Spike Fertility and Duration of Stem Elongation as Promising Traits to Improve Potential Grain Number (and Yield): Variation in Modern Argentinean Wheats

F. G. González,★ I. I. Terrile, and M. O. Falcón

ABSTRACT

The identification of physiological traits that determine grain number (and yield) in modern cultivars, and the possible tradeoffs among them, may help to detect promising traits for breeding to increase yield potential. High-yielding Argentinean wheat (*Triticum aestivum* L.) cultivars were grown under irrigated and high-input conditions during two seasons to study (i) yield and grain number m^{-2} (GN) as a result of stover biomass at harvest (SH) and harvest index (HI); and (ii) spike dry weight at anthesis (SDW$_a$; g m^{-2}) and spike fertility index (SFI; grain number per gram of spike chaff or non-grain spike biomass). Duration of the stem elongation phase (SEP; first node detectable to anthesis) was analyzed as an alternative to increase SDW$_a$. The HI was highly associated with yield differences between cultivars for both years, independently of stem height. In contrast, SH did not vary among cultivars in either season ($P > 0.05$). The GN determined yield differences between cultivars and was highly associated with SFI and SDW$_a$ for both years and cycles. Some cultivars with the same anthesis date showed stable variation for duration of the SEP between years (despite the year × cultivar interaction observed). As the SFI and duration of the SEP were not related, it seems promising to increase GN in a cultivar with high SFI through an increased duration of the SEP (which may yield higher SWD$_a$) or vice versa.

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Abbreviations: BPS$_a$, biomass partitioning to the spike at anthesis; EC, early cultivars; GN, grain number; GW, grain weight; HI, harvest index; LC, late cultivars; PAR, photosynthetic active radiation; RSGR, relative spike growth rate; SDW$_a$, spike dry weight at anthesis; SEP, stem elongation phase; SFI, spike fertility index; SH, stover at harvest.

W HEAT (*Triticum aestivum* L.) production is considered vital to ensure global food security because it provides more calories and protein to the world's diet than any other crop (Chand, 2009). Nevertheless, the growth rate of wheat production has been decreasing since 1985, and nowadays it is even smaller than the population growth rate (Chand, 2009). Under this scenario, there is a general agreement that wheat production has to increase, and most of the increment has to come from improvements in yield, as the cropped area would only marginally increase (Pinstrup-Andersen et al., 1999; Chand, 2009; Reynolds et al., 2009). The improvement of a cultivar's yield potential (i.e., yield without hail, frost, or lodging, and without water, nutrient, or biotic stress) can contribute to improve world production regarding parallel trends between farmers' yield and yield potential in a wide range of environments (Fischer and Edmeades, 2010).

Most past breeding success was based on the increment of the harvest index (HI; proportion of the total biomass partitioned to the grains), without altering the biomass produced at harvest (Austin et
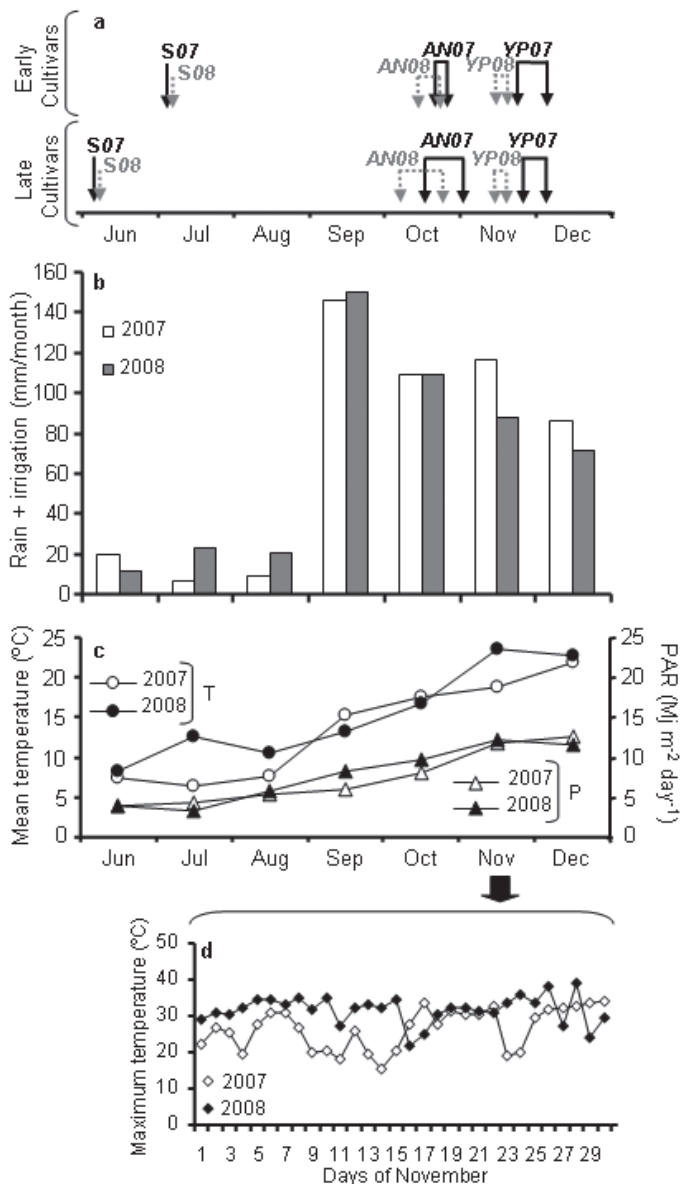
Figure 1. (a) Dates of sowing (S) and range of variation in anthesis (AN) and maturity (estimated as the change in peduncle color from green to yellow, YP) for 2 yr (2007 and 2008) and all cultivars. (b) Monthly rain + irrigation for 2007 and 2008. (c) Mean temperature and photosynthetic active radiation (PAR) for 2007 and 2008. (d) Maximum temperature for November 2007 and 2008.

al., 1980, 1989; Siddique et al., 1989a; Slafer and Andrade, 1991; Sayre et al., 1997; Calderini et al., 1999). The introduction of semidwarf genes to reduce height in the 1960s decreased stem growth and increased assimilate partitioning to the spikes during the stem elongation phase (SEP), improving floret survival and grain number (GN) per spike (Fischer, 1984; Siddique et al., 1989b). During the post–Green Revolution the HI continued to increase, but it has been close to 0.50 since the mid-1980s (Sayre et al., 1997; Reynolds et al., 1999, 2009; Shearman et al., 2005). As the theoretical limit is close to 0.62 (Austin et al., 1980), there still may be scope to increase HI. Alternatively, recent studies observed an increment in yield potential associated with higher biomass at harvest in cultivars released after the mid-1980s (Reynolds et al., 1999; Donmez et al., 2001; Shearman et al., 2005). It has been recently agreed that the GN produced (or sink strength) is still the main factor limiting wheat yield potential in many regions of the world (Reynolds et al., 2009). Understanding the physiology of GN determination in current cultivars in an objective breeding area is useful to identify traits to improve yield potential.

