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RESEARCH

Soybean Genetic Gain in Maturity Groups III to V in Argentina from 1980 to 2015

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ABSTRACT

Genetic progress is assessed to estimate its contribution to on-farm yield increases and to identify traits that have been improved over some period of time. Although Argentina is a major soybean [*Glycine max* (L.) Merr.] producer, there is limited information about genetic progress in this system. Argentinean soybean cultivars were developed from US commercial cultivars. Because the genetic base of US cultivars is narrow, it would be expected that genetic progress in Argentina to be slower than in the United States. We assessed the genetic gain for yield and related traits in cultivars released in Argentina from 1980 to 2015. One hundred and eighty-one cultivars belonging to maturity groups (MGs) III, IV, and V were evaluated in three environments in the northern pampas from Argentina. Genetic gain in yield was 43 kg ha^{-1} yr^{-1} and was not different across MGs. Relative genetic gain was 1.1% yr^{-1}, similar to reports from the United States or Brazil. Newer cultivars from MGs III and IV had increased days to maturity, while cultivars from MG V showed the opposite trend. Vegetative period was also reduced in newer cultivars from MGs IV and V. Seed protein concentration was reduced over the years. Genetic progress explained 50% of total on-farm yield increase. Results from this experiment showed that breeding programs in Argentina were able to attain a similar genetic gain to the United States even though the starting parents were only a few US cultivars selected from an already narrow genetic base.

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Abbreviations: BLUP, best linear unbiased predictor; MG, maturity group; NIRS, near infrared spectroscopy.

Genetic progress is assessed by comparing the performance of cultivars released over a given number of years when grown in the same environmental conditions and under uniform management practices. The aim of this type of study is to quantify the genetic contribution to on-farm yield increases and to identify improved yield-related traits. Soybean, as a major seed oil and protein crop, has been previously subjected to this type of characterization, but these studies were mostly focused on US cropping systems (reviewed in Specht and Williams [1984] and Specht et al. [2014]). The latest collaborative studies conducted in the United States showed an overall genetic gain of 29 kg ha^{-1} yr^{-1} (Specht et al., 2014). This genetic progress varied as a function of productivity and, with just a few exceptions, no major differences in genetic gain were associated with agronomic management practices (e.g., planting date, fertilization, fungicides, cropping system) (Rowntree et al., 2013; Suhre et al., 2014; Weidenbenner et al., 2014; Wilson et al., 2014).

Over the last two decades, South America has become a major producer of soybean on a global scale. In the last season, while the United States continued to be the major soybean producer, with 35% of global production, Brazil was responsible for 28% and Argentina accounted for 17% (FAOSTAT, 2015). Interestingly, so far only four studies have reported genetic gain estimates from South America: three were performed in Brazil and one in Argentina. These studies reported genetic gain through

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the year 2000 or earlier (de Toledo et al., 1990; Alliprandini et al., 1993; Santos et al., 2006; Lange and Federizzi, 2009). When considering these reports, the genetic gain in the United States was faster than in Argentina, Brazil, and Canada (de Toledo et al., 1990; Alliprandini et al., 1993; Voldeng et al., 1997; Cober et al., 2005; Santos et al., 2006; Lange and Federizzi, 2009; Cober and Morrison, 2011). However, estimates from Argentina are based on a limited set of cultivars (only eight cultivars per maturity group) and restricted to cultivars released through the year 2000. Because of the major role of Argentina as a soybean producer, it is critical to have up-to-date estimates of genetic gain for this important production region.

The first varieties registered in Argentina originated from intermating a few previously released US cultivars (Rossi, 2012). Pedigree studies showed that 17 introduced ancestral lines from Asia contributed 95% of the alleles in the current genetic base of US cultivars (Gizlice et al., 1994). This very narrow genetic base from which US cultivars were developed created a genetic bottleneck and limited genetic diversity. Subsequently, Argentina's breeding programs relied on an even narrower genetic base for initial parental selection. Therefore, our working hypothesis is that soybean genetic gain in Argentina should be lower than in the United States. The evaluation of cultivars released from 1980 to the present day is also interesting because it allows testing any possible change in the genetic progress associated with two adopted biotechnological events: the transition from nontransgenic cultivars to Roundup Ready 1 soybean (RR1; Monsanto Co.) (in 1995) and the later (in the last 3 yr) transition to Intacta Roundup Ready 2 Pro soybeans (RR2 IPRO; Monsanto Co.) in Argentina.

Protein meal and oil are the main products produced by the soybean crushing industry, with soybean composition having a direct impact on yield and quality of these products. After oil extraction, protein meal is marketed for animal feed, but profitable marketing requires a meal with at least 47% protein. Producing soybean meal with this characteristic requires raw seeds with protein concentration above certain thresholds (Brumm and Hurburgh, 1990). Despite having an important environmental component, the expression of seed protein and oil concentrations is under genetic control as well (Rotundo and Westgate, 2009; Meckel et al., 2014; Rotundo et al., 2016). At the genetic level, there is a negative correlation between seed yield and protein (Carter et al., 1982; Wilcox and Shibles, 2001; Rotundo et al., 2009). Associated with this, some genetic gain studies showed a decrease in protein concentration associated with year of release (e.g., Wilson et al., 2014). It is critical to estimate how the genetic progress changes the seed composition to maintain the seed quality required by the processing industry.

The specific objectives of this paper were (i) to estimate the genetic gain for seed yield and quality in soybeans adapted to the northern pampas region in Argentina, (ii) to compare these rates among the most representative MG of this region (III to V), and (iii) to explore how the rate of genetic gain is associated with changes in other agronomic traits like phenology and lodging tolerance. To address these objectives, 181 cultivars registered in Argentina from 1980 to 2015 were evaluated in three environments.

