Research Article

Changes in Number and Weight of Wheat and Triticale Grains to Manipulation in Source-Sink Relationship

E. Ballesteros-Rodríguez,[1] C. G. Martínez-Rueda,[1] E. J. Morales-Rosales,[1] G. Estrada-Campuzano [1] and G. F. González[2,3]

[1]*Autonomous Mexico State University, University Campus "El Cerrillo", Toluca, Mexico City 50200, Mexico*
[2]*INTA CRBAN EEA Pergamino, CC31 CP 2700 Pergamino, Buenos Aires, Argentina*
[3]*CITNOBA-CONICET, Monteagudo 2772, 2700 Pergamino, Buenos Aires, Argentina*

Correspondence should be addressed to G. Estrada-Campuzano; gestradac@uaemex.mx

The source-sink ratio experimental manipulation has helped to define whether a crop is limited by source or sink or co-limited by both. There is no evidence in triticale of source-sink manipulations effects on yield and yield components. Two experiments were accomplished during 2008 and 2009 growing seasons at the Universidad Autónoma del Estado de México, México, and one in 2010 at the National Institute of Agricultural Technology in Pergamino, Argentina. Two triticale cultivars (line 4 and 7) and one wheat cultivar (Tollocan) were used. Source-sink relations were modified at anthesis by thinning, degraining, shading, and total defoliation procedures. Changes in the source-sink relation affected yields in both species differentially. The changes in yield due to cultivars and treatments were explained mainly by the number of grains rather than by their individual grain weight. The number of grains was affected by all treatments in both species, while the individual grain weight was increased by thinning and degraining mainly in triticale. A greater number of fertile florets in triticale were associated with their higher rate of abortion compared to wheat. These results could help to better understand crop management and genetic improvement.

1. Introduction

In cereals, yield is defined by the number of grains per unit area and the individual weight of these grains [1]. In general, grain yield is strongly related to the number of grains harvested at physiological maturity [1, 2] while individual grain weight is considered a more stable feature. The number of grains per unit area is defined by the number of spikes per unit area and the number of grains per spike [2]. The number of grains per spike in cereals is determined around to anthesis [3–5], a period that coincides with the maturation of florets that reach the fertile stage [6, 7]. An alteration in the availability of assimilates at anthesis affects the number of grains set per spike and therefore the final yield of the crop.

The source-sink ratio manipulation during setting and grain filling allow defining when the crops are limited by source or sink or co-limited by both [8]. In this sense, the source-sink relationship has been addressed following different approaches and in different crops. For example, treatments involving the partial removal of grains [9–12] and thinning of plants [13, 14] have been successful in defining whether the crops are limited by sink. On the contrary, reductions in source have been addressed through reductions in radiation intercepted by shading and by partial or total crop defoliation [15, 16]. Even though in other species source-sink relationships have been successfully studied, in triticale there is scarce information on the effect of the source-sink manipulations on grain yield and its physiological determinants.

Source-sink manipulation studies in wheat show that this species is not limited by source during grain filling [8]. However, changes in the relationship between source and sink at anthesis can alter the number of grains, since

immediately after anthesis, the grain number is determined [3–5]. Although there is abundant information on changes in grain weight in relation to source-sink manipulations, there is not much knowledge regarding the magnitude of change in the number and weight of grains when the source and sink limitations are imposed exactly at the time of anthesis. The objective of present work was to compare the effect of the source-sink manipulations on grain yield, its physiological determinants, and its components in triticale and wheat. For this purpose, a series of experiments were conducted involving manipulative treatments (shading, defoliating, thinning, and degraining crops at anthesis) under different environmental scenarios. Understanding similarities and differences between triticale and wheat in these traits could help focusing management practices for each species, and known species and environment interactions.

2. Materials and Methods

2.1. Field Experiments General Conditions. Field experiments were carried out during three consecutive growing seasons: 2008, 2009, and 2010. Experiment 1 (2008) and 2 (2009) were performed at the experimental field of the Facultad de Ciencias Agrícolas de la Universidad Autónoma del Estado de México, Toluca, México (19°15′ 33″N, 99°39′ 38″W; 2640 m.a.s.l). The site's soil is characterized as clay loam (Pellic Vertisol; USDA soil survey system). Climate in the region is subhumid with summer rains and little temperature fluctuation, and the average annual temperature is 12.8°C with an average annual rainfall of 900 mm (Garcia, 1988). Experiment 3 (2010) was established on the experimental field of the Instituto Nacional de Tecnología Agropecuaria at Pergamino, Argentina (33°56′S, 60°34′W; 55 m.a.s.l), in winter-spring crop season. The soil is characterized as silt loam (Argiudoll; USDA soil survey system). The sowing date for experiments 1 and 2 was December 3rd and for experiment 3 was July 13th. Experiments were hand sown in plots of 6 rows, 3 m long and 0.20 m apart, at a rate of 350 seeds per m^2. Fertilization consisted of 150-60-30 kg·ha^{-1} (N, P, K); nitrogen was applied in sowing, tillering, and flag leaf stage, whereas P and K were applied at sowing. All experiments were conducted under irrigation conditions, with soil near field capacity throughout the growing season. Weeds were controlled by hand, and for pest control, chlorpyrifos-ethyl insecticide (1500 ml·ha^{-1}) was used twice during crop cycle (experiments 1 and 2).

