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Genetic improvement of peanut in Argentina between 1948 and 2004: Seed yield and its components

Ricardo J. Haro[a,*], Jorge Baldessari[a], María E. Otegui[b]

[a] Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Agropecuaria Manfredi, Argentina
[b] Instituto de Fisiología y Ecología Vinculado a la Agricultura del Consejo Nacional de Investigaciones Científicas y Tecnológicas (IFEVA-CONICET), Facultad de Agronomía, Universidad de Buenos Aires, Argentina

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ABSTRACT

In Argentina, peanut (*Arachis hypogaea* L.) breeding has been based on seed yield *per se* plus defensive and seed quality traits. An important milestone was the shift from cultivars with erect growth habit (CEGH) to cultivars with procumbent (CPGH) growth habit that took place in the 1970s. However, there is no information on the genetic gain obtained for seed yield and related secondary traits (numerical and physiological determinants of seed yield), or on the effect of growth habit shift on these traits. Field experiments were performed to compute this gain and the relationships between traits in potential growing conditions. Eight cultivars released between 1948 and 2004 were evaluated. Introduction of the procumbent habit in 1975 produced a mean increase of 52% in seed yield, which was related to year of cultivar release (YOR) only for CPGH (mean genetic gain of 0.43% y^{-1}). This trend was driven by seed weight, a trait that registered a mean genetic gain of 0.29% y^{-1} ($P = 0.026$) only among procumbent cultivars (56% increase with habit change between 1973 and 1975). No genetic gain was computed for seed numbers, and only a 10% difference was registered between growth habits (CPGH > CEGH). Seed number was related to crop growth rate between R3 and R6.5 ($r^2 = 0.55$, $P < 0.001$). This rate was higher for CPGH than for CEGH. Breeding increased the number of flowers per plant (0.86% y^{-1}), and the number of pods per plant and pod set (CPGH > CEGH). Breeding had a clear effect ($P < 0.001$) on the determinants of seed weight, and a genetic gain of 0.52% y^{-1} was estimated for pod growth rate. Introduction of CPGH enhanced pod growth duration (37% increase). No trade-off was detected between seed number and seed weight because there was no source limitation to seed filling. Therefore, peanut seed yield might be further increased by improving the determinants of seed numbers and seed weight simultaneously.

1. Introduction

During the past six decades, yield performance of many crops has been greatly improved, and this progress can be attributed to genetic improvement as well as enhanced cultural and management practices (Datt et al., 2011; Ramteke et al., 2011; Ci et al., 2012; Manès et al., 2012; Sadras and Lawson, 2013). These trends were also observed for peanut (*Arachis hypogaea* L.), but information on yield gains for this species have not been updated as for other crops and last reports date from the 1980s (Mozingo et al., 1987). During most part of the 20th century, peanut breeders aimed almost exclusively at developing cultivars with enhanced seed yield (Holbrook and Stalker, 2003). Consideration of other traits is relatively recent in breeding programs of this species, and includes physical and chemical seed quality required by the market, and enhanced tolerance to abiotic and biotic stresses (Isleib et al., 1994; Holbrook and Stalker, 2003). This process produced an increase in total flower numbers and reproductive efficiency (percentage of flowers resulting in pods or seeds) of new cultivars as compared to the old ones (Coffelt et al., 1989; Seaton et al., 1992), as well as an improved partitioning of assimilates to reproductive structures (Coffelt et al., 1989; Wells et al., 1991).

In Argentina, peanut genetic improvement has been based on the same general criteria. Selection focused on yield *per se* in trials conducted at sites representative of the target environment, a common practice in extensive grain crops (Austin, 1993; Betran et al., 2004; Orf et al., 2004). However, an important shift occurred in the middle of the 1970s. Up to then, cultivars of the subspecies *fastigiata* were released; these cultivars had a growing cycle of 120–135 days, predominantly erect growth habit and seeds with 48 ± 1%

Abbreviations: Exp, experiment; CGR, crop growth rate; PGR, pod growth rate; SSR_{SF}, source–sink ratio during the effective seed-filling phase; CEGH, cultivars with erect growth habit; CPGH, cultivars with procumbent growth habit; YOR, year of release.