The GN produced depends on spike dry weight per unit area at anthesis (SDW_a) and spike fertility index (SFI; grain number per gram of non-grain or chaff spike at anthesis or harvest) (Fischer, 1984). Yield increments in Argentinean wheat cultivars released during the mid-1980s to mid-1990s were associated with improved SFI (Abbate et al., 1998). Other authors (Shearman et al., 2005; Reynolds et al., 2006) studying different cultivar sets have reported variation of SFI, but found no association of this trait with GN. Most past breeding relied on the increment of SDW_a through improved dry matter partitioning to the spike (BPS_a) (Siddique et al., 1989b; Slafer et al., 1990; Richards, 1992; Slafer and Andrade, 1993; Miralles and Slafer, 1995; Calderini et al., 1999). Further increments of SDW_a could be achieved by lengthening duration of the SEP (which encloses spike growth period) without changing anthesis date (which is close to optimum in common wheat areas) (Slafer et al., 1996, 2001). Altering duration of the SEP through photoperiod environment (Miralles et al., 2000; González et al., 2003; Serrago et al., 2008) or constitution of photoperiod-sensitive genes (*Ppd-1* alleles) (González et al., 2005b) resulted in variations in SDW_a positively associated with the number of fertile florets and grains (González et al., 2003, 2005a; Serrago et al., 2008). Some works have showed cultivar variation in duration of the SEP (Whitechurch et al., 2007), while others found no difference in that trait between cultivars (Abbate et al., 1998; Fischer, 2001). Quantifying the available variation in the traits associated with GN (i.e., SDW_a, SFI, BPS_a, SEP), and the degree of independence between them in current cultivars, may be useful to further improve wheat yield potential. The identification of contrasting cultivars for each one of these traits (but with a similar genetic background for the rest of them) will assist to develop mapping populations, to identify their genetic bases or quantitative trait loci (QTLs) (Slafer, 2003).

In the present study, 39 high-yielding Argentinean wheat cultivars, grouped according to the cycle to anthesis and released to the market from 2000 to 2008, were grown under irrigated and high-input conditions during two contrasting seasons to (i) identify the physiological bases (biomass produced at harvest, HI, SDW_a, SFI, BPS_a, duration of the SEP) of GN (and yield) differences between them; (ii) determine the available variation for those traits and the possible trade-off between them; and (iii) identify contrasting cultivars for each trait to develop mapping populations in the future.

MATERIALS AND METHODS
Growing Conditions and Plant Material

The experiments were performed in the north of Buenos Aires Province (33°51′ S, 60°56′ W), at Pergamino Research Station, National Institute for Agricultural Technology and Husbandry, during 2007 and 2008. The natural rainfall was complemented by irrigation to avoid any sign of water stress (Fig. 1b). At sowing, 110 (2007) or 105 (2008) kg ha^{-1} of a mixed fertilizer (6N, 40P, 5S, 8Ca) were incorporated into the soil together with the application of (i) 275 kg ha^{-1} urea + 25 kg ha^{-1} ammonium sulfate (2007) or (ii) 300 kg ha^{-1} urea (2008). When cultivars reached the beginning of stem elongation (estimated by the detection of the first node, Z3.1) (Zadoks et al., 1974), 160 (2007) or 143 (2008) kg ha^{-1} urea were applied by hand. The total N applied during 2007 was 212 kg ha^{-1}, while the soil N reached 224 kg ha^{-1} during 2008. Pests, diseases, and weeds were controlled by appropriate chemical applications during crop cycle.

The cultivars studied had been released to the market from 2000 to 2008 (Table 1), representing the highest yielding cultivars recommended for the north of Buenos Aires Province (most of them are selected by companies for testing under high-input technology in the National Wheat Cultivar Yield Testing Trials). They were grouped according to their cycle to anthesis in late (LC; 20 cultivars) and early cultivars (EC; 19 cultivars). The cultivars were sown at their optimum dates and plant populations (LC on 4 June 2007 and 3 June 2008 at 250 plants m^{-2}; EC on 3 July 2007 and 1 July 2008 at 300 plants m^{-2}; Fig. 1a).

The temperature during July, August, and November was very contrasting between years (Fig. 1c). 2007 was so cold during the winter that it snowed for 2 d, which is not usual for this region. The average temperature of July and August was 6 and 3°C lower, respectively, during 2007 vs. 2008 (Fig. 1c). The mean temperature in November, when cultivars were filling the grains (Fig. 1a), was 5°C higher during 2008 vs. 2007 (Fig. 1c). This higher mean temperature was associated with maximum temperatures equal to or above 30°C during the first 15 d of November 2008 (Fig. 1d).

Measurements

The dates of emergence (Z1.0) and anthesis (Z6.1) were recorded when 50% of the plants in a plot reached that stage. The dates of first node detectable (Z3.1) were recorded when >50% of 10 main shoots chosen randomly were in that stage. The duration of the SEP (from one node detectable to anthesis) was calculated as days or thermal time (TT = $\sum$mT − bT, where $\sum$ = daily sum during the SEP, mT = mean temperature, and bT = base temperature = 0°C). When each plot reached Z3.1 and Z6.1, the incident radiation over the canopy and the one reaching the soil under the canopy was measured with a 1-m-long integrative bar (Cavadevices.com, Buenos Aires, Argentina) to calculate the intercepted radiation. A linear regression was calculated between the intercepted radiation and the days between Z3.1 and Z6.1. From these equations, the radiation intercepted each day was calculated and multiplied by the daily incoming photosynthetic active radiation (PAR; Mj m^{-2} d^{-1}). Then the accumulated PAR intercepted during the SEP (Mj m^{-2}) was calculated by summing up the daily intercepted radiation. At anthesis, 0.5 m of a central row was sampled and the spikes were removed from the rest of the aerial biomass of the plants. Both fractions were dried for 72

Table 1. Wheat cultivars studied and their year of release (YR) to the market.

