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# Physiological processes associated with soybean genetic progress in Argentina

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**Abstract**

The main physiological processes associated with soybean [*Glycine max* (L.) Merr.] genetic yield progress in central temperate Argentina are largely unknown. This knowledge is critical to identify opportunities to accelerate yield gains via trait-based hybridization. Our objectives were to: (a) evaluate the influence of biomass accumulation vs. harvest index (HI) in explaining genetic progress, and (b) assess the role of radiation and/or N capture and use efficiency (RUE and NUE, respectively) as drivers of biomass accumulation. We tested 173 cultivars released from 1980 to 2014 in two high-yielding environments. Additionally, a crop modeling exercise was performed to demonstrate the physiological perception that any genetic increase in RUE would only translate into more yield if there is enough water for the realization of that RUE. Observed genetic progress was 42 kg ha$^{-1}$ yr$^{-1}$, or ∼1% yr$^{-1}$, and was mostly explained by increased aboveground biomass accumulation. This higher biomass of modern cultivars was associated with increased RUE and total N uptake. This suggests that, if residual genetic variation is still present in current soybean cultivars, future genetic improvements should focus on further improving N uptake to increase RUE. Increases in RUE are associated with increased stomatal conductance and water use. Therefore, it would be expected that genetic progress is faster in environments with increased rainfall. Our modeling exercise was consistent with this hypothesis and showed that soybean genetic progress simulated in different locations within a rainfall gradient was positively associated with cumulative seasonal precipitation.

**Abbreviations:** BLUP, best linear unbiased predictor; ei, radiation interception efficiency; HI, harvest index; MG, maturity group; NDVI, normalized difference vegetation index; NUE, nitrogen use efficiency; Nup, total aboveground nitrogen uptake; PAR, amount of photosynthetically active radiation; PARinc, amount of photosynthetically active radiation incident at the top of the canopy; PARint, amount of photosynthetically active radiation intercepted by the canopy; RUE, radiation use efficiency.

## 1 | INTRODUCTION

Soybean [*Glycine max* (L.) Merr.] is the most widely cultivated oil-seed legume in the world, with ∼80% total production concentrated in United States, Brazil, Argentina, and China (USDA, 2018). Historic soybean yields in these countries are increasing across years, associated with genetic yield improvements (de Felipe, Gerde, & Rotundo, 2016; Lange & Federer, 2009; Morrison, Voldeng, & Cober, 1999;

Specht et al., 2014; Wang et al., 2016). However, the rate of yield increase is not high enough to satisfy global demand for food (Godfray et al., 2010). One strategy to increase the rate of genetic progress is the application of trait-based hybridization in breeding programs (Reynolds et al., 2011). Highest genetic progress would be attained by improving those physiological traits that theoretically have the highest positive impact on yield. Retrospective genetic gain studies are key in determining which traits to manipulate. Even though soybean yield genetic progress has been reported, the description of relevant traits is more limited. We recently reported the genetic progress of the last 35 yr of breeding for the main soybean production region in Argentina (de Felipe et al., 2016). In the present study we report on the underlying mechanisms driving the observed genetic progress in seed yield.

There are different theoretical frameworks to functionally dissect seed yield into underlying physiological mechanisms. The simplest approach is to describe seed yield using the Donald and Hamblin (1976) framework:

$$\text{Seed yield (kg ha}^{-1}) = \text{Total biomass} \times \text{HI} \qquad (1)$$

where total biomass (kg ha$^{-1}$) is aboveground plant dry mass at physiological maturity, and HI (%) is harvest index defined as the proportion of seed dry mass to total plant dry mass. Early genetic gain studies in wheat (*Triticum aestivum* L.) showed increases in yield associated to higher HI but more modern studies are showing a predominant importance of total biomass production (Hall & Richards, 2013). No change over the years was observed in HI for maize (*Zea mays* L.) hybrids, suggesting that genetic progress is more associated with increased total biomass (Duvick, Smith, & Cooper, 2010). For soybean in the northern United States, Suhre et al. (2014) reported a 1.2% yr$^{-1}$ yield genetic progress and HI increase of only 0.1% yr$^{-1}$. However, evidence from the same region showed that both total aboveground biomass and HI increased in modern cultivars (De Bruin & Pedersen, 2009B; Koester, Skoneczka, Cary, Diers, & Ainsworth, 2014). No information is available for breeding programs other than the northern United States, where different breeding pathways may have occurred.

Total aboveground biomass accumulated at physiological maturity as defined by the framework of Donald and Hamblin (1976) can be further described in terms of radiation capture and utilization during the growing cycle. Monteith (1977) provided the theoretical framework to describe biomass accumulation:

$$\text{Total biomass (kg ha}^{-1}) = \text{PARinc} \times \text{ei} \times \text{RUE} \qquad (2)$$

where PARinc (MJ m$^{-2}$) is the incident photosynthetic active radiation at the top of the canopy accumulated during the growing season, ei (%) is the radiation interception efficiency, and RUE (kg MJ$^{-1}$) is the radiation use efficiency. The PAR-

**Core Ideas**
- Genetic progress in soybean was associated with increased radiation use efficiency.
- Increased radiation use efficiency was associated with more N capture.
- Genetic progress rate is higher in most productive environments.

inc depends on days to maturity, which is controlled by E genes associated to maturity groups (MGs) (Bernard, 1971). Optimum days to maturity should be long enough to maximize radiation capture but short enough to minimize losses associated to excessive vegetative growth and consequent HI reduction (Egli, 2011). Breeding for yield in our region have increased days to maturity in MGs III, decreased in MGs V, and did not change it in MGs IV (de Felipe et al., 2016). Beyond shifts in days to maturity, genetic progress information for ei and RUE is limited. Koester et al. (2014) reported genetic gain in ei and RUE when evaluating 28 cultivars in a Midwestern location. The increase in ei was mostly associated to a higher proportion of late maturing cultivars in the most recently released genotypes (Koester et al., 2014). Changes in respiration or photosynthesis could underpin the increase in RUE as suggested by Canadian and Chinese germplasm studies showing that leaf-level photosynthesis has improved with release year (Jin et al., 2010; Morrison et al., 1999). However, Koester, Nohl, Diers, and Ainsworth (2016) showed that maximum photosynthetic capacity, mesophyll conductance, and night-time respiration have not changed with cultivar release date. Regardless of actual increases in field-level RUE in the United States, as reported by Koester et al. (2014), no information is available for other breeding programs or regions.

An alternative to the RUE framework presented above is to explain total aboveground biomass as a function of total N uptake and nitrogen use efficiency (NUE) (Novoa & Loomis, 1981):

$$\text{Total biomass (kg ha}^{-1}) = \text{Nup} \times \text{NUE} \qquad (3)$$

where Nup is (g N m$^{-2}$) is total aboveground N uptake accumulated from emergence to physiological maturity and NUE is the aboveground biomass produced per unit of captured nitrogen (kg kg$^{-1}$). The Nup is strongly correlated with yield, resulting from a combination of mineral N uptake and biological N$_2$ fixation (Rotundo, Borrás, De Bruin, & Pedersen, 2014; Salvagiotti et al., 2008; Santachiara, Borrás, & Rotundo, 2017a). Kumudini, Hume, and Chu (2002) reported that newer soybean cultivars, compared to older ones, accumulate more N during the seed-filling period. The high

correlation between soybean yield and Nup can be explained by the dependence of C assimilation on leaf N (Rotundo et al., 2014; Santachiara, Borrás, Salvagiotti, Gerde, & Rotundo, 2017b; Sinclair & Horie, 1989).

