Combining high grain number and weight through a DH-population to improve grain yield potential of wheat in high-yielding environments

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ABSTRACT

Previous yield gains in wheat have been achieved through increased expression of grain number per unit area, while fruiting efficiency has also been shown to explain improved grain number. However, combining a high grain number and weight in the same genotype is a difficult task in practical breeding. This study evaluated the progeny of a cross between two elite parents that contrast in grain number and grain weight, as a way to better understand how the two desired traits might be combined to achieve a significant boost in yield. The two parents are both high biomass elite spring wheat lines that achieve high yield through contrasting strategies: Bacanora achieves high grain number with a high density of relatively small spikes. Weebil has a lower density of larger spikes in which larger grain size is expressed. The specific objectives of this research were: (i) to evaluate grain yield performance of DH lines and parents over two seasons, (ii) to identify promising physiological traits explaining high yield performance and (iii) to determine whether these traits are also expressed at the low plant densities. Two experiments were carried out under field conditions in southern Chile where the highest yield potential of wheat has ever been recorded. In Exp. 1 the performance of the 105 spring wheat DH lines, their parents and a Chilean spring cultivar (Pandora-INIA) with similar phenology were assessed together. Results showed that it is possible to increase yield potential by combining high grain number and grain weight, thereby reducing the trade-off between both components. 42 and 50% of the DH lines showed transgressive segregation in S_1 and S_2, respectively. 3 and 4% of the DH lines yielded between 15,000 and 16,000 kg ha^{-1}. Grain yield was highly correlated with above-ground biomass ($R^2 = 0.78$, $p < 0.0001$ in S_1 and $R^2 = 0.77$, $p < 0.0001$ in S_2) and grain number ($R^2 = 0.69$, $p < 0.0001$ in S_1 and $R^2 = 0.71$, $p < 0.0001$ in S_2), whereas no correlation was found with either harvest index or grain weight. In Exp. 2, the high-yielding DH lines selected from Exp. 1 showed on average 45% higher grain yield ($p < 0.01$) than the Chilean checks. Differences in yield between the DH lines and the checks were explained by grain number m^{-2}, which was closely related to grain number spike^{-1} and fruiting efficiency. The latter trait was in line with faster post-anthesis spike dry matter accumulation, explaining in turn the higher radiation use efficiency of the selected DH lines recorded during this period. When comparing yield and its components at different plant densities, grain yield and both main yield components showed strong correlations between environments as a result of increased expression of grains spike^{-1} ($p < 0.001$) under low plant density that was able to offset the reduction in spike number m^{-2} ($p < 0.001$).

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1. Introduction

Gains in wheat yield have slowed in recent decades (Acreche et al., 2008; Tweeten and Thomson, 2008; Reynolds et al., 2012). The exponential growth of 3.2% y^{-1} recorded in 1960 declined to 1.5% y^{-1} in 2000, and it is projected to be only 0.9% y^{-1} by 2050 (Fischer et al., 2009), insufficient to match the demand (Tweeten and Thomson, 2008) of a global population that is expected to reach 9.1 billion in 2050 (FAO, 2009). Therefore, crossing strategies aimed at boosting wheat yield potential must be improved, especially in favorable environments where yield gains have the greatest impact on global productivity. In Chile, genetic gain in yield potential has been modest for both spring and winter wheats during the last decades (Mellado, 2000; Labra, 2012; Matus et al., 2012).

Genetic improvement of wheat yield potential carried out in the last 60 years has resulted from the improved expression of harvest index (HI), while biomass has been less affected (Austin et al., 1980; Slafer et al., 1990; Calderini et al., 1999; Foulkes et al.,

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2009). Although HI has a theoretical limit of 62% (Austin et al., 1980), the value of 55% has not been passed in over two decades (Foulkes et al., 2009; Gaju et al., 2009), suggesting further improvement will be challenging. In addition, recent genotypes are within the range of plant height that maximizes yield, i.e. between 0.7 and 0.9 m (Richards, 1992; Miralles and Slafer, 1995b; Flintham et al., 1997). Therefore, it is expected that further improvements in grain yield would be more associated with increases in biomass production, accompanied by higher radiation use efficiency (RUE), while maintaining present HI values (Calderini et al., 1997; Foulkes et al., 2009; Pedro et al., 2011; Sadras and Lawson, 2011). This trend has already been observed for cultivars released in recent decades, which have shown yield genetic gains based on a combination of improved growth rates in the pre-anthesis period and higher RUE (Shearman et al., 2005; Sadras and Lawson, 2011). Improvement in photosynthesis is considered a pre-requisite for increasing genetic yield potential in wheat (Parry et al., 2011; Reynolds et al., 2012).

Regarding numerical yield components, past grain yield increases have been positively associated with grain number per area (Calderini et al., 1999) and grains spikelet^{-1} (Slafer and Andrade, 1993). More recently, fruiting efficiency (the number of grains per spike dry matter at anthesis) has been pointed out as an important trait explaining improved grain number (Abbate et al., 1998; González et al., 2011). Although indirect selection for genotypes with a higher grain number has been effective in the past, the negative correlation often seen between the number of grains and thousand grain weight (TGW) suggests that further increases in the former trait would be partially offset by reductions in average grain weight.

To combine high grain number and weight in the same genotype has been to date a difficult task for wheat breeding. One encouraging strategy to avoid the trade-off between both major yield components has been proposed by Gaju et al. (2009) through selecting genotypes with higher number of spikelets spike^{-1}. These authors showed that genotypes with high spikelet-number also had a higher grain number spike^{-1} and TGW. However, the boost in grains spike^{-1} was reduced as interplant competition increased at conventional plant density. This indicates that selection for higher spikelet number in early generations of core breeding programs may be inefficient in identifying the best lines for improving grain yield and that sensitivity of traits such as fruiting efficiency to plant density needs to be assessed. An alternative strategy, evaluated in the present study, is to cross parental lines contrasting in grain number and grain weight as a way to combine both desired traits. Thus, the objectives of this research were (i) to evaluate grain yield performance of doubled haploid lines derived from the cross between a high grain number and high grain weight cultivars, (ii) to identify promising physiological traits explaining the differences in yield performance and (iii) to determine whether traits enabling genotypes to reach higher yields are maintained at lower sowing densities.

