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Araştırma Makalesi/*Research Article (Original Paper)*

Source–Sink Limitation on Spring Bread Wheat Genotypes in High and Low-Production Environments

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Abstract: Grain yield depends on the number of grains per unit area (sink) and the availability of assimilates (source) to fill these grains. The aim of the current work was to determine whether wheat yield in warm environments is limited in current cultivars by the size of the sink or by assimilates available for grain filling (source) using manipulation. Sink size was reduced at anthesis by removing all the spikelet along one side of the spike and source size was reduced at anthesis by removing all leaf blades from a main stem. This research was conducted with six bread wheat cultivars using randomized complete block design with three replications in two separate experiments in 2011-12 under dryland and full irrigated conditions. After 50% spikelet removal, individual kernel weight was from 42.9 to 53.5 mg with mean change: 9.1% and from 37.9 to 41.8 mg with mean change:10.9% in high input (full irrigation) and low input (dryland) conditions respectively. Defoliation decreased individual kernel weight of all cultivar and a new recently released cultivar for semi-tropical dryland regions of Iran (Karim) showed the lowest reduction. The source–sink modification in two independent experiments suggested that the yield of the current wheat cultivars is more sink- than source-limited and that breeding wheat with a larger sink size than in the current cultivars may lift the yield potential in favourable condition or increase the yield of wheat under heat and drought constraints.

Key words: Assimilate, Bread wheat, Drought, Heat, Tolerance, Yield potential

Yüksek ve Düşük Üretim Koşularında Yazlık Ekmeklik Buğday Genotiplerinde Kaynak-Havuz Sınırlamaları

Özet: Tane verimi, birim alana düşen tane sayısı (havuz) ve bu taneleri dolduracak asimilatların (kaynak) kullanılabilirliğine bağlıdır. Bu çalışmanın amacı ılıman çevre şartlarında mevcut buğday çeşitlerine ait veriminin, havuz büyüklüğünden mi yoksa tane dolumu için (kaynak) manipüle edilmiş asimilatlardan mı sınırlanmadığını belirlemektir. Havuz büyüklüğü çiçeklenme döneminde başağın bir yanı boyunca tüm başakçıkların uzaklaştırılması ile kaynak büyüklüğü ise çiçeklenme döneminde ana gövdedeki tüm yaprak ayalarının uzaklaştırılması azaltılmıştır. Bu araştırma 2011-2012 yıllarında altı ekmeklik buğday çeşidinde kuru ve sulu koşullarda iki ayrı deneme olarak tesadüf bloklarında bölünmüş parseller deneme desenine göre üç tekrarlamalı olarak yürütülmüştür. % 50 başakçık uzaklaştırılmasından sonra tane ağırlığı yüksek girdi (sulu) koşullarında 42.9 ile 53.5 mg arasında değişmiş ve ortalama değişim % 9.1 olmuş; düşük girdi (kuru) koşullarında ise 37.9 ile 41.8 mg arasında değişmiş ve ortalama değişim % 10.9 olmuştur. Yaprak uzaklaştırma bütün çeşitlerde tane ağırlığını azaltmıştır ve en düşük azalma İran'ın yarı-tropik kurak bölgeleri için son zamanlarda geliştirilmiş buğday çeşidinde (Karim) gözlenmiştir. Kaynak-havuz modifikasyonunu içeren bu iki bağımsız çalışma, mevcut buğday çeşitlerdeki verimin kaynaktan ziyade havuz tarafından sınırlandığını ve mevcut çeşitlerden daha geniş bir havuz büyüklüğüne sahip olan buğday ıslahının uygun koşullardaki verim potansiyelini yükseltebileceğini veya sıcak ve kurak kısıtlamalarında buğdayın verimini artırabileceğini göstermektedir.

Anahtar kelimeler: Asimilant, Ekmeklik buğday, Kuraklık, Isı, Tolerans, Verim potansiyeli

Introduction

Under Mediterranean conditions such as the southern part of Iran, heat and drought stress after anthesis is the major grain yield limiting factors in winter sown wheat genotypes (Mohammadi and Karimizadeh 2012). Genetic increases in yield potential is best expressed in optimum environments, it is also associated with enhanced yields under drought (Trethowan et al. 2002; Araus et al. 2002; Slafer and Araus, 2007). Breeding to raise both yield potential and yield further under environmental constraints through improved adaptiveness will be of paramount importance (Slafer et al. 1999; Araus et al. 2002).