Yield progress has been documented in Argentina but a mechanistic understanding of the physiological drivers of the observed genetic progress is currently lacking. Our main objectives were to: (a) evaluate the influence of biomass accumulation vs. HI in explaining genetic progress, and (b) assess the role of radiation and/or N capture and use efficiency as drivers of biomass accumulation. To address these objectives, a set of 173 soybean cultivars released from 1980 to 2014 was evaluated under field conditions close to potential yield. Results showed that the main driver of genetic progress was increased RUE. For high yielding environments, realized RUE equals potential RUE (RUEmax) which is a genetic parameter in several crop models (Sinclair, 1986). We employed modeling to further examine RUE as a driver of genetic gain in high-yielding non-water limited environments for the realization of that RUEmax (Evans & Fisher, 1999). Modeling traits for old and new genotypes supports the expectation of increased genetic progress in locations having increased rainfall.

# 2 | MATERIALS AND METHODS

## 2.1 | Cultivars evaluated, growing conditions, and experimental details

A total of 173 cultivars ranging from MG III to V were evaluated in field conditions. Thirty-five belonged to MG III and were released from 1982 to 2013, 84 were MG IV and were released between 1980 and 2014, and 54 were MG V and were released between 1984 and 2014 (see Supplemental Table S1 for a full description of all cultivars).

Two field experiments (L71415 and Sh1415) were carried out at two sites in Campo Experimental Villarino, located in Zavalla, Santa Fe province, Argentina (33°1′ S, 60°53′ W). Soil type for these sites was a silty clay loam Vertic Argiudoll, Roldán series. Table 1 describes the environmental characterization of these sites. Planting date for both sites was 13 Nov. 2014. Weeds were chemically controlled before crop emergence and hand removed whenever necessary during the crop season. Pests and diseases were controlled following standard agronomic practices for the region. The experiments were planted using a row-cone planter under direct drill. Plant population was set to 35 plants per square meter by over-planting and plot hand-thinning just after emergence. Both experiments were conducted under rainfed conditions as normal farm practice in this region (Di Mauro et al., 2018).

Experimental design was randomized complete blocks with cultivars as experimental factors. Blocks were three in Sh1415 and four in L71415. Individual plots were four rows, 4 m length, and 0.52 m of inter-row spacing.

## 2.2 | Physiological measured traits

Phenological stages (Fehr & Caviness, 1977) were recorded on a plot basis three times a week. Physiological maturity (R7) was determined as the moment when one pod on the main stem turned mature color. At R7, 10 consecutive plants from one central row were hand-clipped and dried at 60 °C for 96 h. The whole sample (seed + non-seed tissues) was weighed for total biomass and then threshed for seed mass determination. At harvest maturity (R8), an area of 2.08-m$^2$ per plot was hand-clipped and threshed on a stationary harvester for yield determination. The seed weight from R7 was added to seed weight from R8 samples for final yield estimation. Seed yield was expressed on a dry weight basis. Seed and non-seed samples from R7 were milled (1 mm) for N determination using Kjeldahl method (Mckenzie & Wallace, 1953).

Potential daily total incident radiation at the top of the atmosphere was calculated based on location and day of year, and converted to potential daily incident radiation at ground level (Angström, 1924). Actual daily incident radiation was calculated using sunshine data measured with a heliograph located less than 2 km from experimental sites. Actual daily incident radiation was converted into photosynthetically active radiation (PARinc, MJ m$^{-2}$ d$^{-1}$) by multiplying the daily incident by 0.5 (Monteith, 1965). The normalized difference vegetation index (NDVI) was measured in each plot every other week during the entire cycle using an active canopy crop sensor (Crop Circle Handheld System, model GeoSCOUT GLS-400, Holland Scientific). Radiation interception efficiency was derived from NDVI using a purposely established relationship between measured ei and NDVI (Supplemental Figure S1). Sellers et al. (1994) showed for the first time that ei can be estimated from NDVI across diverse vegetation types. Since this influential contribution, the concept has proven to be valid and useful. Recently, Gitelson, Peng, and Huemmrich (2014) reported generic relationships between ei and NDVI for soybean and maize. Here we did not use a generic equation but rather created a local calibration for one cultivar. Differences between cultivars might arise by differences in leaf angle that might impact the light extinction coefficient. Gitelson et al. (2014) showed a very small effect of leaf angle (comparing maize and soybean) in the ei/NDVI relationship suggesting that any cultivar difference in leaf angle would be negligible.

**TABLE 1** Environment characterization. Planting date, previous crop, soil characteristic, water availability and environmental index from the two environments employed to evaluate physiological process implicated in yield gain on soybean crop in central Argentina

| Experiment | Previous crop | Soil (0–20 cm) | | | Water | | Environmental index[c] | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Organic matter | P (Bray I) | pH | Soil water[a] | Rainfall[b] | P10 | Average | P90 |
| | | g kg$^{-1}$ | mg kg$^{-1}$ | | ————mm———— | | ————kg ha$^{-1}$———— | | |
| (1) L71415 | Soybean | 25.6 | 32.1 | 5.8 | 326 | 625 | 3,645 | 4,504 | 5,224 |
| (2) Sh1415 | Wheat | 32.4 | 44.1 | 6.1 | 397 | 625 | 4,502 | 5,602 | 6,626 |

[a]Two-meter depth at planting. [b]Between November and March. [c]Based on cultivar mean.

## 2.3 | Calculated physiological variables

Calculated traits followed the same descriptions as Rotundo et al. (2014). Harvest index was calculated as the ratio between seed and total biomass measured at R7. Harvest index was calculated at R7 to avoid possible confounding effects of drop leaves. Total aboveground biomass per unit land area was calculated as seed yield divided HI. Nitrogen uptake (Nup) was calculated from non-seed and seed biomass and N concentrations at R7. Nitrogen use efficiency was calculated as the ratio between total aboveground biomass at physiological maturity and Nup.

Accumulated PARinc from emergence to R7 was calculated as the sum of daily PARinc. Daily ei was linearly interpolated between punctual estimations. Daily PARint was calculated as the product between daily PARinc and daily ei. Finally, accumulated PARint during the whole cycle was estimated as the sum of daily PARint. Light interception efficiency (ei) during the whole cycle was calculated as the ratio between accumulated PARint and accumulated PARinc. In addition, RUE was calculated as the ratio between total aboveground biomass at R7 and accumulated PARint.

## 2.4 | Statistical analysis

Data was analyzed using linear mixed-effect models in R (R Core Team, 2014; version 3.0.2, lme4 package, lmer function). Best linear unbiased predictors of each cultivar were calculated through a model that included environment, cultivars nested in MGs, blocks nested in environments, and cultivar × environment interaction, all as random effects. Since the set of cultivars employed in the current study can be considered as a representative sample of the genotypic commercial diversity used in soybean in Argentina during the period of time studied for the region, cultivar was considered as a random effect (Gizzi & Gambín, 2016). Variance components were estimated for each trait. Parameter estimates for model were obtained using the restricted maximum likelihood method. The best linear unbiased predictor (BLUPs) for individual cultivars are deviation from around the mean across all genotypes.

The single value of BLUP from each cultivar was plotted against year of release and, for each trait, ordinary least square regressions (OLSR) were fitted to estimate absolute genetic gain. Absolute genetic gain was estimated as the resulting slope of the OLSR, while the relative gain was calculated as the absolute gain rate divided by the predicted trait-value of the oldest released year (Boerma, 1979). Slope differences among MGs were tested by an analysis of covariance as implemented in GraphPad Prism version 5.00 for Windows (GraphPad, 2011). Cultivar by trait matrix of BLUPs was generated for principal component analysis (PCA). Traits which were only significant in the ordinary least square regressions have been considered in the analysis. Since traits had different scales normalization was necessary. Matrix was centered within each column through trait mean subtraction and then normalized by division of the remainder by the within column standard deviation. A biplot per each MG of the first two principal components (PCs) was displayed to assess similarities among cultivars in terms of their responses for yield-related traits.