2. Materials and methods

2.1. Field site description, treatments and experimental conditions

Two experiments were carried out on a Typic Hapludand soil at the experimental station of the Universidad Austral de Chile in Valdivia (39°47′S, 73°14′W). Exp. 1 was conducted in two growing seasons: 2008–2009 (S$_1$) and 2009–2010 (S$_2$); whereas Exp. 2 was carried out in 2010–2011. In Exp. 1 the performance of 105 spring wheat DH lines, their parental cultivars and a Chilean spring cultivar (Pandora-INIA), which is widely sown in the country, were assessed. In Exp. 2, the two highest yielding DH lines from Exp. 1

(one was selected in S$_1$ and the other in S$_2$, called hereafter DH1 and DH2 respectively) were compared under two plant densities with two high yielding Chilean cultivars released by two different breeding programs: Pandora-INIA from the National Wheat Program, and Invento-BAER released by one of the most important private-sector Chilean wheat breeders (Semillas Baer).

The DH population derived from the cross of a high number and high weight cultivars with similar grain yield and phenology was especially designed by Drs. Daniel Calderini and Matthew Reynolds to test the above mentioned objectives. The cross between Bacanora and Weebil was carried out in CIMMYT and the DH population was developed by Drs. John Snape and Simon Griffiths in the John Innes Centre (Norwich, UK). The two parents have a coefficient of parentage of 0.305, indicating that they are not close relatives. Both are high biomass elite spring wheat lines that achieve high yield through contrasting strategies: Bacanora produces high grain number with a high density of relatively small spikes. Weebil has a lower density of larger spikes in which larger grain size is expressed. Therefore, the main difference in yield components between Bacanora and Weebil is their high grain number and grain weight, respectively.

Exp. 1 was sown on August 23, 2008 (S$_1$) and September 4, 2009 (S$_2$). In both growing seasons the experiment was set in a randomized complete block design with three replications. Each block consisted of a continuous plot where every genotype was sown in three rows of 1.5 m long (0.15 m between rows), flanked by a row (0.15 m apart and 1.5 m long) of the local spring wheat Pandora INIA at each side and sown at a plant density of 350 plants m^{-2}. In Exp. 2, four genotypes (DH1, DH2, Pandora-INIA and Invento-BAER) were sown on August 22, 2010 at two plant densities (350 plants m^{-2} with conventional plant distribution and at 44 plants m^{-2} with a squared arrangement, i.e. 15 cm × 15 cm). In Exp. 2 the design corresponded to a split-plot arrangement with three replications, where plant density was the main plot and the genotype the sub-plot. Plots of conventional density were 1.35 m wide and 2.0 m long and the ones of low density were squared plots of 1.5 by 1.5 m.

Exp. 1 was fertilized at sowing with 150 kg N ha^{-1}, 300 kg P$_2$O$_5$ ha^{-1} and 150 kg K$_2$O ha^{-1}. An additional fertilization of 150 kg N ha^{-1} was applied at tillering in both seasons. Exp. 2 was fertilized at sowing with 200 kg N ha^{-1}, 300 kg P$_2$O$_5$ ha^{-1} and 150 kg K$_2$O ha^{-1}, while 100 kg N ha^{-1} were added at tillering. All fertilization dosages were designed based on soil analysis guaranteeing that the crop would not suffer for any nutrient limitation. Diseases and insects were prevented or controlled by spraying recommended pesticides as required. Weeds were periodically removed by hand or by chemical applications at the rates recommended by their manufacturers. Water was supplied by irrigation when necessary to complement rainfall in all experiments, avoiding any risk of water stress.

2.2. Plant measurements

In Exp. 1, plants from 0.5 m were harvested from the central row of each experimental unit at maturity and their organs were divided into three categories: spikes, leaf blades and stems plus sheath leaves. After drying for 48 h at 60 °C plant samples were weighed with an electronic balance (Mettler, Toledo XP205DR, Greifensee, Switzerland). Spikes were threshed and grain yield was recorded afterwards. Average grain weight was estimated using three random subsets of grains (100 grains each) per experimental unit. Grain number was calculated as the ratio between grain yield and average grain weight and HI was estimated as the ratio between grain yield and above-ground biomass.

In Exp. 2, phenology was recorded according to Zadoks et al. (1974), following the average phenology of the plot (when 50% of

Table 1
Average minimum (T_{min}), maximum (T_{max}) and mean (T_{mean}) temperatures, and photosynthetically active radiation (PAR) during the emergence-Z31, Z31-flowering and flowering-physiological maturity periods of Exp.1 (S_1 and S_2) and Exp. 2. Values were calculated with the mean duration of the phenological phases of the genotypes.

Exp.	Season	Phenological period											
		Emergence-Z31				Z31-anthesis				Anthesis – physiological maturity			
		T_{min} (°C)	T_{max} (°C)	T_{mean} (°C)	PAR (MJ m^{-2} d^{-1})	T_{max} (°C)	T_{min} (°C)	T_{mean} (C°)	PAR (MJ m^{-2} d^{-1})	T_{max} (°C)	T_{min} (°C)	T_{mean} (°C)	PAR (MJ m^{-2} d^{-1})
1	1	4.0	14.7	9.4	7.7	15.7	6.6	11.1	9.6	19.7	8.7	14.3	11.0
1	2	4.9	14.0	9.5	7.4	18.7	7.6	13.1	12.3	23.2	10.1	16.6	14.3
2	1	5.0	15.4	10.1	7.7	18.5	7.7	13.0	11.0	19.9	8.7	14.4	11.7

the shoots reached a certain developmental stage). Above-ground biomass, leaf area index and radiation interception were registered during the crop cycle. In plots sown at 350 plants m^{-2}, biomass sampling was carried out at Z31, Z32, booting (Z45), heading (Z55), anthesis (Z65), three times during grain filling and at physiological maturity. Thus, 10 biomass samples per plot were harvested during the crop cycle, taking care of always leaving a row acting as border to protect the sampling area. Biomass samples were collected from inner rows of each plot in 0.5 m length, except at maturity, where 1.0 m was harvested. In plots sown at 44 plants m^{-2}, samples of 0.9 m long (six plants) were collected at four time points; i.e. at Z31, Z32, anthesis (Z65) and physiological maturity. In both plant densities, samples were divided into blade leaves, stems plus sheath leaves and spikes when they were present. Individual spike weight was calculated by dividing the total spike weight in the sampling area by the number of spikes present. Leaf area was measured by an area-meter (LI 3100, LICOR, Lincoln, NE, USA) and leaf area index (LAI) was calculated by dividing the leaf area by the sampling surface area. At physiological maturity, grains were separated from other spike structures (chaff) by a blower, similar to in Exp. 1. After that, samples were oven-dried at 60 °C for 48 h and weighed to record grain yield with the same electronic balance than in Exp. 1. TGW was calculated counting all the grains in each sample and dividing total grain biomass by grain number.