Wheat yield improvement in the past was mainly the result of increases in the partitioning of biomass to grains (Miralles and Slafer 2007), whereas biomass increases explained most of the yield progress from the 1980s to the 1990s, that there has been no relevant genetic progress in HI since the 1980s (Sayre et al. 1997; Reynolds et al. 1999; Shearman et al. 2005). Shearman et al. (2005) stated that the recent genetic gains in yield in the UK is based on the combination of an enhanced crop growth rate during pre-anthesis period (by increases in radiation use efficiency, RUE) and larger source during grain filling (by increases in water soluble carbohydrates) and Reynolds et al. (2005) suggested that RUE could be increased by increasing sink-strength (i.e. more grains per unit land area). In this context, the question of whether wheat yield actually is limited by the sink or the source strengths, particularly in modern high-yielding cultivars, is a requirement in order to device alternative opportunities for further increasing yield in favorable or infavorable environments.

Cruz-Aguado et al. (1999) concluded that final grain weight limited by the ability of the source to provide assimilation during grain filling period. In contrast, Slafer and Savin (1994b) and Borra´s et al. (2004) who have reviewed most reported results on source–sink experiments in the literature, and found that wheat grain growth is never source-limited with likely responses varying from only sink-limitation to some degree of co-limitation (with stronger sink- than source-limitation of yield during grain filling). Modern cultivars seem to be relatively less sink-limited during postanthesis than their predecessors (Slafer and Savin, 1994a; Kruk et al. 1997; Shearman et al. 2005), as semidwarf wheats seem less sink-limited than traditional tall wheats (Miralles and Slafer 1995).

The study of contributions made by successful wheat breeding may provide clues to help identify alternatives for breeders to further increase yield. Research into the changes in physiological traits associated with genetic gains in yield potential is essential to improve our understanding of yield-limiting factors and to base future breeding strategies on. The objectives of these experiments were to determine the relative contribution of source/sink reserves to grain yield production under high and low production conditions and also, the responses of the best cultivated genotypes representing adapted cultivars under both conditions were investigated.

Materials and Methods

Two field experiments were conducted at the Gachsaran Agricultural Research Station that is located in South-west of Iran during the 2011-12 seasons. One experiment was carried out under high-inputs and full irrigated conditions (about 200 mm in addition to natural rainfall), while the other was conducted under low-inputs and dry land environment (417 mm rainfall).

Six spring bread wheat cultivars released in Iran for the breeding period from 1996 to 2012 were studied and compared. Chamran and Aflak are the most current cultivars under warm irrigated condition and also, Zagros, Gahar, Koohdasht and Karim are cultivated in semitropical dryland regions.

Each plot was 7.03 m long with six rows spaced 17.5 cm apart and sown by a small-plot planter (Wintersteiger) with a density of 300 and 400 seeds/m^2 in irrigation and dry land environments respectively. The soil texture was silty-clay loam, with pH= 7.3-7.8, and less than 1% organic matter. Fertilizers were applied completely before sowing (90 kg N ha^{-1} and 75 kg P_2O_5 ha-1) in dry land condition, while more 50 kg P_2O_5 ha^{-1} (before sowing) and 50 kg N ha^{-1} at tillering and booting (25 and 45 Zadoks scale) additional under irrigated condition. The harvested plot size for grain yield was 6 m^2 and the grain yield of each individual plot was separately harvested and measured.

-The dry weight of 10 spikes at anthesis were determined by oven dried 48 h at 65 °C. Kernel number per m^2 was calculated by dividing grain yield (gm^{-2}) by kernel weight (mg) (Hobbs and Sayre 2001).

The source–sink ratios were manipulated the sink–source relationships in both experiments:

- To increase the source, spikelets were removed on main stems in 10 plants; while the other part of the spikes remained unaltered as controls.
- To decrease the source, all leaves on 10 main stem were removed during anthesis.
- Ten plant samples (main stem) were marked during anthesis in middle part of central rows for each plot. They were taken at maturity.

Results and Discussion

In all cultivars, medium drought stress decreased main stem yield in addition to grain yield significantly, but in Koohdasht, Gahar and Karim cultivars which are adapted to dryland areas decreasing rate was less than the other cultivars (Table 1).