## 2.5 | Simulation of genetic gain across varying production environments

An implementation of a soybean crop growth model (Sinclair, 1986; Soltani & Sinclair, 2012) was utilized to simulate seed yield across different environments. Genetic coefficients for the earliest and latest release year were calculated for each MG to define an old and a new "in-silico" genotype. The coefficients were calculated using the linear equations relating measured phenotypes and year of release for RUE and HI from this paper; flowering (R1) and maturity (R7) dates were obtained from de Felipe et al. (2016). Since RUE is estimated in field experiments at near to potential conditions, this estimation is considered potential RUE (Sinclair, 1986). The potential RUE is by definition not affected by environmental conditions. In Sinclair's model, the realized RUE is estimated based on a water stress function. Harvest index is also considered a trait very stable across environmental conditions for a given cultivar. For example, Spaeth, Randall, Sinclair, and Vendeland (1984) tested the stability of HI across four different environmental conditions: interplant competition,

extended photoperiod, drought stress timing, and drought stress intensity. Results indicated that changes in HI across environmental conditions were negligible. These authors concluded that HI is a conservative trait within each cultivar. That is why we would expect no changes in HI beyond the ones associated with different genetics. Further experimentation also confirmed this finding (Bindi, Sinclair, & Harrison, 1999). The data from de Felipe et al. (2016) was used to calculate cumulative temperature for phenological development using base temperature of 8 °C (Soltani & Sinclair, 2012). Days to emergence was set at 8 and beginning seed-fill (R5) date was calculated as the mid-point between R1 and R7 (Setiyono et al., 2007). For simplicity, temperature accumulates when it is higher than base temperature without considering an optimum temperature threshold (Zhao et al., 2019). The influence of photoperiod of phenological development was considered negligible since planting date was fixed and latitude across simulation locations was similar.

To ensure the crop growth model reflected observed light interception, species-level parameters impacting leaf area growth were fit to the observed light interception data from Zavalla 2014; specifically, the parameters of the expolinear growth equation of LAI (Sinclair, 1986) were adjusted. Parameters $c$, $r$, and $t$ in the function

$$LAI(x) = \left(\frac{c}{r}\right) log(1 + exp^{r(x-t)} pop$$

were adjusted to fit seasonal intercepted PAR, where $x$ is the plastochron index and pop is the plant population (Sinclair, 1986). Parameter values of $c = 0.021$, $r = 0.02$, and $t = 4$ minimized the difference between observed PAR intercepted over the season, 1,444 (MJ m$^{-2}$) and simulated PAR intercepted, 1307 (MJ m$^{-2}$). The genotype/cultivar-specific parameters, RUE, HI, and time to physiological maturity, varied for each cultivar based on the measurements taken.

The model was run for 129 production environments generated by the combination of three locations (Zavalla [–33.016 S, –60.883 W], Marcos Juarez [32.697 S, 62.105 W], and Rio Cuarto [–33.123 S, –64.349 W]) and weather data from years 1973–2015. These locations had similar latitudes but were distributed across a rainfall transect. Simulation locations were selected to expose the model to a gradient of water availability. The same latitude was selected to avoid the need of incorporating a photoperiod response subroutine to deal with variation in daylength expected to occur at different latitudes. Planting date was set at 13 November. The cumulative precipitation from planting to maturity was used as an index for the potential productivity of the simulated production environment. The relative genetic progress (% yr$^{-1}$) for each environment (location × year combination) was calculated as the absolute yield difference between the new and old genotype, divided by the yield of the old genotype, and then divided by the numbers of release years between the new and the old genotype. The use of relative genetic progress instead of absolute is better suited for the comparison across environments (Slafer & Andrade, 1991).

## 3 | RESULTS

### 3.1 | Environmental characterization and seed yield

Available soil water at planting was 326 and 397 mm for sites L71415 and Sh1415, respectively, and total rainfall from emergence to maturity was 625 mm for both environments (Table 1). Average minimum and maximum air temperatures were 16.4 and 28.4 °C, respectively, while average air temperature was 22.3 °C.

Average yield for each site was 4504 and 5602 kg ha$^{-1}$ (~24% variation) (Table 1). Lowest yields (10th percentile) ranged from 3645 to 4502 kg ha$^{-1}$ (~24% variation) (Table 1),

**TABLE 2** Variance components (seen as a percentage of total variance) associated with environments (E), maturity group (MG), cultivars (C) nested within MG, ExC interaction, block nested within E, and residual are described

| Source of variation | Seed yield | Accumulated biomass | Harvest index | Incident radiation | Radiation interception efficiency | Radiation use efficiency | N uptake | N use efficiency |
|---|---|---|---|---|---|---|---|---|
| Environment (E) | 47 | 49.2 | 0.1 | 0.2 | 67.2 | 49.4 | 53.5 | 0.7 |
| Block (E) | 0.1 | 0.1 | 0 | 0 | 4.2 | 0 | 0.4 | 1.1 |
| Mat. group (MG) | 5.3 | 5.1 | 47 | 77.8 | 2.6 | 1.3 | 1 | 33.6 |
| Cultivar (C$_{MG}$) | 25.2 | 16.5 | 19.1 | 15.8 | 20.5 | 15.1 | 19.3 | 22.7 |
| E × C$_{MG}$ | 4.3 | 3.7 | 4.4 | 1.1 | 6 | 4.1 | 3.7 | 4.8 |
| Residual | 18.1 | 25.4 | 29.4 | 5.1 | 39.9 | 30.2 | 22.1 | 37.1 |
| C$_{MG}$/(E × C$_{MG}$) | 5.8 | 4.5 | 4.4 | 14.2 | 3.4 | 3.7 | 5.2 | 4.7 |
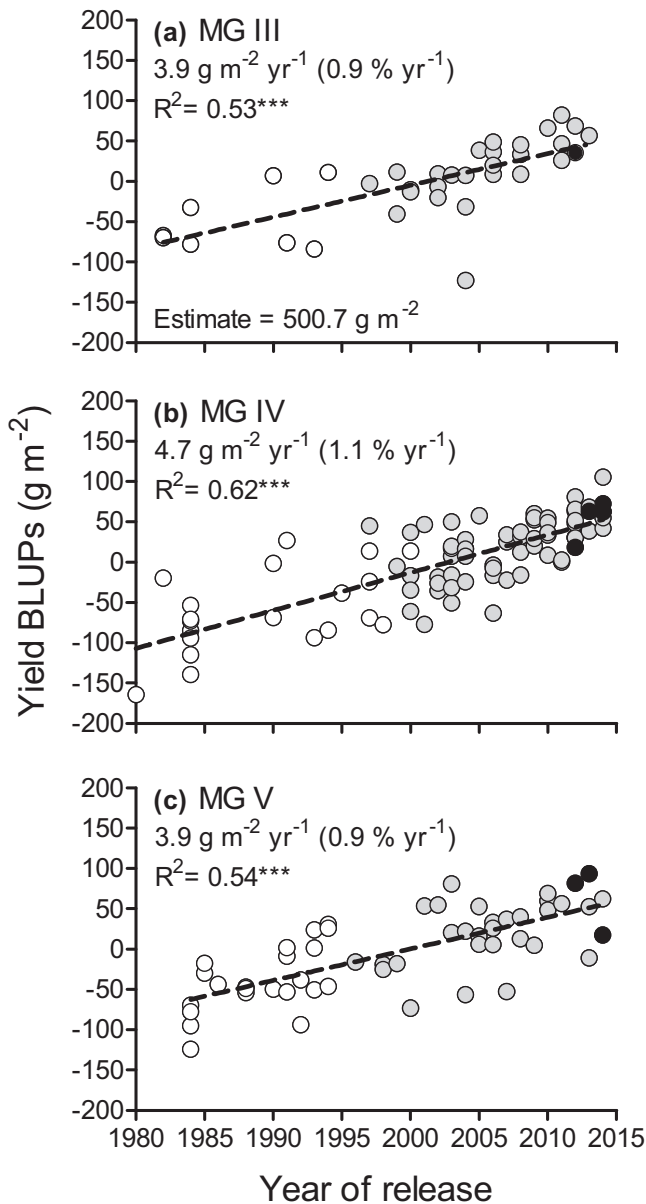
**FIGURE 1** Relationship between seed yield best linear unbiased predictors (BLUPs) and year of release for maturity groups (a) III, (b) IV, and (c) V. Empty symbols indicate non-transgenic cultivars, grey symbols indicate RR1 cultivars, and full symbols indicate RR2IPRO. The absolute and relative genetic progresses are displayed on each figure. The seed yield estimate is the average across cultivars