2.2. Treatments and Experimental Design. All experiments included two triticale cultivars (line 4, BULL_10/MAN ATI_1//FARAS/CMH 84.4414; line 7, POLLMER_2.2 ∗ 2/FARAS/CMH 84.4414) and one wheat cultivar (Tollocan). The cultivars were chosen because of presenting similar times to anthesis (1400°Cd on average). Five source-sink manipulation treatments were used: (1) shading (by reducing 90% of incident radiation during 10 days after anthesis); (2) defoliation (removing all the plants leaves); (3) degraining (all the spikelets were removed from one side of the spikes); (4) thinning (removing alternately three rows of each plot); and (5) control. All treatments were applied in a 1.2 m^2 area when 50% of the plants in the plot were at anthesis. The factorial combination of three cultivars and five source-sink manipulation treatments were arranged in a random complete block design with three replications.

2.3. Measured Variables. The cultivars' main development stages (emergence, terminal spikelet, flag leaf, anthesis, and physiological maturity) were recorded during the crop cycle. To determine the number of fertile florets per spike in all plots, five spikes of main shoots of equal number of spikelets were randomly selected at anthesis. The number of fertile florets per spike was determined by observing under a stereoscopic microscope and florets found according to the scale of Waddington et al. [17], at stage W10 or immediately before that stage (when the stigmatic branches were curved with green anthers). After the count of fertile florets, the spikes were dried for 72 h at 60°C until constant weight.

At physiological maturity, plants from two central rows of 100 cm length were harvested and separated into main stems and tillers. Spikes and shoots were separated within each category and were dried at 60°C for 72 h until constant weight. In this sample, grain yield, number of grains per unit area, individual grain weight, number of spikes per m^2, and number of grains per spike were determined. The number of grains per spike (main stem) was determined by selecting randomly five spikes of equal number of spikelets. For comparison purposes, the data from treatment THIN (per square meter) were multiplied by a factor of two according to Jedel and Hunt [18].

2.4. Statistical Analysis. Data were analyzed by using factorial ANOVA for each experiment. When the ANOVA revealed significant differences, mean treatment values were compared by using honest significant difference (HSD) of the Tukey test. The relationships between variables were analyzed using linear regressions [19].

3. Results

3.1. Changes in Yield Components. When considering the three experiments, variations in grain yield were related to changes in biomass (Figure 1(a)), and the relationship between grain yield and harvest index (HI) was found poor ($r^2 = 0.36$). However, within each experiment, the relationship between grain yield and HI was good (Figure 1(b)), particularly in the experiments 2008 and 2010 ($r^2 = 0.54$, $r^2 = 0.68$, respectively).

