

Genetic progress in Argentine bread wheat varieties released between 1918 and 2011: Changes in physiological and numerical yield components

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ABSTRACT

The objective of this study is to update the data of genetic progress in bread wheat cultivars released in Argentina from 1918 to 2011 (emphasizing the last 20 years) characterizing different agronomic traits of interest for breeders. Experiments were carried out with a wide range of bread wheat cultivars and conducted under field conditions without nutritional and water restrictions. Yields showed a significant ($R^2 = 0.68$) tri-linear trend when associated with the cultivar's year of release. Until the 40s, when the first inflection point occurred, the genetic progress in terms of yield was $0.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($0.02\% \text{ yr}^{-1}$). Between 1940 and 1999, yield genetic progress reached its highest value ($51 \text{ kg ha}^{-1} \text{ yr}^{-1}$; $1.17\% \text{ yr}^{-1}$) but changed after 1999 when values became lower compared to the previous period, showing a value of $14 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($0.18\% \text{ yr}^{-1}$). Changes in grain yield were mostly explained by increases in harvest index and not by those in above-ground biomass. Plant height showed a negative bi-linear trend with the year of release, reaching an inflexion point well before the introgression of semi-dwarfing genes in commercial cultivars. Grain number increased ca. 63% when modern cultivars were compared to older ones, which explains most of the grain yield changes. In contrast to grain number, no significant differences between old and modern cultivars were found for grain weight, with average values of ca. 30 mg grain^{-1} for all environments explored.

1. Introduction

As a strategy to increase global and/or regional wheat production and considering the inability to increase the planted area on a large scale, efforts should be focused on yield increments per unit area. One of the most important ways to achieve increments in yields genetic gain is associated with the release of new cultivars with higher yield potential (Reynolds et al., 1996; Sinclair et al., 2004; Reynolds et al., 2009).

In Argentina, the grain yield increases were mainly associated with an increase in grain number and by changes in the partitioning of biomass. The first semi-dwarf varieties, derived from crossings involving cultivar Norin 10, were released in the late '70s and breeders quickly included dwarfing genes from CIMMYT into the breeding programs. By late '90s more than 95% of Argentine commercial varieties had Rht-B1 and/or Rht-D1 alleles in their background (Appendino et al., 1993). Slafer and Andrade (1989), Slafer et al. (1990) and Calderini et al. (1995, 1997) analyzed the genetic gain in Argentinean bread wheat varieties released from 1920 to 1990 and did not find any significant differences in above-ground biomass at harvest between old

and modern cultivars. However, they did find significant differences in harvest index associated to a marked reduction in plant height when old and modern cultivars were compared. These differences in plant height favored biomass partition to spikes, increasing harvest index by ca. 39%.

When the numerical yield component changes were analyzed in Argentina between 1920 and 1990, new cultivars consistently showed a significant increment in grain number per spike compared to the old ones. However, changes in grain weight associated with the year of release showed contradictory results. Calderini et al. (1995) did not find significant temporal trends in grain weight, but they observed different trends in grain weight when analyzing local cultivars released between 1920 and 1990. In cultivars released before the '80s, yield gains were the consequence of an increment in grain number as from late '80s and up to the '90s (last period analyzed in that work) grain weight increments determined yield gain. Similar results were observed by Sadras and Lawson (2011) for Australian wheat cultivars released between 1958 and 2007 who showed that up until the '80s grain yield increases were attributed to increments in grain number per unit area that was counterbalanced by partial reductions in grain weight. After the '80s

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the increments in yields were associated with higher grain weight. Conversely to Calderini’s et al. (1995) report, Slafer and Andrade (1989) observed lower grain weight in modern cultivars compared to old ones, possibly caused by a greater contribution of grains fixed in distal positions within spikelet’s with lower potential grain weight than those placed in basal positions (Miralles and Slafer, 2007). This situation determines a smaller grain weight contribution to grain yield that reduces average weight without necessarily reflecting a reduction of the source needed to complete the growth of the grain (Miralles and Slafer, 2007).

There are no studies analyzing the genetic gain of Argentinian bread wheat cultivars released in the last 25 years. The last studies were published in the mid-’90s considering cultivars released up until 1990 (Calderini et al., 1995, 1997). Other papers, such as Abbate et al. (1998), have only analyzed a narrow time period in terms of year of release for Argentinian cultivars (between 1984 and 1994). During the last 20 years an important number of European cultivars with high yield potential were introduced into the Argentinian breeding programs and crossed with adapted local cultivars (Brieva, 2007). It is important to perform an upgrade of retrospective studies in order to assess the current genetic gain for wheat in Argentina as well as analyzing other fine tuning traits that are important for breeding purposes as these traits are not commonly measured in genetic progress analyses. The aim of this study is to update the data of genetic progress in bread wheat cultivars released in Argentina during different periods characterizing different agronomic and breeding traits of interest related to physiological and numerical yield components.

2. Materials and methods

2.1. Genetic material and experimental design

Seventeen commercial wheat bread cultivars released in Argentina between 1918 and 2011 were selected according to their relative importance in the area sown to wheat in each period, an indicator which is closely related to the degree of adoption by farmers. Cultivars were grown under field conditions during two consecutive years in three different environments and most of the cultivars were included in all environments (Table 1). The cultivars corresponded to Argentinian breeding programs with the exception of three materials released from 1999 to 2011 which correspond to European introgressions from French Breeding Programs. The experimental design was a completely

Table 1
Cultivars used in the experiments of genetic progress. The crosses indicate which location (BA and BC correspond to Buenos Aires and Balcarce, respectively) and in which experimental year (13 and 14 correspond to 2013 and 2014, respectively) each variety of wheat was used.