[*] Corresponding author at: Estación Experimental Agropecuaria INTA Manfredi, CC 5988 Córdoba, Argentina. Tel.: +54 3572493053; fax: +54 3572493058.
E-mail address: ricardoharo@manfredi.inta.gov.ar (R.J. Haro).

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oil content. Since then, with the release of genotypes of the subspecies *hypogaea*, on-farm yield increased substantially, whereas seed oil content remained unchanged (Giandana, 2006). The new genotypes were also characterized by longer cycles (ca. 140–145 days from sowing to harvest) and a procumbent growth habit. Currently, evaluation of peanut genotypes is based on final pod yield and seed grades.

It is well recognized that selection for yield *per se* has several constraints (Reynolds et al., 1996; López Pereira et al., 1999; Peng et al., 1999; Araus et al., 2002), because yield is characterized by low heritability and high genotype × environment interaction (Wallace et al., 1993; Jackson et al., 1996; Richards et al., 2001). Up to the present, however, the inclusion in breeding programs of traits representative of the physiological determinants of grain yield (e.g. crop growth rate during critical periods and source/sink relationships) has not been significant for any species, probably due to difficulties for assessing those related to biomass production on a large number of genotypes and environments (Araus et al., 2001). Consequently, a better understanding of the impact of these traits on genetic gains in seed yield has become essential for assisting conventional (Jackson et al., 1996; Boote et al., 2001; Araus et al., 2002) and molecular (Miflin, 2000) breeding approaches for hastening yield improvement. An effective approach to the analysis of physiological determinants is achieved by dissecting yield into component traits (Yin et al., 2004; Lee and Tollenaar, 2007). Crop yield is often viewed as the product of seed number and seed weight, two variables for which there are evidences of a negative association in some crops but not in others (Slafer et al., 1996; López Pereira et al., 1999; Luque et al., 2006; Gambín and Borrás, 2010). There is no evidence on the trends caused by peanut breeding on this topic.

Starting with the work of Austin et al. (1980), comparing cultivars released in different eras became a useful method to estimate the contribution of genetic improvement to crop yield and its determinants. Richards (1997) highlighted the value of identifying yield determinants by comparing historical sets of cultivars because any increase in yield potential must have a physiological basis. Accordingly, Richards (1997) proposed that, by targeting the components contributing to greater yield, we should be able to select for them more easily and efficiently and to identify the most appropriate germplasm to be used as parents. This comparative approach has been applied to a number of species (Wells et al., 1991; Slafer, 1994; López Pereira et al., 1999; Luque et al., 2006), but no previous attempt has been made to elucidate the physiological differences that account for the large increase in on-farm yield among Argentine peanut genotypes over the years. As mentioned previously, a clear breakpoint occurred in the 1970s, when Spanish and Valencia genotypes of predominantly erect habit were substituted by procumbent runner varieties that were better suited for exporting as hand picked and selected peanuts to Europe. Additionally, the harvest work of digger-shaker-inverter machines was facilitated by the shift in growth habit because procumbent plants were inverted easily (too many pods remained in contact with the soil among machine-harvested erect genotypes). So far, no information was produced on how this shift affected seed yield determination from the physiological point of view. A better understanding of the differences among genotypes and how these differences relate to their yield potential may contribute to the selection process and future yield improvement in peanut.

The objective of our study was to investigate the genetic gain in seed yield and seed yield components among peanut cultivars of contrasting growth habit (erect and procumbent) released between 1948 and 2004 in Argentina. For this purpose we used the analytical framework proposed by López Pereira et al. (1999) for the study of sunflower breeding. We evaluated (i) the relationship between seed yield and yield components, (ii) the relationship between seed number and seed weight, and (iii) the response of seed number and seed weight to their physiological determinants (e.g. crop and pod growth rates, source/sink relationships).