The highest grain per spike belonged to Aflak cultivar at both conditions. Maximum 1000-grain weight was observed in Karim (49.7 gram) and Chamran (42.6 gram) under well-watered condition (Table 1). In all cultivars 1000-grain weight decreased under drought stress compared to well-watered condition. However, the lowest decreasing rate of 1000-grain weight was observed in Zagros. Removal of all leaves in main stem caused a reduction of individual kernel weight in main spike by 15.9%, and 17.2%, respectively in favorable and infavorable environments. Defoliation decreased kernel weight of all wheat cultivars.

Obtained results showing that defoliation reduced grain weight in both groups of genotypes and there is no considerable difference between the cultivars grown under stress and favorable conditions. In contrast, Plaut et al. (2004) reported that considerable reduction was occurred in the plants grown under stress. However, Karim cultivar which was recently released for semitropical dryland of Iran (Mohammadi, 2012) had maximum kernel weight after defoliation and 50% spikelet removal at both conditions. It had less grain per spike. This is in line with Schonfeld et al. (1988) and Plaut et al. 2004) results which showed drought resistant cultivars have heavier individual kernel weight and less grain per spike. Selection and culture of cultivars that maintain high kernel weight capability might be a useful strategy in yield improvement of wheat in areas where the water availability is low.

It appears that kernel weight of Aflak and Koohdasht were more sensitive to source restriction compared to the other cultivars (Table 1) It means assimilate availability in defoliated main stem was insufficient to fully satisfy grain The grain number and potential grain size usually affected sensitive cultivars to heat and drought stress which, limiting the capacity of grains to store newly produced biomass. But, it this study, there was no clear difference between irrigation advisable group (Chamran and Aflak) and dryland advisable group (Koohdasht, Zagros, Gahar and Karim). It may contributed to partially drought tolerance of Chamran and Aflak cultivars and lack of high intensity of drought stress due to 417 mm rainfall during crop season (Tables 2 and 3). Leaves are the major sources of assimilate production and the influential factor on sink growth, but Cruz-Aguado et al. (1999) and Junmin et al. (1999) reported that defoliation of some leaves in the plant increases the sink requirement in the remained leaves and by considering the relationship between source - sink in the plant, photosynthesis rate will be increased to compensate the sink reduction in the residual leaves and also, genotypes of wheat differ considerably in effects of temperature on utilization of reserves for filling of grain (Al-Khatib and Paulsen, 1990).

A 50% reduction in the kernel weight in main stem is expected after post-anthesis ear halving; however, we found reduction of only 40.9% under well watered environment and 39.1%, in drought environment. Increasing grain weight was 42.9 to 53.5 mg and 37.9 to 41.8 mg or 9.1 and 10.9% change in individual kernel weight average under irrigation and drought conditions respectively (Tables 2 and 3). Although the effect of reduced grain numbers on the final yield may be compensated for during grain filling by the production of larger grains, the yield losses could be still considerable. A higher availability of assimilates for spikelets in the half remaining of the ear increased grain set which indicates the potential for further increases in grain weight and grain set if ample assimilates are provided. This is in line with an earlier suggestion by cultivars are that modern cultivars are simultaneously limited by source and sink-strength during grain filling and also, more sink- than source-limited during grain filling (Borra´s et al.,2004; Shearman et al. 2005).

Growth of grains is reduced depending upon the degree of water deficit and the stage of grain development. Drought before anthesis influences both the number and size of spikes in a wheat crop, and thus determines the potential number of grains. Water deficit during early grain development curtails the grain sink potential by reducing both the rate and duration of grain filling (Saini and Westgate, 2000). There are increasing evidences that suggest sink strength is still a critical yield limiting factor in wheat (Fischer 1985; Slafer and Savin 1994b; Abbate et al. 1995; Miralles et al. 2000; Borras et al. 2004; Miralles and Slafer 2007) and that improving the balance between source and sink is currently the most promising approach for raising yield, biomass, and RUE (Reynolds et al. 2001, 2005; Shearman et al. 2005; Foulkes et al. 2007).