Radiation intercepted by the crop was measured from 21 days after emergence to physiological maturity at each experimental unit in Exp. 2. Incident and radiation transmitted to ground level were measured twice a week using a 1 m long linear sensor (LI 191 S, Licor Inc., Lincoln, NE, USA). Transmitted radiation was measured on clear days at noon, by placing the line sensor in the in the left, center and right of the inter-row space between two central rows of each plot. The average of the three measurements was taken as transmitted radiation (Slafer et al., 1990). After anthesis, transmitted radiation was measured along the green line, that is, by rising up the linear sensor as senescence progressed. Intercepted radiation (IR) was calculated as the ratio of the difference between incident and transmitted radiation to incident radiation. The dynamic of IR with time from emergence was estimated by fitting the experimental data to the following polynomial equation:

$$y = ax^5 + bx^4 + cx^3 + dx^2 + ex + f \tag{1}$$

where y is the IR and x represents the days after emergence. To calculate photosynthetically active radiation (PAR) intercepted by the canopy day^{-1}, the corresponding value of incident PAR was multiplied by the intercepted radiation of that day. Incident PAR was averaged every 15 min at the meteorological station of the Universidad Austral de Chile, approximately 200 m from the experimental plots. RUE was calculated as the slope of the linear regression of accumulated above-ground biomass against accumulated PAR intercepted (IPARa) between (a) Z21 and anthesis (RUE pre-anthesis) and (b) between anthesis and physiological maturity (RUE post-anthesis).

In Exp. 2, floral development was measured in DH1 and Invento-BAER in three main shoots per plot by harvesting the shoots once a week from terminal spikelet initiation to 10 days after anthesis. The developmental stage of all florets from one of the central spikelets was assessed using the semi-quantitative scale developed by Waddington et al. (1983), which recognizes different stages from W3 (glume primordia present) to W10 or fertile floret (style curve outwards and stigmatic branches spread wide, pollen grains on well-developed stigmatic hairs). Within each spikelet, florets were identified from proximal to distal positions, with F1 being the floret position closest to the rachis.

2.3. Statistical analysis

The effects of genotype (Exps. 1 and 2), season (Exp.1) and plant density (Exp. 2) on yield and associated traits were assessed by analysis of variance. The LSD test (5%) was employed to evaluate differences among treatments. Potential effects of time to flowering on grain yield were assessed by a log-likelihood ratio test, where time to flowering was considered as a random term. Linear and quadratic regression analyses were used to evaluate the degree of association between variables.

3. Results

3.1. Climatic conditions during the crop cycle in Experiments 1 and 2

The three climatic conditions explored (S_1 and S_2 of Exp. 1 and Exp. 2) had very similar temperatures during the whole crop cycle, as shown in Table 1 (the absolute minimum and maximum recorded over all environments were −1 and 33 °C, respectively). No big differences in levels of radiation were observed between sowings either. Only S_2 of Exp. 1 showed slightly higher values of PAR, especially from Z31 onwards (Table 1).

3.2. Experiment 1: Grain yield and associated traits in the doubled haploid lines, parents and the Chilean cultivars

Grain yield of the DH population, averaged across lines, was 11,912 and 12,143 kg ha^{-1} in S_1 and S_2, respectively (Table 2). Transgressive segregation was found for this trait; i.e., 42 and 50% of the DH lines out-yielded the average yield of the parents in S_1 and S_2, respectively. Moreover, 9 and 8% of the lines yielded between 14,000 and 15,000 kg ha^{-1} in S_1 and S_2; while 3 and 4% yielded between 15,000 and 16,000 kg ha^{-1}, depending on the season (Fig. 1). Variation between seasons was very low as 78% of the DH lines showed less than 10% yield variation, while the highest observed change was 33%. Crop phenology was similar amongst the cultivars and both the highest and lowest yielding DH lines as it was shown by the period between sowing and anthesis, i.e. between 87 and 96 days in S_1 and between 95 and 104 days in S_2 (Table 2). No effect of the length of the crop cycle on final grain yield was observed in this experiment as no association between

Table 2
Grain yield (GY), above-ground biomass (biomass), harvest index (HI), grain number (GN), thousand grain weight (TGW) and days between sowing and anthesis (So–At) of the highest and lowest yielding doubled haploid lines (DH) recorded at each growing season, and average values calculated across the DH lines or parent cultivars (Cvs.) in the first (S_1) and second (S_2) growing season of Exp. 1.

Season	Genotype	GY (g m^{-2})	Biomass (g m^{-2})	HI (%)	GN (grains m^{-2})	TGW (g)	So–At (days)
1	Highest DH (DH1)	1506 a	2780 a	54.3 a	36,224 a	41.7 d	87
	Lowest DH	589 e	1697 d	34.7 e	14,239 e	41.2 d	92
	DH average	1191 bcd	2399 bc	49.5 bc	27,148 c	44.2 c	92
	Bacanora	1164 bcd	2226 c	52.3 ab	30,014 bc	38.7 e	88
	Weebil	1290 b	2443 bc	52.6 ab	28,344 c	45.6 c	93
	Pandora-INIA	1030 d	2298 c	45.0 cd	19,995 d	51.5 a	96
2	Highest DH (DH2)	1607 a	3103 a	51.7 ab	33,634 ab	47.8 b	99
	Lowest DH	607 e	1664 d	36.5 e	14,639 e	41.6 d	99
	DH average	1214 bcd	2514 bc	48.2 bc	27,301 c	44.7 c	97
	Bacanora	1192 bcd	2423 bc	49.3 bc	30,905 bc	38.6 e	95
	Weebil	1262 bc	2615 bc	48.7 bc	27,574 c	45.7 c	99
	Pandora-INIA	1072 cd	2547 bc	42.1 d	21,127 d	50.8 a	104
	Genotype	***	***	***	***	***	
	Season	n.s.	*	*	n.s.	*	
	GxS	n.s.	n.s.	n.s.	n.s.	***	
	S.E.M.	51	73	1.1	1200	0.7	