2. Materials and methods

2.1. Experimental design and crop husbandry

Field experiments were conducted during the 2009–2010 (Exp1), 2010–2011 (Exp2 and Exp3), and 2011–2012 (Exp4) growing seasons at the research station of the National Institute of Agricultural Technology (INTA), located in Manfredi (31°49′ S, 63°46′ W), Córdoba province, Argentina. The soil is silty loam Typic Haplustoll (USDA Soil Taxonomy). The experiments included eight cultivars (Table 1) of contrasting growth habit developed for this region and released between 1948 and 2004. The cultivars employed for the experiments were representative of the most widely used by Argentine peanut farmers at their time of release. The fact that all cultivars corresponded to the breeding program of INTA (used in 90% of the land cropped with this species in the country) allowed us to better understand effects of breeding, which is not always possible when cultivars from completely different breeding programs are tested (Luque et al., 2006). Sowing was performed on November 10 (Exp1), October 19 (Exp2), November 10 (Exp3) and November 1 (Exp4). Exp1 and Exp2 were aimed to understanding breeding effects at the crop level, for this reason seeds were hand-planted in rows 0.7 m apart using a stand density of 14 plants m^{-2}. In these experiments, treatments (cultivars) were arranged in a completely randomized block design with three replicates and plots were four rows wide and 15 m long. Exp3 and Exp4 were developed for the analysis of traits at the individual plant level, and for this reason they were grown with almost no interference among them (ca. 1.5 m between plants) and treatments were arranged in a completely randomized block design with five replicates (i.e. each experimental unit had one plant).

Experiments received drip irrigation to keep the uppermost 1 m of the soil near field capacity throughout the growing season. Experimental units were maintained free of weeds by frequent hand removal, and received periodical applications of 125 mL ha^{-1} of tebuconazole (α-[2-(4-chlorophenyl) ethyl]-α-(1,1-dimethylethyl)-1*H*-1,2,4-triazole-1-ethanol) to prevent foliar diseases. Daily mean air temperature was measured within 10 m from the experimental plots to calculate thermal time. Thermal unit calculations (in °Cd) were linearly accumulated from a base temperature of 11 °C (Williams and Boote, 1995).

2.2. Measurements

In Exp1 and Exp2, crop phenology (Boote, 1982) was followed in each plot on three plants tagged at R1 (first flower visible in at least 50% of the plants). Starting from initial pod growth (R3) and fortnightly, all plants in samples of 0.35 m^2 were harvested from the two central rows (i.e. between 6 and 7 sampling dates along the cycle). Plants were separated into leaves plus stems (vegetative biomass) and pods (reproductive biomass), and dried at 70 °C until constant weight. At final harvest (R8), total seed number was counted manually and seeds were weighed for quantification of final seed yield. Seed weight was computed as the quotient of seed yield and seed number. Crop growth rate (CGR, in g m^{-2} d^{-1}) and pod growth rate (PGR, in g m^{-2} d^{-1}) at different growth stages were estimated by linear interpolation. CGR between R3 and R6.5 ($CGR_{R3–R6.5}$) was taken as representative of the critical period for pod and seed set (Haro et al., 2007). PGR between R3 and R8 was used as indirect estimator of seed growth. The source–sink ratio during the effective seed-filling phase (SSR_{SF}, in mg $seed^{-1}$) was

Table 1
Characteristics of cultivars included in the experiments.

Cultivar	Year of release	Growth habit	Seeds per pod	Maturity group[a]	Pod type	Breeding method[b]
Colorado Manfredi	1948	Erect	3	110	Valencia	PL
Blanco Santa Fe	1950	Erect	2	120	Spanish	PL
Blanco Manfredi 68	1962	Erect	2	130	Spanish–Runner	H + S
Colorado Irradiado INTA	1973	Erect	3	110	Valencia	I + S
Virginia 5 INTA	1975	Procumbent	2	150	Virginia	H + S
Florman INTA	1985	Procumbent	2	150	Runner	PL
ASEM 485 INTA	2000	Procumbent	2	145	Runner	H + S
ASEM 505 INTA	2004	Procumbent	2	145	Runner	H + S

[a] Days to achieve 40% of pods with endocarp coloration.
[b] PL = pure line selection, H + S = hybridization followed by selection, and I + S = irradiation followed by selection.

estimated as crop growth per seed during that period (Ruget, 1993), and computed as the quotient of total biomass production between R5 and R8, and final seed numbers. Final seed weight may be: (i) larger than SSR_{SF}, which is indicative of reserve use for accomplishing seed growth demand; (ii) smaller than SSR_{SF}, indicative of assimilate production in excess of seed demand; or (iii) similar to SSR_{SF}, which suggests an equivalence between assimilate production and seed demand.