The range of variation in the number of grains per unit area was 6556 to 21031, depending on cultivar, treatment, and environment (Figure 2(a)). The variations in grain yield due to the effect of cultivars and source-sink manipulation treatments were associated to the number of grains per unit area. No relationship was observed between grain yield and individual grain weight. Grain weight ranged between 32 and 58 mg·grain^{-1}, being this magnitude of change mainly
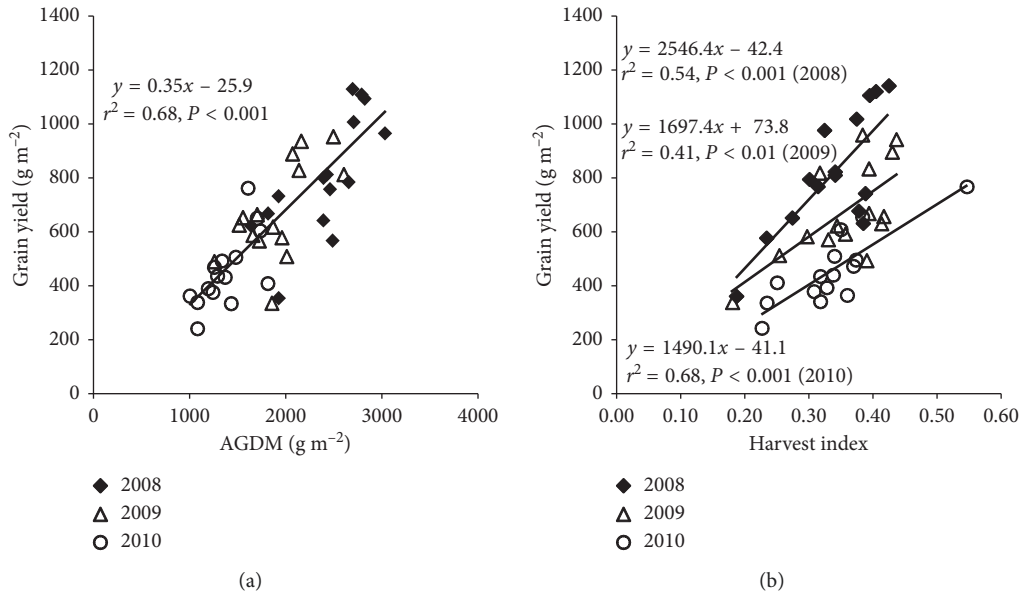
FIGURE 1: Relationships between grain yield and above-ground dry matter (AGDM) at physiological maturity (a) and harvest index (b) in two triticale and one wheat cultivars. Data correspond to three experimental cycles.
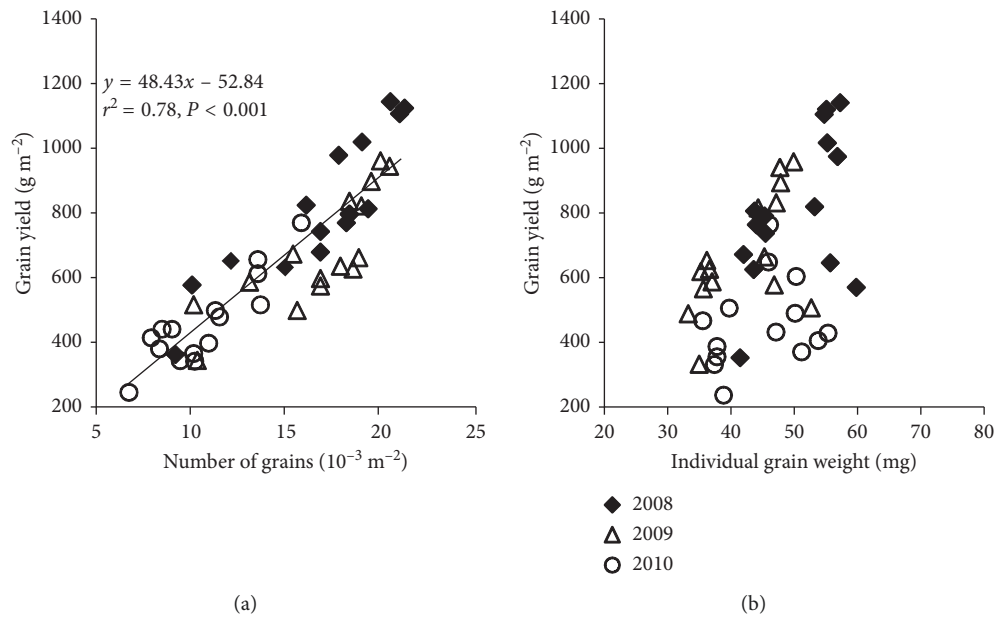

FIGURE 2: Relationships between grain yield and number of grains (a) and individual grain weight (b) in two triticale and one wheat cultivars. Data correspond to three experimental cycles.

due to the differences between species and treatments (Figure 2(b)).

3.2. Changes in Physiological and Numerical Components of Grain Yield.
Genotypes differed in AGDM and GY ($P < 0.001$; Table 1), and these differences were consistent across years despite the significant year's effects ($P < 0.001$), and significant effects were observed when comparing TCL *vs* W and between two TCL genotypes. In general, mean values of AGDM and GY were higher in 2008 than those of

2009 and 2010 cycles (Table 1) and, across genotypes and years, the range explored for these traits varied between 1639 and 3044 g·m^{-2} for AGDM and 247 and 1144 g·m^{-2} for GY, but a year × genotype interaction was detected for this trait ($P < 0.001$). Genotypes showed significant differences in HI, across genotypes and years, this varied from 0.18 to 0.43.

Grain yield was affected differentially by source-sink manipulations; defoliation treatment at anthesis decreased grain yield in L4 by 44%, 30%, and 30%, in L7 by 33%, 24% and 28%, and for wheat by 16%, 13% and 29% in 2008, 2009, and 2010 years, respectively (Table 1). Reductions in incident

Table 1: Grain yield (GY), above-ground dry matter at physiological maturity (AGDM), and harvest index (HI); genotypes (G), years (Y), and five source-sink manipulation treatments (T) (defoliation (Df), shading (S), degraining (D), thinning (Th), and control (C)). Data correspond to average of each year.