Cultivars	Breeding program	Year of release	Cultivars used		
			BA13	BA14	BC14
38 MA.	Argentinean	1918	X	X	X
Americano 26n	Uruguay	1918	X	X	X
K. Favorito	Argentinean	1920	X	X	X
Eureka FFCC Sur	Argentinean	1936	X	X	X
K. Rendidor	Argentinean	1954	X	X	X
B. Manantial	Argentinean	1964	X	X	X
B. Pucará	Argentinean	1980	X	X	X
B. Ombú	Argentinean	1984			X
B. Poncho	Argentinean	1986		X	X
K. Cacique	Argentinean	1991		X	X
K. Pegaso	Argentinean	1997	X	X	X
Baguette 10	France	1999	X	X	X
BioINTA 3005	Argentinean	2009	X		
ACA 906	Argentinean	2010	X		
K. Gladiador	Argentinean	2010	X	X	X
Baguette 601	Argentinean/France	2011	X	X	X
B. Sy 110	Argentinean/France	2011	X	X	X

randomized one with three replications in all environments.

2.2. Growing conditions

The experiments were conducted during 2013 and 2014 at (i) the experimental field of the School of Agronomy, University of Buenos Aires (34°35’S, 58°29’O) (BA₁₃ and BA₁₄, respectively) and (ii) during 2014 at the experimental field of the company Agrar del Sur S.A. (37°58’S, 58°23’O) located in Balcarce, Province of Buenos Aires (BC₁₄). In BA soils are classified as vertic Argiudolls, while Balcarce has a silty soil classified as typical Argiudoll.

Sowings were done mechanically with a 7 rows seeder spaced at 0.175 m in BA₁₄ while in BC₁₄ and in BA₁₃ 7 rows were spaced at 0.21 m. Each plot occupied an area of 2.94; 3.06; and 6.12 m² (for BA₁₃, BA₁₄ and BC₁₄, respectively). Planting dates were June 7 and May 29 for BA₁₃ and BA₁₄, respectively and July 23 for BC₁₄. The target density was 280 plants per square meter. In all experiments weeds, pests and diseases were chemically controlled throughout the crop cycle. For weed control Proflufenoxuron + Triasulfuron + Dicamba (10 g ha⁻¹; 10 g ha⁻¹ and 150 cm³ ha⁻¹, respectively) was applied. For diseases and pests control Azoxystrobin + Isopyrazam (500 cm³ ha⁻¹) and Lambda cyhalothrin (35 cm³ ha⁻¹) was applied in DC3.9, respectively.

The BA₁₃ and BA₁₄ experiments were supplemented with irrigation to avoid water deficiencies, while BC₁₄ was conducted under rainfed conditions. However, BC₁₄ did not suffer severe water deficiencies due to the accumulated rainfall between July and December, which was ca. 535 mm. All experiments were fertilized at sowing with 80 kg ha⁻¹ of di-ammonium phosphate and at tillering 150 kg N ha⁻¹ was applied (DC2.5, Zadoks et al., 1974). As soils had no sulphur and potassium deficiencies, the fertilization with phosphorus and nitrogen was made with the objective of avoiding nutritional deficiencies of those elements during the whole cycle.

Mean temperature during the 2013 and 2014 crop cycle was 15.4 and 16.0 °C in BA, respectively, while in Balcarce mean temperature was 15.7 °C. The average incident PAR Radiation values between emergence and physiological maturity was similar in both years in BA (average 1508.7 MJ m⁻²); and 1410.4 MJ m⁻² in BC₁₄ (Fig. 1).

2.3. Sampling and measurements

Different physiological variables related to biomass and yields were measured and are detailed below:

Phenology: In all experiments flag leaf appearance (DC39) (Zadoks et al., 1974), anthesis time and physiological maturity were recorded (when 50% of plot plants reached that particular stage) for each particular genotype. Physiological maturity was determined visually by the color of the spike peduncle.

Above-ground biomass: Three samples of above-ground biomass were taken at the stages of: (i) initiation of the critical period in coincidence with the flag leaf appearance (DC39), (ii) end of the critical period (10 days post anthesis) and (iii) physiological maturity. All phenological stages were recorded separately for each particular cultivar and the timing of sampling adjusted to cultivar phenology. Samples were obtained from two 0.5- m row sections, away from plot borders and previously sampled areas. Were dried in an oven at 60 °C for 72 h and then weighed. The crop growth rates during the critical period (for each cultivar according to the phenological events described above) were calculated using the biomass difference between samples taken at DC3.9 and 10 days after anthesis (equation 1).

$$CGR (g m^{-2} d^{-1}) = [AGB_{eCP} (g m^{-2}) - AGB_{iCP} (g m^{-2})] / D_{eCP-iCP} (days) \tag{1}$$

where CGR is the crop growth rate during the critical period, AGB_{eCP} and AGB_{iCP} correspond to the above-ground biomass at the end and the start of the critical period, respectively, and $D_{eCP-iCP}$ corresponds to the

