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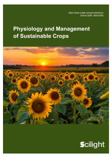

Article

Soybean Breeding Effects on Seed Yield Determination Under Contrasting Water Supply

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Abstract: Soybean seed yield (SY) gains have been achieved through both genetic improvement and advances in agronomic practices. However, the contribution of genetic gain (GG) to overall yield improvement can vary depending on specific environmental conditions, particularly under contrasting water supply. In this study, we analyze the impact of traditional soybean breeding on SY, its physiological determinants, and numeric yield components across contrasting water supply conditions. Field trials included a representative set of widely adopted commercial varieties from maturity groups (MGs) IV–V released between 1982 and 2016, grown in the core production zone of the humid Pampas region in Argentina. Results showed a biphasic GG trend for SY, which declined at a rate of 0.64% year^{-1} until 2004 and increased at 1.9% year^{-1} from 2004 onwards. These trends were mirrored by changes in harvest index (HI) and, to a lesser extent, by aboveground biomass (B_T), particularly under water-limited conditions. Changes in B_T were reflected in similar trends in radiation and water use efficiencies, as no significant breeding effects were observed on resource capture. The most consistent effects of breeding were observed on seed number and pod number, with no clear trends in individual seed weight. The absence of differences in crop evapotranspiration among genotypes suggests that recent genetic progress improved the efficiency of biomass production rather than increasing water use. This study highlights the importance of analyzing GG within specific MGs and environments, revealing previously undetected shifts in SY trends within MG IV–V adapted to humid temperate regions.

Keywords: *Glycine max* (L.) Merr.; genetic gain; seed yield; secondary traits; resource use; resource use efficiency

1. Introduction

Globally, increases in soybean seed yield (SY) have resulted from both genetic improvements and advances in agronomic practices. In the United States, Rincker et al. [1] estimated a long-term global yield gain (GYG) of 23.3 kg·ha^{-1}·y^{-1} between 1924 and 2012, with two-thirds attributed to breeding efforts across time. The rate of change in SY, which is associated with the annual release to the market of new genotypes, is commonly known as genetic gain (GG) [2,3]. In Argentina, the estimated GYG for the same period is similar (22.4 kg·ha^{-1}·y^{-1}) [4], but the relative contribution of GG to GYG appears to be lower than in the United States. A re-analysis of data from Santos et al. [5] suggests that genetic contributions account for approximately 33% of the GYG, though this estimate covers a wide range of maturity groups (MGs, III-VIII) and does not reflect significant genetic progress within each group. Different MGs are adapted and sown by farmers across a wide range of environmental conditions in Argentina [6]. Consequently, studies focusing on specific MGs and a wider range of environments provide further insight into genetic trends [7]. For example, de Felipe et al. [8] analyzed genotypes released to the Argentine market between 1980 and 2015 (MGs III-V) and estimated a GG of 1.10% y^{-1} under non-limiting water conditions (i.e., >650 mm water supply). These GG estimates were consistent across MGs. However, in a simulation study, de Felipe et al. [9] reported that GG may range from 0.27–0.30% y^{-1} under low water availability to 0.87–1.11% y^{-1} under favorable conditions, suggesting that SY improvements associated to breeding effects depend on environmental factors, particularly rainfall. In a recent study, however, GG for MG IV genotypes was found to be higher under well-watered than water-stressed conditions (31.6 and 12.8 kg ha^{-1} y^{-1}, respectively), although the relative rate of increase remained similar across both environments (1% y^{-1}) [10].

The observed breeding effects on SY have primarily been linked to increases in total aboveground biomass (B_T) at physiological maturity (R7) [11], its partitioning to seeds represented by harvest index (HI), and the number of harvestable seeds per m^2 (SN) at R7 [8,9]. For short-cycle genotypes adapted to high-latitude environments, Kumudini et al. [12] estimated that 78% of GG was explained by B_T gains, with the remaining 22% attributed to HI. Similar trends were reported for MGs III and IV [9], whereas for MG V, genetic progress involved both B_T and HI in equal proportions. In Canadian soybean genotypes (MGs < II), Morrison et al. [13] attributed GG in SY to increased HI and photosynthetic rate (a key determinant of B_T), while observing a gradual reduction in leaf area index over time. The former increased at a rate of 0.5% y^{-1} and the latter decreased at a rate of 0.4% y^{-1}.

Aboveground biomass production, its partition between vegetative and reproductive organs, and the numerical components of SY (pod number, SN, and individual seed weight) are key determinants of SY that have been unintentionally shaped by genetic improvement (i.e., without being directly targeted in selection). A similar pattern applies to water use efficiency (WUE) and radiation use efficiency (RUE) for B_T production, both of which could enhance soybean SY in increasingly challenging environments (IPCC, 2014) [14]. While positive breeding effects on RUE have been documented in humid environments [9], the effects on WUE remain less understood. Feng et al. [15] reported that breeding for improved WUE in arid and semi-arid regions of China was accompanied by reduced water use, whereas de Felipe et al. [9] found that increases in RUE were associated with greater stomatal conductance and higher water use in humid conditions. These contrasting findings suggest that the GG in SY should be faster in high-rainfall environments, highlighting the need for a simultaneous evaluation of both efficiencies under diverse water supply conditions. In summer-grown cereal species like maize, there is general agreement that breeding has not significantly altered total crop water use in humid temperate regions [16,17], despite a reduction in biomass allocation to roots [18]. This shift in biomass allocation supports the documented increments in B_T and WUE [16].

In this study, we analyze the impact of traditional soybean breeding on SY, its physiological determinants, and numeric yield components across contrasting water supply conditions. To achieve this, we evaluated a representative set of widely adopted commercial varieties (MGs IV-V) released between 1982 and 2016, grown in the core production zone of the humid Pampas region in Argentina. By integrating historical genetic trends with a resource efficiency perspective, this study provides insights into physiological and environmental drivers shaping soybean genetic progress.

2. Materials and Methods

2.1. Crop Husbandry and Experimental Design

Field experiments were carried out at the experimental station of the National Institute of Agricultural Technology (INTA), located in Pergamino (33°56′S, 60°33′W), province of Buenos Aires, Argentina, on a silty clay loam soil (Argiudol típico, Pergamino series) with an effective soil depth greater than 2 m. Experiments (Exp) were performed during two seasons (Exp1: 2016–2017; Exp2: 2017–2018). Twelve (Exp1) or fourteen (Exp2) genotypes were included in the analysis, which were released to the local market between 1982 and 2016 (Table 1). All corresponded to the MGs most used and adapted in the region (IV and V) [6,19]. At least two varieties, and at least one of each MG, were selected for each decade of market release. The varieties were chosen among the most widely cropped by farmers according to official statistics (INASE, 2016) and by consultation with specialists from various seed companies (Nidera Semillas, Grupo Don Mario, Santa Rosa Semillas) and previous work carried out in Argentina [5,8]. Sowing dates (23 and 17 Nov for Exp1 and Exp2, respectively) were within the range used for soybean cultivated as a single crop (i.e., not double-cropped after a winter crop harvest) in the region [19]. Seeds were inoculated with *Bradyrhizobium japonicum* strains before sowing, and stand density was always 30 plants m^{-2}. Genotypes were distributed in a completely randomized block design with three replicates. Each experimental unit consisted of 6 rows (width) and 5 m (length), with a row spacing of 0.35 m (Exp1) or 0.52 m (Exp2). Experiments were kept free of biotic constraints using appropriate controls.