while highest yields (90th percentile) ranged from 5224 to 6626 kg ha$^{-1}$ (~27% variation) (Table 1). The results of variance components showed that most of the variation in seed yield was due to environmental effects suggesting that growth conditions, mostly associated to soil conditions, differed among the experimental sites (47%; Table 2).

Genetic yield progress, estimated as the linear relationship between seed yield and cultivar release year, was 42 kg ha$^{-1}$ yr$^{-1}$ from 1980 to 2014 when all the MGs were

pooled in the analysis. The relative genetic gain was 1% yr$^{-1}$. No difference in absolute or relative yield genetic gain was observed across the three MGs evaluated (Figures 1a, 1b, and 1c). No discontinuities in the linear regression were observed across the non-transgenic, RR1, and RR2 IPRO soybean cultivars, suggesting there were no additional benefits of these biotechnological events.

## 3.2 | Total aboveground biomass and harvest index

Significant cultivar differences in total aboveground biomass at maturity were evident (Table 2). Cultivars explained ~17% of total variance, and environment accounted for ~50% (Table 2). Cultivar explained 4.5 more times variation when compared to the cultivar x environment interaction, suggesting cultivar ranking was consistent across environments. Maturity group and the interaction environment × cultivar, explained a reduced proportion of the total variance (~5 and ~4%, respectively; Table 2). Regression analysis showed that total aboveground biomass increased 6.2 g m$^{-2}$ yr$^{-1}$ for MG III (Figure 2a), 7.3 g m$^{-2}$ yr$^{-1}$ for MG IV (Figure 2b), and 4.1 g m$^{-2}$ yr$^{-1}$ for MG V (Figure 2c). The relative increase was 0.7, 0.8 and 0.4% yr$^{-1}$, respectively. Covariance analysis indicated significant differences in absolute slope; slopes for MG III and IV were significantly higher than the one from MG V. This showed that biomass at maturity increased in all MGs, but the increase was higher in the shorter MGs.

Cultivar differences in HI were also evident. The proportion of variance in HI explained by cultivar effects was ~20% while the variation explained by environmental effects was less than 1% (Table 2). Cultivar explained ~4.5 times more variation when compared with environment × cultivar interaction. However, the variance explained by MG was ~47% (Table 2), suggesting that variation in HI was mainly associated to MG. Regression analysis showed that HI did not change over year of release for cultivars MG III (Figure 2d). However, HI increased 0.15 and 0.35% yr$^{-1}$ for MGs IV and V, respectively (Figures 2e and 2f). Analysis of covariance showed that genetic gain in HI was significantly higher in MG V when compared to MG IV ($P < .05$). As such, the longer the MG the higher the HI increase over year of release.

