخیره‌ای از ساقه به دانه، میزان مشارکت ذخایر ساقه در عملکرد دانه، کارایی‌ساقه در انتقال ذخایر به دانه، کارایی انتقال مجدد کربوهیدرات‌ها از ساقه به دانه و وزن ویژه میانگره‌ها اندازه‌گیری شد. نتایج حاکی از کفایت مدل افزایشی- غالبیت در همه صفات به جز دوره موثر پر شدن دانه و میزان مشارکت ذخایر ساقه در عملکرد دانه بود. وجود غالبیت ناقص، غالبیت کامل و فوق غالبیت در کنترل صفات مشاهده شد. به طور کلی، وراثت پذیری عمومی صفات بالا بود و از ۰/۷۲ (کارایی انتقال مجدد کربوهیدرات‌ها) تا ۰/۸۸ (سرعت موثر پر شدن دانه) متغیر بود. در حالی که وراثت پذیری خصوصی از ۰/۱۷ تا ۰/۶۶ در نوسان بود. در بین صفات، سرعت پر شدن دانه بیشترین وراثت پذیری خصوصی (۰/۶۶) را داشت و انتقال مجدد مواد ذخیره‌ای (۰/۴۶) و وزن ویژه میانگره‌ها (۰/۴۴) در مراتب بعد قرار گرفتند. نتایج همچنین نشان داد که بین غالبیت و مقدار وزن ویژه میانگره‌ها رابطه مثبت وجود دارد که در مورد این صفت آلل‌های غالب مطلوب بودند. بر اساس روش گریفینگ، ارقام رصد، کونیا ۲۰۰۲ و پیشتاز دارای ترکیب پذیری عمومی بالاتر و در نتیجه آلل‌های مطلوب برای سرعت پر شدن دانه بودند. در حالی که در مورد انتقال مجدد مواد ذخیره‌ای، ارقام رصد و کونیا ۲۰۰۲ ترکیب پذیری عمومی بالاتری داشتند.

واژه‌های کلیدی: انتقال مجدد؛ تنش خشکی؛ دیالل؛ ذخایر ساقه؛ وراثت پذیری