Table 1- Grain yield components of wheat cultivars under favorable (full irrigation) and unfavorable (dryland) conditions

Cultivars	**Grain per spike**		**1000 grain weight (g)**		**Grain yield (kg/ha)**	
	Favorable	**Unfavorable**	**Favorable**	**Unfavorable**	**Favorable**	**Unfavorable**
Chamran	51.6b	50.4a	42.6b	38.8b	6156ab	4129b
Aflak	57.9a	52.3a	38.1c	33.2b	6770a	4079b
Koohdasht	50.0bc	44.6ab	41.9b	39.2b	5885b	4308ab
Zagros	49.5bc	44.3ab	38.9c	38.2b	6311ab	4314ab
Gahar	47.9bc	40.3ab	34.0d	32.0b	6357ab	4473ab
Karim	45.8cd	45.0ab	49.7a	46.5a	6735a	4702a
LSD(0.05)	6.1	8.3	2.4	6.2	1122	566

Table 2- Effects of manipulation in source (defoliation all leaves of main stem) and sink (removal 50% spikelet of main stem) on individual grain weight of wheat cultivars under full irrigation condition

Cultivars	**Defoliation all leaves**		**Removal 50% spikelet**		**Main stem yield (mg)**
	Mean (mg)	**Change to control (%)**	**Mean (mg)**	**Change to control (%)**	
Chamran	37.5a	12.0	42.9b	0.7	1814c
Aflak	30.3b	20.5	43.2b	11.7	2202a
Koohdasht	33.8b	19.3	46.2b	9.4	2089ab
Zagros	32.4b	16.7	43.0b	9.6	1928bc
Gahar	30.8b	9.4	44.4b	15.8	1768c
Karim	40.9a	17.7	53.5a	7.1	2270a
LSD (0.05)	5.1		4.0		269.8

In our experiments, there was significant positive correlation between spike dry weight and grain number/m^2 in irrigation and dryland conditions(r=0.66 and r=0.44 respectively). Although grain number/m^2 being generated during the whole period from sowing to immediately after anthesis (Slafer and Rawson 1994), is extremely responsive to changes in growth/partitioning during only few weeks before anthesis (Fischer 1985). It is during this period when the spikes, where floret development takes place, are growing at the fastest rate (Kirby 1988). Consistent relationship between number of grains per unit land area and the spike dry mass at anthesis the impact of semi-dwarf genes is an increase of the number of grains per m^2 (Fischer and Stockman 1986; Youssefian et al. 1992; Flintham et al. 1997; Miralles et al. 1998).

Yield potential, and actual yields in a wide range of conditions, would be increased, if we could further increase the spike dry weight per unit land area at anthesis. Lengthening the duration of the phase when spike growth takes place would result in higher spike dry matter at anthesis and subsequently more grains per m^2. In fact, artificially extending the duration of stem elongation by exposing the crop to different photoperiods did raise the number of grains (Miralles et al. 2000; González et al. 2003, 2005). Partitioning to spikes could be increased by reducing competition from alternative sinks, especially during stem elongation when grain number is determined (Foulkes et al. 2011; Reynolds et al. 2011).

Table 3- Effects of manipulation in source (defoliation all leaves of main stem) and sink (removal 50% spikelet of main stem) on individual grain weight of wheat cultivars under dryland condition

Cultivars	Defoliation all leaves		Removal 50% spikelet		Main stem yield (mg)
	Mean (mg)	Change to control (%)	Mean (mg)	Change to control (%)	
Chamran	32.9b	15.2	41.8bc	7.7	1644b
Aflak	27.7b	16.5	37.9c	14.1	1736ab
Koohdasht	29.9b	23.7	43.9b	12.0	1728ab
Zagros	30.9b	19.1	40.9bc	7.1	1694ab
Gahar	28.1b	12.2	38.0c	18.7	1596b
Karim	38.9a	16.3	49.3a	6.0	2090a
LSD(0.05)	7.4		4.1		433

Conclusions

The conclusions reached that investments in raising wheat yield in favorable and stress conditions should simultaneously focus on improving source and sink. Further increasing yield in wheat breeding programe must be preference to increases in sink size during grain filling, either by increasing the potential size of the grains or by further increasing grain number/m^2. Although, the fact that the some genotypes in our experiments had the lowest decrease in grain weight showed at least in part, its relatively high response to higher resource availability. Spike dry matter at anthesis as an alternative trait is much simpler than the complex genes controlling ultimately yield itself under a wide range of conditions.

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