Table 1. Soybean genotypes included in each experiment (Exp).

Year of Release	Genotype	Technology	Company	MG	Exp1	Exp2
1982a	Asgrow 4268	Non-transgenic	Nidera Semillas	IV	X	X
1982b	A 5618	Non-transgenic	Nidera Semillas	V	X	X
1984	Asgrow 5308	Non-transgenic	Nidera Semillas	V	X	X
1990	DK CX 458	Non-transgenic	Dekalb	IV	X	X
1994	A 5780	Non-transgenic	Nidera Semillas	V	-	X
1997	A 5402	Non-transgenic	Nidera Semillas	V	X	X
2000	ADM4800	Glyphosate resistant	Grupo Don Mario	IV	X	X
2006	DM 5.8i	Glyphosate resistant	Grupo Don Mario	V	X	X
2007	NA 4990 RG	Glyphosate resistant	Nidera Semillas	IV	X	X
2008a	DM 4250	Glyphosate resistant	Grupo Don Mario	IV	X	X
2008b	DM 4670	Glyphosate resistant	Grupo Don Mario	IV	X	X
2012	DM 4612	Glyphosate resistant	Grupo Don Mario	IV	X	X
2014	NS 5258	Glyphosate resistant	Nidera Semillas	V	-	X
2016	DM 40R16	Glyphosate resistant	Grupo Don Mario	IV	X	X

MG: maturity group.

Incident photosynthetically active radiation (PARinc, in MJ·m^{-2}), maximum air temperature (Tmax, in °C) and minimum air temperature (Tmin, in °C) were recorded daily by an automatic station located less than 1 km from the experiments. Rainfall (in mm) was registered in situ. Experiment 1 received supplementary irrigation (sprinkler system) to have the rainfall plus irrigation (in mm) amount close to the potential evapotranspiration (PET, in mm), whereas Exp2 was conducted under dryland farming. These management, together with interannual differences in weather, ensured contrasting growing conditions between years both in the vegetative-pod set (VE-R5) [11] and pod-filling (R5-R7) phases (Table 2).

Table 2. Growing conditions (averaged across genotypes).

Stage	Characteristic	Experiment 1 (Irrigated)	Experiment 2 (Dryland)
VE-R5 phase	Cumulative PARinc (MJ m^{-2})	2108	2488
	Mean maximum Temperature (°C)	30.2	31.9
	Mean minimum Temperature (°C)	16.5	16.8
	Rainfall and Irrigation (mm)	468	217
	Potential evapotranspiration (mm)	441	525
R5-R7 phase	Cumulative PARinc (MJ m^{-2})	803	621
	Mean maximum Temperature (°C)	28.4	30.9
	Mean minimum Temperature (°C)	16.3	15.2
	Rainfall and Irrigation (mm)	150	23
	Potential evapotranspiration (mm)	142	144

PARinc: incident photosynthetically active radiation. VE, emergence, R5, beginning of seed filling, R7, physiological maturity according to Fehr and Caviness [11] scale.

2.2. Measurements, Computations and Statistical Analyses

Soil water content was surveyed fortnightly throughout the cycle, gravimetrically in the 0–30 cm layer and by neutron probe (Troxler 3400, NC, USA) from 30 to 200 cm soil depth. One access tube was placed in the middle of each plot immediately before sowing. The probe was calibrated with volumetric soil samples and converted into soil water content (SWC, in mm) as described in Dardanelli et al. [20]. Seasonal crop evapotranspiration (ETc, in mm) was calculated as in Equation (1).

$$\mathrm{ETc} = \Delta\mathrm{SWC} + \mathrm{Rainfall} + \mathrm{Irrigation} \quad (1)$$

Variation in SWC (ΔSWC) derived from the difference in SWC between successive measurements. Runoff was considered negligible due to the flat topography of the landscape.

The light interception efficiency (ei) was also surveyed fortnightly during the whole cycle. A 1-m linear ceptometer (Cavadevices, Argentina) was used to quantify ei according to Equation (2)

$$\text{ei} = 1 - \text{PARb}/\text{PARa} \tag{2}$$

being PARa the amount of PARinc above the canopy and PARb, the amount of PARinc immediately below the lowermost green leaves of the canopy. Measurements were performed between 11:00 and 14:00 hs on clear days. In each plot, PARb was computed as the average of three measurements, obtained by placing the ceptometer diagonally between two successive interrows and centered in the row. Daily ei was estimated by linear interpolation between successive measurements. The seasonal amount of PARinc that was intercepted by the crop (PARint) was calculated as in Equation (3)

$$\text{PARint} = \sum_{VE}^{R7} ei \times PARinc \tag{3}$$

The B_T (in g·m^{-2}) was estimated by sampling 1 m from a central row of each plot at R7. The pods were separated to obtain the number of pods per m^2 (PN) and pod biomass (B_P, in g·m^{-2}). The biomass samples were weighed after being air-dried at 60 °C up to constant weight.

Pods were hand shelled and SY (in g·m^{-2}) was registered and expressed on a 13% seed moisture. Individual seed weight (SW, in mg) was assessed on a sample of 500 seeds, and SN was computed as the quotient between SY and SW. The HI was computed as in Equation (4)

$$\text{HI} = \text{SY}/B_T \tag{4}$$

Both WUE (in g·m^{-2}·mm^{-1}) and RUE (in g·MJ^{-1}) were estimated as in Equations (5) and (6), respectively.

$$\text{WUE} = B_T/\text{ETc} \tag{5}$$

$$\text{RUE} = B_T/\text{PARint} \tag{6}$$

The effect of treatments and their interactions on all measured traits was evaluated by ANOVA. The ANOVA was performed according to the model in Equation (7), where the environment (E) represented by each Exp and the genotype (G) were considered as fixed main effects. Only genotypes evaluated in both experiments were included in the ANOVAs.

$$Yijk = \mu + Ei + Gj + (E \times G)ij + B(E)ik + \varepsilon ijk \tag{7}$$

where $Yijk$ is the observation of genotype j in environment i and block k, μ is the overall mean, Ei is the fixed effect of the environment, Gj is the fixed effect of genotype, $(E \times G)ij$ is the fixed interaction effect between environment and genotype, $B(E)ik$ is the random effect of block k nested within environment i, and εijk is the residual error. Means were compared using Tukey's test with a significance level of $\alpha = 0.05$.

A Pearson correlation analysis was performed to explore the degree of association between seed yield and each of the evaluated variables. Additionally, a principal component analysis (PCA) was performed to comprehensively interpret the discrimination of each $G \times E$ combination with respect to the set of variables. For the latter, the values were previously standardized. Both the correlation analysis and the PCA were conducted using the InfoStat program [21] and included all genotypes.

The genetic gain (GG) was estimated by means of the best linear unbiased predictors (BLUPs) of each genotype in each environment obtained by linear mixed models fitted with the lmer function in R (lme4 package; R Core Team, 2024). For each trait, the breeding effect across time was estimated as the slope of the relationship of the BLUPs with respect to the year of release (YOR), and was expressed both in absolute terms and annual percentage (% y^{-1}). Each percent gain was calculated as the quotient between the absolute gain and the mean value of all cultivars [22]. To determine whether or not there were significant differences between the models adjusted to each experiment, slopes were compared using GraphPad Prism 9 [23].