MATERIALS AND METHODS

Cultivars Evaluated and Growing Conditions

A total of 181 cultivars ranging from MG III to V were evaluated under field conditions. Thirty-six belonged to MG III and their release year ranged from 1982 to 2013 (eight nontransgenic, 27 RR1, and one RR2 IPRO); 90 cultivars were MG IV and were released between 1980 and 2014 (20 nontransgenic, 65 RR1, and five RR2 IPRO); and 55 cultivars were MG V and were released between 1984 and 2015 (23 nontransgenic, 27 RR1, and five RR2 IPRO; See Supplemental Table S1 for a full list of cultivars). Intacta Roundup Ready 2 Pro soybeans express Cry1Ac insecticidal protein and provide protection from feeding damage caused by lepidopteran pests in addition to resistance glyphosate herbicide.

Field experiments were conducted at Campo Experimental Villarino, located in Zavalla, Santa Fe province, Argentina (33°1′ S, 60°53′ W). Soil type was a silty clay loam Vertic Argiudoll, Roldán series. Three environments were explored by a combination of field and season conditions (Table 1). Environment 1 (Sh1314) was planted on 2 Dec. 2013. Environments 2 and 3 (L71415 and Sh1415, respectively) were planted on 13 Nov. 2014 in different fields. Table 1 summarizes soil characteristics, water availability, and observed yields for those environments. Weeds were chemically controlled before crop emergence and mechanically removed whenever necessary during the remainder of the season. Pests and diseases were controlled by spraying commercially recommended products based on a fixed schedule.

Experimental Details and Measurements

The experiment was planted using a row cone planter under direct drill. Plant population was set to 35 plants m^{-2} by overplanting and hand-thinning the plots at emergence. Plots were two or four rows in 2013 to 2014 and 2014 to 2015, respectively. Rows were 0.52 m apart and plot length was 4 m. Experimental design was randomized complete block with block and cultivars as experimental factors. All cultivars were included in each block. Blocks were two in Sh1314, four in L71415, and three in Sh1415.

Phenological stages (Fehr and Caviness, 1977) of initial flowering (R1), beginning seed filling (R5), and physiological maturity (R7) were registered on a plot basis three times per week. Lodging was estimated at physiological maturity based on a 1 (fully erect) to 5 (fully prostrate) scale. Plants from two rows (center two rows in 2014–2015) were hand-clipped at R8 in a 2.08 m^2 section and threshed on a stationary harvester. Since plots were hand-clipped, there was not any issue related with the difference in days to maturity across cultivars differing in maturity group. Seeds were weighed and moisture content recorded.

Table 1. Characterization of planting date, previous crops, soil characteristics, water availability and environmental index for the three environments used to evaluate genetic gain in soybean in Argentina.

				Soil (0–20 cm)			Water		Environmental index§		
Environment	Year	Planting date	Previous crop	Organic matter	P (Bray I)	pH	Soil water†	Rainfall‡	P10	Average	P90
				g kg^{-1}	mg kg^{-1}		mm		kg ha^{-1}		
(1) Sh1314	2013–2014	2 Dec.	Pasture	32.4	44.1	6.1	208	671	3681	4416	5022
(2) L71415	2014–2015	13 Nov.	Soybean	25.6	32.1	5.8	326	625	3649	4504	5224
(3) Sh1415	2014–2015	13 Nov.	Soybean	32.4	44.1	6.1	397	625	4502	5602	6626

† Two-meter depth at planting.

‡ Between November and March.

§ Based on cultivar means.

Table 2. Variance components (as percentage of total variance) associated with environments and cultivars for different response variables.

	Percentage of total variance								
Source of variation	Seed yield (kg ha^{-1})	Seed number (seed m^{-2})	Seed mass (mg seed^{-1})	Days to R7 (d)	Duration vegetative phase (proportion of total cycle)	Lodging (1–5 scale)	Seed protein (mg mg^{-1} × 100)	Seed oil (mg mg^{-1} × 100)	Protein yield (kg ha^{-1})
	%								
Environment	39.2	24.1	14.0	65.7	24.9	5.9	21.5	42.0	23.4
Block(environment)	0.0	0.1	1.4	0.0	0.4	1.1	1.5	1.2	0.2
Cultivar	30.7	44.8	63.5	31.1	66.0	40.8	48.2	40.0	42.7
Environment × cultivar	4.7	6.2	6.0	0.6	1.6	16.1	6.0	1.5	6.8
Residual	25.4	24.7	15.1	2.6	7.1	36.1	22.8	15.4	26.9
Cultivar/environment × cultivar ratio	6.5	7.2	10.7	54.7	42.0	2.5	8.0	26.7	6.2

A subsample of 200 seeds was weighed to estimate individual seed mass and seed number on an area basis. Seed yield and seed mass were expressed on a dry weight basis. Protein and oil concentrations were estimated by near infrared spectroscopy (NIRS; NIRSystems 5000, Foss) and expressed on a dry weight basis. The NIRS equipment was fitted with calibration equations developed by the University of Rosario in cooperation with Foss Argentina. Protein and oil yield was estimated by multiplying seed yield by seed protein or oil concentrations.

Statistical Analysis

Conducting a genetic gain study for any specific trait requires having a single estimate for each cultivar included in the analysis. This estimate should predict the true genotypic effect of each particular cultivar regardless of environmental effects or missing data. The use of best linear unbiased predictors (BLUPs) (Robinson, 1991) gives an adequate estimate of the cultivar effect across different environments. Best linear unbiased predictors of each cultivar were obtained using estimate statements in a model that included environment (combination of field × year), blocks within environment, cultivar, and cultivar × environment interaction as random effects (Rincker et al., 2014). For each trait, variance components were determined by fitting a linear mixed-effects model using the lmer function in the lme4 package (Bates et al., 2014) in R (R Development Core Team, 2014). Parameter estimates for the model were obtained using the restricted maximum likelihood method.

The slope of the regression of trait BLUPs (instead of means) for each respective cultivar release year provides an estimate of the annual genetic gain. Significance of slope differences among MGs were tested by an analysis of covariance as implemented in GraphPad Prism version 5.00 for Windows (GraphPad, 2011). Whenever genetic gain was not different among MGs, data are reported for the three MG together. Ordinary least squares regressions were calculated to estimate average genetic gain over time. A quantile regression at the 90th percentile was used to estimate genetic gain for the top 10% of cultivars across years of release (de la Vega et al., 2007; Gizzi and Gambin, 2016). The genetic gain for any of the evaluated traits was expressed both in absolute and relative change per year. Relative gain was calculated as the absolute gain divided by the predicted yield of the oldest release year (Boerma, 1979). The same approach was used for the estimation of the relative genetic gain at the 90th percentile.