## 3.3 | Radiation capture and use efficiency

Cultivars differed in accumulated PARinc, and cultivar effects accounted for ~16% of total variance (Table 2). Cultivar variance in accumulated PARinc was several times higher than the environment × cultivar interaction variance (Table 2),
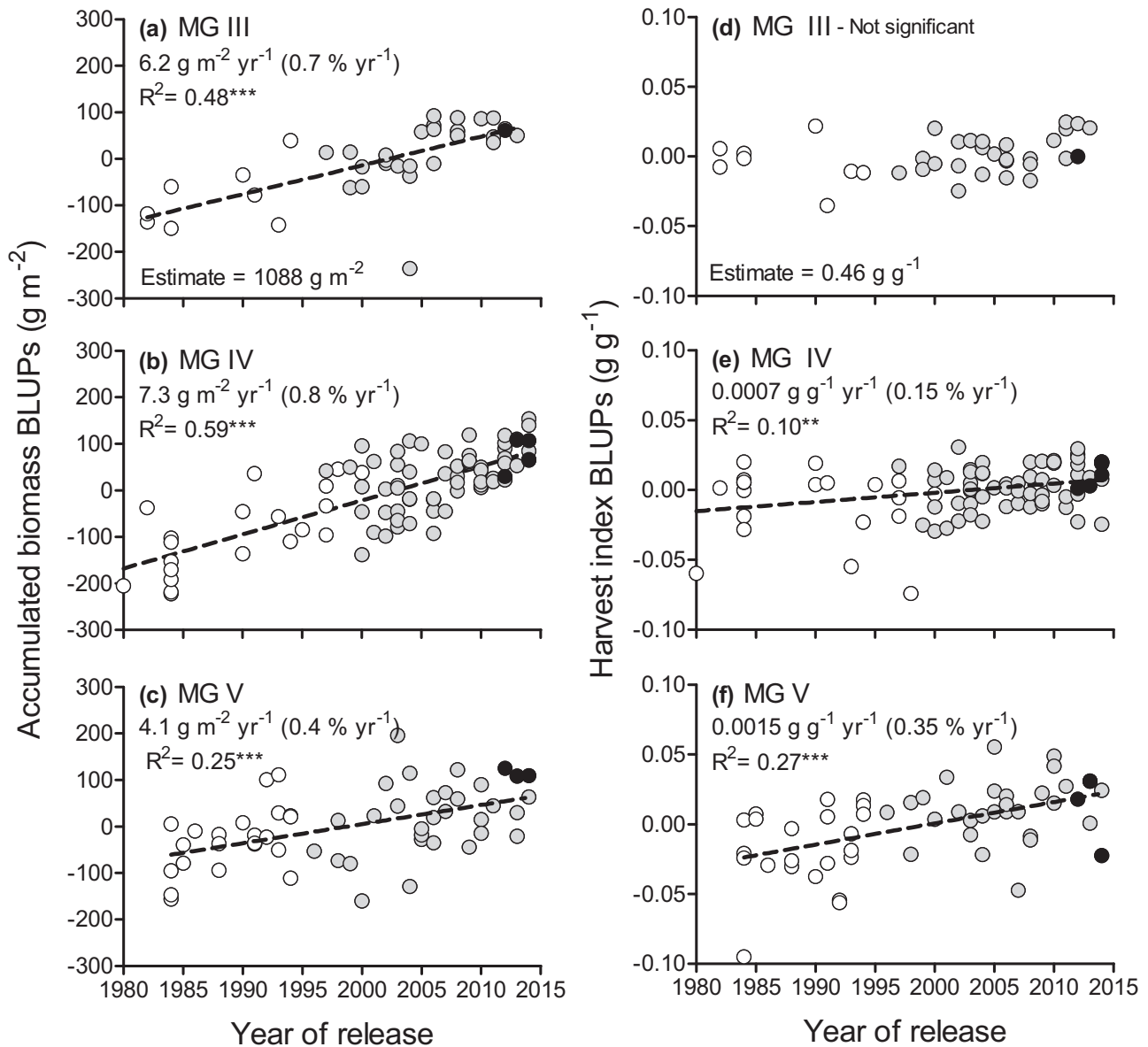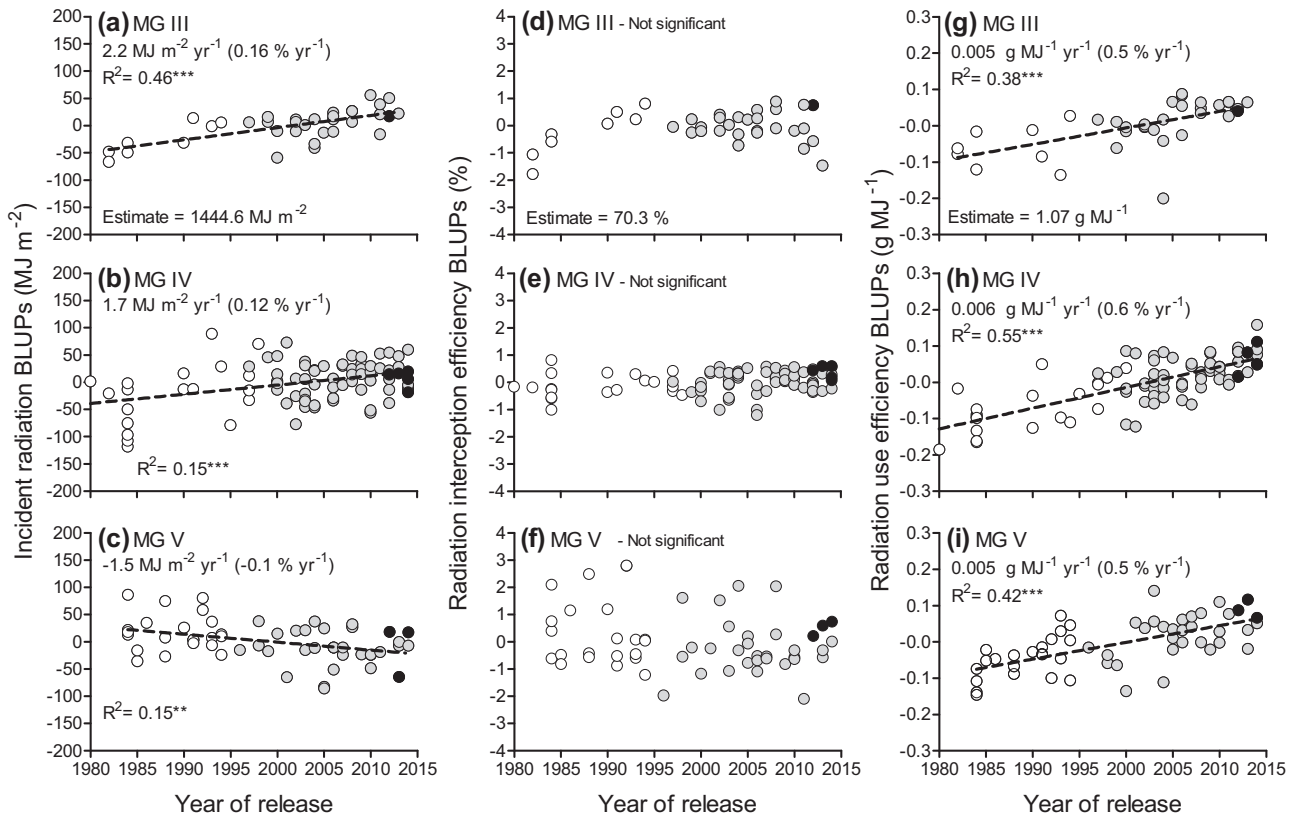
**FIGURE 2** Relationship between (a–c) accumulated biomass and (d–f) harvest index with year of release for maturity groups III, IV, and (f) V. Empty symbols indicate non-transgenic cultivars, grey symbols indicate RR1 cultivars, and full symbols indicate RR2IPRO. The absolute and relative genetic progresses are displayed on each figure. The seed yield estimate is the average across cultivars. The accumulated biomass and harvest index estimate indicate the average across cultivars

suggesting that cultivar behavior was fairly constant across environments. Maturity group effect accounted for more than 70% of the variance, indicating that changes in cycle duration impacted directly on the accumulation of PARinc. Regression analysis indicated accumulated PARinc increased 2.2 MJ m$^{-2}$ yr$^{-1}$ for MG III (Figure 3a) and 1.7 MJ m$^{-2}$ yr$^{-1}$ for MG IV (Figure 3b) over time. For MG V, accumulated PARinc was reduced at a rate of −1.5 MJ m$^{-2}$ d$^{-1}$ (Figure 3c). Covariance analysis revealed that these rates of genetic gain from MGs III and IV were significantly higher than the one for MG V ($P < .05$).

Radiation interception efficiency also showed differences among cultivars, and the cultivar effect accounted for ∼20% of the variance in ei while environment explained ∼65% (Table 2). The ratio between cultivar and environment × cultivar variance was the lowest of all variables evaluated. There were no changes in ei over time for any of the MGs tested (Figures 3d, 3e, and 3f). Average ei for the whole growing season was 0.7 and remained fairly constant after 35 yr of soybean breeding.

Cultivars also showed differences in RUE, and the cultivar effect accounted for ∼15% of the variance in RUE, while

**FIGURE 3** Relationship between (a–c) incident radiation, (d–f) radiation interception efficiency, and (g–i) radiation use efficacy with year of release for maturity groups III, IV, and V. Empty symbols indicate non-transgenic cultivars, grey symbols indicate RR1 cultivars, and full symbols indicate RR2IPRO. The absolute and relative genetic progresses are displayed on each figure. The incident radiation, radiation interception efficiency, and radiation use efficiency estimates indicate the average across cultivars

the environment effect explained ∼50% (Table 2). However, cultivar explained approximately four times more variation in RUE than cultivar × environment interaction indicating similar cultivar ranking across environments. Maturity group effect explained a reduced proportion of the total variance (1.3%; Table 2). Regression analysis showed genetic gain for RUE was 0.005 g MJ$^{-1}$ yr$^{-1}$ for MG III, 0.006 g MJ$^{-1}$ yr$^{-1}$ for MG IV, and 0.005 g MJ$^{-1}$ yr$^{-1}$ for MG V (Figures 3g, 3h, and 3I, respectively). The relative gain was 0.5% yr$^{-1}$ for MGs III and V (Figure 3g and 3h) and 0.6% yr$^{-1}$ for MG IV (Figure 3i). Analysis of covariance showed no significant differences in slopes among MGs ($P > .05$), concluding that the average gain across MGs was 0.005 g MJ$^{-1}$ yr$^{-1}$ or 0.5% yr$^{-1}$ when expressed as relative gain.

## 3.4 | Nitrogen capture and use efficiency

Cultivars differed in Nup at maturity, and cultivar effect accounted for ∼19% of variance while environment effect explained ∼54%. Cultivar explained five times more variation

than the environment × cultivar interaction, suggesting high consistency of cultivar ranking across environments. Maturity group explained a reduced proportion of the variance (1%; Table 2). Absolute genetic gain in Nup over time was 0.23 g m$^{-2}$ yr$^{-1}$ for MG III, 0.27 g m$^{-2}$ yr$^{-1}$ for MG IV, and 0.18 g m$^{-2}$ yr$^{-1}$ for MG V (Figures 4a, 4b, and 4c). The relative rates were 0.8, 0.9, and 0.6% yr$^{-1}$, for MGs III, IV, and V, respectively (Figures 4a, 4b, and 4c). The rate of gain in Nup was not significantly different across MGs ($P > .05$), and the average rate was 0.23 g m$^{-2}$ yr$^{-1}$ or 0.8% yr$^{-1}$ when expressed as relative gain.