Different letters indicate LSD test differences ($p < 0.05$). n.s., *, ** and *** mean no significant difference at $p = 0.05$, difference at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. Different letters indicate significant differences between genotypes and seasons.
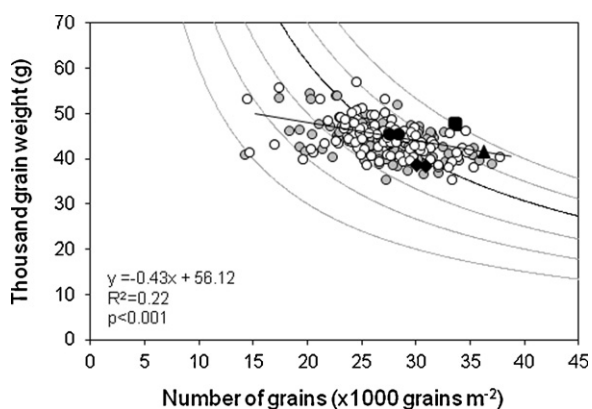

Fig. 1. Relationship between thousand grain weight and number of grains of 105 DH lines in S_1 (white circles) and S_2 (gray circles). The highest yielding line in S_1 (closed triangle), S_2 (closed square), parental cultivars Bacanora (closed diamonds) and Weebil (closed circles) are also shown. Gray isolines show yields of 6000, 8000, 10,000, 14,000 and 16,000 kg ha^{-1}. Black isoline represents 11,270 kg ha^{-1} (yield averaged across the parental cultivars).

grain yield and time to flowering was found in the entire population including Bacanora, Weebil and Pandora-INIA ($R^2 = 0.05$ and 0.01 for S_1 and S_2, respectively). In contrast, grain yield was highly associated with above-ground biomass across all DH lines and cultivars (Fig. 2). A lower association was found between grain yield and HI in this experiment ($R^2 = 0.54$, $p < 0.0001$ in S_1 and $R^2 = 0.41$, $p < 0.0001$ in S_2).

In S_1, the best performing DH line (DH1) out-yielded the average of the parental cultivars by 23% and Pandora-INIA by 46% (Table 2), whereas the highest yielding line in S_2 (DH2) out-yielded the average of the parental cultivars by 31% and Pandora-INIA by 50% (Table 2). Higher yields reached by DH1 and DH2 than the cultivars can be ascribed to greater biomass and grain number and due to higher HI when compared with the Chilean cultivar Pandora-INIA (Table 2). Considering the performance of DH1 and DH2 in the second and first season, respectively, DH1 ranked sixth in S_2 (14,676 kg ha^{-1}) and DH2 reached the second highest grain yield (15,031 kg ha^{-1}) in S_1.

A wide range of grain number and TGW was observed across the lines, i.e. from 14,239 to 37,646 for grains m^{-2} and between 36 and 57 g for TGW. As expected, grain yield was linearly associated with grain number in both growing seasons ($R^2 = 0.69$, $p < 0.0001$ in S_1 and $R^2 = 0.71$, $p < 0.0001$ in S_2) and no correlation between grain yield and TGW was observed in either S_1 or S_2 ($R^2 = 0.01$, $p = 0.437$ in S_1 and $R^2 = 0.01$, $p = 0.36$ in S_2). When the relationship between TGW and number of grains was plotted, only a slightly negative relationship was observed across the lines (Fig. 1). However, when the relationship between grain yield and grain number was evaluated in the highest yielding lines, a curvilinear relationship
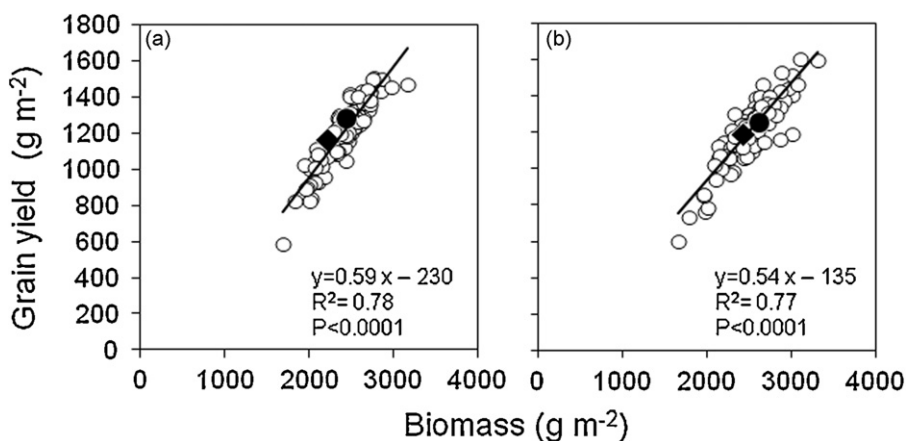
Fig. 2. Relationship between grain yield and biomass of 105 DH lines in S_1 (a) and S_2 (b). The parental cultivars Bacanora (closed diamonds) and Weebil (closed circles) are also shown.
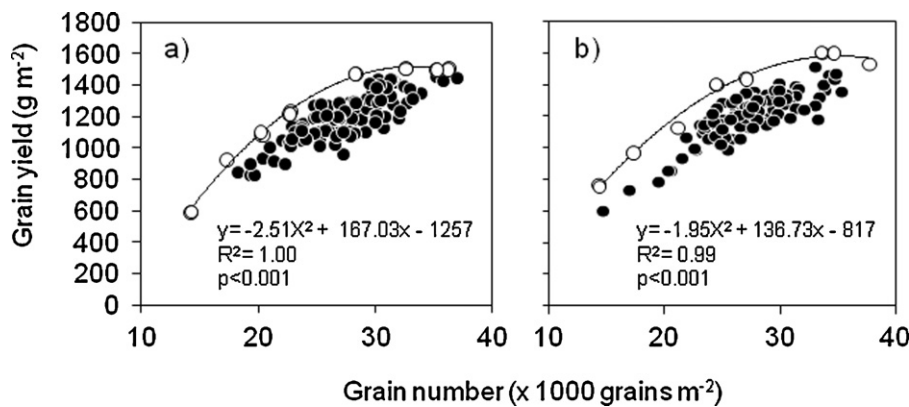
Fig. 3. Relationship between grain yield and grain number of 105 DH lines in S_1 (a) and S_2 (b) of Exp. 1. The highest yields for different grain numbers (open circles) were fitted by a quadratic regression. The other lines are shown as closed circles.

was found (Fig. 3a and b), showing that the strategy of increasing grain yield by higher grain number could be less efficient in the future.