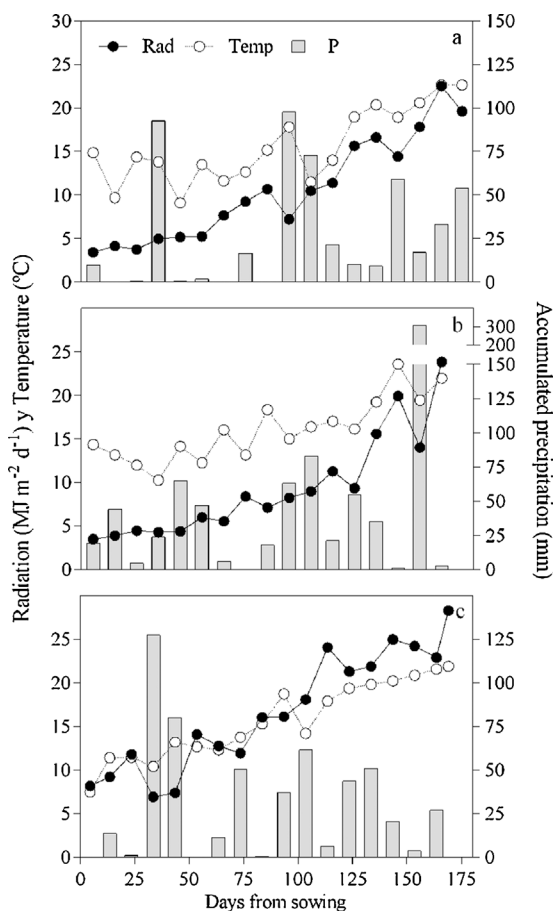


Fig. 1. Relationship between incident radiation (Rad – MJ m⁻² d⁻¹), average (T_{average} – °C), maximum (T_{max}) and minimum (T_{min}) temperatures and accumulated precipitation (Rainfall – mm-) as a function of days from planting. The panels (a), (b) and (c) correspond to the climatic data of the three environments (BA₁₃, BA₁₄ and BC₁₄, respectively).

days between those two moments.

Intercepted Radiation: Photosynthetically Active Radiation interception efficiency (IPAR) was measured twice a week during the critical period for yield generation (between DC3.9 to DC7.1) with a 1 m long PAR quantum sensor (BAR-RAD 100, Cavadevices.com, Buenos Aires, Argentina) between 12:00 and 14:00 on clear days. For this purpose, for each individual plot the line quantum sensor was placed just above the canopy in order to determine incident PAR (I_0) as well as at soil level with a 45° angle in relation to rows, to record transmitted PAR (I_t). In order to estimate the intercepted radiation during the crop cycle, intercepted radiation values were fitted using sigmoid models to obtain the daily dynamics intercepted radiation and thereby calculate cumulative radiation. The fraction of PAR intercepted at midday (F) was calculated as $(I_0 - I_t)/I_0$. Daily fraction interception (F_D) was calculated as indicated in Eq. (2) (Charles-Edwards and Lawn, 1984):

$$F_D = 2F/(1 + F) \quad (2)$$

Daily incident PAR was calculated as the total solar incident radiation measured with a standard weather station 50 m from the plots multiplied by 0.48 (Demotes-Mainard and Jeuffroy, 2004). Cumulative intercepted PAR was estimated for the critical period. For experiments conducted in Buenos Aires radiation use efficiency (RUE) during the critical period was calculated as the ratio between cumulative biomass and cumulative intercepted radiation during that period.

Plant height: five main stems of each sample were randomly selected at harvest and plant height was measured from the base of the plant to the insertion of the spike.

Yield and its components: total aerial biomass, harvest index, yield and its numerical components (grain number per unit area, average grain weight, spikes m⁻² and grains spike⁻¹) were determined at harvest (i.e. after physiological maturity).

2.4. Analysis

In order to establish the genetic progress for cultivars released in different eras, values of all measured variables were analyzed as a function of the year of release. Cultivar deviations from the mean of each environment and variable were used for environments comparison. Bi- or tri-linear models (according to the best fit) were fitted in order to establish the relationship between each particular variable and the year of release, according to Eqs. (3) and (4).

For bi-linear models the equation was:

$$y = a + bx \text{ if } x \leq c; \text{ and}$$

$$y = a + bc + d(x-c) \text{ if } x > c \quad (3)$$

where x indicates the year of release, a is the intercept, b is the first slope representing the genetic progress, c indicates the year where a breaking point occurred and d indicates the second slope of genetic progress.

When points were fitted using a tri-linear model, the equation was:

$$y = a + bx \text{ if } x \leq c;$$

$$y = a + bc + d(x-c) \text{ if } e \leq x < c; \text{ and}$$

$$y = a + bc + d(e-c) + f(x-e) \text{ if } x > e \quad (4)$$

where x indicates the year of release, a is the intercept, b is the first slope representing the genetic progress, and c indicates the first year when a break point occurred, d indicates the second slope of genetic progress, e indicates the second year when a breaking point occurred and f indicated the third slope of genetic progress. Box plots were used to show the range of variation, the mean and the median of each variable in the three environments.

3. Results

Flowering time for the whole cultivars occurred in a narrow time period on the three environments. The range of flowering time was: October 18th to 22nd, September 18th to 20th and from October 29th to November 3rd, for BA₁₃, BA₁₄ and BC₁₄, respectively. Thus, the differences in flowering time were 4, 2 and 5 days for BA₁₃, BA₁₄ and BC₁₄, respectively.