Genotypes	Treatments	GY (g m^{-2})			AGDM (g m^{-2})			HI		
					Years					
		2008	2009	2010	2008	2009	2010	2008	2009	2010
	Df	633	660	345	1639	1568	1091	0.39	0.42	0.32
	S	1021	898	380	2715	2082	1258	0.38	0.43	0.30
L4	D	577	515	437	2494	2021	1389	0.23	0.25	0.31
	Th	1144	962	611	2705	2506	1748	0.42	0.38	0.35
	C	1123	945	498	2796	2173	1352	0.40	0.43	0.37
	Df	743	633	475	1927	1526	1273	0.39	0.41	0.37
	S	825	672	441	2433	1716	1311	0.34	0.39	0.34
L7	D	653	585	414	2397	1972	1822	0.27	0.30	0.23
	Th	979	821	770	3044	2613	1618	0.32	0.31	0.39
	C	1108	837	655	2828	2148	1717	0.39	0.39	0.38
	Df	679	496	365	1818	1271	1015	0.37	0.39	0.36
	S	769	626	396	2466	1879	1215	0.31	0.33	0.33
W	D	362	341	247	1929	1869	1097	0.19	0.18	0.23
	Th	796	595	341	2660	1671	1449	0.30	0.36	0.24
	C	812	574	514	2398	1736	1500	0.34	0.33	0.34
HSD ($P \le 0.05$)		307	153	165	697	536	898	0.10	0.08	0.08
Years (Y)			***			***			ns	
Genotype (G)			***			***			***	
TCL vs W			***			***			***	
L4 vs L7			***			***			***	
Y * G			***			ns			ns	
Treatments (T)			***			***			***	
Y * T			***			**			ns	
G * T			***			*			ns	
Y * G * T			**			ns			***	

TCL: triticale; W: wheat.

radiation during 10 days from anthesis reduced yield for L4 only in 2010 by 24%, 23% in wheat only in 2010, and for L7 by 26%, 19%, and 33% in 2008, 2009, and 2010, respectively. The 50% elimination of the spikelets at anthesis resulted in reductions of 35% in L4, 36% in L7, and 49% in wheat when averaged across years was considered. Thinning at anthesis had no effects on grain yield in both species in 2008 and 2009; however, in 2010, this treatment reduced grain yield in wheat by 34%, and in triticale grain, yield was increased in 23% for L4 and 18% for L7.

Defoliation decreased AGDM in both species being the magnitude in 30%, 29%, and 28% for L4, L7, and wheat, respectively. Shading marginally affected AGDM, being L7 the most affected (19%) and wheat the least affected (only 3%, Table 1). The degraining treatment reduced AGDM in 5%, 6%, and 13% for L4, L7, and wheat, respectively. The HI was affected only by degraining treatment 34% L4, 31% for L7, and 41% for wheat cultivar when the average of years was considered, as the other treatments were statistically similar to their respective controls (Table 1).

Genotypes differed in NG m^{-2}, IGW, NGS, and NGSP ($P < 0.001$; Table 2) between the environments explored. There was significant ($P < 0.01$) variation for all variables among the genotypes examined, and these differences between genotypes were due to differences between TCL and W, and among the TCL genotypes (Table 2). Triticale genotypes had higher NG m^{-2} in the three experiments. As

expected, degraining at anthesis reduced NG m^{-2}; likewise, the defoliation and shading decreased NG m^{-2}. A significant ($P < 0.05$; Table 2) year × genotype interaction was observed in NG m^{-2} ($P < 0.001$; Table 2). The removal of all leaves at anthesis reduced the number of grains per unit area in 30%, 8%, and 10% for L4 compared to control (Table 2), 20%, 3%, and 16% for L7, and 13%, 7%, and 26% in wheat in the years 2008, 2009, and 2010, respectively. Reductions of the incident radiation minimized the number of grains per unit area for 2008, 2009, and 2010 cycles in 11%, 5%, and 26% for L4, 24%, 16%, and 34% for L7, and 31% for wheat only in 2010 (Table 2). A similar trend but of greater magnitude was observed in the degraining treatment, where L4 had reductions of 53%, 51%, and 25%, similar values of reduction for wheat (53%, 39%, and 51%), while for L7, it only was reduced by 43%, 29%, and 42% (Table 2). The thinning treatment did not cause significant reductions in the number of grains per unit area, except in 2010 by 20% for wheat.

Individual grain weight showed a wide range of variation among genotypes and treatments ($P < 0.001$; Table 1). Values of IGW varied from 35 to 58 mg·grain^{-1} in L4, in L7 from 35 to 55 mg·grain^{-1}, and from 32 to 44 mg·grain^{-1} for wheat in the three experimental years.