3. Results

3.1. Genotypic and Environmental Effects on Seed Yield Determination

The environment had a significant effect ($p < 0.05$) on all the evaluated variables except the PARint and ei, while the genotypes affected all variables except ETc (Table 3). By contrast, there was no effect attributable to the $G \times E$ interaction. Seed yield was maximized under the more favorable water supply of Exp1 (5133 kg·ha^{-1};

averaged across genotypes) and decreased 40.8% (3037 kg·ha^{-1}) in response to the reduced water budget of Exp2 ($p < 0.01$). Among the genotypes, DM 40R16 (YOR 2016) and DM 4670 (YOR 2008) stood out as the highest yielding (4850 and 4476 kg·ha^{-1}, respectively) and DM 5.8i (YOR 2006) as the lowest yielding (3314 kg·ha^{-1}).

Total biomass production showed interannual variability similar to that of SY, with mean values in Exp1 being 41.6% higher than in Exp2 ($p < 0.01$; Table 3). The genotypes, on the other hand, did not hold the ranking registered for SY, and B_T was on average maximum for genotypes A 5618 (YOR 1982) and Asgrow 5308 (YOR 1984), belonging to MG V, and minimum for DM 4250 (YOR 2008), from MG IV. The HI had lower interannual variability than SY and B_T ($p < 0.05$), but it was also higher (21.8%) in Exp1 than in Exp2. For this variable, the maximum value also corresponded to the genotypes with the highest SY (i.e., DM 40R16 and DM 4670) and the minimum value to that with the lowest SY (i.e., DM 5.8i).

Although no significant difference was found between Exp1 and Exp2 for the PARint and ei (Table 3), there were differences ($p < 0.001$) among genotypes, with A 5618 standing out for presenting the highest values of both traits (894 MJ·m^{-2} accumulated during the season, as a result of having intercepted 62% of all PARint) and DM 4250 for presenting the lowest values (719 MJ·m^{-2} and 0.54, respectively). Regarding crop water use (ETc), there was a slight effect of the environment ($p = 0.06$) on this trait, which was only 7.5% higher in Exp1 than in Exp2 (although it represented 88% of the total potential evapotranspiration in Exp1 and only 71% in Exp2). No differences were detected among genotypes in ETc.

About the resource use efficiencies (RUE and WUE), the significant environmental ($0.001 \leq p < 0.05$) and genotypic ($p < 0.001$) effects stand out for both traits (Table 3). Regarding the environment, the drought recorded during Exp2 meant a decrease in RUE of 30.8% and in WUE of 24.6% compared to Exp1. Regarding genotypes, the maximum RUE value corresponded to Asgrow 5308 (1.61 g·MJ^{-1}) and the minimum to DM 5.8i (1.32 g·MJ^{-1}), while for WUE the maximum value corresponded to A 5618 (26 kg·ha^{-1}·mm^{-1}) and the minimum to DM 4250 (20.3 kg·ha^{-1}·mm^{-1}).

Regarding B_P and SY numerical components, there were significant effects of the environment ($0.001 < p < 0.05$) and the genotype ($p < 0.001$) for all of them (Table 4). The poor water condition of Exp2 produced a decrease of 40.6% in B_P with respect to Exp1, 20.5% in PN, 30% in SN and 15% in SW. Among the genotypes, the highest B_P (683 g·m^{-2}) and PN (1470 m^{-2}) values corresponded to A 5618, the highest SN to DM 40R16 (3143 m^{-2}) and the highest SW to Asgrow 5308 (164 mg). On the other hand, the lowest values corresponded to DM 4670 for B_P (468 m^{-2}), DM 5.8i for PN (966 m^{-2}), DM 5.8i for SN (2220 m^{-2}) and Asgrow 4268 (YOR 1982) for SW (140 mg).

Table 3. Mean values for seed yield and its main physiological determinants corresponding to twelve soybean genotypes grown in two experiments with contrasting water supply.

Year of release	Genotype	SY	B_T	HI	PARint	ei	RUE	ETc	WUE
		kg·ha^{-1}	g·m^{-2}		MJ·m^{-2}		g·MJ^{-1}	mm	g·m^{-2}·mm^{-1}
1982a	Asgrow 4268	4111	11245	0.36	789	0.58	1.43	493	22.7
1982b	A 5618	4336	13419	0.32	894	0.62	1.52	495	27.0
1984	Asgrow 5308	4220	13097	0.32	823	0.58	1.61	496	26.3
1990	DK CX 458	3961	10501	0.37	734	0.54	1.43	493	21.3
1997	A 5402	3838	11400	0.33	866	0.60	1.34	496	22.9
2000	ADM4800	3696	10876	0.34	771	0.58	1.41	486	22.4
2006	DM 5.8i	3314	10650	0.31	817	0.56	1.32	490	21.7
2007	NA 4990 RG	4017	11178	0.35	769	0.56	1.45	477	23.3
2008a	DM 4250	3914	9856	0.39	719	0.54	1.36	488	20.2
2008b	DM 4670	4476	11885	0.37	764	0.56	1.56	498	23.8
2012	DM 4612	4291	10460	0.41	762	0.56	1.38	485	21.6
2016	DM 40R16	4850	11880	0.41	751	0.56	1.58	460	25.9
Exp1		5133	13329	0.39	777	0.59	1.72	514	26
Exp2		3037	9412	0.32	799	0.55	1.19	461	21
Exp		**	**	*	ns	ns	**	ns	*
G		***	***	***	***	***	***	ns	***
G × E		ns	ns	ns	ns	ns	ns	ns	ns

B_T: total aboveground biomass at physiological maturity; E: environment; ei: seasonal light interception efficiency; ETc: seasonal crop evapotranspiration; Exp: experiment; G: genotypes; HI: harvest index; ns: not significant, PARint: seasonal cumulative intercepted photosynthetically active radiation, RUE: seasonal radiation use efficiency; SY: seed yield; WUE: seasonal water use efficiency for biomass production; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: not significant.

Table 4. Mean values for pod biomass and seed yield components at physiological maturity corresponding to twelve soybean genotypes grown in two experiments with contrasting water supply.

Year of Release	Genotype	B_P	SN	SW	PN
		g·m^{-2}	# m^{-2}	mg	# m^{-2}
1982a	Asgrow 4268	562	2729	140	1109
1982b	A 5618	683	3064	148	1470
1984	Asgrow 5308	513	2486	164	1057
1990	DK CX 458	531	2755	150	1081
1997	A 5402	554	2575	147	1103
2000	ADM4800	545	2343	157	991
2006	DM 5.8i	548	2220	147	966
2007	NA 4990 RG	590	2798	141	1178
2008a	DM 4250	595	2736	141	1160
2008b	DM 4670	468	3100	143	1236
2012	DM 4612	596	2883	148	1203
2016	DM 40R16	599	3143	153	1303
Exp1		709	3217	160	1287
Exp2		421	2255	136	1023
Exp		**	**	*	**
G		***	***	***	***
G × E		ns	ns	ns	ns

#: number; E: environment; Exp: experiment; G: genotypes; B_P: pod biomass; ns: not significant, PN: pod number; SN: seed number; SW: individual seed weight; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: not significant.