Early cultivars		Late cultivars	
Name	YR	Name	YR
Aca 601	2003	Aca 303	2002
Aca 801	2004	Aca 304	2004
Aca 901	2006	Aca 315	2006
Baguette P 13	2001	Baguette P 11	2004
Baguette 9	2007	Baguette 19	2006
BioINTA 1001	2004	BioINTA 2002	2006
BioINTA 1002	2005	BioINTA 3000	2004
BioINTA 1003	2005	BioINTA 3004	2006
BioINTA 1005	2008	Buck Guatimozin	2001
Buck Brasil	2000	Buck Norteño	2006
Buck Bigua	2002	Buck Malevo	2006
Buck Pingo	2002	Buck Ranquel	2006
DM Onix	2004	Buck Baqueano	2007
DM Cronox	2005	DM Themix-L	2007
INIA Condor	2005	INIA Tijetera	2001
INIA Churrinche	2005	INIA Torcaza	2005
Klein Castor	2005	Klein Capricornio	2004
Klein Tauro	2005	Klein Gavilan	2004
Klein Zorro	2007	Klein Guerrero	2007
		Sursem Nogal	2006

h at 65°C in a forced-air oven and then weighed to estimate the SDW$_a$ (g m^{-2}) and the BPS$_a$ as the relation between SDW$_a$/(the rest of the aerial biomass + SDW$_a$). The relative spike growth rate (RSGR; g m^{-2} d^{-1}) was estimated as the relation between SDW$_a$ and the duration of the SEP. At harvest, 0.5 m of another central row was sampled and the spikes were removed from the rest of the aerial biomass. Both fractions were oven-dried and the total biomass was estimated as the sum of the two components. The spikes were drilled in a single spike machine to estimate yield (g m^{-2}) and its components, grain number (m^{-2}) and 1000 grain weight (GW; g). The non-grain biomass produced at harvest, or stover at harvest (SH), was estimated as the total biomass minus yield (g m^{-2}). The SFI (grains g^{-1}) was calculated as the relation between the grain number and the dry weight of spike chaff (non-grain biomass of the spike). Although chaff weight at maturity exceeds spike weight at anthesis, resulting in smaller values of SFI at harvest vs. anthesis, the ranking of cultivars would be unaffected (Fischer, 2001). The HI was calculated as the ratio between yield and the total biomass.

Experimental Design and Statistical Analysis

One experiment was performed each year for each group of cultivars (late and early) and each one was arranged as a randomized complete block design with three replicates. Plots consisted of seven rows 0.21 m apart and 5 m long. The ANOVA was performed (within each group of cultivars) considering years as random effects and cultivars as fixed effects (Infostat/P; Di Renzo et al., 2010). Pearson correlations were used to determine the relationship between some of the analyzed variables.

RESULTS
Main Yield Components

Average yield was higher during 2007 than 2008 for both cycles, LC and EC (632–583 g m^{-2} for LC- and EC-2007, and 474–423 g m^{-2} for LC- and EC-2008) (Fig. 2), but
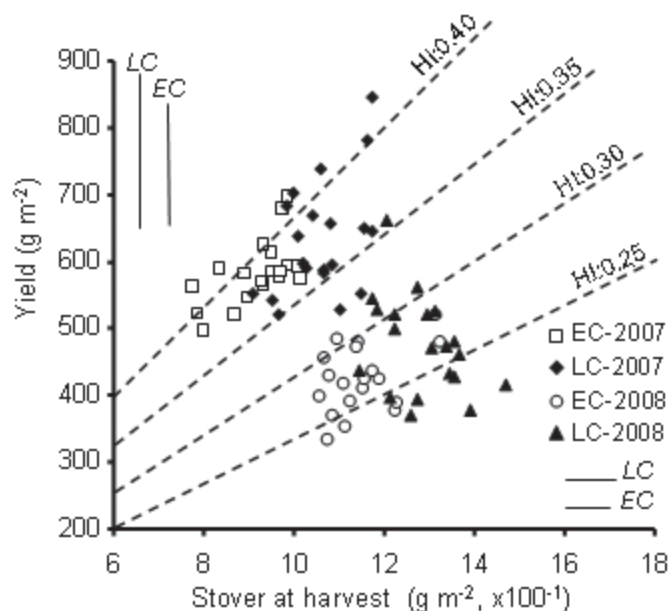
Figure 2. Relationship between yield and stover at harvest for early (EC) and late (LC) cultivars. The dotted lines represent isolines of harvest index (HI) from 0.25 to 0.40. The lines parallel to the *y*-axis and *x*-axis represent 2× standard error of the cultivars' means.

it depended on the year × cultivar interaction for LC (Table 2). The yield of LC ranged from 521 to 845 g m^{-2} during 2007 and from 369 to 661 g m^{-2} during 2008.

The LC tended to increase yield by 364 kg ha^{-1} yr^{-1} (2001–2007), considering for each year of release only the highest yielding cultivar and the better environment of 2007, but it was not statistically significant ($P > 0.05$).

The SH was affected by years, but it was not statistically different between cultivars in any of the cycles (LC or EC) (Table 2). Nevertheless, a positive association between yield and SH was observed for cultivars within each cycle and year ($r = 0.61$ for LC–2007 and LC–2008; $r = 0.66$ for EC–2007 and $r = 0.63$ for EC–2008, $P < 0.001$). In contrast, the HI was greatly modified by the year (it was smaller during 2008 than

2007) and by the year × cultivar interaction, in both cycles (Table 2), ranging from 0.21 to 0.42. The HI explained most yield variations observed in LC and EC within each year and when considering all data together (Fig. 2).