The higher grain yield reached by DH1 was mainly explained by the biomass and grain number achieved by this line over the cultivars (Table 2). Transgressive effects were found in grain number ($p < 0.05$), supporting the strategy of crossing contrasting parents in grain components. Moreover, although grain number was highly increased in DH1, TGW recorded in this line was not different from the parents' average (Fig. 1 and Table 2), reinforcing the hypothesis that it is possible to combine both desired traits and reduce the trade-off between grain number and grain weight. DH1 surpassed the Chilean cultivar Pandora-INIA by 46; 21 and 81% in biomass, HI and GN respectively. In contrast, TGW was 18% lower than in Pandora.

3.3. Experiment 2: assessment of high-yielding DH lines and Chilean cultivars under conventional plant density

In Exp. 2, the two highest yielding lines recorded in Exp. 1 (DH1 and DH2) were evaluated together with the Chilean cultivars Pandora-INIA and Invento-BAER, which were used as checks. These cultivars are widely sown in Chile, especially in the high-yielding environments in the south. As in Exp. 1, similar phenology was recorded in the evaluated genotypes (Table 3). Both DH lines showed higher yield ($p < 0.01$) than the Chilean cultivars, being on average 45% higher than the mean of the checks (Table 3). This difference to the domestic checks is similar to those observed with Pandora-INIA in Exp. 1. In spite of the yield consistency of the DH lines, different strategies were observed between them to achieve the higher yield. For instance, DH2 gain was reached mainly by the higher biomass, while HI was the key trait in DH1 (Table 3). DH2 also showed higher HI than Pandora-INIA but similar to Invento-BAER.

The vegetative biomass recorded at harvest was similar among DH2, Pandora-INIA and Invento-BAER, and lower in DH1 (Table 3). Although genotypes differed in plant height ($p < 0.001$), this trait did not show the same trend as grain yield across genotypes, i.e. the tallest genotypes (Invento-BAER and DH2), reached the lowest and highest grain yield in Exp. 2, respectively.

The highest biomass achieved by DH2 was mainly due to a higher crop growth rate, showing a positive relationship ($R^2 = 0.84$, $p = 0.054$) between both traits across genotypes. Differences in IPARa between genotypes were associated with differences in radiation interception dynamics (Fig. 5a), which can be attributed to the slower increase of LAI shown by DH1 and to the later senescence of Invento-BAER (Fig. 5b). It is noteworthy that DH1 showed smaller LAI during the whole crop cycle, reaching a maximum value of $4.4\,m^2\,m^{-2}$ (Fig. 5b). Despite this, DH1 was able to achieve full radiation interception at the same time as the other genotypes (Fig. 5a), while values of 5.4, 5.6 and $6.0\,m^2\,m^{-2}$ were recorded for Pandora-INIA, DH2 and Invento-BAER, respectively, suggesting a different extinction coefficient between these genotypes. Although these differences no association between total biomass and IPARa was found ($R^2 = 0.01$, $p = 0.94$). On the other hand, both DH lines showed higher RUE compared to the checks, especially at the post-anthesis period (Table 4).
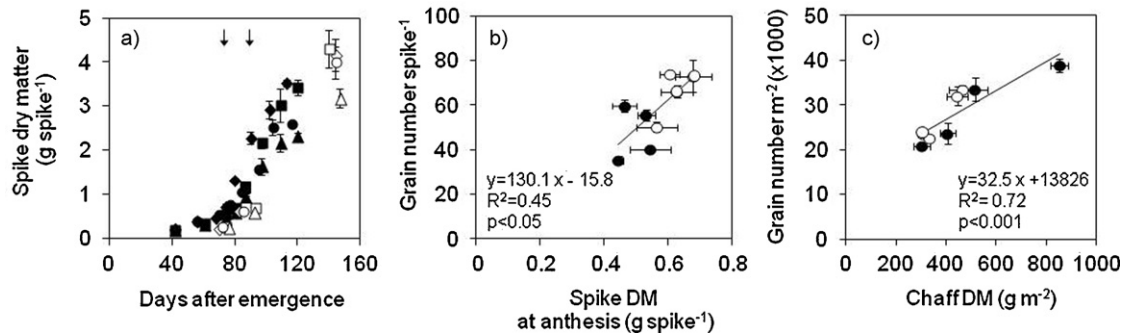
Regarding numerical yield components, grain number consistently explained differences in grain yield ($R^2 = 0.98$, $p < 0.01$). This trait was 62% higher in both DH lines than in the check cultivars (Table 3). Between the DH lines, DH2 reached higher grain number m^{-2} due to increased number of spikes compared with DH1, while grains spike^{-1} was clearly higher in both DH lines than in the checks (Table 4). The later trait was more explanatory of grain yield ($R^2 = 0.83$, $p = 0.057$) than the number of spikes m^{-2} ($R^2 = 0.29$, $p = 0.45$). However, the higher grain number spike^{-1} was not correlated to spike dry weight at anthesis

Table 3
Grain yield (GY), total above-ground biomass (Biomass), harvest index (HI), grain number (GN), vegetative biomass, grain number m^{-2} (GN), thousand grain weight (TGW), plant height and days between sowing and anthesis (So–At) recorded in the doubled haploid lines (DH) selected from Exp. 1 as well as in the check cultivars Pandora-INIA and Invento-BAER sowed at conventional plant density (350 plants m^{-2}). Genotypes are shown according with the ranking of grain yield recorded in Exp. 2.

Genotype	GY (g m^{-2})	Biomass (g m^{-2})	HI (%)	Vegetative biomass (g m^{-2})	GN (grains m^{-2})	TGW (g)	Plant height (cm)	So–At (days)
DH2	1656 a	3573 a	47 ab	1137 a	38,829 a	42.7 d	81.7 ab	100
DH1	1524 a	2990 b	51 a	951 b	33,502 a	45.5 c	75.2 cd	93
Pandora-INIA	1116 b	2684 b	41 c	1139 a	23,656 b	47.2 b	78.5 bc	98
Invento-BAER	1075 b	2516 b	43 bc	1162 a	20,876 b	51.5 a	84.6 a	100
	**	*	**	*	***	***	***	
S.E.M	84.4	142	0.01	33	2338	1.05	1.2	

Different letters indicate LSD test differences ($p < 0.05$). n.s., *, ** and *** mean no significant difference at $p = 0.05$, difference at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. Different letters indicate significant differences between genotypes.