The numeric determinants of final seed number (flowers per plant, pods per plant and seeds per pod) were evaluated in Exp3 and Exp4 (i.e. potential values at low stand density). The number of flowers that had opened by 0800 h was counted daily and recorded for each plant during the growing season. Plants used for flower counts were harvested at R8; seed number per pod and pod number were assessed at this stage. A fertility index was computed as the quotient of pod number at R8 and total flower number.

2.3. Statistical analyses

Analysis of variance (ANOVA) was performed for detecting differences among cultivars for all evaluated traits, and breeding effects were estimated as the genetic gain for the attributes under study. This gain was computed as (i) the response of the attribute to the year of release (YOR) of cultivars included in the analysis (i.e. parameter *b* of the linear relationship), and (ii) mean percent genetic gain, obtained as the quotient between parameter *b* described in (i) and the mean value of all cultivars (Donmez et al., 2001). Linear models were fitted between variables by means of an optimization technique (Jandel Scientific, 1991). Significance of differences between the parameters of fitted linear models was evaluated using the *F* test (Statistix V7, 2000). To further analyze interactions between seed yield and its components, these traits were expressed in relative terms using values of cultivar Virginia 5 INTA (Table 1) as a reference.

3. Results

3.1. Breeding effects on seed yield and yield components

Differences in seed yield were detected among cultivars, which were due predominantly to the growth habit ($P < 0.0001$). Within each growth habit group, differences in seed yield ($P = 0.07$) were detected only among procumbent cultivars, and a genetic gain of 2.01 $g\,m^{-2}\,y^{-1}$ ($P = 0.033$) was computed for the 1975–2004 period (mean genetic gain of 0.43% y^{-1}). The change in growth habit that took place between 1973 and 1975 produced a mean increase of 52% in seed yield of cultivar Virginia 5 INTA with respect to cultivar Colorado Irradiado INTA. Seed yield values ranged between 246 and 505 $g\,m^{-2}$ (2.1-fold increase with respect to minimum), with means of 271 and 467 $g\,m^{-2}$ for CEGH and CPGH (Fig. 1b), respectively.

Seed number varied between 867 and 1134 seeds m^{-2} (1.3-fold increase with respect to minimum), with random fluctuations across cultivars and years (Fig. 1c) that yielded no genetic gain. On average, CEGH and CPGH set 972 and 1075 seeds m^{-2} (Fig. 1d), respectively (i.e. 10% increase of the latter with respect to the former). Cultivars of the same growth habit did not differ in number of seeds m^{-2}. Individual seed weight differed markedly between growth habits (CPGH > CEGH; $P < 0.0001$) and among CPGH ($P < 0.05$). As for seed yield, a significant genetic gain ($P = 0.026$) could be verified only among procumbent cultivars, (0.0013 g $seed^{-1}\,y^{-1}$; mean genetic gain of 0.29% y^{-1}). The change in growth habit (years 1973 and 1975) caused a mean increase of 56% in seed weight of cultivar Virginia 5 INTA with respect to cultivar Colorado Irradiado INTA. Mean seed weight was 0.276