RESULTS

Environment Characterization

Average yield across environments ranged from 4416 to 5602 kg ha^{-1} (~27% variation) (Table 1). Lowest yields (10th percentile) ranged from 3641 to 4502 kg ha^{-1} (~24%), while highest yields (90th percentile) were from 5022 to 6626 kg ha^{-1} (~32%) (Table 1). Variance components for yield showed environment accounting for 40% of total variation and cultivar 30% (Table 2). Cultivar explained six times more variation than the cultivar by environment interaction, suggesting cultivar rankings were consistent across environments.

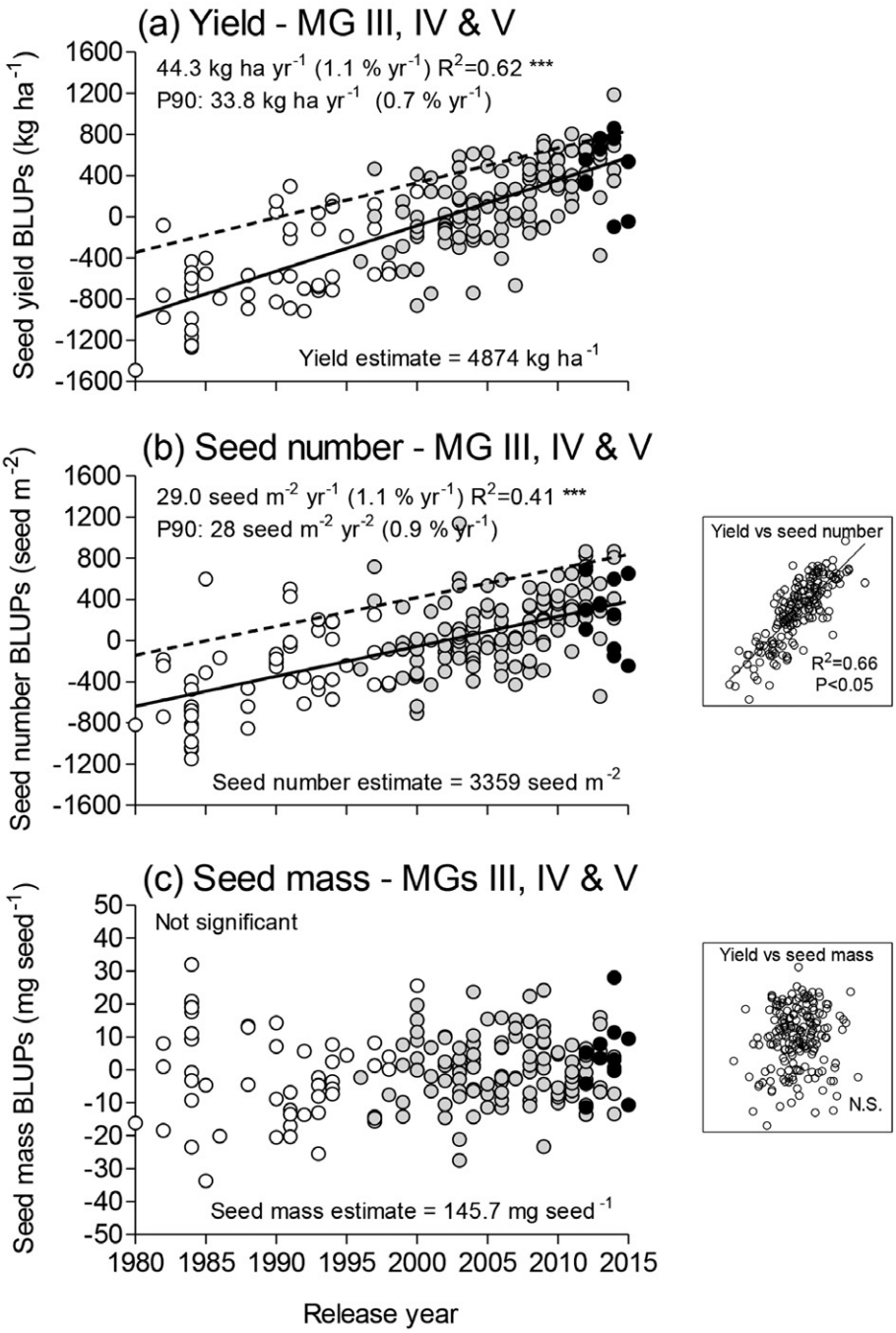

Fig. 1. Relationship between best linear unbiased predictors (BLUPs) for (a) seed yield, (b) seed number, and (c) individual seed mass and release year for maturity groups III, IV, and V. Empty symbols indicate nontransgenic cultivars, grey symbols indicate Roundup Ready 1 soybean cultivars, and full symbols indicate Roundup Ready 2 IPRO soybean cultivars. The full line is the ordinary least square regression. The dashed line is the 90th percentile regression. Insets show the relationship between seed yield and seed number and between seed yield and individual seed size. The seed yield, number, and mass estimates indicate the average across cultivars. The relative genetic gain is indicated in parenthesis.