3.2. Relationship between Phenotypic Variables

Seed yield had a highly significant ($p < 0.01$) and positive correlation (r) with all the evaluated variables, except with the PARinc that was negative (−0.83; $p < 0.001$) and PARint that was not significant (Supplementary Table S1). Regarding the magnitude of the correlation with SY, the order of importance in absolute value was RUE (0.96) > SN (0.94) > B_T (0.91) > WUE (0.89) > B_P (0.86) > PARinc (0.83) > PN (0.80) > HI = SW (0.77) > ei (0.60) > ETc (0.56).

A PCA accommodated 83.8% of the total variability among these traits across environments (Figure 1), with 66% explained by the first component (PC1) and 17.8% by the second component (PC2). The PC1 accommodated most of the variation in SY, B_T, SN, PN, B_P, SW, RUE and WUE in the positive direction of the ‘x’ axis. The PC2 accommodated the variation in PARint (with relatively higher values towards the positive direction of the ‘y’ axis) and HI (with relatively higher values towards the negative direction of the ‘y’ axis). The other variables (PARinc, ei and ETc) were distributed between both PCs. The PC1 also distinguished the two experimental years, with all the data corresponding to Exp1 (filled symbols) towards positive values of the component and all those of Exp2 (empty symbols) towards negative values of the component. Additionally, a greater variability among genotypes along the PC2 was detected during Exp2 than during Exp1.

Supporting the correlation analysis, the vectors corresponding to SY, RUE, SN and B_P were of similar length and in marked acute angle, denoting the strong association among these traits. This trend was also true for SW, although its shorter vector indicated a lower variability in the data of this trait and consequently comparatively less relative participation in the analysis. Next in relative importance for SY determination were WUE, PN and B_T, and to a much lesser extent HI and ETc. Across the entire dataset, ei and PARint had no impact on the determination of the SY (vectors in an almost right angle), while the cumulative PARinc had a clear negative effect on SY (vectors in obtuse angle).

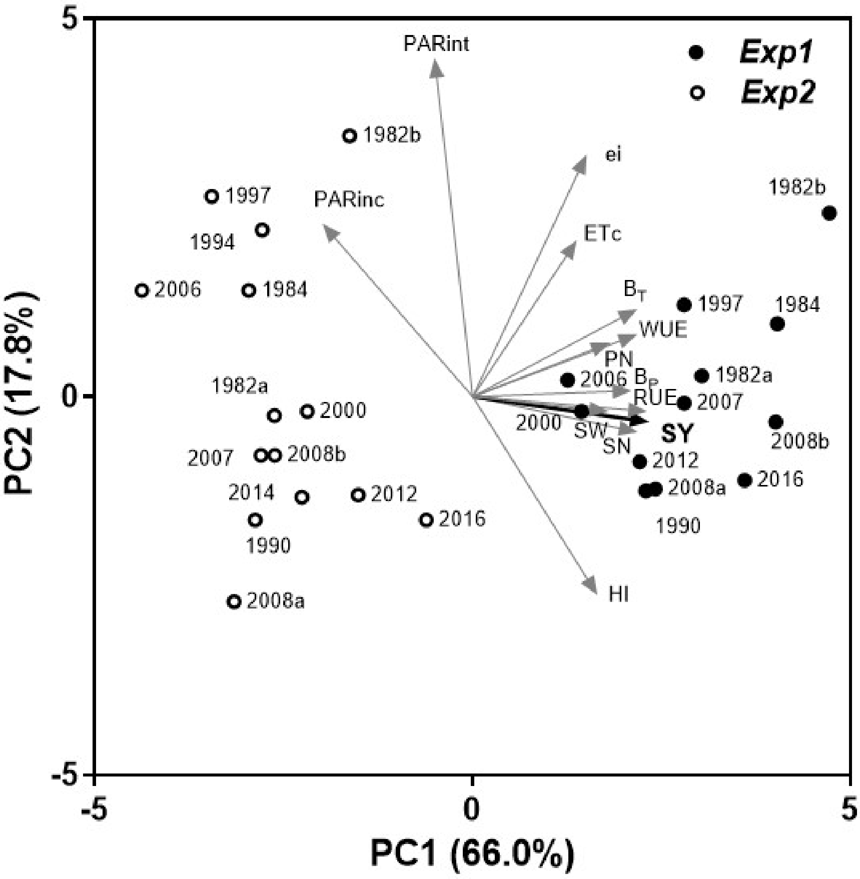

Figure 1. Biplot for the first (PC1) and second (PC2) principal components corresponding to key ecophysiological and yield related traits: total biomass (B_T), pod biomass (B_P), light interception efficiency (ei), radiation use efficiency (RUE), water use efficiency for biomass production (WUE), crop evapotranspiration (ETc), harvest index (HI), seed number (SN), pod number (PN), individual seed weight (SW), seed yield (SY), cumulative incident photosynthetically active radiation (PARinc), and cumulative intercepted photosynthetically active radiation (PARint). Experiment 1 (irrigated), represented by filled symbols, and Exp2 (dryland), represented by empty symbols. Soybean genotypes were released to the Argentine market between 1982 and 2016 (number next to each symbol).

Regarding genotypic discrimination by the evaluated variables across experiments ($G \times E$), it was noteworthy (i) the high SY achieved by old (1982b and 1984) as well as modern (2008b and 2016) genotypes in the high yielding environment of Exp1, but in the first case attributable to a proportionally higher production of B_T with comparatively lower HI and in the second case the opposite trend (comparatively lower B_T and higher HI), (ii) the poor overall performance across experiments of the genotype released in 2006 (DM 5.8i), always placed towards the lowest relative values of the SY vector, both in its explicit positive (Exp1) and implicit negative (Exp2) trajectory, (iii) the low variability in SY of genotypes released in 2000 (ADM4800) and 2012 (DM 4612), with their data towards the center of the diagram, and (iv) the higher range in SY along the PC1 of the old genotypes 1982b and 1984, which in the poor environment (Exp2) was mainly due to a strong penalization of their HI. In addition to their higher B_T production, the old genotypes released in 1982b (A 5618) and 1984 (Asgrow 5308) were also characterized by a proportionally higher seasonal resource use (i.e., ETc and PARint).

3.3. Breeding Effects on Seed Yield, Its Physiological Determinants and Numeric Components

For the set of genotypes analyzed in this study, the two contrasting environments did not determine significant differences between the regression models fitted to the response of SY to the YOR (Figure 2), and a clear biphasic trend was established ($r^2 = 0.509$; $p < 0.0001$). The first phase corresponded to the 1982–2004 period and was characterized by a decrease in the genetic progress for SY at a rate of −25.7 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$, equivalent to −0.64% y^{-1}. The second phase corresponded to the 2004–2016 period, for which a strong and sustained increase in genetic progress occurred at a rate of 76.5 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$, equivalent to +1.9% y^{-1}.