The GN produced depended on the year × cultivar interaction for LC (Table 2), showing a similar range of variation between years (Fig. 3). For EC the range of GN produced was also similar between years (Fig. 3), but it depended only on the cultivar (Table 2). Although a great year impact was observed in grain weight ($P < 0.001$, 21 mg vs. 32 mg 2008 vs. 2007, average for all cultivars), it depended on the year × cultivar interaction for both cycles ($P < 0.001$) (Fig. 3). As expected, GW and GN showed a negative correlation within each year and cycle (Fig. 3), and almost all yield levels could be achieved by different combinations of these components. For example, the cultivars DM Cronox and Baguette 9 pro–duced 22,746 and 17,373 GN (during 2007), respectively, but this difference was balanced by the GW yielding 696 and 681 g m^{-2}, respectively (Fig. 3). In the LC the impact of GN was more evident: yields ≥700 g m^{-2} were only achieved with GN > 20,000 and GW ranging from ca. 35 to 25 g. The general lower yield (and HI) during 2008 in relation to 2007 was due to lower GW and may be associated with the high tempera–ture experienced during November (Fig. 1d), when the grains were actively filling. The GW variations and the effect of temperature (continuous moderate high temperature [Chow-dhury and Wardlaw, 1978]) or heat stress by short periods of high temperature (Stone and Nicholas, 1994), the relationship to GN, and the degree of source limitation during grain fill-ing will be reported in a following paper. From now on, this paper will focus on traits determining GN variations.

Grain Number: Tillers, Spike Dry Weight at Anthesis, and Spike Fertility Index

The number of tillers m^{-2} produced by LC ranged from 528 to 1030, depending on year and cultivar ($P < 0.05$), and was positively associated with GN during both years.

Table 2. Mean squares of the main analyzed variables†.

Source of variation	Yield (× 10³)	SH (× 10⁴)	HI (× 10⁻²)	GN (× 10⁵)	SDW$_a$ (× 10¹)	SFI	SEP	BPS$_a$ (× 10⁻³)
				Late cultivars				
Year (Y)	747*	154*	33.0	801	89.6	410	1672***	0.52
Cultivar (C)	23.2	2.51	0.41	365*	474***	1133*	98.4***	1.90***
Y × C	14.8***	1.38	0.24***	148*	50.4	416*	10.7***	0.11
Error	3.70	3.16	0.06	81.0	111	206	3.60	0.17
CV (%)	11.0	15.1	7.8	13.5	18.4	17.2	4.8	8.5
				Early cultivars				
Year (Y)	724***	152*	41.0***	151	265	115	480***	2.30
Cultivar (C)	9.33	1.93	0.17	16.2*	318**	522***	19.2	2.70***
Y × C	5.21	1.55	0.06*	6.31	78.9	88.9*	11.6***	0.24
Error	3.53	0.97	0.03	5.26	83.2	45.5	2.65	0.26
CV (%)	11.8	9.5	5.5	11.9	17.7	8.0	5.0	10.2

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

† SH, stover at harvest; HI, harvest index; GN, grain number; SDW$_a$, spike dry weight at anthesis; SFI, spike fertility index; SEP, stem elongation phase; BPS$_a$, biomass par-titioning to the spike at anthesis.
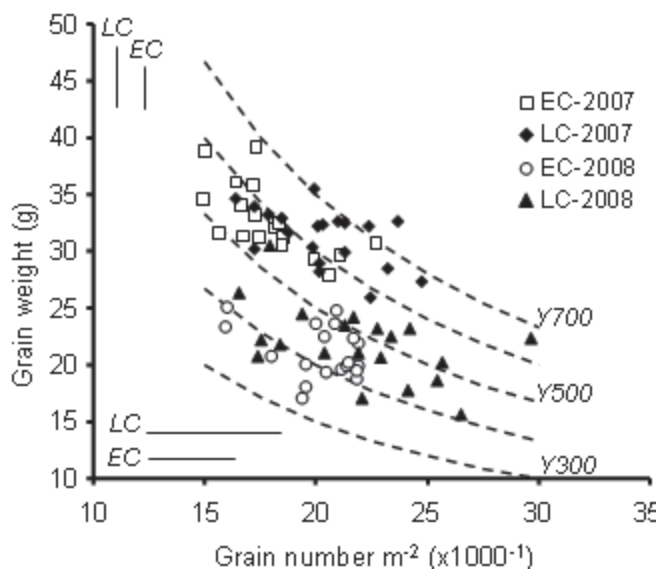
Figure 3. Relationship between grain weight and grain number for early (EC) and late (LC) cultivars (LC-2007, $r = -0.36$; LC-2008, $r = -0.31$; EC-2007, $r = -0.57$; EC-2008, $r = -0.28$; $P < 0.05$ for all cases). The dotted lines represent isolines of yield, from 300 to 700 g m^{-2}. The lines parallel to the y-axis and x-axis represent 2× standard error of the cultivars' means.
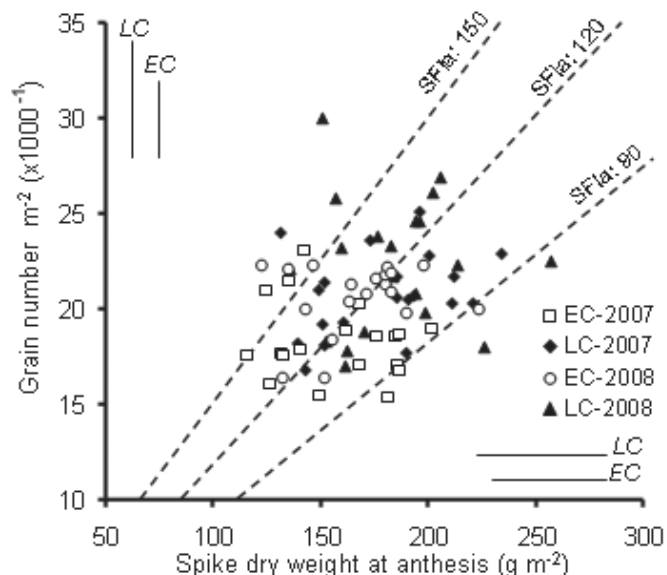

Figure 4. Relationship between grain number and spike dry weight at anthesis for early (EC) and late (LC) cultivars (LC-2007, $r = 0.14$; LC-2008, $r = 0.05$; EC-2007, $r = -0.09$; EC-2008, $r = 0.11$; $P > 0.10$ for all cases). The dotted lines represent theoretical isolines of spike fertility index (SFI) at anthesis (i.e., grain number per gram of spike at anthesis), from 90 to 150 grains g^{-1}. The lines parallel to the y-axis and x-axis represent 2× standard error of the cultivars' means.