3.1. Grain yield and biomass partition

Grain yield showed a significant ($R^2 = 0.68$) tri-linear trend with the cultivar's year of release. The first slope of the relationship was observed until the 40's, when the first inflection point occurred (Fig. 2a). The genetic progress in terms of yield (reflected by the slope of the relationship) was 0.8 kg ha⁻¹ yr⁻¹ (0.02% yr⁻¹) starting at the beginning of the century until 1940. After this first inflection point (1940), the highest genetic gain was reached (51 kg ha⁻¹ yr⁻¹; 1.17% yr⁻¹), and maintained until 1999 (Fig. 2a). However, the genetic progress for the last period (1999–2011) was clearly lower compared to the previous period showing a value of 14 kg ha⁻¹ yr⁻¹ (0.18% yr⁻¹) (Fig. 2a).

The average yield and the range explored by the cultivars were not significantly different between environments ($p > 0.05$). In BA₁₃ and BA₁₄ average yields were similar on both years (ca. 5800 kg ha⁻¹, exploring a yield range of between 2560 and 8670 kg ha⁻¹). The average yield in BC₁₄ was higher than that in Buenos Aires (ca. 6630 kg ha⁻¹) with a range between 3850 and 9630 kg ha⁻¹. However, as was stated, differences were not significant (Fig. 2b).

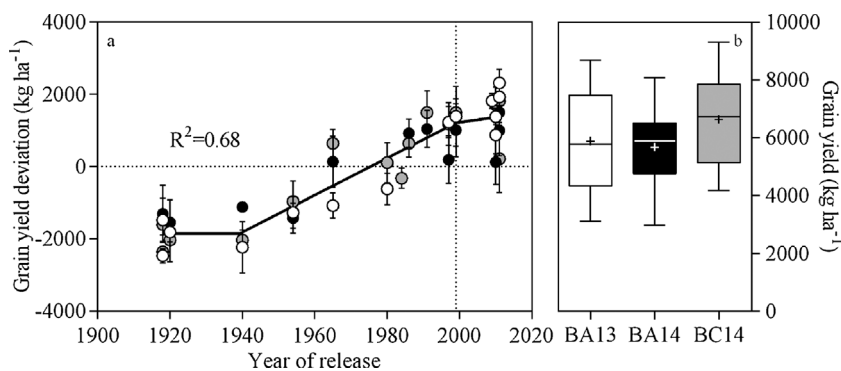


Fig. 2. (a) Grain yield deviation for each cultivar with respect to the average yield for each environment (dotted horizontal lines) for wheat varieties released in Argentina between 1918 and 2011. The vertical lines for each point represent standard error of the mean, and the dashed vertical line represents the second breakpoint of the tri-linear equation; (b) Grain yield box-plots for experiments conducted in Buenos Aires during 2013 and 2014 (BA13 and BA14) and in Balcarce in 2014 (BC14). The horizontal line and the cross indicate the median and average values in each environment; the limits of the boxes represent the 25 and 75 percentile (lower and upper limit, respectively); and vertical bars represent the 5 and 95 percentile. The colors of the symbols in (a) correspond to the color code of the environments in (b).

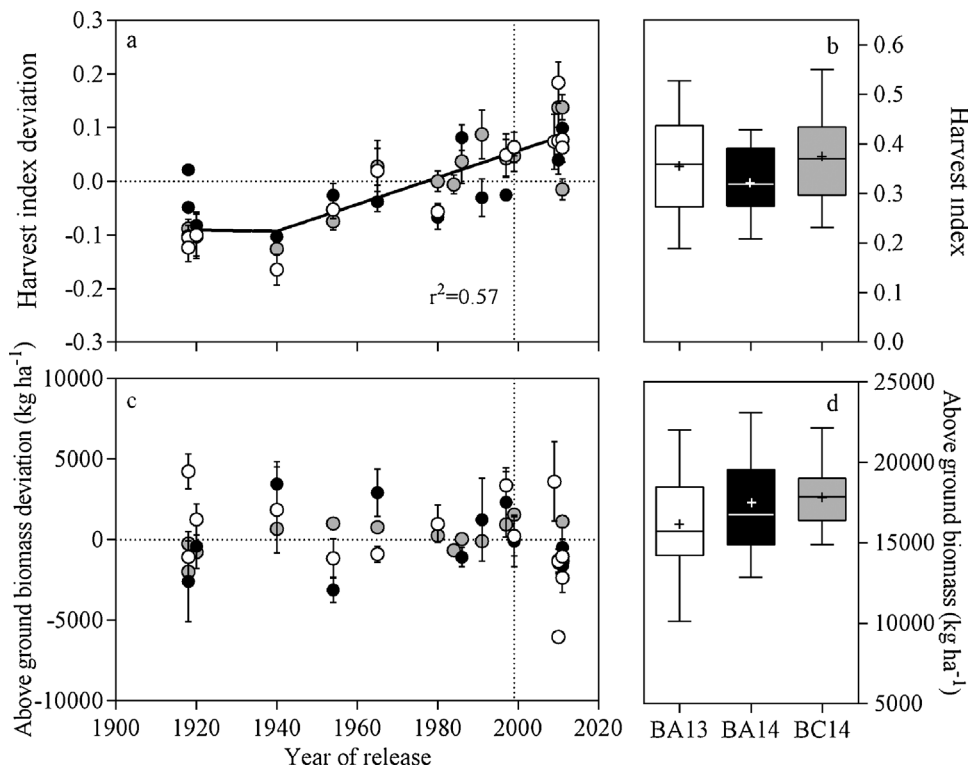


Fig. 3. (a) Harvest index deviation and (c) above-ground biomass deviation at harvest for wheat varieties released in Argentina between 1918 and 2011. (b) Box-plot for harvest index and (d) above-ground biomass at harvest for experiments conducted in Buenos Aires in 2013 and 2014 (BA13 and BA14) and in Balcarce in 2014 (BC14). The methodology for estimation of cultivar deviations for each trait and symbol color-coding as in Fig. 2.