Yield Genetic Gain

The genetic gain for yield, estimated as the slope of the linear relationship between seed yield and release year, was not significantly different among MGs. The overall genetic gain for the three MGs was 44.3 kg ha^{-1} yr^{-1} while the genetic gain relative to the earliest release years was 1.1% yr^{-1} (Fig. 1a). No discontinuities in the linear regression were observed across the nontransgenic, RR1, or RR2 IPRO soybeans. When focusing on the cultivars yielding in the top 10th percentile, the absolute and relative genetic gains dropped to 33.8 kg ha^{-1} yr^{-1} and 0.7% yr^{-1}, respectively (Fig. 1a). Seed number per unit land area increased at a significant rate over the release years, while the individual seed mass did not change (Fig. 1b, c). Average individual seed mass was ~146 mg seed^{-1} and was constant across the release years. For the average data,

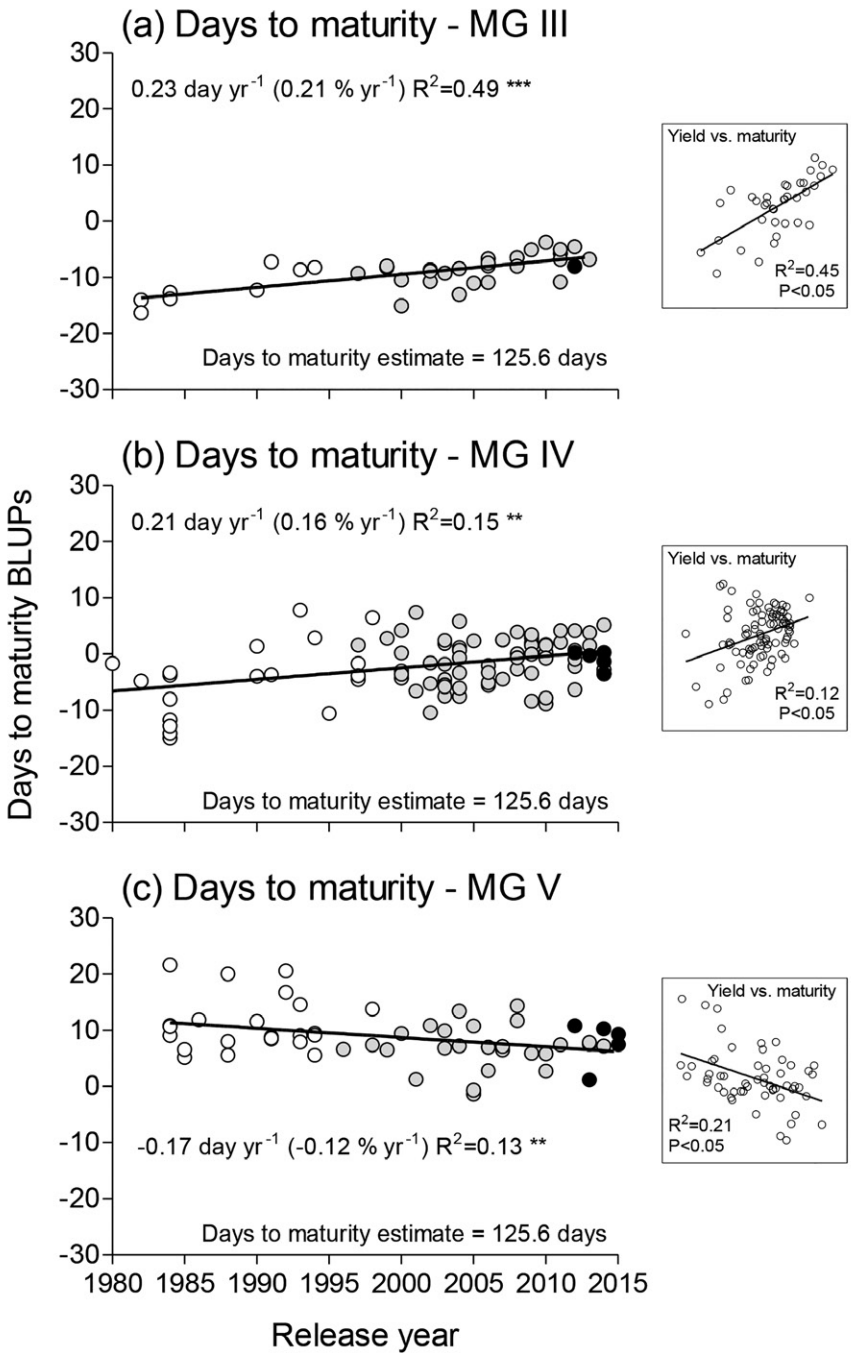

Fig. 2. Relationship between best linear unbiased predictors (BLUPs) for days to maturity and release year in cultivars maturity group (a) III, (b) IV, and (c) V. Empty symbols indicate nontransgenic cultivars; grey symbols indicate Roundup Ready 1 soybean cultivars; and full symbols indicate Roundup Ready 2 IPRO soybean cultivars. Insets show the relationship between seed yield and days to maturity. The days to maturity estimate indicates the average across cultivars. The relative genetic gain is indicated in parenthesis.

the relative genetic gain for seed number was similar to that for seed yield (1.1% yr^{-1}), but in the case of the 90th percentile it was slightly slower (Fig. 1a, b). Regardless of the release year, seed number explained more than 60% of the observed yield variation; there was no correlation between yield and individual seed mass (insets Fig. 1b, c).

Release Year and Phenology

Environment accounted for >60% of variation in days to physiological maturity (R7), while cultivar explained 30% (Table 2). Cultivar explained 54 times more variation than the environment × cultivar interaction, suggesting high consistency of cultivar behavior across environments. There were statistical differences among MG in the slope that relates days to maturity to release year ($P < 0.05$). These variables were positively associated for MGs III and IV while negatively associated for MG V (Fig. 2). Regardless of the year of release, there was a positive correlation between seed yield and days to maturity for MGs III and IV (Insets, Fig. 2a, b). On the contrary, there was