In the same group of cultivars, the number of grains per spike, ranging from 22 to 42, was positively associated with GN only during 2008. For EC, the number of tillers m^{-2}, ranging from 433 to 936, was associated with GN only during 2007. Although the number of grains per spike varied from 21 to 40 in the EC, no relation was observed with GN for any year. As expected from numerical component analyses, for both LC and EC, there was a strong negative relationship between the number of grains per spike and the number of tillers m^{-2}.

Considering the crop physiological traits, GN was studied analyzing the SDW$_a$ and the SFI. The SDW$_a$ depended on cultivar for both LC and EC (Table 2), ranging from 130 g m^{-2} (Baguette 11) to 250 g m^{-2} (Buck Guatimozin) for LC and from 120 g m^{-2} (Baguette 13) to 200 g m^{-2} (BioINTA 1002) for EC (Fig. 4). When GN was plotted against SDW$_a$, no single relationship was observed, mainly due to the great differences between cultivars in SFI (Fig. 4). When variation of SFI was considered using isolines of SFI at anthesis (grain number per gram of spike at anthesis), then a relationship could be seen between SDW$_a$ and GN (Fig. 4). Although the cultivar explained most of the variation observed in SFI (see mean squares in Table 2), it depended on the year × cultivar interaction (Table 2). For LC the SFI ranged from 59 to 136 grains g^{-1} and, for similar values of SDW$_a$, it was positively associated with GN during both years (Fig. 4). The EC showed less variation of the SFI, from 64 to 113 grains g^{-1}, but for similar values of SDW$_a$ it was also associated with GN during both years (Fig. 4). Despite the year ×

cultivar interaction for the SFI, extreme cultivars showing no change of their ranking between years were identified within each cycle (e.g., for LC BioINTA 2002 and Buck Baqueano with 63 grains g^{-1} vs. Baguette 11 and Baguette 19 with 106 grains g^{-1}; and BioINTA 1002 with 64 grains g^{-1} vs. Baguette 13 with 100 grains g^{-1}). It is worth mentioning that almost any combination of SFI and SDW$_a$ could be observed in the range from 100 to 200 g m^{-2} of SDW$_a$, but no cultivar was observed with >200 g m^{-2} of SDW$_a$ and >120 SFI at anthesis (Fig. 4).

Spike Dry Weight at Anthesis and Duration of Stem Elongation Phase

The SDW$_a$ is the result of (i) duration of spike growth, here assessed as duration of the SEP, which would modify the amount of accumulated PAR intercepted during that period; and (ii) rate of spike growth, here estimated as the RSGR. Duration of the SEP depended on the year × cultivar interaction, for both cycles (Table 2). Within LC, duration of the SEP ranged from 28 to 40 d and from 32 to 48 d, depending on the year (2007 vs. 2008) (Fig. 5a). In EC duration of the SEP ranged from 26 to 34 d and from 30 to 38 d, also depending on the year (2007 vs. 2008) (Fig. 5a). Duration of the SEP was positively associated with SDW$_a$ for both cycles within each year (r's from 0.34 to 0.39; Fig. 5a). As the intercepted radiation was high (≥80% for all cultivars) from the onset of stem elongation (Z3.1), and achieved >95% at heading, variation in the duration of the SEP resulted in differences in the accumulated PAR intercepted during the SEP (from
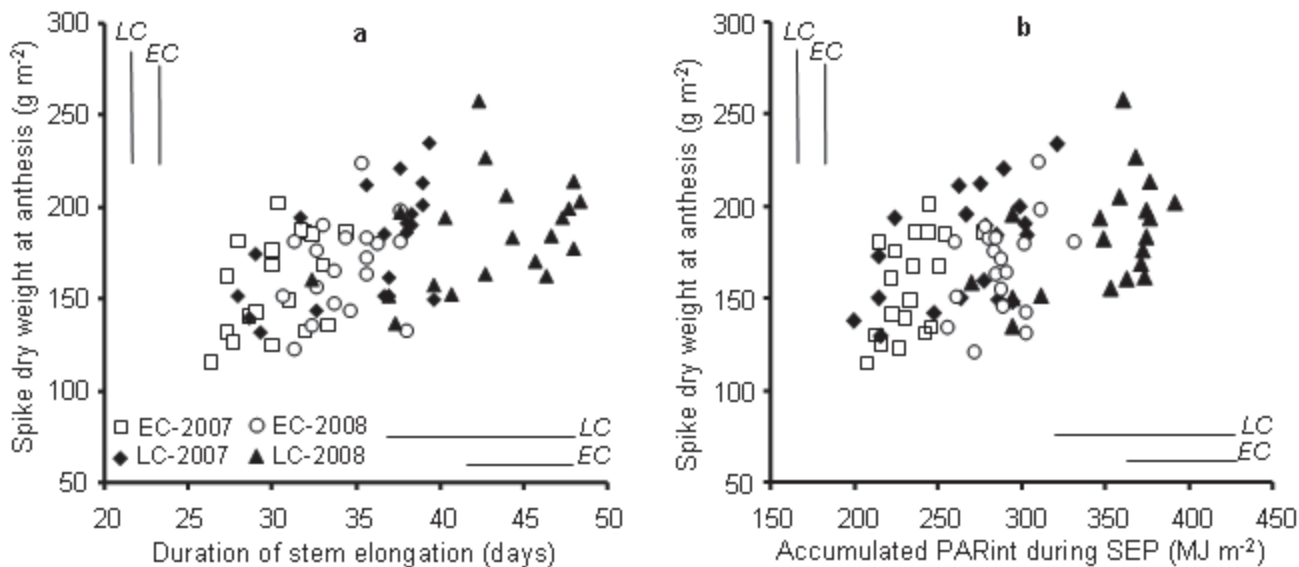
Figure 5. Relationship between spike dry weight at anthesis and (a) duration of stem elongation phase (SEP) for early (EC) and late (LC) cultivars (LC-2007, $r = 0.39$; LC-2008, $r = 0.36$; EC-2007, $r = 0.39$; EC-2008, $r = 0.34$; $P < 0.05$ for all cases); and (b) accumulated photosynthetic active radiation intercepted (PARint) during the SEP (LC-2007, $r = 0.55$; LC-2008, $r = 0.48$; EC-2007, $r = 0.54$; EC-2008, $r = 0.37$; $P < 0.05$ for all cases). The lines parallel to the *y*-axis and *x*-axis represent 2× standard error of the cultivars' means.