Changes in grain yield were mostly explained by increases in harvest index ($R^2 = 0.61$; data not shown). However, harvest index showed a bi-linear response, with similar dates for the first inflection point (i.e. 1940) followed by a positive linear trend (Fig. 3a). On average, cultivars released before 1940 had a harvest index of ca. 26%, while modern cultivars registered values of ca. 44% with a genetic progress for this attribute of $0.32\% \text{ y}^{-1}$ and without significant differences ($p > 0.1$) when the three environments were compared (Fig. 3b). Above-ground biomass at harvest did not show any particular temporal trend in any environment explored, and no significant association was found between above-ground biomass at harvest and the year of release (Fig. 3c). However, a more detailed inspection of the 1999–2011 period showed a reduction of above-ground biomass at a rate of $15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (i.e. $0.9\% \text{ y}^{-1}$) in opposition to harvest index that showed increases of $0.25\% \text{ y}^{-1}$ for the same period (see Fig. 3). In absolute terms, the ranking of above-ground biomass values at harvest between environments was $BC_{14} > BA_{14} > BA_{13}$ with 17770, 17490 and 16820 kg ha^{-2} , respectively; without significant differences between environments (Fig. 3d).

In agreement with the lack of association between above-ground biomass and the year of release, the analysis of physiological components associated with biomass production (radiation interception and

radiation use efficiency –RUE-) and the crop grow rate, did not show any association with the cultivar year of release (Supplementary Fig. S1). However, when focusing on the last period analyzed (i.e cultivars released between 1997 and 2011), a decreasing trend was found (although the negative regression was not significant) in the three physiological variables (Supplementary Fig. S1).

3.2. Numerical yield components and functional relationships

Plant height showed a bi-linear trend with the year of release but in the opposite direction to that observed for yield and harvest index. Thus, plant height was significantly reduced when old and modern cultivars were compared, presenting values of ca. 93–65 cm in BC_{14} (ca. 30%) and ca. 130–79 for BA_{13} and BA_{14} cm (ca. 40%, average for both experimental years) (Fig. 4). Until 1940 no significant changes ($p > 0.01$) were observed for this trait with average values of ca. 118 cm, but since the '40s plant height was reduced at a rate of 0.62 cm yr^{-1} .

Grain number increased ca. 63% between old and modern cultivars, and was the variable that best explained the changes in grain yield in both absolute ($R^2 = 0.58$; $p < 0.0001$), as well as in relative terms (data not shown). Similar to yield, grain number increased at a very low

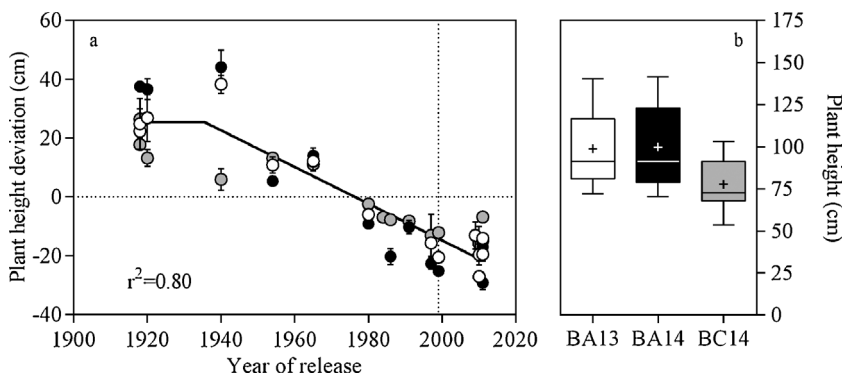


Fig. 4. (a) Plant height deviation for wheat varieties released in Argentina between 1918 and 2011. (b) Box-plot for plant height for experiments conducted in Buenos Aires in 2013 and 2014 (BA13 and BA14) and in Balcarce in 2014 (BC14). The methodology for estimation of cultivar deviations for each trait and symbol color-coding as in Fig. 2.