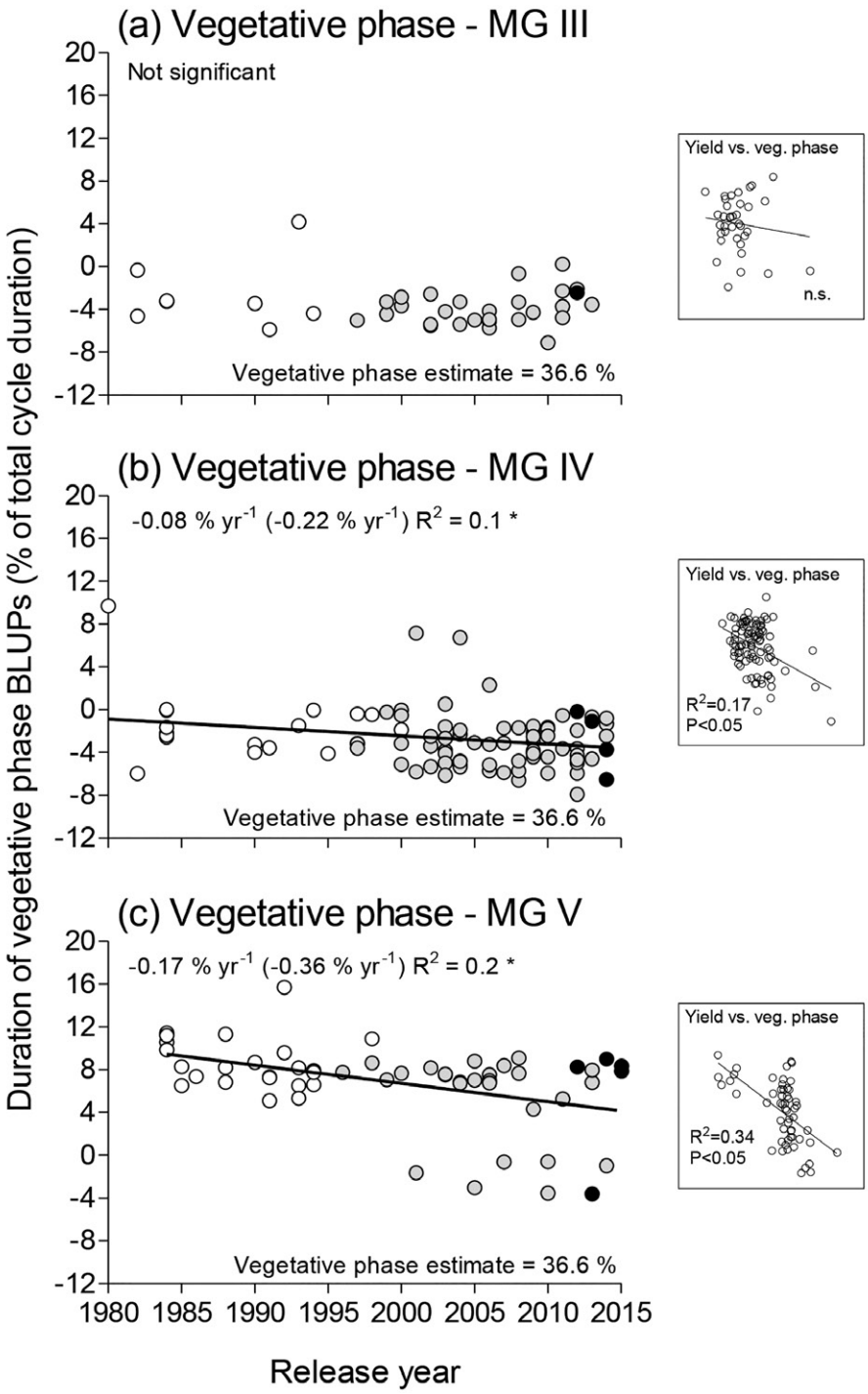

Fig. 3. Relationship between best linear unbiased predictors (BLUPs) for duration of vegetative phase (percentage days from total cycle) and release year in cultivars maturity group (a) III, (b) IV, and (c) V. Empty symbols indicate nontransgenic cultivars, grey symbols indicate Roundup Ready 1 soybean cultivars, and full symbols indicate Roundup Ready 2 IPRO soybean cultivars. Insets show the relationship between seed yield and duration of vegetative phase (days). The duration of vegetative phase estimate is the average across cultivars. The relative genetic gain is indicated in parenthesis.

a negative correlation between seed yield and maturity for MG V. The duration of the vegetative phase (planting to R1) was expressed as a fraction of the total cycle. More than 60% of the variation observed for this trait was accounted for by cultivar (Table 2). The magnitude of the variance of cultivar was >40 times higher than the environment × cultivar interaction, suggesting that cultivars behave similarly in different environments. For the earliest release year, the vegetative phase represented 33, 35, and 45% of the total cycle for MGs III, IV, and V, respectively. The duration of this phase was significantly reduced over the release years in cultivars belonging to MGs IV and V (Fig. 3b, c) but was unchanged for MG III (Fig. 3a). After >30 yr of breeding, the duration of the vegetative phase

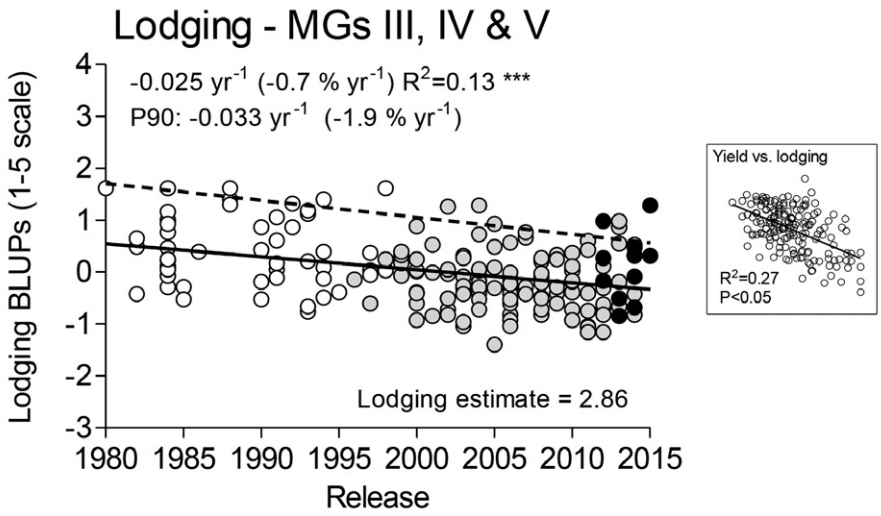

Fig. 4. Relationship between best linear unbiased predictors (BLUPs) for lodging and release year for maturity groups III, IV, and V. Empty symbols indicate nontransgenic cultivars, grey symbols indicate Roundup Ready 1 soybean cultivars, and full symbols indicate Roundup Ready 2 IPRO soybean cultivars. The full line is the ordinary least square regression. The dashed line is the 90th percentile regression. Inset show the relationship between seed yield and lodging. The lodging estimate indicates the average across cultivars. The relative genetic gain is indicated in parenthesis.

was reduced to ~32% of the total cycle in MG IV and to ~40% in MG V cultivars. For these MGs, there was a significant negative correlation between the duration of the vegetative phase and seed yield (Insets Fig. 3b, c). This relationship was not observed for MG III (Inset Fig. 3a).