Table 4

Crop growth rate, accumulated intercepted photosynthetically active radiation (IPARa), radiation use efficiency during pre-anthesis (RUE_{pre}), radiation use efficiency during post-anthesis (RUE_{post}) spikes per square meter (spikes m^{-2}), grains per spike and grains per gram of spike dry matter at anthesis (fruiting efficiency) recorded in the DH lines selected from Exp. 1 as well as by the check cultivars Pandora-INIA and Invento-BAER sown at conventional plant density (350 plants m^{-2}). Genotypes are shown according with the ranking of grain yield recorded in Exp. 2.

Genotype	Crop growth rate (g day^{-1})	IPARa (MJ)	RUE_{pre} (g MJ^{-1})	RUE_{post} (g MJ^{-1})	Spikes m^{-2}	Grains spike^{-1}	Fruiting efficiency (grains spike DM$_{at}$$^{-1}$)
DH2	37.9 a	915.5 a	3.8 a	4.7 a	702 b	56 a	129 a
DH1	31.1 a	831.8 b	3.7 a	4.0 a	560 b	60 a	136 a
Pandora-INIA	26.9 c	878.9 ab	3.2 ab	1.9 b	587 ab	40 b	86 b
Invento-BAER	28.9 bc	932.1 a	2.9 b	2.1 b	591 ab	35 b	90 b
	***	*	*	**	*	***	**
S.E.M.	1.3	15	0.1	0.5	22	3	8

Different letters indicate LSD test differences ($p < 0.05$). n.s., *, ** and *** mean no significant difference at $p = 0.05$, difference at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. Different letters indicate significant differences between genotypes.

Fig. 4. Time course of the spike dry matter dynamics of DH1 (diamonds), DH2 (squares), Invento-BAER (triangles) and Pandora-INIA (circles) (a), Relationship between grain number spike^{-1} and individual spike dry matter at anthesis (b), and relationship between grain number m^{-2} and chaff dry matter at maturity (c) sown at 44 plants m^{-2} (open symbols) and at 350 plants m^{-2} (closed symbols). Arrows show the time of anthesis of plants grown at 44 (right arrow) and 350 plants m^{-2} (left arrow).

($R^2 = 0.01$, $p = 0.48$, Fig. 4a), but to increased fruiting efficiency (grain number per unit of spike dry matter at anthesis, Table 4). This finding was confirmed by the performance of DH1, taking into account that it showed a higher number of fertile flowers (Fig. 6) than Invento-BAER (DH1 and Pandora-INIA were not evaluated for floral score). For example, seven to eight flower primordia spikelet^{-1} were initiated at the central spikelets of the spikes in each genotype assessed and only 4–5 and 3–4 primordia reached the fertile stage in DH2 and Invento-BAER, respectively (Fig. 6). Differences in fruiting efficiency were also in line with faster post-anthesis spike dry matter accumulation and spike dry weight at maturity (Fig. 4a). These results could be ascribed to the higher RUE during post-anthesis shown by DH1 and DH2 (Table 4). Although no biomass differences were found at anthesis ($p = 0.26$), the DH2 line reached higher above-ground biomass at maturity, which might be due to the faster allocation of biomass to the growing grains.

3.4. Experiment 2: DH1, DH2, Pandora-INIA and Invento-BAER under low plant density

Despite the eight-fold reduction in plant density, no significant effect ($p = 0.239$) of this variable on grain yield was detected. Low plant density increased HI by 10% ($p < 0.01$), while it reduced above-ground biomass by 13% ($p < 0.01$) and plant height by 14% ($p < 0.001$) and delayed development. In addition, grain number m^{-2} and TGW were not affected. The similar grain number m^{-2} recorded under high and low densities was accompanied by an increase in grains spike^{-1} ($p < 0.001$) under low plant density that compensated for the reduction in spike number m^{-2} ($p < 0.001$). The reduction in number of spikes was relatively smaller than the reduction in plant density because of the increased number of tillers, reaching up to 11 fertile tillers plant^{-1}.

Between genotypes, both DH lines surpassed the checks by 31% when plant density was reduced. A key trait was grain number m^{-2}, which was 42% higher ($p < 0.001$) in both DH lines (Table 5). The higher grain number m^{-2} attained by both DH lines was accompanied by a higher number of grains per unit of spike dry matter at anthesis, reflecting a 94% differences in fruiting efficiency relative to both checks (Table 6). This response is also supported by the higher number of fertile flowers in the evaluated DH lines, reaching 5–6 flowers in DH2 and 4–5 in the Invento-BAER. Although genotypic differences were found among them in biomass, HI and TGW, they showed a less clear association with grain yield than grain number across genotypes (Table 5). DH lines reached on average 17% higher biomass ($p < 0.05$) and 31% higher RUE ($p < 0.01$) than the checks, and when both variables were plotted a positive correlation ($R^2 = 0.93$, $p < 0.05$) was found. However, these calculations need to be taken with caution since only four time points were used for RUE under low density. No association was recorded between biomass and IPARa ($p = 0.84$), which was smaller ($p < 0.001$) than at conventional plant density (Table 6). Invento-BAER reached almost full interception though a lower LAI was recorded (4.2 and 6.0 at low and high densities, Fig. 5b).

Across genotypes and densities, spike fertility was a key trait for attaining similar grain number at conventional and low plant densities. For example, grain number spike^{-1} was positively associated with individual spike weight at anthesis (Fig. 4b) as well as grains m^{-2} and chaff dry matter m^{-2} ($R^2 = 0.72$, $p < 0.01$, Fig. 4c). Further evidence was the higher number of fertile flowers in the central spikelets in both genotypes evaluated here: DH1 and Invento-BAER at 44 and 350 plants m^{-2} (Fig. 6). These genotypes were also the most contrasting in grains spike^{-1} among the four genotypes evaluated. In addition, no interaction ($p < 0.05$) between genotype and plant density was found for any trait, suggesting that selection for increased grain yield, biomass, HI, grain number and TGW in early generations of core breeding programs could be efficiently evaluated in order to identify promising genotypes.

Table 5
Grain yield (GY), total above-ground biomass (Biomass), harvest index (HI), grain number (GN), vegetative biomass, grain number m^{-2} (GN), thousand grain weight (TGW) and plant height shown by the DH lines selected from Exp. 1 as well as by the check cultivars Pandora-INIA and Invento-BAER sown at low plant density (44 plants m^{-2}). Genotypes are shown according with the ranking of grain yield recorded in Exp. 2.