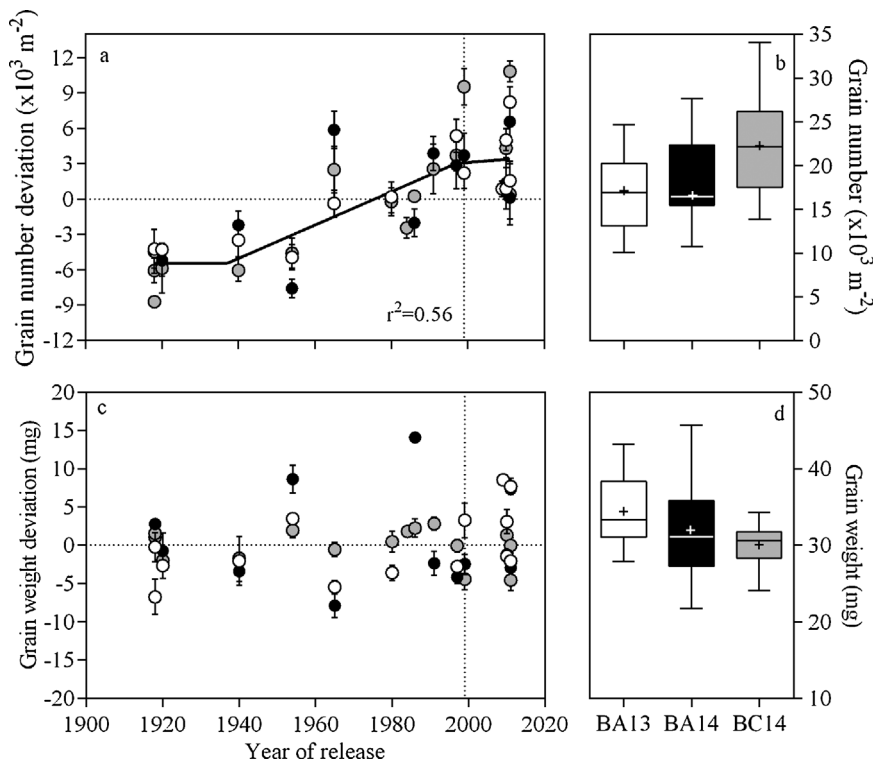


Fig. 5. (a) Grain number deviation and (c) grain weight deviation for wheat varieties released in Argentina between 1918 and 2011. (b) Box-plot of grain number and (d) grain weight for experiments conducted in Buenos Aires in 2013 and 2014 (BA13 and BA14) and in Balcarce in 2014 (BC14). The methodology for estimation of cultivar deviations for each trait and symbol color-coding as in Fig. 2.

rate (ca. 2.5 grains m⁻² yr⁻¹) in cultivars released before 1940, and thereafter the rate increased at 141 grains m⁻² yr⁻¹ until 1999. In agreement with yield trends, from 1999 to 2011 grain number increased at a lower rate than in the previous period (26 grains m⁻² yr⁻¹) (Fig. 5a). Experiments carried out in Buenos Aires had fewer grains (ca. 17100 and 18900 grains m⁻² in BA₁₃ and BA₁₄, respectively) than in Balcarce (ca. 22250 grains m⁻²) (Fig. 5b). No significant differences between old and modern cultivars were found for grain weight, with average values of ca. 30 mg grain⁻¹ for all environments explored (Fig. 5c,d).

Regarding the sub-components of grain number (spike number per square meter and grain number per spike), the spike number did not show any consistent pattern when the whole period was considered. However, a consistent positive temporal trend of spike number was evident up to 1940 without any trend after that year (Fig. 6a). Conversely, grain number per spike showed slight reductions from 1918 to 1940, but from 1940 onward it was consistently increased (Fig. 6c). Thus, grain number per unit area was associated with changes in grain number per spike ($R^2 = 0.56$) without any association with the number of spikes per m² ($p > 0.1$).

When some of the grain number sub-components were analyzed, focusing on the equation proposed by Fischer (2008, 2011) (grain

number = stem elongation phase duration x crop growth rate x biomass partitioning to spike x fruiting efficiency), it was observed that spike dry weight deviations (measured in g m⁻²) did not show any particular trend when plotted against cultivar's year of release (Fig. 7a). However they were significantly affected by environments, showing in BC₁₄ the lowest average and maximum values. In contrast to spike dry weight, the fruiting efficiency did not show changes until ca. 1960 when it increased with the year of release ($r^2 = 0.37$) following the same trend observed for grain yield and grain number at a rate of 8.3 grains g⁻¹ yr⁻¹. (Fig. 7c). It is important to highlight that both traits were negatively associated following a curvilinear relationship (Supplementary Fig. S2).

4. Discussion

4.1. Genetic yield progress

The present paper showed that genetic progress, from 1940 to the end of the '90s, was 51 kg ha⁻¹ yr⁻¹ (in absolute value) or 1.17% yr⁻¹ (in relative value, calculated as the ratio between the genetic progress and the grain yield average for all cultivars), similar to those reported by Calderini et al. (1995) for Argentinian cultivars released up to