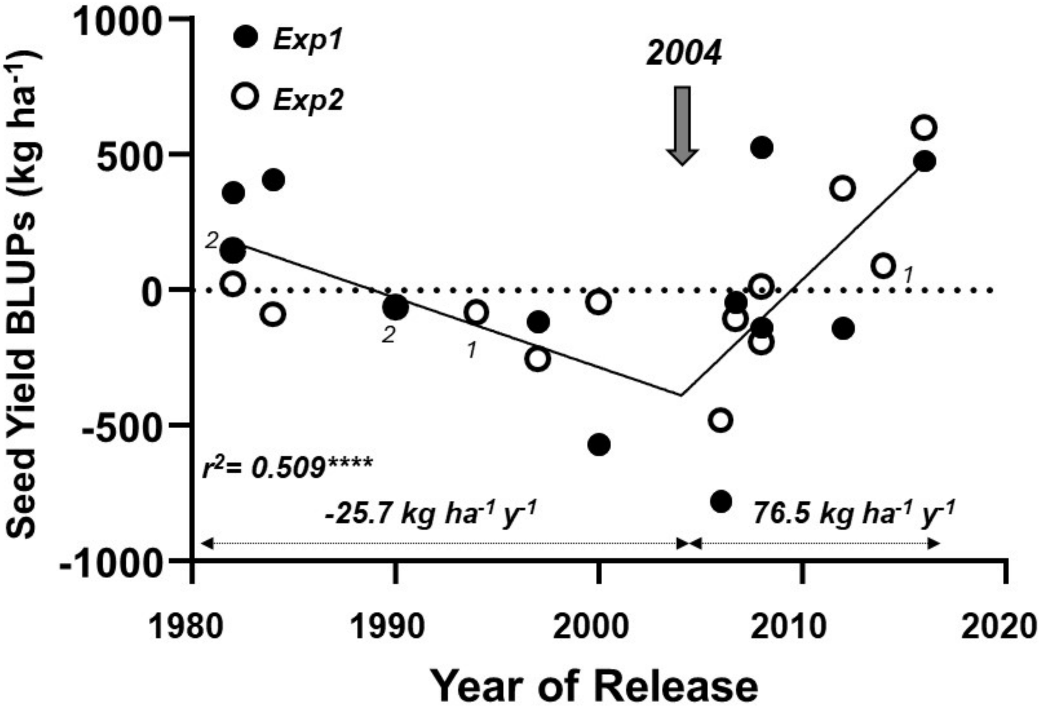

Figure 2. Breeding effects on seed yield of fourteen soybean genotypes of maturity groups IV-V released to the Argentine market between 1982 and 2016. The data correspond to the best linear unbiased predictors (BLUPs) of seed yield obtained in two experiments with contrasting water supply: Experiment 1 (irrigated), represented by filled symbols, and Exp2 (dryland), represented by empty symbols. The solid line corresponds to the bilinear model fitted to the whole data set (no significant difference detected between experiments), and the vertical arrow indicates the breakpoint between phases (2004). The values above the horizontal arrows represent the slopes computed for each phase. The numbers next to some symbols indicate (i) the overlapping of two data (2), or (ii) the existence of a single data (1) in the case of genotypes included only in Exp2. **** indicates $p < 0.0001$.

The biphasic trend described for SY was clearly replicated by the HI (Figure 3A) but only partially by the B_T (Figure 3B). A single bilinear model accommodated breeding effects on HI across environments, which decreased at a rate of 0.3% y^{-1} until 2005 and then increased at a rate of 1.03% y^{-1} ($p < 0.01$). By contrast, significant ($p < 0.05$) breeding effects on B_T were detected only during Exp2. For this trait, breeding had no effects under non-limited water conditions but would have begun to produce some benefits in water-limited environments among genotypes released from 2010 onwards. The improvement under such conditions was estimated at 2.9% y^{-1}.

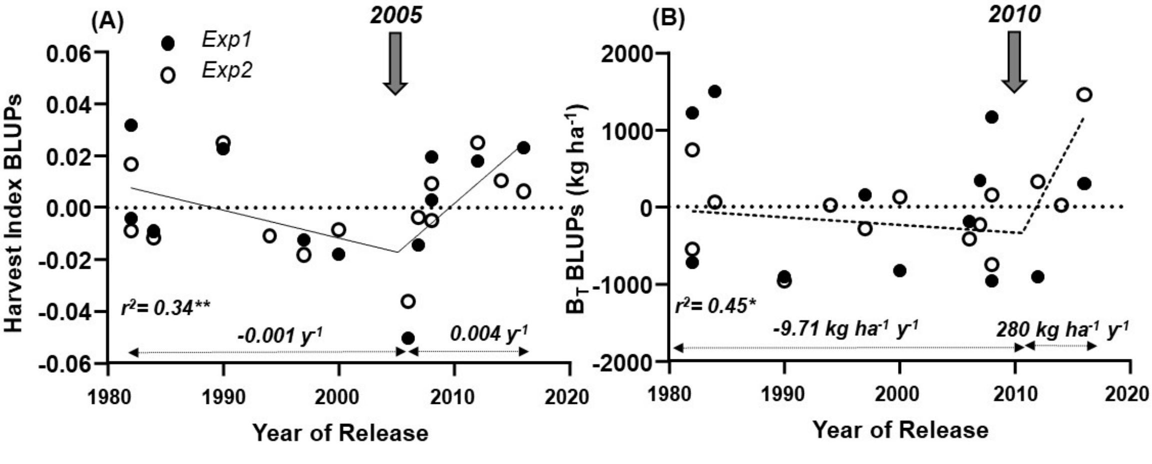

Figure 3. Breeding effects on (**A**) harvest index, and (**B**) total aboveground biomass (B_T) at physiological maturity. Symbols and references as in Figure 2. The solid line in (**A**) represents the model fitted to the whole dataset, whereas the dashed line in (**B**) corresponds only to Exp2 data. Asterisks indicate $p < 0.05$ (*) and $p < 0.01$ (**), respectively.

Regarding the numerical components of SY, genetic improvement had consistent effects across environments only on SN (Figure 4A) and PN (Figure 5A), but were limited to the unfavorable environment in the case of B_P (Figure 5B) and were null in the case of SW (Figure 4B). The trend verified for SN and PN was similar to that described for SY, i.e., bilinear and unique across environments. For SN, the loss rate during the first phase was estimated at 0.7% y^{-1}, which was followed by a gain rate of 1.32% y^{-1} during the second phase. The breakpoint between the two phases was estimated to occur in 2002. The estimated rates for PN were similar to those of SN, with an initial drop of 0.8% y^{-1} followed by an increase of 1.23% y^{-1} from 2001 onwards. The trend registered in B_P was similar to that described for B_T, stable across genotypes in the well-watered environment of Exp1 and bilinear in the drought environment of Exp2. In the latter, it registered a first phase of minimal decline followed by an increase at a rate of 2.9% y^{-1} from 2007 onwards.