Genotype	GY (g m^{-2})	Biomass (g m^{-2})	HI (%)	Vegetative biomass (g m^{-2})	GN (grains m^{-2})	TGW (g)	Plant height (cm)
DH2	1440 a	2767 a	52 a	881 b	32,027 a	44.9 b	69.9 a
DH1	1481 a	2785 a	53 a	770 b	33,421 a	44.2 b	63.9 b
Pandora-INIA	1048 b	2141 b	49 ab	1097 a	22,447 b	46.7 ab	69.8 a
Invento-BAER	1182 b	2585 ab	46 b	792 b	23,533 b	50.2 a	71.4 a
	**	*	*	**	***	*	*
S.E.M	62	100	0.01	44	1568	0.89	1.1

Different letters indicate LSD test differences ($p < 0.05$). n.s., *, ** and *** mean no significant difference at $p = 0.05$, difference at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. Different letters indicate significant differences between genotypes.

Table 6
Crop growth rate, accumulated intercepted photosynthetically active radiation (IPARa), radiation use efficiency (RUE), spikes per square meter (spikes m^{-2}), grains per spike and grains per gram of spike dry matter at anthesis (fruiting efficiency) shown by the DH lines selected from Exp. 1 as well as by the check cultivars Pandora-INIA and Invento-BAER sown at low plant density (44 plants m^{-2}). Genotypes are shown according with the ranking of grain yield recorded in Exp. 2.

Genotype	Crop growth rate (g day^{-1})	IPARa (MJ)	RUE (g MJ^{-1})	Spikes m^{-2}	Grains spike^{-1}	Fruiting efficiency (grains spike DM$_{at}$$^{-1}$)
DH2	35.3a	625.2	4.8 a	442 a	73 a	248 a
DH1	33.0 a	558.6	5.0 a	454 a	74 a	220 a
Pandora-INIA	29.2 ab	677.1	3.4 c	341 b	66 a	116 b
Invento-BAER	24.3 b	697.4	4.1 bc	472 a	50 b	125 b
	**	n.s.	**	**	**	*
S.E.M.	1.5	19	0.2	17	3	20

Different letters indicate LSD test differences ($p < 0.05$). n.s., *, ** and *** mean no significant difference at $p = 0.05$, difference at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. Different letters indicate significant differences between genotypes.

4. Discussion

This paper aims to evaluate traits that form part of a selection strategy in the context of crosses between parents with high grain weight on the one hand and high number of grains m^{-2} on the other. This is especially valuable in environments with high yield such as those in southern Chile, where it would be easy to take advantage of improved yielding cultivars, and given that that breeding gains have been low in recent decades (Mellado, 2000; Labra, 2012; Matus et al., 2012).

The gain in grain yield (from 23 to 31%) over the parental cultivars and between 37 and 54% above the Chilean checks demonstrates a quantum leap above the 0.9% y^{-1} predicted worldwide (Fischer and Edmeades, 2010). The fact that the relationship between grain number and TGW observed for the 107 genotypes assessed in Exp. 1 (105 DH lines plus the parental cultivars) was much smaller (less negative) than the one observed in previous experiments (Sadras and Lawson, 2011) might have contributed to the high genetic gain.

An important set of DH lines (42 and 50% in S$_1$ and S$_2$, respectively) combined both desirable traits, reaching a higher grain yield

potential than the parents. This suggests that crossing genotypes expressing high grain number with others expressing high TGW (and with similar yield and biomass) might be a useful strategy to increase yield potential, particularly if the chance to put together both yield components in the same genotype could be facilitated by increasing the number of possible outcomes through a DH population. However, only one cross was evaluated in this paper and although similar levels of transgressive segregation have been observed in other cereals as barley (Borràs et al., 2009), it would be interesting to compare our results with further crosses before making a general recommendation for breeders. Additionally, it would be interesting to assess whether the changes that occurred in TGW could also be achieved at specific positions, to have bigger beneficial impact on quality traits (Calderini and Ortiz-Monasterio, 2003) and milling efficiency (Marshall et al., 1986). In previous papers no consistent grain weight reduction was found in proximal grains when grain number was increased by both breeding (Miralles and Slafer, 1995a) and crop management (Acreche and Slafer, 2006). However, given the curvilinear association between grain yield and grain number due to the higher proportion of smaller distal grains, further increases in grain number would be less effective in the
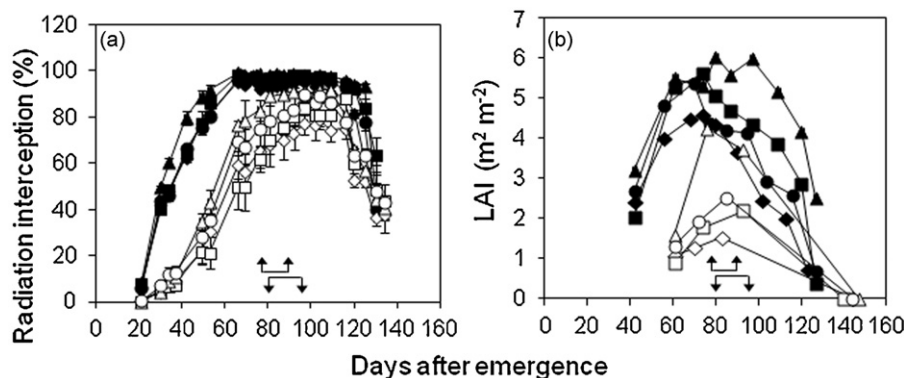
Fig. 5. Time course of radiation interception (a) and leaf area index (b) during the growth cycle for DH1 (diamonds), DH2 (squares), Invento-BAER (triangles) and Pandora-INIA (circles) grown at 44 plants m^{-2} (open symbols) and at 350 plants m^{-2} (closed symbols). Arrows pointing up show the range of observed flowering timing for the four genotypes sown at conventional plant density, whereas arrows pointing down show the range of flowering timing at low plant density.
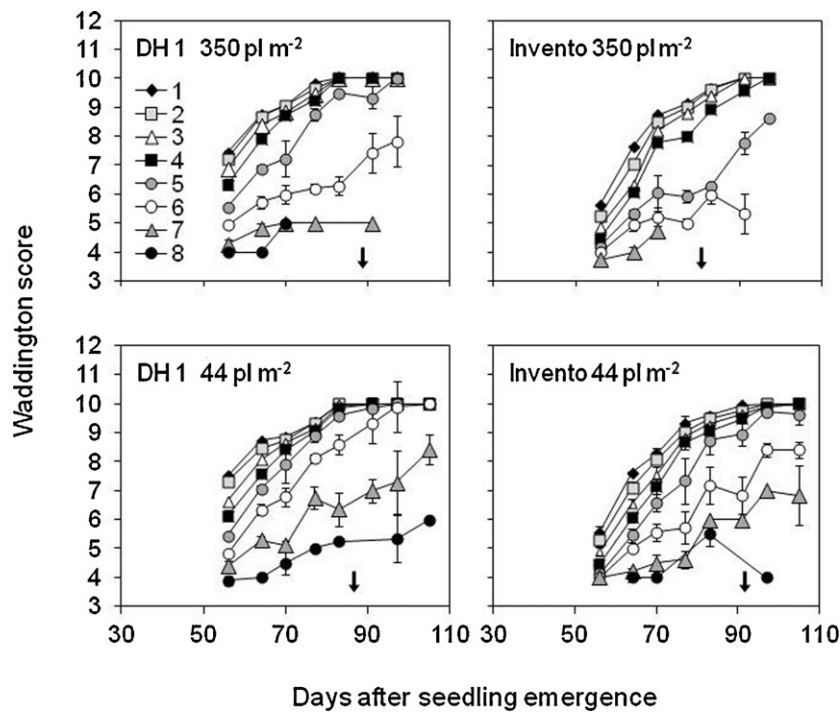
Fig. 6. Time course of floret development within the central spikelet of DH1 and Invento-BAER sown at 44 plants m^{-2} and at 350 plants m^{-2}. Measurements were taken from terminal spikelet initiation to 10 days after anthesis. Timing of anthesis is shown by an arrow and different symbols represent floret positions, with F1 being the floret closest to the rachis and F8 the most distal floret in the spikelet.