200 to 400 MJ m^{-2}). As the accumulated PAR intercepted during the SEP increased, the SDW$_a$ also increased, for both cycles within each year (Fig. 5b). Nevertheless, for the same accumulated PAR intercepted during the SEP, great variation in SDW$_a$ was observed (Fig. 5b). These differences were partially explained by the RSGR, which ranged from 3.5 to 7 g m^{-2} d^{-1}. Neither the years nor the cycles (LC or EC) showed differences in the range or average RSGR (4.7 ± 0.8 vs. 5.1 ± 0.7, LC vs. EC considering the two years). The differences in RSGR resulted in high variation in the BPS$_a$. The BPS$_a$ was clearly a cultivar effect within both LC and EC (Table 2), ranging from 0.11 to 0.19. The BPS$_a$ was not associated with differences in height of the cultivars ($p > 0.10$, except for EC during 2008, $r = -0.83$, $P < 0.01$). The biomass produced at anthesis (without considering SDW$_a$) differed between cultivars within each cycle ($P < 0.05$ for both LC and EC), and was mainly associated with differences in anthesis date (ranging from 14 to 18 d in LC and from 6 to 10 d in EC; LC-2007, $r = 0.45$; LC-2008, $r = 0.55$; EC-2007, $r = 0.25$; EC-2008, $r = 0.63$; $P < 0.05$).

Duration of the Stem Elongation Phase: Variability for the Same Anthesis Date

In previous paragraphs, it was shown that duration of the SEP depended on the year × cultivar interaction, with a variation of 12 to 16 d for LC and 8 d for EC (considering both years). This variability was similar to that observed if the analysis is restricted to those cultivars showing the same anthesis date (Fig. 6). Despite the year × cultivar interaction, at least one pair of cultivars was identified showing similar anthesis date but different durations of the SEP within each cycle (Fig.

6). Although some degree of vernalization requirement was observed for both pairs of cultivars (the thermal time to anthesis was reduced during 2007, which was colder than 2008; Fig. 1c), the differences in duration of stem elongation between the identified pairs were maintained (Fig. 7).

Traits Relationships and Trade-offs

There was no relationship between BPS$_a$ and duration of the SEP (Fig. 8a, except for EC-2007), suggesting that variations of RSGR between cultivars may be associated with differences in daily biomass partitioned to the spike instead of being an artifact due to the methodology used to estimate RSGR. In contrast, a negative relationship was observed between SFI and BPS$_a$ (Fig. 8b). Also, no relationship was found between SFI and duration of the SEP (Fig. 8c), suggesting that they may be improved independently.

DISCUSSION

The improvement of yield potential of cultivars has been a major contributor to increase crop yields (Reynolds et al., 2009; Fischer and Edmeades, 2010) because cultivars with higher yield potential generally express their advantage under a wide range of suboptimal environments (Fischer, 1984, 2007; Calderini and Slafer, 1998; Slafer and Araus, 2007; Reynolds et al., 2009; Fischer and Edmeades, 2010), including water deficits (Richards, 1992), high temperatures (Reynolds et al., 1998), and salinity (Richards, 1995). It is important to quantify the available variation and possible trade-off between the traits associated with GN (and yield) determination in current cultivars to identify useful traits to improve yield potential. In the present study, 39 high-yielding cultivars were studied during two
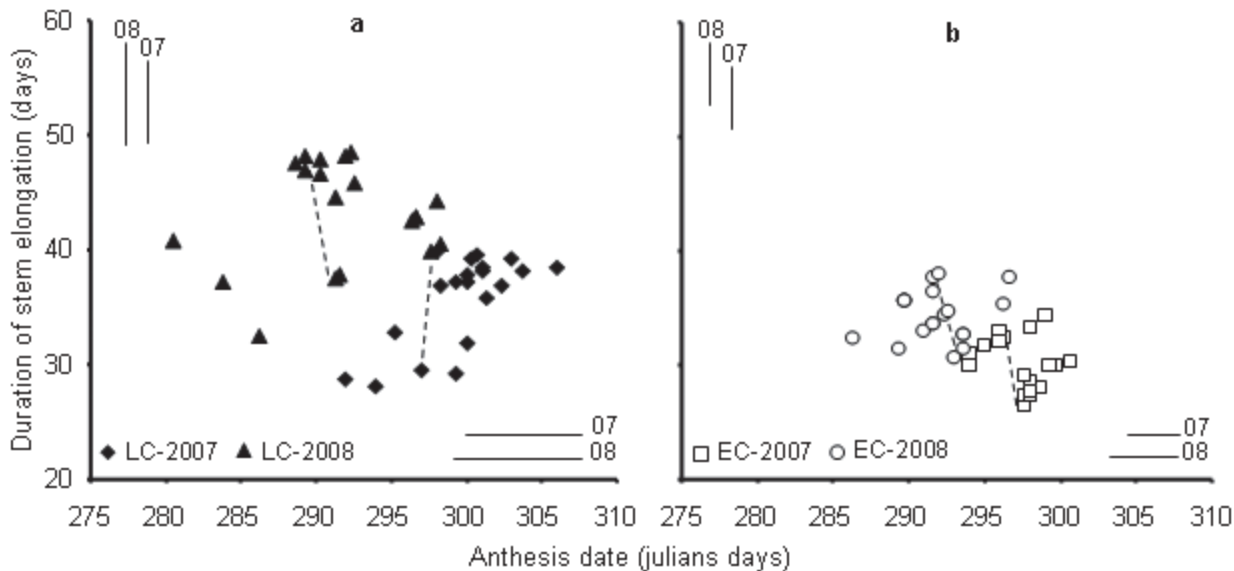
Figure 6. Duration of stem elongation (SEP) vs. anthesis date for (a) late cultivars (LC) and (b) early cultivars (EC). The dotted lines join pairs of cultivars showing similar anthesis date but different duration of the SEP during the 2 yr. The lines parallel to the *y*-axis and *x*-axis represent 2× standard error of the years' means.

contrasting seasons under irrigation, high nutrition, and controlled diseases and pests.