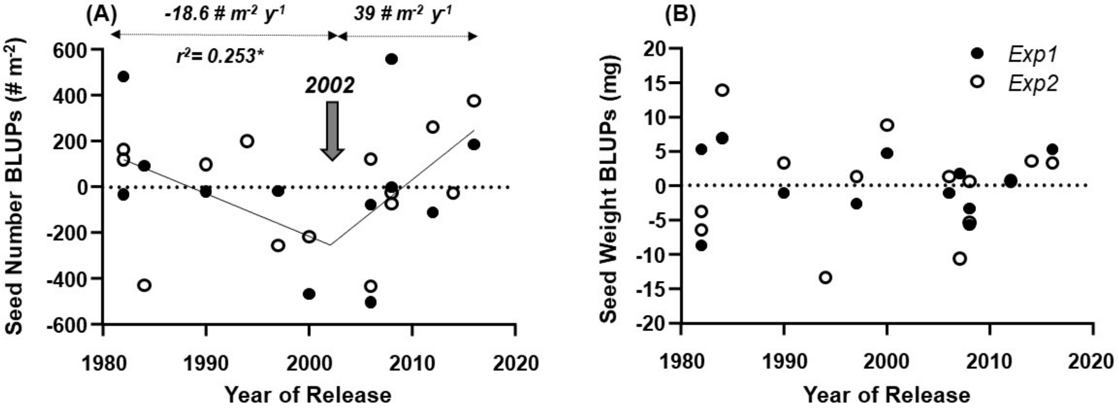

Figure 4. Breeding effects on (**A**) seed number, and (**B**) individual seed weight. Symbols and references as in Figure 2. The solid line in (**A**) represents the model fitted to the whole dataset, and the asterisk indicates $p < 0.05$. #: number.

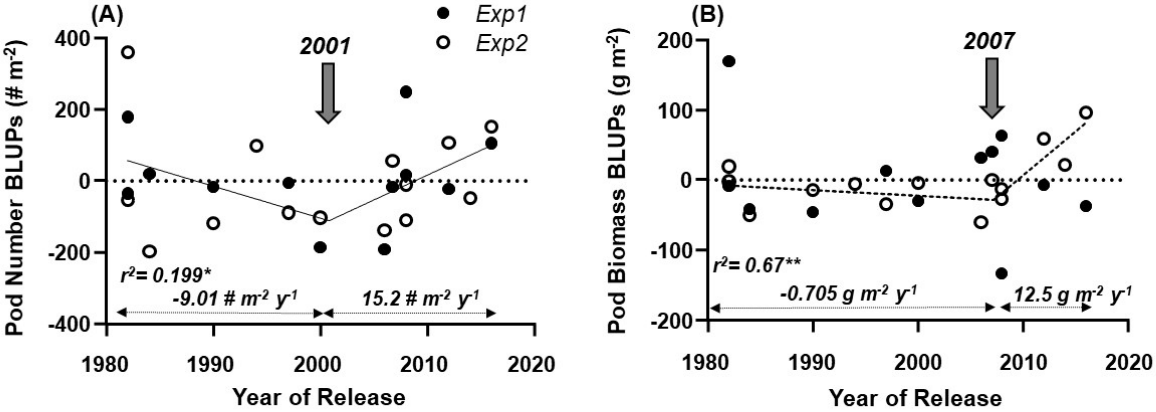

Figure 5. Breeding effects on (**A**) pod number, and (**B**) pod biomass at physiological maturity. Symbols and references are as in Figure 2. The solid line in (**A**) represents the regression model fitted to the whole dataset, whereas the dashed line in (**B**) corresponds only to Exp2 data. Asterisks indicate $p < 0.05$ (*) and $p < 0.01$ (**), respectively. #: number.

Despite the differences among genotypes in ei and PARint (Table 3) and their significant relationship with SY (Supplementary Table S1), these traits related to resource capture (ei) and use (PARint, ETc) showed no trend associated with genetic improvement (data not shown). By contrast, significant breeding effects were detected on resource use efficiencies, but only under the water-limited condition explored in Exp2 (Figure 6). In this environment, both efficiencies tended to decrease until 1997 (RUE) or 1999 (WUE) and then increase. In the first phase, the loss rate was 0.57% y^{-1} and 0.55% y^{-1} for RUE and WUE, respectively. In the second phase, the former increased at a rate of 0.85% y^{-1} and the latter at a rate of 0.99% y^{-1}.

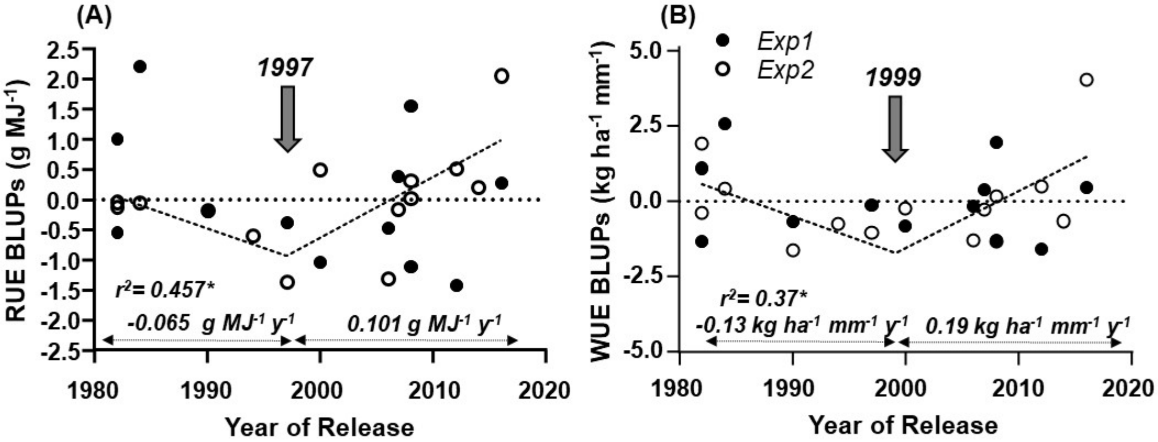

Figure 6. Breeding effects on (**A**) radiation use efficiency (RUE), and (**B**) water use efficiency (WUE) for biomass production at physiological maturity. Symbols and references are as in Figure 2. The dashed line corresponds to models fitted to data from Exp2 data. Asterisks indicate $p < 0.05$.

4. Discussion

4.1. Genotypic and Environmental Effects on Seed Yield and Secondary Traits

Field trials conducted over two growing seasons with contrasting water availability in a representative humid temperate region of Argentina revealed significant genotypic differences in SY among 12–14 widely used soybean genotypes (MG IV–V) released to the Argentine market between 1982 and 2016. Although the drought condition caused a foreseeable reduction in SY [24,25], no significant $G \times E$ interaction was detected, indicating that genotype rankings remained stable across environments [10,26].

The behavior described for SY (i.e., significant main effects but no G × E effect) was also verified for its physiological determinants (BT, BP and HI) and numerical components (PN, SN and SW). The differences between experiments corroborated what has been documented for this crop when it is exposed to water shortages during its critical reproductive stages: a significant decrease in all mentioned traits [25,27,28]. However, despite these environmental contrasts, no significant differences were observed in ei or cumulative PARint at R7. This was unexpected, as water deficits typically reduce both early-stage canopy expansion and late-stage leaf area persistence, ultimately affecting seasonal ei [28–30]. The lack of response registered in current research could be attributed to compensatory effects from interannual variation in seasonal PARinc (Exp2 > Exp1; Table 2) and shifts in its distribution across growth stages due to changes in their relative duration [31].

In contrast to the environment, genotypic differences were evident for mean seasonal ei and PARint. As expected in [32–34], longer-cycle MG V varieties exhibited higher values for these traits than shorter-cycle MG IV genotypes. Interestingly, the absence of differences in PARint between environments and the higher value of this variable in MG V genotypes promoted a higher B_T value among some varieties of this group (e.g., A5618 and A5308) but not in all (e.g., A5402 and DM5.8i), due to variations in the opposite direction in RUE. Genotypic differences in RUE within the same MG may stem from differences in foliar photosynthetic capacity [35] and/or light distribution within the canopy [31,36,37].