Release Year and Lodging

Cultivar accounted for ~40% of the variance for lodging (Table 2). Even though environment accounted for <6% variation, the ratio between cultivar and environment × cultivar variances was the lowest of all variables evaluated. This indicates that there were some cultivars that were more sensitive to lodging in the different environments. Regardless of this interaction, there was a negative correlation between lodging and release year (Fig. 4). The rate of lodging reduction was not different across MGs. For all three MGs lodging was reduced on average from 3.41 in 1980 to 2.53 in 2015 (Fig. 4). The reduction in lodging of the highest lodging cultivars (90th percentile) was higher than the average decay.

Release Year and Seed Quality

Cultivar accounted for >40% of the variance in seed protein and oil (Table 2). Environments explained around 20 and 40% of seed protein and oil variances, respectively. However, the cultivar variance was several times higher than the environment × cultivar variance. This indicated that, for both traits, the ranking of cultivars was fairly constant across environments. In terms of genetic change, there was a negative association between cultivar release year and seed protein concentration. Although the explanatory power of the relationship was low ($R^2 = 0.10$), there was a highly significant ($P < 0.001$) decline from 38.6% protein in 1980 to 37.6% in 2015 (Fig. 5a). When considering the 90th percentile values, we observed that in both absolute and relative terms, seed protein concentration decreases were very similar to the average decay (Fig. 5a). Variation in seed oil concentration was not associated with release year (Fig. 5b). Across all cultivars, regardless of release year, there was a strong negative correlation between seed protein and oil concentration (Inset Fig. 5).

Cultivar accounted for >40% of variation in seed protein yield, expressed as kilograms protein per hectare (Table 2). The ratio of cultivar variance to that of environment × cultivar interaction was >6, indicating a high degree of consistency of cultivars across environments (Table 2). Seed protein yield across all MGs increased with increasing release year at a rate of 9.95 kg ha^{-1} yr^{-1}; however, there were differences across the MGs evaluated. The rates of genetic gain in protein yield were 10.5, 12.4, and 7.1 kg ha^{-1} for MGs III, IV, and V, respectively (Fig. 6), while the relative genetic gains were 1.0, 1.3, and 0.6% yr^{-1}, respectively. The genetic gain of the highest yielding cultivars was similar, both in absolute and relative terms, to that of the average cultivars. Regardless of the release year, there was a significant negative correlation between seed protein concentration and seed yield for the three MGs evaluated (Insets Fig. 6). The slopes of these negative correlations were −0.00072, −0.00052, and −0.00075% protein per kg ha^{-1} yield increase for MG III, IV, and IV, respectively.

DISCUSSION

Results from our experiment have demonstrated significant genetic progress in soybean cultivars released in the main production area of Argentina. Genetic gain for seed yield was not different when comparing MGs. Recently,

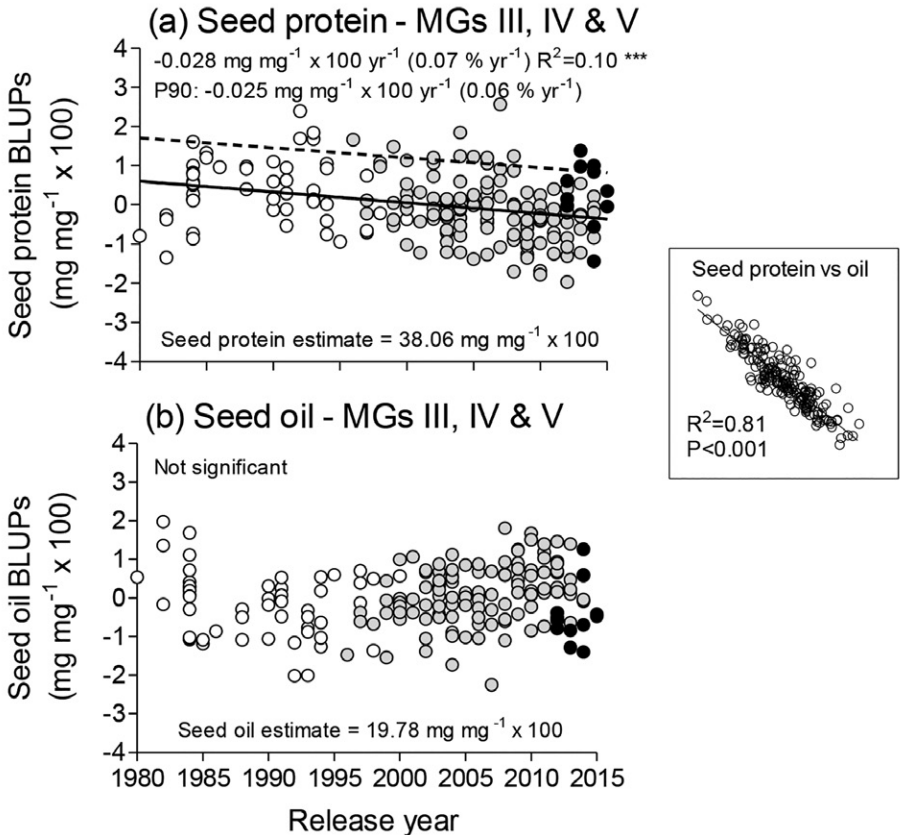

Fig. 5. Relationship between best linear unbiased predictors (BLUPs) for (a) seed protein and (b) oil concentrations and release year for maturity groups III, IV, and V. Empty symbols indicate nontransgenic cultivars, grey symbols indicate Roundup Ready 1 soybean cultivars, and full symbols indicate Roundup Ready 2 IPRO soybean cultivars. The full line is the ordinary least square regression. The dashed line is the 90th percentile regression. Inset show the relationship between seed protein and oil concentrations. The seed protein and oil concentrations estimates indicate the average across cultivars. The relative genetic gain is indicated in parenthesis.