The individual grain weight (IGW) in triticale was 26% higher than wheat when considering only the controls in 2008 (Figure 3(a)), 29% in 2009 (Figure 3(b)), and 22% in 2010 (Figure 3(c)). The IGW was more stable in wheat than

TABLE 2: Number of grains per unit area (NG m^{-2}) (grain number from tillers and main shoots), individual grain weight (IGW), number of grain per spike (NGS), and number of grains per spikelet (NGSP) for two triticale cultivars (L4 and L7) and one of wheat (W) in five source-sink manipulation treatments. Data correspond to three experimental cycles.

Cultivars	Source-sink treatments	NG (m^2)			IGW (mg grain^{-1})			NGS			NGSP		
						Years							
		2008	2009	2010	2008	2009	2010	2008	2009	2010	2008	2009	2010
	Defoliation	14736	18632	10019	42	35	42	67	71	54	2.2	2.5	1.9
	Shading	18810	19280	8162	54	47	50	73	79	45	2.5	2.8	1.6
L4	Degraining	9866	9952	8274	58	51	54	43	53	42	2.8	3.5	3.0
	Thinning	20287	19775	13315	56	49	49	82	94	66	2.7	3.3	2.1
	Control	21031	20251	11094	54	47	49	73	78	66	2.3	2.9	2.3
	Defoliation	16626	17693	11281	44	36	35	42	48	40	1.5	1.9	1.9
	Shading	15849	15176	8805	52	44	46	47	49	43	1.7	2.0	1.8
L7	Degraining	11903	12899	7724	54	46	52	30	36	33	2.1	3.0	2.5
	Thinning	17592	18772	15596	55	43	45	58	68	52	2.1	2.7	2.0
	Control	20734	18173	13359	53	46	45	57	67	44	2.1	2.6	1.8
	Defoliation	16588	15398	9954	41	32	37	36	36	39	1.6	1.6	2.3
	Shading	17980	18333	10773	43	34	37	39	41	41	1.7	1.8	2.1
W	Degraining	8989	10135	6556	40	34	37	22	22	24	2.0	2.0	2.7
	Thinning	18137	16623	9222	44	36	36	42	43	47	1.9	1.9	2.3
	Control	19101	16615	13461	43	35	39	41	41	45	1.8	1.8	2.6
HSD ($P \leq 0.05$)		6041	4127	4344	4.4	6.1	5.9	4.2	6.0	4.2	0.3	0.3	1.1
Years (Y)			***			***			***			ns	
Genotype (G)			**			***			***			***	
TCL vs. W			***			***			***			***	
L4 vs. L7			***			***			***			***	
Y * G			*			***			***			***	
Treatments (T)			***			***			***			***	
Y * T			***			**			***			***	
G * T			***			***			***			***	
Y * G * A			**			ns			***			***	

TCL: triticale; W: wheat.

triticale in the source-sink manipulation treatments in the three experimental cycles (Figure 3).

The individual grain weight (IGW) in triticale was reduced ca. 19% with defoliation treatment in 2008 and 2010 (Figures 3(a) and 3(c)) and 24% in 2009 (Figure 3(b)) compared to wheat that was not affected (Figures 3(a)–3(c)). The thinning and shading treatments did not significantly affect the IGW of the three cultivars in the three experimental cycles. However, the degraining treatment increased the IGW in L4 9% in 2008 (Figure 3(a)) and 17% in 2009 and 2010 (Figures 3(b) and 3(c)), while in L7, IGW observed only increases of 10% in 2010 (Figure 3(c)), whereas the increases observed in wheat were not significant (Figure 3).

The cultivars differed significantly in the number of grains per spike, where triticale showed a significantly higher number of grains per spike (72% in L4 and 34% in L7 in average for the three experimental cycles) than wheat when only the controls were considered (Table 2). Reductions in the source size (defoliation at anthesis) affected the number of grains per spike in both species, being L7 the most affected (21% in average in the three experimental cycles) (Table 2); the reduction in wheat was only 13% and 12% for L4. On the contrary, reductions in incident radiation affected only triticale cultivars; L4 was affected only in 2010 in 32%, while L7 was affected in 18% and 27% in 2008 and 2009, respectively. In the contrary, thinning treatment in triticale

significantly increased the number of grains per spike in 12% and 21% in 2008 and 2009 for L4 and 18% for L7 in 2010, while wheat showed no changes in this component (Table 2).

The number of fertile florets at anthesis was positively correlated with the spike's dry weight at anthesis, with an average higher dry weight in triticale than wheat, producing more fertile florets per spike (Figure 4). For all treatments, the number of grains per spike was related to the number of fertile florets at anthesis mainly in the 2008 and 2009 cycles ($r^2 = 0.87$, $P < 0.001$; Figure 5(a); $r^2 = 0.82$, $P < 0.001$; Figure 5(b)).