Regarding water use, seasonal ETc did not exhibit significant environmental, genotypic, or interaction effects. Consequently, environmental and genotypic differences in WUE arose from variations in B_T, which influenced the numerator of this efficiency metric (Table 3). While previous studies have documented genotypic variation in soybean water use, including responses to vapor pressure deficit [38] or soil water content leading to the regulation of transpiration [39], the ETc values in the present study did not differ among genotypes, even when accounting for MG-associated cycle differences. This trend suggests that variations may exist in water partitioning throughout the growth cycle and/or in the efficiency to convert transpired water into biomass [40,41].

4.2. Relationship among Variables and Seed Yield Determination

Although SY had a high and significant correlation with almost all analyzed variables, for the set of genotypes included in the study we can underscore (i) among the physiological determinants of SY, the larger effect of B_T production over its partition to grains (i.e., HI), and (ii) among the components of SY, the larger effect of SN over SW. Regarding the physiological determinants, there is consensus about a decrease in HI with cycle lengthening [42], which is usually compensated through an increase in radiation capture [33] and consequently in biomass production [34,43]. In the present study, the greater relative importance of B_T would be attributable to the fact that a limited number of MGs were included in the analysis. Regarding the numerical components, the results confirm the importance of both SN and SW on soybean SY determination [44] and the greater relative influence of the former with respect to the latter [45,46]. Also in this case, the limited number of MGs together with the use of an early sowing date in both experiments would have contributed to the result, by avoiding severe limitations by the source of assimilates for grain filling linked to the delay of the growing cycle [47,48].

The joint analysis of the evaluated variables discriminated between environments according to their SY potential and among genotypes according to the different strategies to achieve it. Regarding the environment, it confirmed a relatively stable response pattern among genotypes through both environments in terms of their discrimination by the SY vector (Figure 1), coinciding with the absence of $G \times E$ effects detected by the ANOVA and similar results from previous research [8]. Regarding the strategies to generate SY, the MG V genotypes that achieved relatively high SYs were characterized by a comparatively higher B_T and lower HI, while those with relatively high SY among those of MG IV exhibited the opposite behavior (HI effect > B_T effect). Both patterns could be expected in a comparison between MGs [33,34]. However, the PCA also detected some useful trends for breeding purposes, such as genotypes with comparatively lower relative variation in SY across both environments (e.g., ADM4800 released in 2000 and DM 4612 released in 2012) concerning others with greater relative variation (e.g., Asgrow 5308 released in 1984), or genotypes with relatively higher SY in both environments (e.g., DM 40R16 released in 2016) or lower in both environments (e.g., DM 5.8i released in 2006).

4.3. Breeding Effects on Soybean Seed Yield

The genetic improvement process is under permanent evaluation in terms of its ability to hold the necessary gains to meet the estimated increase in global demand, particularly for species that are highly required, such as soybean [49]. Different approaches are used to assess GG, including retrospective or era studies where a variable number of representative historical genotypes are evaluated [8,50] as well as those based on multi-environment trials [7,51]. The inclusion of ecophysiological traits generally limits the number of genotypes and, consequently, a careful choice is needed if robust conclusions are to be reached [52]. In the present work, the retrospective approach was used, including a limited set of 14 genotypes, given the large number of ecophysiological determinations proposed, in particular to meet the objective of characterizing water use and its seasonal use efficiency. The chosen genotypes are highly representative of those most grown by farmers over the last 40 years, as evidenced by the inclusion of most of them (12 out of 14) in previous studies carried out in the same region to estimate the GG in SY exclusively [5] or also of ecophysiological nitrogen or radiation-based traits for explaining B_T production [8–10].

The most striking finding of this study is the identification of two opposing trends in soybean GG for MGs IV–V, selected for the central humid Pampas region of Argentina. The first trend shows a decline in SY at a rate of 0.64% y^{-1} from 1982 to 2004, while the second trend reveals an increase in SY at a rate of 1.9% y^{-1} from 2004 to 2016. Evidence of shifts in soybean GG over time is scarce in the literature. Rincker et al. [1] reported only moderate and consistently positive values for MGs II-IV in the U.S., with breakpoints occurring in the 1960s. They attributed the acceleration of GG since the 1970s to increased investment by private seed companies, driven by the enactment of the Plant Variety Protection Act (PVPA) in 1970. This legislation not only incentivized private breeding efforts but also expanded the number of public-sector plant breeders. The apparent discrepancy between our findings and previous studies from Argentina—where no loss in GG was detected—can be largely explained by differences in the number of genotypes, MGs, and environments considered in the analyses. Larger datasets tend to reveal broader, long-term trends, but they may obscure genetic improvement shifts due to breeding strategy modifications or fail to capture true underlying trends within specific environments, MGs, or time periods. Additionally, variations in cycle duration among MGs and their interaction with environmental factors may further influence GG estimates [7]. The studies by Santos et al. [5] and de Felipe et al. [8] illustrate the impact of these methodological differences. Santos et al. [5] conducted both a pooled analysis across MGs and a separate analysis for each MG (from III to VIII), incorporating a large number of growing seasons and environments. The pooled analysis estimated a GG of 14.3 $kg \cdot ha^{-1} \cdot y^{-1}$, corresponding to a national rate of 0.33% y^{-1}. However, the within-MG analysis indicated no genetic gain, aligning partially with our findings. A later study by de Felipe et al. [9] confirmed a stable GG of 0.9–1.1% y^{-1} for each evaluated MG (from III to V). However, this study was limited to a single growing season, unlike the previous research, and did not report trends in the top-performing genotypes, where percentage GG tends to decline [8]. Notably, neither Santos et al. [5] nor de Felipe et al. [8] conducted a segmented analysis of GG, which could be crucial for detecting trend reversals like those observed in the present study. In summary, the exclusive inclusion of widely adopted genotypes from a limited number of MGs, evaluated in their target selection environment under climatic conditions that effectively captured the expected interannual variability in water availability, enabled the detection of GG trends that had not been previously documented. This analysis revealed a two-phase pattern: an initial decline in GG until 2004, followed by a sharp increase, with an estimated improvement rate of 1.9% y^{-1} in the second phase. This rate is substantially higher than the 0.9–1.1% y^{-1} rate reported by de Felipe et al. [9,10] for the same MGs over a longer period (1984-2015). It also exceeds the 0.9% y^{-1} estimated by Abdala et al. [7] using a different approach (multi-environment trials) in high-yield environments in Argentina for the 2005–2021 period. Notably, Abdala et al. [7] reported smaller gains (0.3–0.6% y^{-1}) in lower-yielding environments, a pattern that was not observed between the wet (Exp1) and dry (Exp2) conditions analyzed in current research, yielding a single model that was able to describe GG trends across environments.