Rincker et al. (2014) evaluated genetic gain across different locations in the United States and specifically tested differences across MGs II to IV. They found that when cultivars differing in MGs were grown in the same environment, the genetic gain rate was not differentially associated with MGs. This finding, together with our current results, suggests that contrasting MGs have no intrinsic differences in genetic gain potential. Also, our dataset is unique in that it includes two transgenic milestones in soybean breeding: the transition of non-GMO to RR1 soybeans and the transition for RR1 to RR2 IPRO soybeans. We found no discontinuities in the relationship between seed yield and release year that would suggest any qualitative yield advantage associated with these transgenic events.

Regardless of the maturity group, the rate of genetic gain in central Argentina was 44.3 kg ha^{-1} yr^{-1} in absolute terms and 1.1% yr^{-1} relative to the predicted oldest cultivar yield. The absolute genetic gain that we observed is among the highest ever recorded. Some similar values were observed in Paraná, Brazil (41 kg ha^{-1} yr^{-1}; de Toledo, 1990), but several other recent reports from the United States showed a lower genetic gain than the one we observed (~29 kg ha^{-1} yr^{-1}; Specht et al., 2014). Because the genetic gain in kilogram per hectare per year is positively associated with the quality of the environment (Rincker et al., 2014), it is important to use the relative genetic gain as a way to compare productive systems that have different starting points or average yields (Slafer and Andrade, 1991). Thus, when the genetic gain is expressed relative to the predicted yield for the oldest release year considered in the experiment, the rates that we observed for central Argentina are similar to those reported for the United States and Brazil, ~1.2% yr^{-1} (de Toledo, 1990; Rincker et al., 2014). The genetic progress in the United States is constrained by a narrow genetic base because most cultivars were developed from just a handful of ancestral lines imported from Asia (Gizlice et al., 1994). Since Argentina's breeding programs were derived from US commercial lines released in the 1960s and 1970s (Rossi, 2012), we expected to observe a lower genetic gain than that observed in the United States. The results from our experiment show that breeders have been able to overcome this constraint and attain high genetic gains. In addition, it can be hypothesized that at least part of the genetic bottleneck expected to occur in Argentina was relieved by a likely continuous exchange of materials between Argentina and the United States.

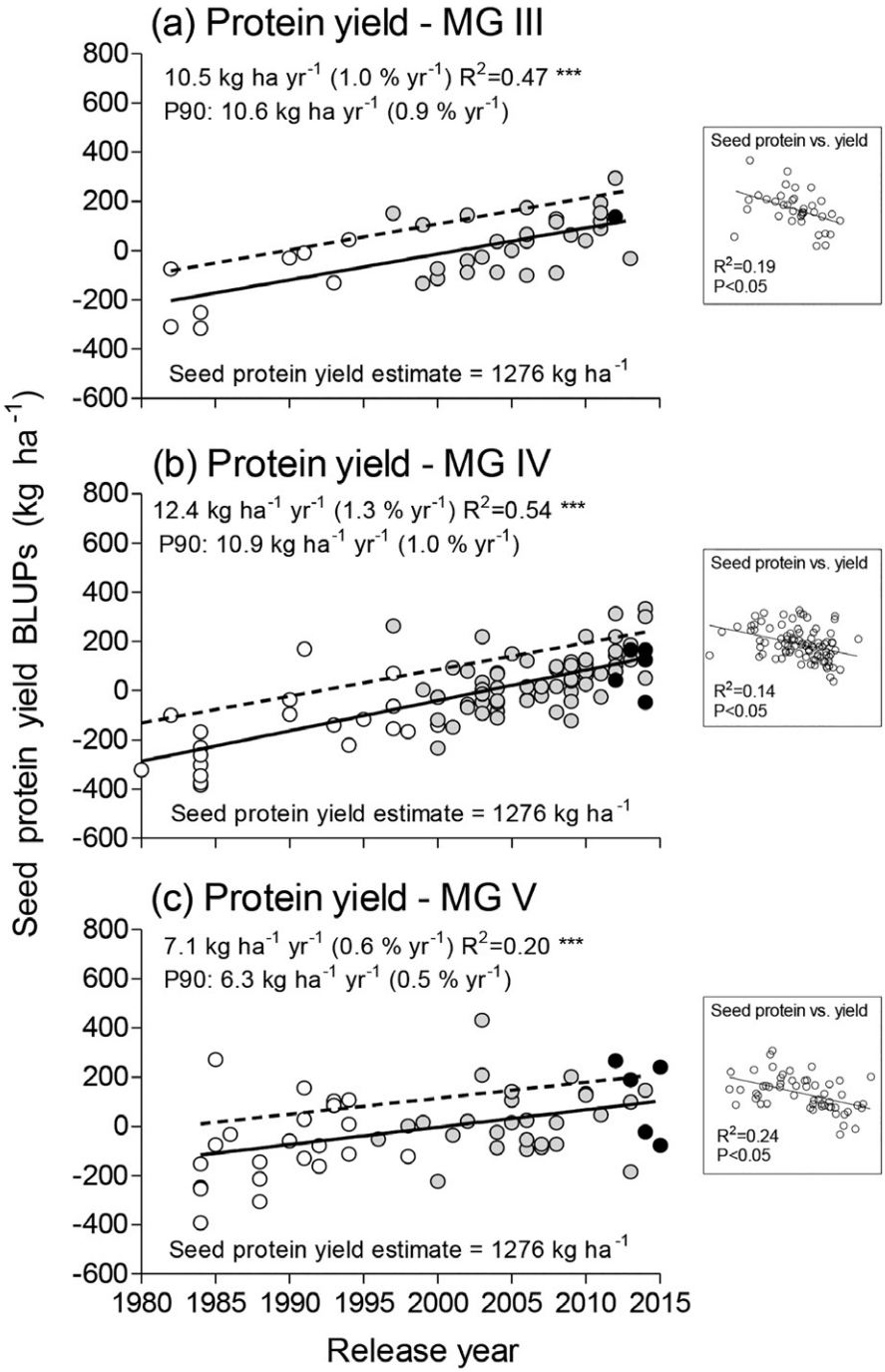

Fig. 6. Relationship between best linear unbiased predictors (BLUPs) for seed protein yield and release year in cultivars maturity group (a) III, (b) IV, and (c) V. Empty symbols indicate nontransgenic cultivars, grey symbols indicate Roundup Ready 1 soybean cultivars, and full symbols indicate Roundup Ready 2 IPRO soybean cultivars. Insets show the relationship between seed protein concentration and seed yield. The seed protein yield estimate is the average across cultivars. The relative genetic gain is indicated in parenthesis.