In this sense, the source-sink manipulation treatments differentially affected both species, as increasing source (thinning and degraining) increased set of number of grains immediately after anthesis (Figure 5). It was clear that almost 100% of fertile florets at anthesis set as grain in wheat in the three experimental cycles, while in triticale (L4) the percentage of fertile florets with no grain setting (abortion) was around 18%, 22%, and 36% for the controls in 2008, 2009, and 2010 respectively (Figure 5). The decrease of source in triticale (defoliated) increased the abortion of fertile florets by 26%, 31%, and 49% average of two cultivars, respectively (Figure 5).

On the contrary, the shading treatment increased the abortion of fertile florets by 21%, 26%, and 41% in 2008, 2009, and 2010, respectively. Degraining treatment favored
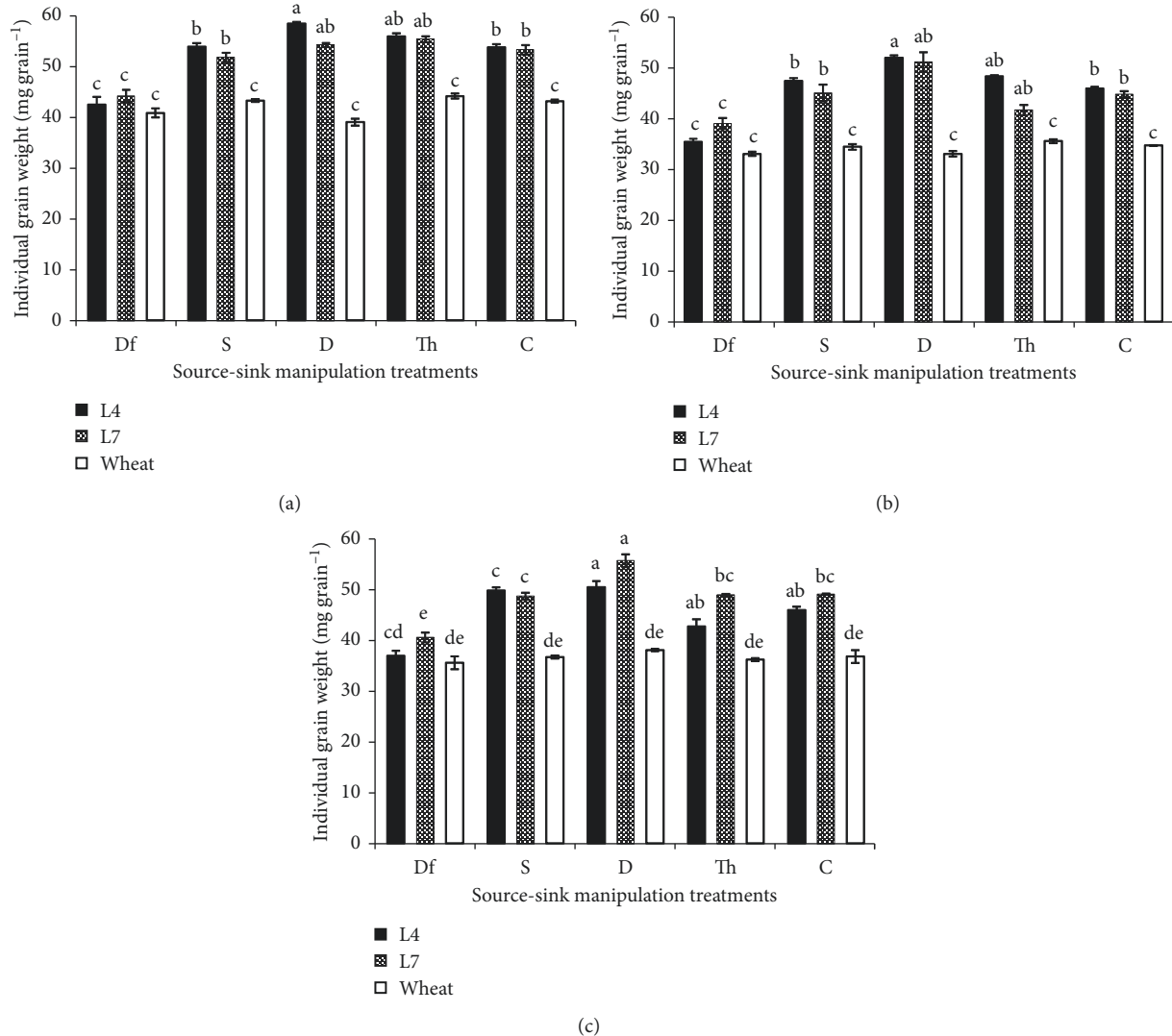
(a)

(b)

(c)

FIGURE 3: Individual grain weight (IGW) in 2008 (a), 2009 (b), and 2010 (c) for the control (C), degraining (Dg), thinning (Th), shading (S), and defoliation (Df) in two triticale cultivars (L4 and L7) and one wheat. Same letter above bars indicate no difference at 0.05 of the HSD test.

setting grain ca. 100% in both cultivars of triticale only in 2008 and 2009, while in 2010, the setting of grains was only 83% in triticale.