Cultivars differed in NUE, and this effect accounted for ∼23% of the total variance in NUE. The environment explained less than 1% (Table 2). The cultivar effect explained five times more of the observed variation than the environment x cultivar interaction effect, suggesting cultivars behaved similarly across the environments. The proportion of variance explained by MG was ∼34%. There was no correlation between NUE and release year for MGs III (Figure 4d) and IV (Figure 4e). For MG V, ordinary least square regression analysis showed that absolute gain in was
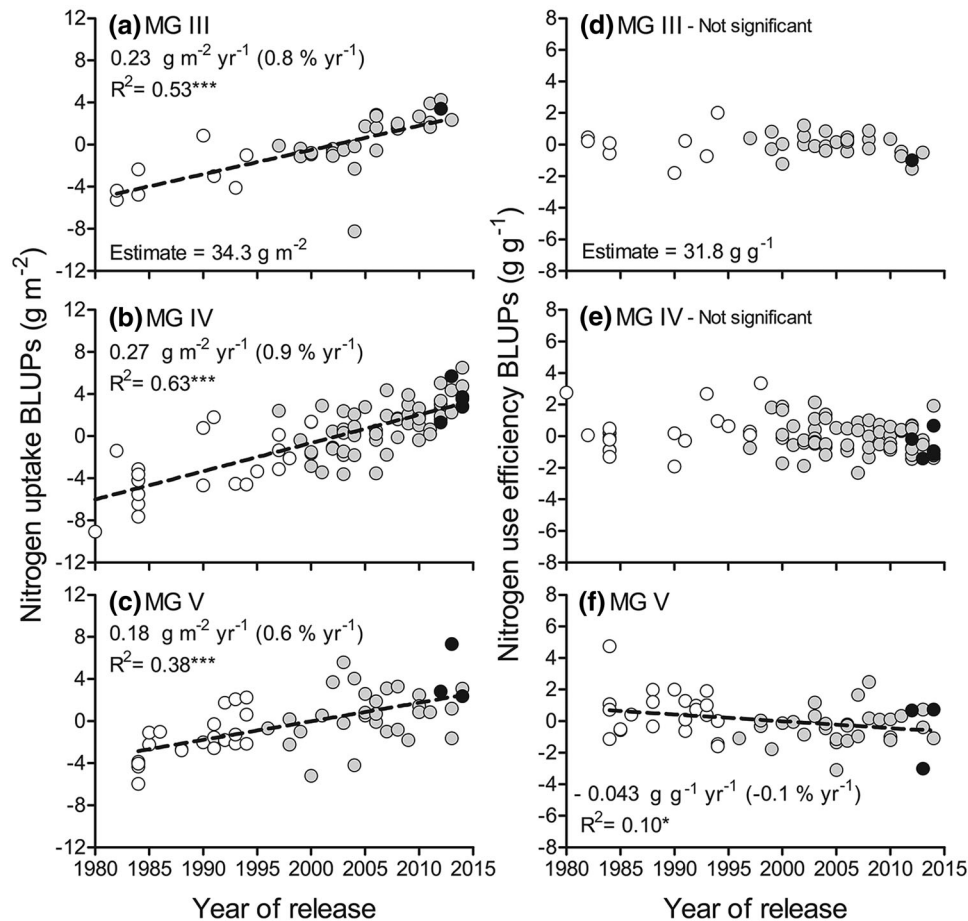
**FIGURE 4** Relationship between (a–c) N uptake and (d–f) N use efficiency with year of release for maturity groups III, IV, and V. Empty symbols indicate non-transgenic cultivars, grey symbols indicate RR1 cultivars, and full symbols indicate RR2IPRO. The absolute and relative genetic progresses are displayed on each figure. The N uptake and N use efficiency estimates indicate the average across cultivars

$-0.043$ g g$^{-1}$ yr$^{-1}$ or $-0.1\%$ yr$^{-1}$ when expressed as relative gain (Figure 4f). However, this significantly negative relationship, the proportion of variation explained by the model is low ($R^2 = .1$), showing that NUE has remained fairly stable across years.

## 3.5 | Multi-trait analysis

The two PCA dimensions retained 98% of original information for MG III cultivars (Figure 5a). Seed yield was positively correlated with Nup, RUE, and biomass at physiological maturity ($r > .9$, $P < .0001$; Table 3a). Nitrogen uptake was highly correlated with RUE ($r = .92$, $P < .0001$; Table 3a). A relationship between RUE and biomass was clearly evident, suggesting RUE was the main trait for increased canopy biomass ($r = .97$, $P < .0001$; Table 3a).

Figure 5b depicts the relationships between cultivars and traits for MG IV. The first two PCA dimensions retained 92% of original information. The biplot (Figure 5b) showed a relationship among seed yield, Nup, RUE, and biomass at physi-

ological maturity ($r > .9$, $P < .0001$; Table 3b). Harvest index was also correlated to yield ($r = .55$, $P < .0001$; Table 3b). Nitrogen uptake was highly correlated to biomass production ($r = .92$, $P < .0001$; Table 3b) through improvements in RUE ($r = .91$, $P < .0001$; Table 3b), which showing to be highly correlated with biomass at physiological maturity ($r = .96$, $P < .0001$; Table 3b). There was no significant correlation between HI and biomass at maturity (Table 3b).

The first two PCA dimensions explained 90% of original information for MG V (Figure 5c). The diagram showed that seed yield was positively correlated with Nup, RUE, biomass at physiological maturity, and HI ($r > .7$, $P < .0001$; Table 3c). No correlation was observed between HI and biomass at physiological maturity. However, Nup showed a strong correlation with biomass ($r = .85$, $P < .0001$; Table 3c) through the relationship between biomass and RUE at maturity ($r = .89$, $P < .0001$; Table 3c). Nitrogen uptake and RUE were highly correlated ($r = .89$, $P < .0001$; Table 3c). Radiation use efficiency showed a weak correlation with PARinc ($r = -.33$, $P < .05$; Table 3c). Nitrogen use efficiency was not correlated with biomass at physiological maturity.
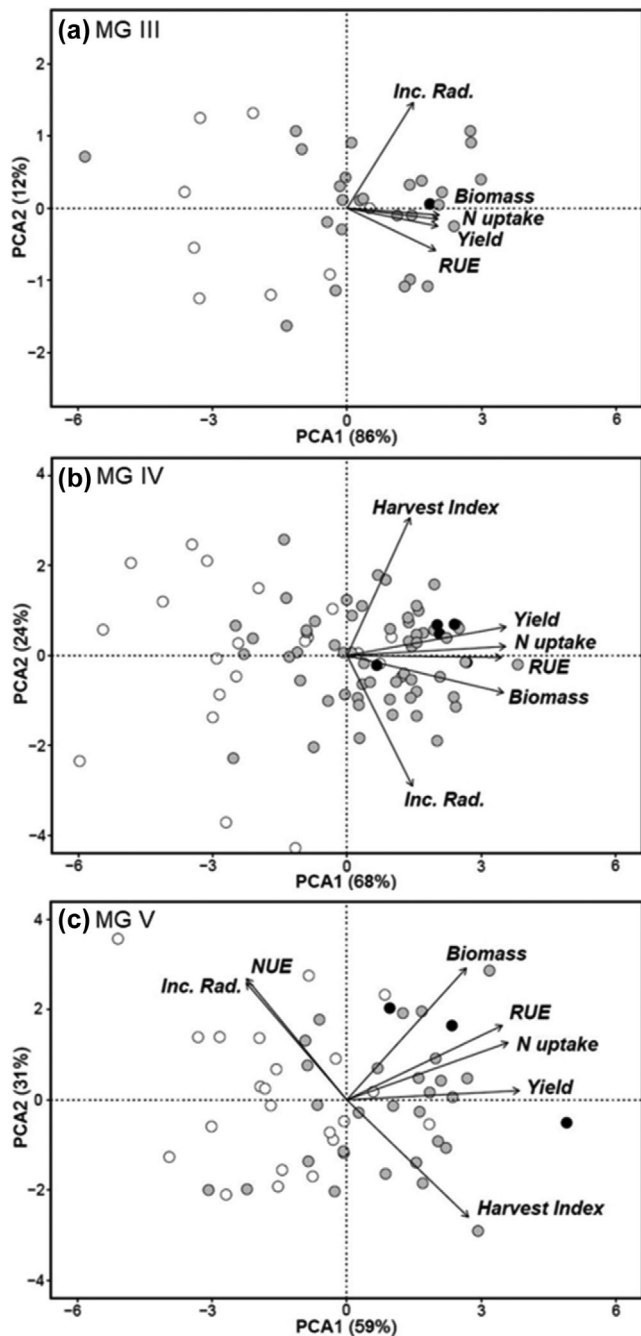
**FIGURE 5** Biplot of the first and second principal components for those variables that were associated with the year of release for maturity groups (a) III, (b) IV, and (c) V. Empty symbols indicate non-transgenic cultivars, grey symbols indicate RR1 cultivars, and full symbols indicate RR2IPRO. See text for details