Regarding the possible reasons behind the bilinear trend observed, with a breakpoint in 2004, one key factor to consider is the shift in the breeding focus to genetically modified (GM) soybean genotypes with resistance to glyphosate herbicide. These genotypes were introduced to the Argentine market in 1996 and reached an adoption rate of 98.8% by 2002–2003 [19,53]. Among the genotypes analyzed in this study, the earliest GM genotype was ADM4800, released in 2000, which, along with DM 5.8i (released in 2006), exhibited the poorest trends in SY (Figure 2). While this technology more than doubled the rate of soybean acreage expansion, leading to a near-proportional increase in national production [19], previous studies have documented a yield penalty associated with the introduction of glyphosate-resistance genes. On average, GM genotypes yielded 5% less than their conventional counterparts [54], with yield losses reaching up to 18% under certain conditions [55–57]. However, improvements in genetic engineering and breeding strategies have mitigated these drawbacks in more recent GM events; for example, in Intacta technology launched in 2013. Recently in Argentina, no differences were reported between GM and non-GM commercially available genotypes belonging to MGs V-VI [58]. The adoption of GM genotypes has contributed to the crop's technological progress, leading to average global SY increases of 9.2% in Argentina, Brazil, Paraguay, and Uruguay [59].

4.4. Breeding Effects on Secondary Traits

Genotypes included in previous retrospective studies are primarily the product of traditional breeding, which focuses on SY as the main selection criterion, along with secondary agronomic and defensive traits such as resistance to lodging and diseases [8,60]. Although glyphosate resistant GM genotypes were incorporated in this study (Table 1), there are still no commercial soybean genotypes with transgenic traits for abiotic stress tolerance or other selection criteria beyond those mentioned [61]. Consequently, the trends described in this study for the ecophysiological determinants of SY and its numerical components are an unintended outcome of this selection process.

As expected, given the strong relationship between SY, SN and PN (Supplementary Table S1 and Figure 1), these SY numeric components followed a biphasic trend similar to SY, with comparable breakpoints (2001 for PN and 2002 for SN). By contrast, no significant breeding effects were detected for SW. This trend aligns with previous studies that have evaluated yield components and consistently found significant GG in PN and SN but not in SW [1,8,46,62–64]. Furthermore, the absence of significant changes in SW—or, in some cases, a concurrent increase in both SN and SW [60]—suggests that variations in SN did not substantially alter the source-sink relationship during the seed-filling period. An exception to this general pattern has been reported in Japan, where a complete trade-off between increased SN and decreased SW resulted in no net SY improvement [65].

Among the ecophysiological determinants, SY showed a stronger relationship with B_T than HI (Supplementary Table S1). However, the observed breeding effects on HI were more similar to those observed for SY than to those for B_T (Figures 2 and 3). In the case of B_T, significant breeding effects were detected only in the environment with a strong water deficit (Exp2). While the adjusted model for B_T resembled the one fitted for SY, the rates of change in each phase and the inflection point between them were less consistent compared to those observed for HI. As a result, this study reaffirms the greater relative importance of breeding on HI than on B_T, as documented in some studies [60,64,66], in contrast to others [9,67], which suggest the opposite (i.e., B_T > HI). Regardless of the predominant ecophysiological determinant in the trends observed for SY, the underlying causes of these differences, particularly in relation to the environment, remain to be clarified.

Regarding seasonal resource use (PARint and ETc) and resource use efficiencies (RUE and WUE), the absence of breeding effects on the former resulted in both efficiencies mirroring the response observed for B_T. These effects were only significant under the water-limited conditions of Exp2, though the turning point for both efficiencies occurred much earlier than for B_T. Unlike the previously analyzed traits, fewer studies have investigated the effects of breeding on resource use efficiencies at the crop level. Among the few available studies, de Felipe et al. [9] reported no breeding effects on ei but a significant improvement in RUE. However, using a modeling approach due to the lack of contrasting environments in terms of water supply and quantification of ETc, they suggested that improvements in RUE would only lead to gains in SY if water availability was sufficient. A priori, the results of the current research reject this hypothesis, as we observed gains in RUE and WUE without changes in ETc. This finding is consistent with what has been documented for maize improvement in a similar target environment [16] and for soybeans in arid and semi-arid environments [66]. Yang et al. [66] indicated that traditional soybean breeding has led to more conservative water use, which increased WUE for seed production. This was achieved through mechanisms such as greater stomatal sensitivity, lower root hydraulic conductivity, and a higher HI. Similarly, He et al. [40] noted that modern genotypes have adopted conservative water use strategies, including early flowering, reduced leaf area, and lower stomatal conductance, optimizing WUE under water-stressed conditions. Feng et al. [15] observed that traditional genotypes used more water during the growing season, while modern genotypes exhibited higher efficiency for grain production. Specht et al. [68] also noted that modern soybean genotypes achieved higher transpiration efficiency, producing more biomass with less water. However, these strategies may not be as successful in predominantly humid environments, where genotypes with such traits may compromise performance in water-abundant conditions [69], such as those found in the central humid Pampas region.

5. Conclusions

In the current study, we evaluated the unintended effects of traditional soybean breeding (i.e., that focused primarily on SY and defensive traits) on key ecophysiological traits of genotypes released between 1982 and 2016 for the Central Pampas region of Argentina. Our analysis identified two distinct phases: an initial decline in SY at a rate of 0.64% y^{-1} up to 2004, followed by a sustained increase of 1.9% y^{-1} from 2004 to 2016. When weighted by the duration of each phase (22 years for the first phase and 12 years for the second), the overall GG for the entire period was estimated at only 0.256% y^{-1}. These trends in SY were mirrored almost exactly by trends in HI and, to a lesser extent, by B_T, with significant breeding effects on B_T recorded only under water deficit conditions. These effects on B_T were similar to those observed for SY and HI, exhibiting a biphasic pattern. Moreover, changes in B_T were reflected in similar trends in resource use efficiencies (RUE and WUE), as no significant breeding effects were observed on resource capture. The lack of response in ETc suggests that breeding did not exert pressure to increase its utilization, potentially indicating a smaller root system without compromising its overall functionality.

Supplementary Materials

The additional data and information can be downloaded at: https://media.sciltp.com/articles/others/2507161618318387/PMSC-1130-supplementary.pdf. Table S1: Pearson's correlation (r) matrix for evaluated traits.

Author Contributions

L.J.A.: Conceptualization, Visualization, Writing, review and editing. S.A.B.: Data collection, Conceptualization, Formal analysis, Methodology, Visualization, Writing original draft. G.D.M.: Conceptualization, Visualization, Writing, review and editing; M.E.O.: Conceptualization, Formal analysis, Methodology, Visualization, Writing original draft, Funding acquisition.

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Institutional Review Board Statement

Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

Data will be available upon request to the corresponding author.

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Conflicts of Interest

The authors declare no conflict of interests.

Abbreviations

ANOVA	analysis of variance
BLUP	best linear unbiased predictor
B_P	pod biomass
B_T	total aboveground biomass
E	environment
ei	light interception efficiency
ETc	crop evapotranspiration
Exp	experiment
G	genotype
GYG	global seed yield gain
GG	genetic gain
GM	genetically modified
HI	harvest index
MG	maturity group
PAR	photosynthetically active radiation
PARinc	incident PAR
PARint	intercepted PAR
PCA	principal component analysis
PC1	first principal component
PC2	second principal component
RUE	radiation use efficiency
SN	seed number per square meter
SW	individual seed weight
SWC	soil water content
SY	seed yield
Tmax	maximum air temperature
Tmin	minimum air temperature
WUE	water use efficiency
YOR	year of release
ΔWater storage	Variation in soil water storage

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