In triticale, source increases by thinning treatment resulted in setting grain ca. 94% in 2008 and 2009 (Figures 5(a) and 5(b)), while in 2010, the setting grain was ca. 83% because the reduced abortion of fertile florets respect to its controls (Figure 5(c)).

4. Discussion

The source-sink manipulation treatments allow understanding whether a crop is limited by the source or sink or co-limited by both [8]. In this work, different source-sink manipulation treatments were evaluated to elucidate the physiological bases of changes in the yield of triticale and wheat.

Triticale produced more above-ground biomass at physiological maturity than wheat, and this is consistent

with previous reports in the literature [20], indicating that triticale may be more efficient for radiation use than other cereals. The higher grain yield of triticale compared to wheat was associated with increased biomass production, like that reported in other studies (e.g., [21, 22]). On the contrary, variations in yield due to cultivars and treatments were explained mainly by variations in the number of grains per unit area rather than the individual grain weight, and this relationship has been reported in other cereals [2, 20].

The source-sink manipulation treatments differentially affected the physiological and numerical components of yield in triticale and wheat. Reductions in source (defoliation and/or shading from anthesis) show that the yield of triticale was more sensitive (38% defoliation and 19% shading) than wheat (19 and 6%, respectively) to these treatments. Reductions in grain yield due to defoliation at anthesis observed in this study for wheat agree with those found by Zhenlin et al. [23], who reported reductions of
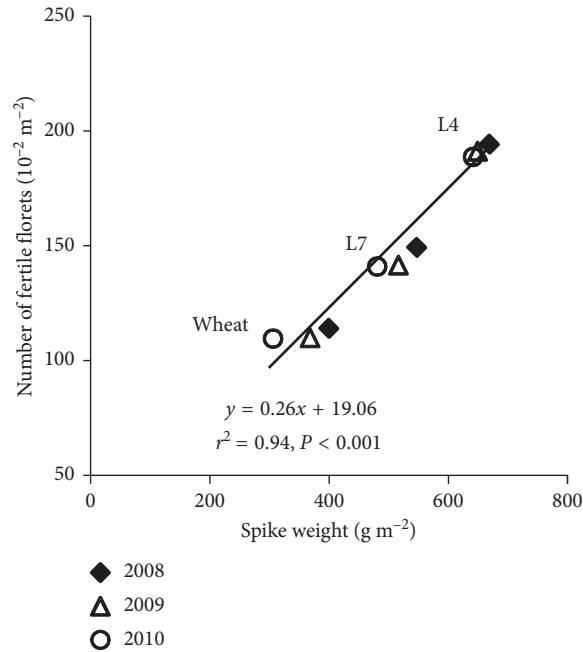
FIGURE 4: Relationships between number of fertile florets and spike weight at anthesis (only main shoots) in two triticale and one wheat cultivars. Data correspond to three experimental cycles.
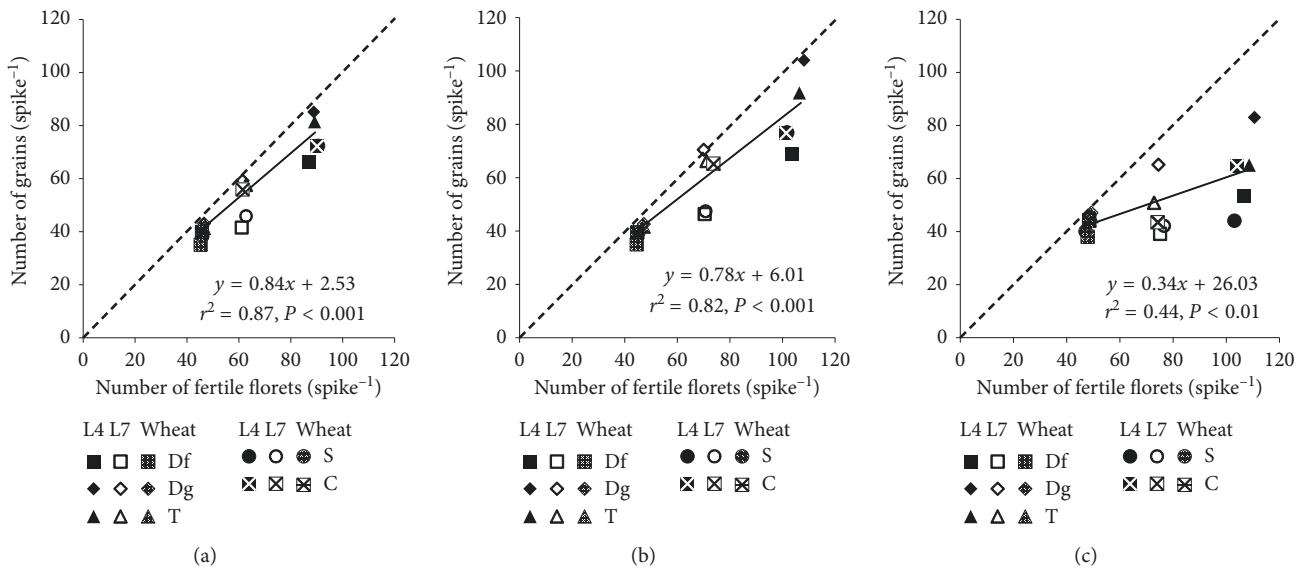