## 3.6 | Simulation of genetic gain across varying production environments

The simulated yield of the oldest and newest soybean cultivars was compared to the observed yield BLUPs for Zavalla 2014. Across MGs, the relative mean absolute error (RMAE) for

yield prediction given the model fit to observed light interception was 9.1%. The relative root mean squared error (RRMSE) of yield prediction was 10.9%. The simulated relative genetic progress was also compared to the observed one for Zavalla 2014–2015 season. Across the MGs evaluated, the RMAE for genetic progress was 11.2%, and the RRMSE was 14.0%. The correlation between observed and simulated yield is presented in Supplemental Figure S2. Genetic parameters for simulations are presented in Supplemental Table S2. These results indicated that the model was able to capture both seed yield and genetic progress.

The average relative genetic progress across 129 simulated environments were 0.62, 0.71, and 0.60% $yr^{-1}$ for MGs III, IV, and V, respectively. The maximum simulated genetic progress was 1.00, 1.11, and 0.87% $yr^{-1}$ for the three MGs; the minimum was 0.27, 0.30, and 0.19% $yr^{-1}$. Our results showed a positive correlation between simulated relative genetic progress and productivity of the evaluation environment estimated as cumulative precipitation during the growing season (Figure 6). This result was evident for the three evaluated MGs. The genetic progress response to seasonal precipitation was higher for MGs III and IV than the one observed for MG V (Figure 6, $P < .05$).

## 4 | DISCUSSION

Soybean genetic progress rate in Argentina during the last 35 yr was 42 kg $ha^{-1}$ $yr^{-1}$ (1% $yr^{-1}$). Reports from the United States and Brazil ranged from ∼23 to 41 kg $ha^{-1}$ $yr^{-1}$ (de Toledo, de Almeida, de Souza Kiihl, & Menosso,1990; Rincker et al., 2014; Specht et al., 2014). Yield progress was not different across MGs and was consistently explained by increased total aboveground biomass at physiological maturity. Harvest index improvement was also associated to genetic progress for MG V, but to a lesser degree for MGs IV and III. Reports of the association between yield progress and HI have been contradictory in the past (Board & Modali, 2005; Koester et al., 2014; Pedersen & Lauer, 2004; Shibles & Weber, 1966). This might have been related with the unaccounted effect of different MGs evaluated in some studies. These results suggest future genetic progress should seek continuing increases in total accumulated biomass across MGs but efforts to increase HI should focus on longer MG cultivars.

Genetic improvement of total accumulated biomass at maturity was explained by changes in PARinc during crop cycle and RUE, but not by increased ei. Our previous study showed MGs III and IV increased days from sowing to physiological maturity (de Felipe et al., 2016), mainly due to increases in the duration of reproductive stages. However, MG V showed a decrease in days to maturity due to shortening in vegetative phase. These changes impacted differentially the amount of PARinc during the growing season for each

**TABLE 3** Pearson correlations for variables (best linear unbiased predictors, BLUPs) significantly associated with year of release for cultivars maturity group (MG) (a) III, (b) IV, and (c) V. Variables seed yield (yield), accumulated biomass at R7 (Biomass), accumulated incident radiation at R7 (incident radiation, inc. rad.), radiation use efficiency (RUE), nitrogen uptake (N uptake), harvest index (HI), and nitrogen use efficiency (NUE)

| (a) MG III | Yield | Biomass | Inc. rad. | RUE | N uptake | |
|---|---|---|---|---|---|---|
| Yield | 1 | | | | | |
| Biomass | 0.94*** | 1 | | | | |
| Inc. rad. | 0.61*** | 0.67*** | 1 | | | |
| RUE | 0.94*** | 0.97*** | 0.48** | 1 | | |
| N uptake | 0.96*** | 0.95*** | 0.64*** | 0.92*** | 1 | |
| **(b) MG IV** | **Yield** | **Biomass** | **Inc. rad.** | **RUE** | **N uptake** | **HI** |
| Yield | 1 | | | | | |
| Biomass | 0.90*** | 1 | | | | |
| Inc. rad. | 0.28** | 0.52*** | 1 | | | |
| RUE | 0.91*** | 0.96*** | 0.27* | 1 | | |
| N uptake | 0.95*** | 0.92*** | 0.35** | 0.91*** | 1 | |
| Harvest Index | 0.55*** | 0.14 | −0.36*** | 0.26* | 0.42*** | 1 |
| **(c) MG V** | **Yield** | **Biomass** | **Inc. rad.** | **RUE** | **N uptake** | **HI** |
| Yield | 1 | | | | | |
| Biomass | 0.69*** | 1 | | | | |
| Inc. rad. | −0.47*** | 0.1 | 1 | | | |
| RUE | 0.86*** | 0.89*** | −0.33* | 1 | | |
| N uptake | 0.87*** | 0.85*** | −0.23 | 0.89*** | 1 | |
| Harvest Index | 0.70*** | −0.03 | −0.75*** | 0.31* | 0.37** | 1 |
| NUE | −0.46*** | 0.11 | 0.62*** | −0.14 | −0.42** | −0.77*** |

*Significantly different from zero at $P < .05$.