The higher yield potential (particularly within LC) was associated with harvest index (HI) according to most previous papers showing that improved yield potential is generally associated with higher partitioning of biomass to reproductive organs (Austin et al., 1980, 1989; Siddique et al., 1989a; Slafer and Andrade, 1991; Sayre et al., 1997; Calderini et al., 1999; Reynolds et al., 1999; Donmez et al., 2001). Considering the theoretical limit to HI of 0.62 (Austin et al., 1980) and the maximum actual values observed in other areas, ca. 0.50 (Sayre et al., 1997; Calderini et al., 1999; Donmez et al., 2001; Shearman et al., 2005), there seems to be still scope to increase HI in modern breeding, as the maximum observed in the present study was 0.42 (with the highest-yielding cultivars of this region). How to increase HI by increasing GN without altering actual height of the cultivars, which is within the optimum (Richards, 1992; Miralles and Slafer, 1995) is hard to assess, but we discuss various options in the following paragraphs. Few papers reported that increments in biomass at harvest were also associated with increased yield potential (Reynolds et al., 1999; Donmez et al., 2001; Shearman et al., 2005), but in the present study no statistical difference was observed between cultivars for biomass at harvest.

The GN produced was highly associated with yield within cultivars of both cycles, though it showed year interaction in LC. The impact of GN agrees with most previous evidence showing that GN may explain yield potential differences between cultivars in different years and regions (Siddique et al., 1989b; Slafer et al., 1990; Slafer and Andrade, 1993; Sayre et al., 1997; Abbate et al., 1998; Calderini et al., 1999; Reynolds et al., 1999; Shearman et al., 2005; Acreche et al., 2008).

The increased number of grains per spike was the main determinant of improved GN through breeding in wheat (Siddique et al., 1989b; Slafer et al., 1990; Slafer and Andrade, 1993; Calderini et al., 1999), but in the present
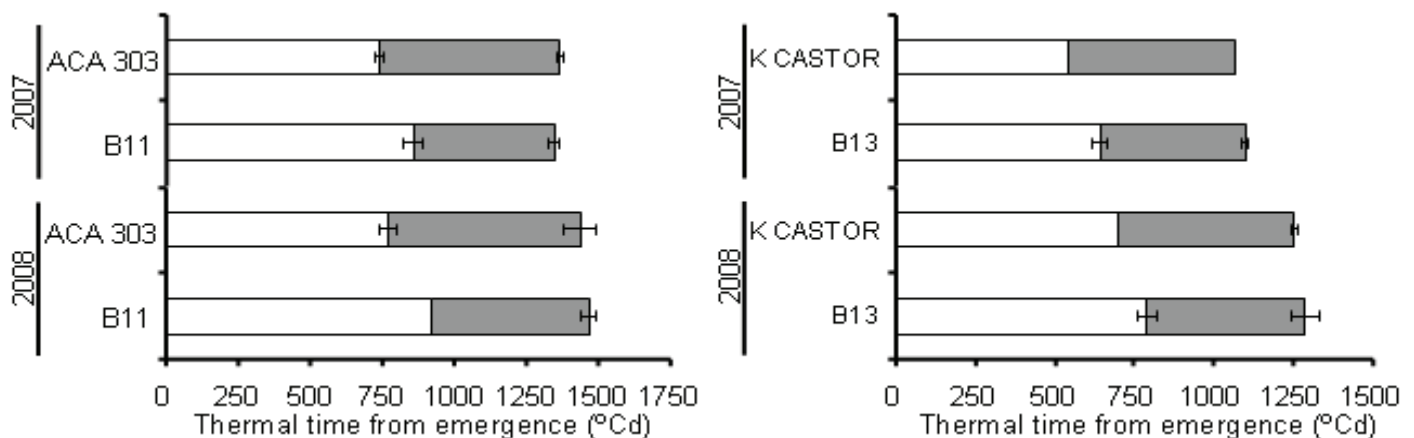

Figure 7. Thermal time from emergence to beginning of stem elongation (Z3.1) and from then to anthesis (Z6.1), that is, stem elongation phase (SEP), for the two pairs of cultivars showing similar anthesis date but different duration of the SEP (see Fig. 6). Means ± standard error.
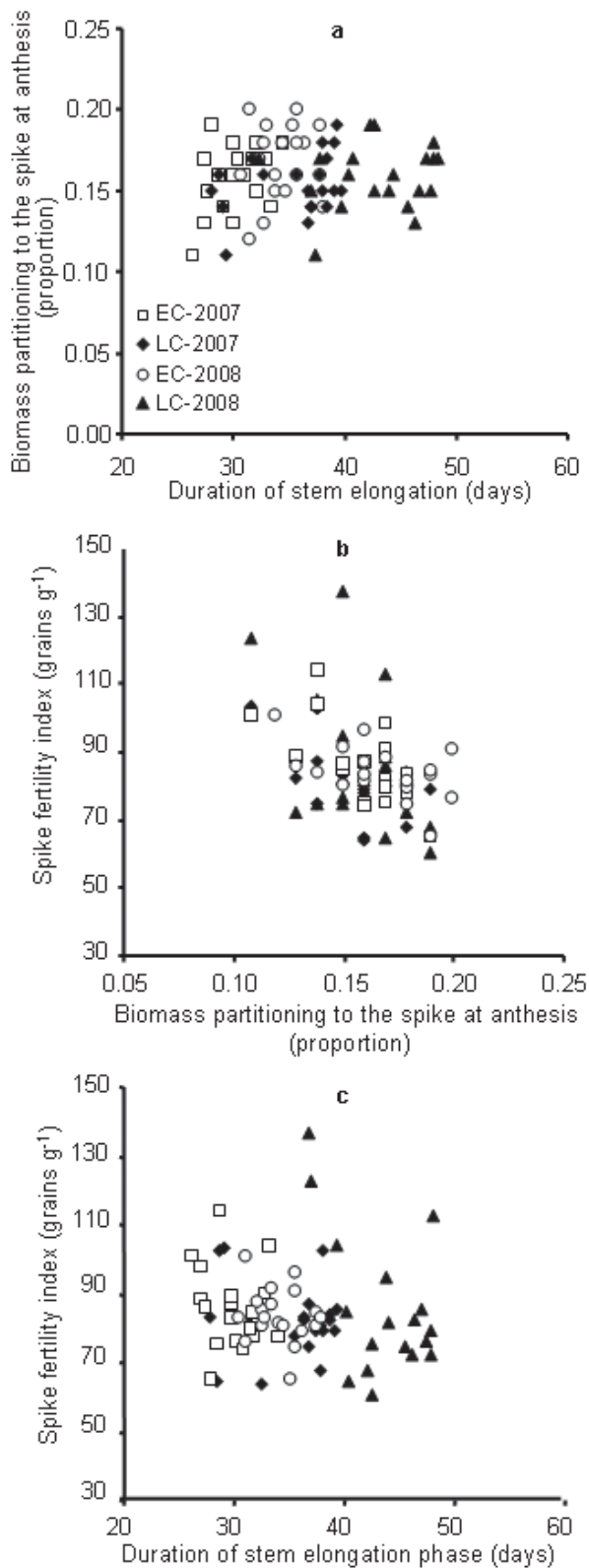
Figure 8. Relation between (a) biomass partitioning to the spike at anthesis (BPS$_a$) and duration of the stem elongation phase (SEP) for early (EC) and late (LC) cultivars (LC-2007, r = 0.21; LC-2008, r = 0.06; P > 0.1 for both years; EC-2007, r = 0.36, P < 0.01; EC-2008, r = 0.07, P > 0.1); (b) spike fertility index (SFI) and BPS$_a$ (LC-2007, r = −0.25; LC-2008, r = −0.47; EC-2007, r = −0.48; EC-2008, r = −0.37; P < 0.05 for all cases); and (c) SFI and duration of the SEP (LC-2007, r = −0.15; LC-2008, r = −0.23; EC-2007, r = −0.12; EC-2008, r = −0.09; P > 0.05 for all cases).