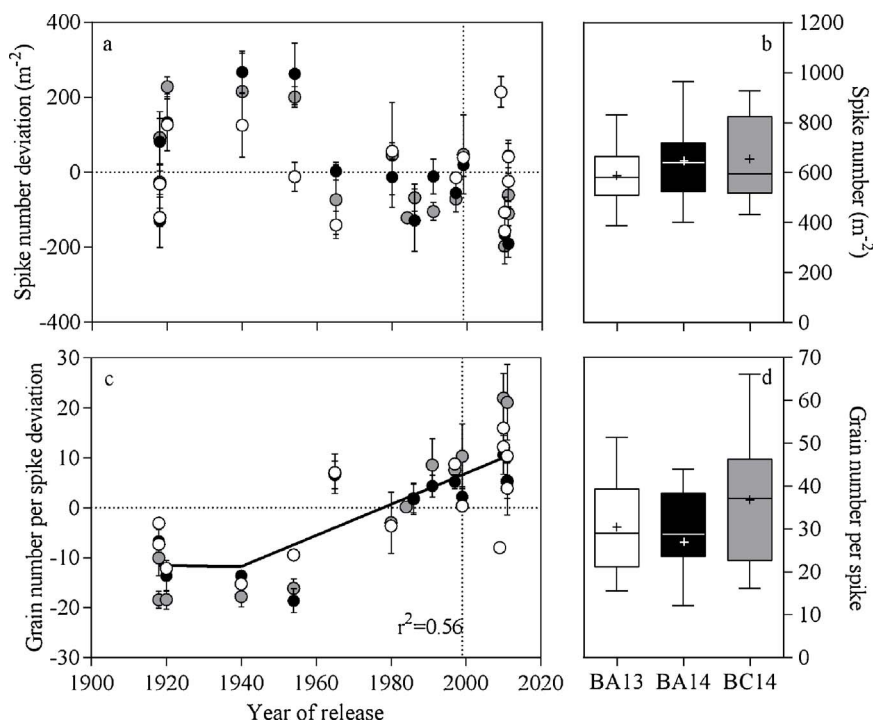


Fig. 6. (a) Spike number (m^{-2}) and (c) grain number per spike deviations for wheat varieties released in Argentina between 1918 and 2011. (b) Box-plot of spike number and (d) grain number per spike for experiments conducted in Buenos Aires in 2013 and 2014 (BA13 and BA14) and in Balcarce in 2014 (BC14). The methodology for estimation of cultivar deviations for each trait and symbol color-coding as in Fig. 2.

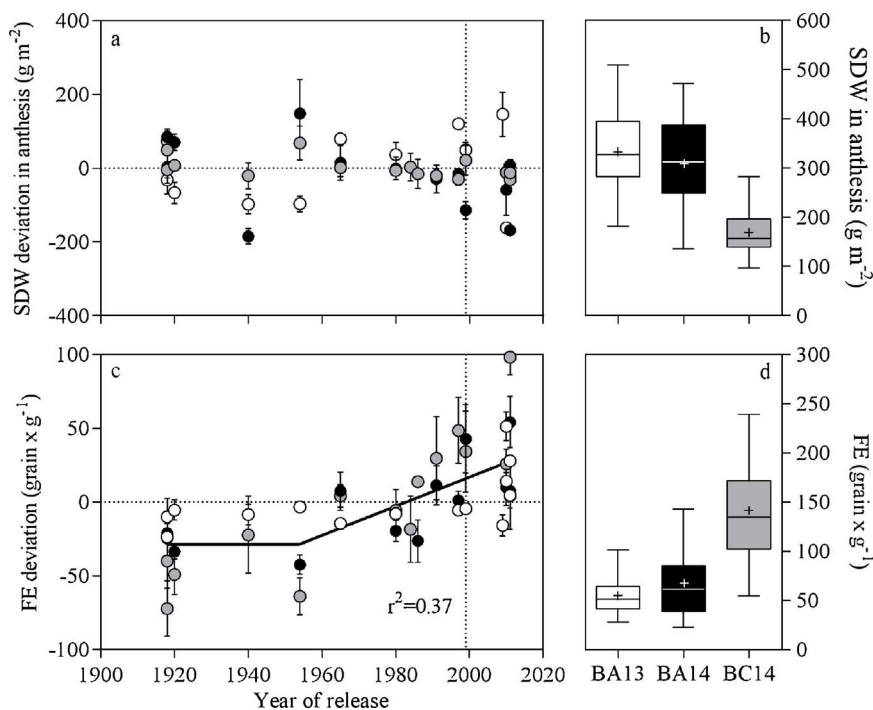


Fig. 7. (a) Spike dry weight (SDW) and (c) fruiting efficiency (FE) deviation for wheat varieties released in Argentina between 1918 and 2011. (b) Box-plot of SDW and (d) FE for experiments conducted in Buenos Aires in 2013 and 2014 (BA13 and BA14) and in Balcarce in 2014 (BC14). The methodology for estimation of cultivar deviations for each trait and symbol color-coding as in Fig. 2.

middle of the “90 s ($50 \text{ kg ha}^{-1} \text{ yr}^{-1}$ or $0.96\% \text{ yr}^{-1}$). However, genetic yield progress was drastically reduced ($0.18\% \text{ yr}^{-1}$ averaging all cultivars) from the end of the ’90 s to 2011, demonstrating that (i) the genetic progress of new wheat varieties released in Argentina during the last 13 years was substantially lower than the historical genetic progress (i.e. from the middle of the ’70s to the end of the ’90s) (Calderini et al., 1995) and (ii) yields are close to stable, as found for other countries (Acreche et al., 2008; Fischer and Edmeades 2010). Sanchez-Garcia et al. (2013) analyzed the genetic gains of Spanish cultivars and observed that those have declined in the last years from $35 \text{ kg ha}^{-1} \text{ year}^{-1}$ or $0.88\% \text{ yr}^{-1}$ (< 1940–1955) to $18 \text{ kg ha}^{-1} \text{ yr}^{-1}$ or $0.41\% \text{ yr}^{-1}$ (1969–2001). A similar situation was found in Brazilian

cultivars by Beche et al. (2014) in which rates of genetic gain decreased in modern cultivars from $29 \text{ kg ha}^{-1} \text{ year}^{-1}$ or $0.92\% \text{ yr}^{-1}$ (1940–2009) to $16 \text{ kg ha}^{-1} \text{ year}^{-1}$ or $0.45\% \text{ yr}^{-1}$ (1999–2009). Genetic gains in Mexican cultivars released to the market in the last 25 years, also showed a decrease with respect to the previous period (Aisawi et al., 2015). These authors reported a genetic gain of $30 \text{ kg ha}^{-1} \text{ year}^{-1}$ for Mexican cultivars released between 1966 and 2009. However, a reanalysis of the database, made by us in the context of the present paper and focusing on the cultivars released after 1990, showed that genetic gain was only $9 \text{ kg ha}^{-1} \text{ yr}^{-1}$. In contradiction to the yield stabilization described above in Australia (Sadras and Lawson, 2011) and Chile (del Pozo et al., 2014) the modern wheat cultivars

released during the recent period continued increasing yield showing positive yield gains (25 and 43 kg ha⁻¹ yr⁻¹ or 0.51% yr⁻¹ and 1.10% yr⁻¹) in both countries.