future, as was shown in a preliminary evaluation of 60 wheat genotypes (Calderini et al., 2012). Fruiting efficiency has been suggested as constitutive component for grain weight reduction in cultivars maximizing the number of grains set per unit of spike dry weight at anthesis (Ferrante et al., 2012). One strategy to overcome this problem could be to increase grain weight potential at specific positions within the spikelet (Calderini and Reynolds, 2000), rather than breeding for higher TGW.

Only TGW showed genotype by season interaction, suggesting that the response of most of the traits recorded in this study were highly conservative across both seasons. The higher yield attained by the DH1 and DH2 could be ascribed to increased biomass production as well as to improved HI. This is consistent with the trend observed in cultivars released over the last few decades, which showed that biomass production has been improved, albeit only slightly, in the most modern genotypes (Shearman et al., 2005; Sadras and Lawson, 2011).

The higher biomass attained by both DH lines was accompanied by an improved RUE. Although even the checks had a slightly higher RUE compared to that recorded in other environments, e.g. 2.6 g MJ^{-1} (Muurinen and Peltonen-Sainio, 2006; Foulkes et al., 2009) the values of Invento-BAER and Pandora-INIA are similar to previous experiments performed in Valdivia (Valle et al., 2009; Sandaña et al., 2012). Nonetheless, both DH lines showed a higher RUE (29% higher than the checks), especially during the post-anthesis period. This suggests that sink strength can be boosted through combining grain number and grain weight, especially in favorable environments as southern Chile.

There was no clear trend for IPAR among genotypes, supporting the idea that the improvement in RUE holds greater promise than enhancing IPARa to gain a higher biomass (Reynolds et al., 2012). This is especially true when taking into account the highest yielding cultivars released in the last decades, which exhibit source-sink co-limitation after anthesis (Acreche et al., 2009) and under high source reduction in high-yielding environments (Sandaña

et al., 2009). Therefore, higher sink strength, induced by increased spike fertility, could promote faster biomass accumulation during post-anthesis (Ferrante et al., 2012). The former is supported by the fact that RUE during grain-filling can be increased in response to the need for more assimilates (Calderini et al., 1997; Miralles and Slafer, 1997; Reynolds et al., 2005), highlighting the importance of fruiting efficiency to yield determination and the regulatory effect of the sink size on RUE during post-anthesis. However, other complementary traits such as plant height need to be considered in addition to biomass so as to avoid grain loss due to lodging (Foulkes et al., 2011) since DH1 is one of the tallest genotypes and lodging risk is to be expected.

Although conservation of grain yield under an 8-fold reduction in plant density seems surprising, this result agrees with previous studies where similar responses were observed (Spink et al., 2000; Whaley et al., 2000). Regular spacing and delayed development might have contributed to a better radiation capture by the crop. We hypothesize that lower inter-plant competition might have favored spike weight at anthesis, allowing for a higher number of fertile flowers, in agreement with the evidence show by González et al. (2011). Furthermore, Pedró et al. (2012) recently published a paper where low density (<20 plants m^{-2}) and regular spacing were used. In that paper, grain yield was positively correlated to both grain number m^{-2} and spike weight at anthesis. Nevertheless, yield components were not able to fully compensate for the reduction in plant density. This emphasizes the need for a better understanding of the mechanisms involved in yield response to plant density and suggesting that these mechanisms might show a threshold after which wheat plants are no longer able to compensate for reductions in plant density.

5. Conclusions

This study shows that it is possible to increase yield potential by combining high grain number and grain weight and thus reducing

the trade-off between the 2 components. In the DH population evaluated in this study, 3 and 4% of the genotypes yielded between 15,000 and 16,000 kg ha^{-1} in S_1 and S_2, respectively, showing transgressive segregation. Grain yield was highly correlated with above-ground biomass and grain number, while no correlation was found with either HI or grain weight. However, considering the uppermost yield level for a given grain number, a curvilinear relationship was found.

The two highest yielding DH lines attained between 22 and 31% increment compared to the parents and between 37 and 54% higher yields than the Chilean check cultivars. Differences in yield were explained by higher biomass and grain number m^{-2}, which was closely related to grain number spike^{-1} and fruiting efficiency. Differences in fruiting efficiency were also in line with faster post-anthesis spike dry matter accumulation. This might be the cause of the 29% higher RUE observed for both DH lines during grain filling. No general association between total biomass and IPARa was observed, suggesting that RUE played a more important role in biomass accumulation.

Grain yield and grain number m^{-2} evaluated at very low plant density were similar to those recorded for 350 plants m^{-2} due to higher grain number spike^{-1} expression under low density, which in turn compensated for the reduction in spike number m^{-2}.

Acknowledgments

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