study no stable association was observed between these numerical components. The number of tillers per unit area being positively associated with GN (particularly in LC) may be reflecting a trend to increase tolerance to density (Shearman et al., 2005). Increased tolerance to density (through higher number of tillers) has been reported as the main factor increasing yield potential of barley (*Hordeum vulgare* L.) in different regions (Martiniello et al., 1987; Wych and Rasmusson, 1983; Abeledo et al., 2003).

From the physiological point of view, both SDW$_a$ and SFI were associated with GN production. The SDW$_a$ was clearly a cultivar effect while the SFI depended on the year × cultivar interaction, but with high ANOVA sums of squares, explained by cultivars in both LC and EC. Most previous evidence showed that the main factor explaining GN production is the SDW$_a$ (Fischer and Stockman,1980; Stockman et al., 1983; Thorne and Wood, 1987; Slafer et al., 1990; Savin and Slafer, 1991; Abbate et al., 1997; Demotes–Mainard et al., 1999), and although variation in SFI could be found (Shearman et al., 2005; Reynolds et al., 2006; Dreccer et al., 2009), generally there has been no association with GN (Shearman et al., 2005; Reynolds et al., 2006). In the present paper, the SFI was highly associated with GN, suggesting that breeding success in Argentina retains the strategy reported for cultivars released from the mid-1980s to mid-1990s (Abbate et al., 1998). The range of variation of SFI was slightly higher (Abbate et al., 1998; Shearman et al., 2005) or similar (Dreccer et al., 2009) than the ones reported previously. As the SFI is a complex trait that includes the assimilate partitioning inside the spike (or spike structure), development and survival of florets, and grain set, few papers have studied its physiological bases. Abbate et al. (1998) observed that the SFI estimated as GN per gram of non–grain spike at anthesis was similar to that of GN per gram of rachis, suggesting that the rest of the spike chaff or the development of florets and grain set were not involved in the differences in SFI.

The lack of correlation between SFI and SDW$_a$ observed in the present study suggest that one trait could be manipulated without altering the other, as proposed by Fischer (1984). Previous studies where SDW$_a$ was altered by manipulating duration of spike growth (González et al., 2003, 2005a), or by shading the canopy during stem elongation (Stockman et al., 1983; González et al., 2005a), or by altering the dwarfism genes (Miralles et al., 1998), did not alter the SFI showing the same relation between GN (or fertile florets) and SDW$_a$, supporting the idea that these traits are more or less independent. Nevertheless, in the present study no cultivar showed SDW$_a$ heavier than 200 g m^{-2} and SFI at anthesis higher than 120 grains g^{-1}, suggesting that increments of SDW$_a$ over that value may increase the non–grain part of the spike (Acreche et al., 2008). If this limit could be overcome by breeding remains a speculation, but both traits seem promising based on the results of the present study, showing some degree of independence between them during two contrasting seasons.

One alternative to increase SDW_a may be to increase duration of the SEP by advancing the beginning of stem elongation without altering anthesis date, considering that developmental phases could be manipulated more or less independently (Slafer et al., 1996, 2001). In the present study the cultivars showing increased duration of stem elongation accumulated more intercepted radiation during that period, as was reported for experiments where duration of the SEP was altered by changing photoperiod environment during that phase (González et al., 2003, 2005a) or photoperiod-sensitivity genes (*Ppd-1*) (González et al., 2005b). Despite the year × cultivar interaction, stable differences in duration of the SEP were observed between pairs of cultivars showing similar anthesis date, as was observed whenever a large set of cultivars or lines were studied in wheat (Whitechurch et al., 2007) or barley (Borrás et al., 2009). The actual potential of introducing this trait as a selection criterion in future breeding would depend on identification of the genetic bases of duration of pre- and postbeginning of stem elongation (associated with photoperiod sensitivity, vernalization, and/or intrinsic earliness). The lack of genetic correlation between the two phases was recently shown in barley (Borrás et al., 2009), but so far, no combination of genes or QTLs has been identified controlling particularly the duration of the SEP, with small effects in previous phases in barley (Borrás et al., 2009) or wheat (González et al., 2005b). The differences in RSGR explaining part of the variation in SDW_a between cultivars may be associated with daily biomass partitioned to the spike during the SEP (as no relation was observed between BPS_a and duration of the SEP). The differences of BPS_a between cultivars were not associated with height, suggesting that reduced partitioning to other organs may have occurred (Reynolds et al., 2009, and citations therein). However, from the present study it is hard to explain the differences in RSGR. Further experiments measuring biomass production at beginning of stem elongation and dynamics of growth of different organs in a reduced set of cultivars should be performed to understand the basis of the differences observed.

CONCLUSIONS

The high yield potential was associated with increased HI and GN, which was determined by the SFI and the SDW_a. Duration of the SEP (which encloses duration of spike growth) showed stable variation between years for two pairs of cultivars showing similar anthesis date, supporting the idea that increased SDW_a could be achieved by lengthening duration of the SEP. As the SFI and duration of the SEP were not related, both traits seem promising for increasing GN and yield potential in wheat.

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