Changes in maturity, vegetative phase duration, and lodging resistance were associated with release year and yield. Results from our experiment showed increased days to maturity for MG III and IV across release years and decreases in MG V. Rincker et al. (2014) found increases in maturity for cultivars grown in the United States in later years of release. It is generally established that late-maturing cultivars tend to yield greater than early ones because the extended period of the growth cycle allows for more C assimilation and, therefore, more yield (Board and Tan, 1995). However, in some cases, excessively long growth cycle duration is associated with reduced yield resulting from drops in harvest index (Edwards and Purcell, 2005). Therefore, the optimum MG for a location (without serious risk of drought) is one that is not too short to be limited by radiation capture and not too long to be limited by excessive vegetative growth and reduced harvest index (Egli, 2011). The difference in days to maturity between MG III and V in cultivars released in 1980 was 24 d, while in cultivars released in 2015, it was 12 d. These results indicate

adjustments in maturity toward intermediate maturities that would balance radiation capture and optimum partitioning of assimilates. Moreover, MG IV and V also showed a significant reduction in the vegetative phase duration, and this duration was negatively associated with yield in these MGs. This is in agreement with Kantolic and Slafer (2001, 2005) who demonstrated the yield benefits of increasing the reproductive phase to increase seed set and yield.

Lodging was another trait that was reduced in modern cultivars. Several reports showed reductions in lodging as a consequence of breeding (e.g., Specht et al., 1999; Morrison et al., 2000; Jin et al., 2010). Some authors suggest that the reduction in lodging is associated with increased radiation use efficiency (Cooper, 1971), while others suggest that it improves canopy light interception (Zhu et al., 2010). In fact, Koester et al. (2014), using a set of cultivars from the United States, have recently demonstrated that soybean yield increases associated with breeding are related to increased radiation use and interception efficiency while lodging is reduced.

Soybean seed composition is becoming an important characteristic for marketing. Protein deficits in the seeds preclude attaining quality standards established by international markets for high-protein meal (Meckel et al., 2014). There is evidence that selecting for seed protein concentration is possible, but negative correlations between seed protein concentration and both yield and seed oil concentration hinder the development of competitive high-protein lines (Carter et al., 1982; Wilcox and Zhang, 1997; Wilcox and Shibles, 2001). In general, genetic gain studies showed a negative correlation between seed protein concentration and release year (e.g., Morrison et al., 2000; Rincker et al., 2014; Rogers et al., 2015). There is evidence that some management practices can reduce the relative decrease in soybean protein concentration with release year such as N fertilization (Wilson et al., 2014), later planting date (Rowntree et al., 2013), and fungicide applications (Weidenbenner et al., 2014). In all these cases, relative reductions in protein concentration are lower than increases in yield over year of release. Therefore, seed protein yield increased with modern cultivars. Our study shows, however, that the genetic gain of seed protein yield was differently associated with MGs. Cultivars belonging to MG V showed half of the relative genetic gain observed in the other two MGs with statistically different slopes. The result is a higher negative correlation between seed protein concentration and yield for these longer MGs.

The importance of this type of study is that it provides the means to explain the causes of increases in production and identifies future prospects for continued gain from selection. The production increase, in relative terms, on farms within the same county where our experiments were performed and for the same time period, was 2.3% yr^{-1}, as estimated by Argentina's agricultural data agency (Sistema integrado de Información Agropecuaria, 2016). Comparing this value with our observed genetic gain (1.1% yr^{-1}) suggests that ~50% of production improvements were associated with better genetics, while 50% was associated with better production practices. The 50% we attribute to better genetics contrasts with that in the United States where genetic improvement was responsible for ~67% of on-farm yield increases (Specht et al., 2014). Regardless of the proportion of on-farm yield increases explained by management or genetics, there is a need to increase the annual rate of genetic gain of crops to satisfy a steadily growing food demand (Cassman, 1999; Specht et al., 1999). Increasing the annual rate of genetic gain in a crop like soybean with a narrow genetic base (Gizlice et al., 1994) would require, among other things, increasing its genetic diversity by taking advantage of the genetic variation in wild relatives, which may provide yield-enhancing alleles (Concibido et al., 2003; Gur and Zamir, 2004).

CONCLUSIONS

Genetic gain studies provide the opportunity to estimate the relative contribution of breeding and agronomic management in past on-farm yield increases. Breeding of soybean in the central region of Argentina produced 1.1% yr^{-1} yield increases over the last 35 yr. This value accounts for 50% of the on-farm yield increases over the same years and location. The observed genetic gain in Argentina is similar to the genetic progress observed in the United States and Brazil. The transition from conventional non-transgenic soybeans to RR1 soybean in the 1990s, and the further transition to RR2 IPRO in 2013, did not show any discontinuity in the relationship between yield and release year that could indicate an extra contribution from these biotechnological events to genetic gain.

This study also provides the opportunity to identify yield-related traits that may have changed in response to breeding. Over the release years, there were some adjustments in phenology associated with increasing days to maturity in early and intermediate cultivars and decreasing days to maturity in late cultivars. Also, the duration of the vegetative phase was reduced in intermediate and late maturity cultivars. Seed protein concentration was reduced in modern cultivars, but increases in seed yield compensated for this reduction.

Supplemental Information Available

Supplemental information is available with the online version of this manuscript.

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