4.2. Biomass partitioning, capture of radiation and radiation-use efficiency

Both physiological yield components (above-ground biomass and harvest index) showed different trends when plotted against the cultivar's year of release. Above-ground biomass did not change with the year of release up until the end of the '90, in contrast to that reported in China (Wu et al., 2014) and Mexico (Aisawi et al., 2015) where the biomass at harvest increased with year of release. However, for the 1999–2011 period, above-ground biomass showed a reduction tendency compared to the previous period. In line with the biomass reduction, radiation interception, RUE and the crop grow rate were also reduced in the last 13 years, which explains the negative trend observed in biomass.

According to many other published reports, yield increases in Argentina were mostly related to the decrease in plant height that resulted in harvest index increments due to a greater biomass partition to the reproductive organs (Siddique et al., 1989; Borrell et al., 1991; Calderini and Slafer, 1999). During the last decade increases in harvest index were more than proportional to decreases in above ground biomass, determining positive genetic gains (although at a lower rate than in the past).

4.3. Numerical yield components

Grain number per unit area was the main driver of grain yield increments in modern cultivars compared to old ones (Foulkes et al., 2009). The trends found in genetic progress evaluated through grain yield or grain number are different between different countries. In Argentina the reduction in the genetic yield gain for the last decade (as was reported in the present study) was paired with reductions in grains per unit area.

In relation to the other numerical yield component (grain weight), Calderini et al. (1995) reported that grain weight for Argentinian cultivars released between 1920 and 1990 registered reductions up to the '80s (although they were lower than the increments in grain number per m² when both changes were measured in proportional terms), followed by a grain weight increment up to the '90s. In contradiction to Calderini et al. (1995), our results demonstrated that grain weight did not show a consistent pattern with the cultivar year of release.

So far we have discussed the most common eco-physiological traits that are usually addressed in this type of analysis. However, other "fine tuning" traits associated with grain number per unit area (e.g. fruiting efficiency), and which are not usually considered in retrospective analysis of genetic progress, were also analyzed in this paper. Several works have concluded that spike dry weight at flowering was the main physiological component of grain number (Slafer and Andrade, 1993; Abbate et al., 1998; Demotes-Mainard et al., 1999; González et al., 2003) when old and modern wheat cultivars were compared. However, in line with that reported by Shearman et al. (2005) and Aisawi et al. (2015) in our work spike dry weight did not show any trend when plotted against the year of release. This lack of association can be related to the fact that spike dry weight was measured in g m⁻² and according to Fig. 6 there was a positive trend in spike m⁻² and year of release up until ca. 1960. Therefore, it is possible to speculate that the benefits in biomass partitioning to the main shoot spikes in those cultivars released from 1918 to 1960 were counterbalanced by an increased contribution of tiller spikes which are lighter than those of main stems. In the present work, deviation in grain number per unit area was explained by deviations in fruiting efficiency more than in spike dry weight in line with data from Abbate et al. (1998) in cultivars released from 1960 to 1990. González et al. (2011) and García et al. (2014) also found a positive correlation between grain number per unit area and

fruiting efficiency when testing the performance of modern cultivars.

It is important to highlight that in the present work there was a negative curvilinear relationship between the fruiting efficiency and spike dry weight, suggesting a possible trade-off between them as heavier spikes could be less efficient establishing grains than lighter spikes. García et al. (2014) working with an elite wheat population, found a similar trade-off as the one observed in the present work. The improvements in fruiting efficiency could be either associated to a better intra-spike partitioning with a concomitant increment in biomass being transferred to the growth of developing florets instead of structural components of the spike (Slafer and Andrade, 1993), or to increase the number of distal florets of smaller size than those proximal to the rachis (Dreccer et al., 2009). In the first case, potential grain weight would not be affected (Acreche et al., 2008) but in the second case, increments in grains per spike due to the appearance of grains in distal positions, respect to the rachis, within the spikelets would determine compensations in grain weight due to the association between the floret's ovary and grain size (i.e. the smaller the size of the fertile florets, the smaller the potential weight of the grains, Calderini and Reynolds 2000). In the present study no significant negative relationship was found between average grain weight and fruiting efficiency ($R^2 = 0.02$, $p > 0.1$) suggesting that yield could be increased throughout more grains per unit area without compensatory changes in potential grain size.

5. Conclusions

Summarizing, the rate of genetic progress in yield of cultivars released in Argentina in recent years has declined and this has been associated with a stabilization in grain number without changes in grain weight. Although harvest index was increased with the cultivar's year of release, in modern cultivars these increases were partially counterbalanced by decreases in above ground biomass, resulting in reduced yield progress over the last 10 years. Modern cultivars increased grains per spike without changes in spikes per unit area, and fruiting efficiency was the trait that better explained the changes in grains per unit area. Thus, fruiting efficiency could be the way to promote increments in grain number without negative consequences in grain weight.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fcr.2017.08.014>.

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