FIGURE 5: Relationship between number of grains per spike and number of fertile florets per spike in 2008 (a), 2009 (b), and 2010 (c) for the control (C), degraining (Dg), thinning (Th), shading (S), and defoliation (Df) in two triticale cultivars (L4 and L7) and one wheat (W).

15% when defoliation was partial and only in the main stem. In contrast, Singh and Singh [24] showed up to 40% reductions in grain yield in wheat when the main stem defoliation was total, coinciding with the observed reductions in triticale in this study. The restriction of incident radiation (shading) more affected grain yield of triticale than wheat mainly by changes in the number of grains per unit area. It has been reported that triticale is mostly affected by reductions in the levels of incident radiation around anthesis compared to wheat [5] or during spike growth stage [25, 26]. The IGW was greater in triticale than wheat; however, the grain weight in wheat was much more stable than that of triticale to changes in the availability of assimilates, agreeing with previous reports by Miralles et al. [27] who observed that increasing the source-sink relationship did not modify the grain weight in wheat. In contrast, Chowdhary et al. [28] reported that defoliation in spring wheat causes a decreased weight of 13.27%. The elimination of spikelets on one side of the spike (degraining) increased in grain weight about 8% in triticale,

whereas no change was observed in wheat. Contrary defoliation reduced grain weight in triticale (20%) and wheat (6%) with respect to the controls. The observed value in triticale is consistent with Simmons et al. [29] and Álvaro et al. [30] who reported that the reduction in the number of grains per spike in wheat increased the final grain weight, while defoliation reduced it. On the contrary, Alam et al. [31] showed that the elimination of 50% of spikelets increased the weight of grains by 9.44% and reported that the elimination of 25% of spikelets increased the weight of grains in a 4.08%. Roy and Salahuddin [32] studied the effect of the removal of spikelets at anthesis in wheat and reported that this treatment increased the average grain weight by 14%. The results show that the increased availability of assimilates (thinning and degraining) had a clear impact on grain setting in triticale, but not in wheat as it remained without significant changes.

The number of fertile florets in anthesis was related with the dry weight spike in the same stage, and this is in line with evidences reported in wheat [6], barley [7], and triticale [5] that showed that dry weight spike at anthesis explained the variations observed in the number of fertile florets. However, differences were observed between triticale and wheat in the number of fertile florets because triticale had a greater dry weight spike at anthesis that wheat. The results show that there is a threshold number of fertile florets that the plant can sustain with current assimilates, which is consistent with evidence in wheat [6] and triticale [5], who state that above 70 fertile florets abortion tends to increase. Accordingly, future studies should be designed to elucidate the causes of high percentage of florets abortion characterized as fertile at anthesis in triticale, which could make the most profitable crop in comparison with wheat.

Data Availability

The data of the analyzed variables are found on the one hand in the relationships shown in the manuscript, in the table that contains the averages of each one of them and in the bar figures. The way in which they were obtained is described in materials and methods.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this article.

Acknowledgments
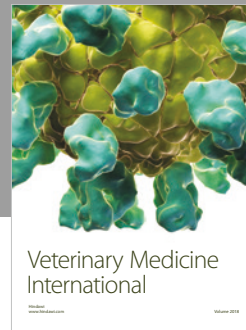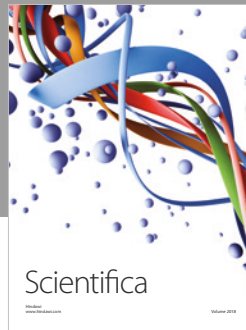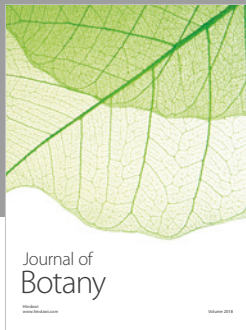
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