**Significantly different from zero at $P < .01$.
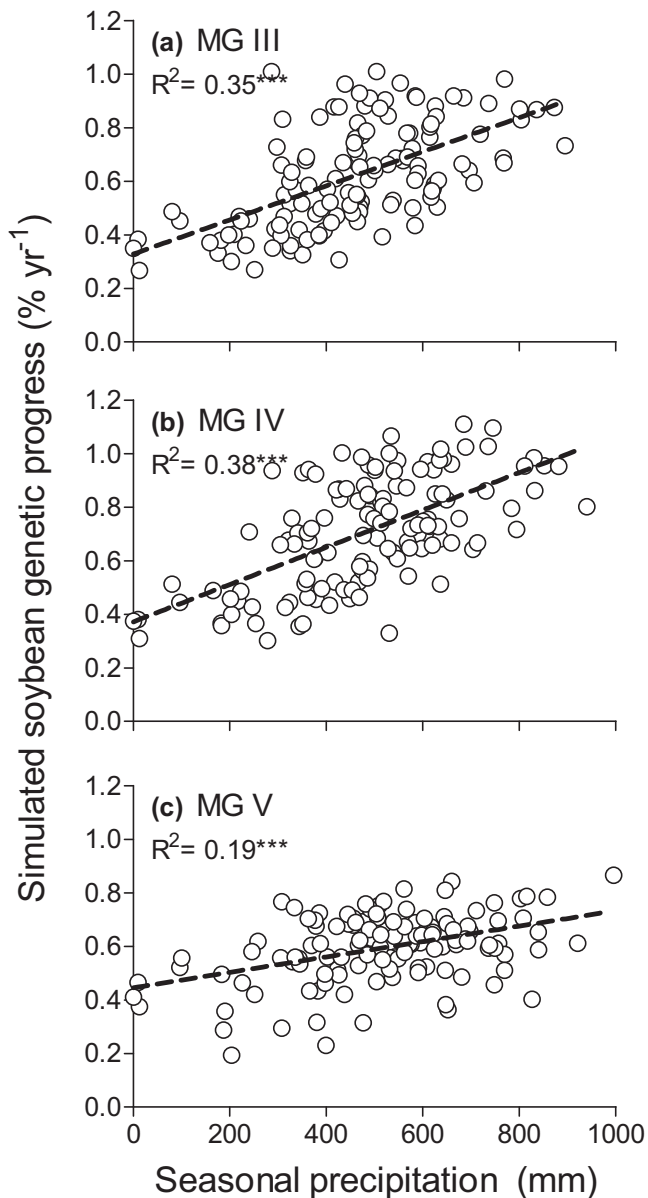
***Significantly different from zero at $P < .001$.

evaluated MG. Increased PARinc was positively associated to the genetic progress of MGs III and IV only.

Radiation use efficiency is a critical trait determining C assimilation at the crop level (Muchow & Sinclair, 1994; Sinclair & Horie, 1989). Improvements in RUE are relevant to improve biomass accumulation, but the degree of improvement across years of release is poorly understood (Koester et al., 2014). Our results show that RUE improved at a rate of 0.5% $yr^{-1}$ across all MGs. Koester et al. (2014) reported RUE improved 0.43% $yr^{-1}$ across U.S. soybean germplasm. Genotypic differences in soybean leaf photosynthesis per unit leaf area exist, and increased leaf photosynthesis has been observed in most modern soybean cultivars (Liu et al., 2012; Morrison et al., 1999). This increased leaf photosynthesis might explain, at least in part, the observed increase in field-level RUE observed in our study (Sinclair & Horie, 1989). Our results showed that RUE played a critical role in past genetic progress in soybean. From a theoretical and practical point of view, RUE is still a fundamental target for improving soybean yield (Ainsworth, Yendrek, Skoneczka, & Long, 2012; De Bruin & Pedersen, 2009).

Radiation interception efficiency was ~70% when the whole crop cycle from planting to physiological maturity is considered and showed no changes across release years. Previous work showed a decrease in leaf area across years of release in soybean, suggesting potential reduction in ei for the newer genotypes (Jin et al., 2010; Morrison et al., 1999). However, leaf area of newer cultivars might still be well above the critical LAI needed for maximizing ei. Koester et al. (2014) showed substantial improvements in ei of newer soybean cultivars. However, this effect was confounded because newer cultivars were longer MGs. Here, when controlling for this confounding effect, ei showed no significant progress throughout the evaluated time period.

Leaf N is considered the main driver of increases in RUE across species (Sinclair & Muchow, 1999). Our results showed substantial improvements in total Nup associated to year of release. This improvement in Nup was correlated with improvements in RUE. Increased RUE is probably associated to higher leaf N and consequently photosynthesis (Koester et al., 2016; Muchow & Sinclair, 1994). Our results agree with previous evidence supported by Sinclair and Horie (1989) and Muchow and Sinclair (1994), revealing the strong importance of N in seed yield determination (Rotundo et al., 2014). In spite of changes observed for Nup at R7, no shifts in NUE were detected, except for a slight negative tendency

**FIGURE 6** Soybean genetic gain (% yr$^{-1}$) for maturity groups (a) III, (b) IV, and (c) V simulated across different season rainfall environments. Seasonal rainfall was determined by the combination of three locations and 43 yr per location. See text for details on modeling approximation

ciated to biological $N_2$ fixation constrain the possibilities of obtaining low N supply environments and thus the expression of NUE variability across cultivars. Besides any speculation related to NUE, the tight correlations between Nup, RUE, and seed yield across the three MGs clearly suggest a mechanistic link between N, C assimilation, and yield (Sinclair & Horie, 1989).

The simulation study showed increased genetic progress in more productive environments. This is consistent with the idea that commercial breeding selected for traits associated with increased yield potential (Blum, 2005). Even though there is evidence that genetic variation for stress tolerance exists (Sadok & Sinclair, 2011) and that it has potential value to increase yield (Sinclair, Messina, Beatty, & Samples, 2010), our results suggest increased changes of genetic progress expression in more productive, relatively stress-free, environments. The explanation for this result might be associated with RUE being the main driver of genetic progress in Argentinean soybean. The impact of increased RUE on soybean yield is through increased growth. Assuming a constant transpiration efficiency (Tanner & Sinclair, 1983), the increased growth is only supported by additional water and nutrient consumption. This is consistent with the observed increased genetic progress expressed in more productive environments. Other crops like maize showed a consistent association between increased yield due to genetic progress and stress tolerance (Duvick et al., 2010). On the contrary, past evidence relating genetic progress and productivity in soybean was limited and contradictory. For example, newer cultivars were more tolerant to increased plant density stress (Cober, Morrison, Ma, & Butler, 2005), but estimates of genetic gain dropped as weed stress increased (Cober & Morrison, 2011) or under soil water deficits (Frederick, Woolley, Hesketh, & Peters, 1991). This evidence highlights the importance of understanding which trait (i.e., RUE) is driving the observed genetic progress to better understand possible associations with environmental conditions.

## 5 | CONCLUSIONS

Different breeding trajectories were evident when comparing the physiological determinant of yield genetic progress of contrasting MGs in soybean. Genetic progress in seed yield across MG cultivars was ~1% yr$^{-1}$. Relatively short cycle cultivars (MGs III and IV) improved seed yield by increasing (a) seasonal PARinc (~0.15% yr$^{-1}$), and (b) RUE (~0.6% yr$^{-1}$). These trends resulted in increased total biomass accumulation but no consistent changes in HI. On the contrary, MG V cultivars improved seed yield by increasing (a) RUE (~0.5% yr$^{-1}$) and (b) HI (~0.35% yr$^{-1}$). These effects overcompensated for the observed decrease in PARinc associated to newer cultivars. For the most part, genetic

for MG V. When studied at leaf level, highest NUE values were observed for soybean wild relatives (Rotundo & Borrás, 2016). This would indicate that breeding has been usually selecting for reduced NUE. Another hypothesis regarding the lack or even negative NUE observed across release years would be that high values of NUE are only expressed at low soil N conditions, as were shown before by Hirel, Le Gouis, Ney, and Gallais (2007) for maize and by Robinson et al. (2007) for sugarcane (*Sacharum officinarum* L.). In soybean, the relative independence of Nup from soil supply asso-

progress in PARinc and RUE for short MGs, and RUE and HI for longer MGs, account for most of the observed progress in seed yield. These results confirm the concept that different physiological pathways to increase yield exist, as previously reported (Rotundo, Borrás, De Bruin, & Pedersen, 2012). Our study shows evidence of the critical role of increased N uptake over the observed RUE improvement, reinforcing results describing the direct relationship between soybean canopy N uptake and yield. Possible limitation of the current study is the reduced number of environments explored for experimentation.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest.

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