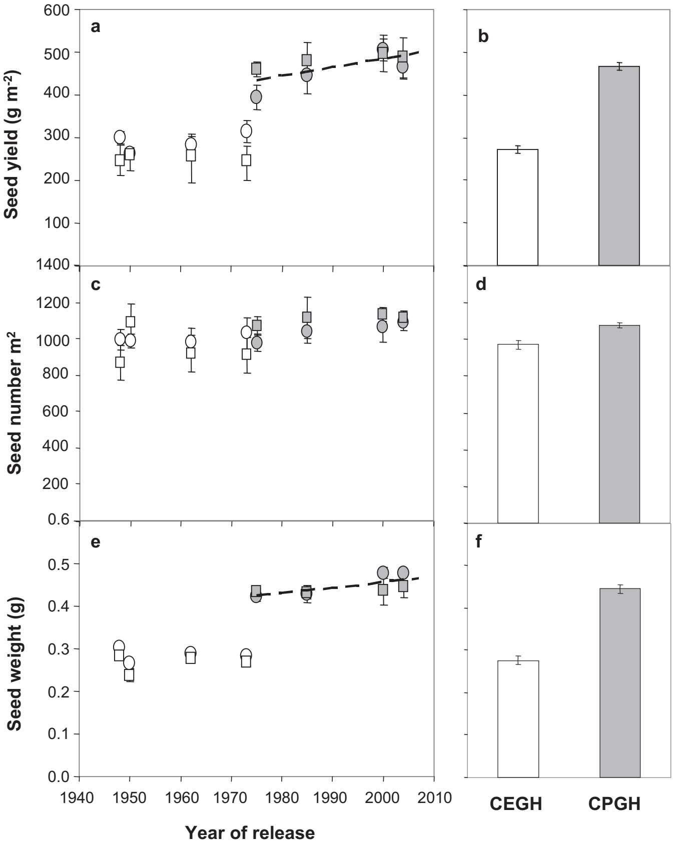

Fig. 1. Evolution of (a) seed yield, (c) seed number, and (e) seed weight of peanut cultivars released in Argentina between 1948 and 2004. Average (b) seed yield, (d) seed number, and (f) seed weight of cultivars with erect (CEGH) and procumbent (CPGH) growth habit. In (a), (c) and (e), CEGH in white symbols, and CPGH in gray symbols; Exp1 in circles, and Exp2 in squares. Each symbol represents a cultivar mean ($n = 3$). Bars are the standard error of the mean. Dashed lines represent models fitted to CPGH in (a) $Y = 2.0159X - 3544.8$, $r^2 = 0.50$, $P = 0.033$ and (e) $Y = 0.0013X - 2.0621$, $r^2 = 0.53$, $P = 0.026$.

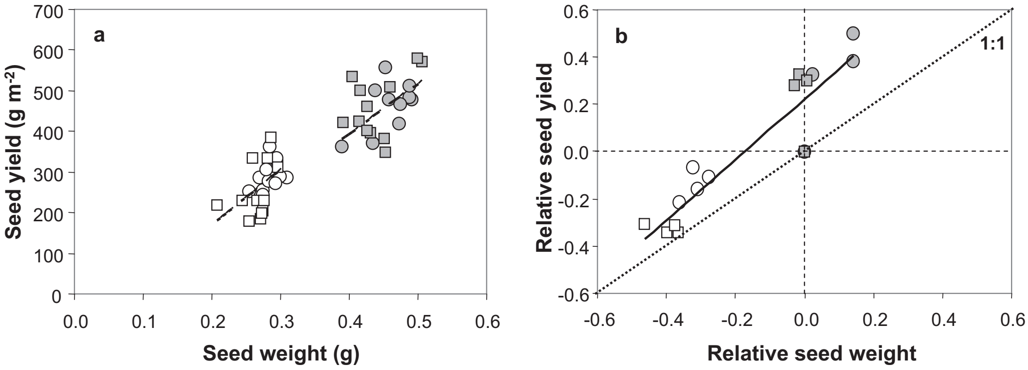

Fig. 2. Response of seed yield to seed weight in (a) absolute values, where each point represents an individual replicate, and (b) normalized dimensionless values, where each symbol represents a cultivar mean ($n = 3$). Symbols as in Fig. 1. The dashed lines in (a) represent linear models fitted to each growth habit group ($Y = -98.59 + 1341.5X$, $r^2 = 0.25$, $P = 0.009$ for CEGH; $Y = -101.04 + 1235.8\,X$, $r^2 = 0.31$, $P = 0.004$ for CPGH), and the solid line in (b) represents the linear model fitted to the whole data set ($Y = 0.2218 + 1.2808X$, $r^2 = 0.86$, $P < 0.0001$). The dotted line in (b) represents the 1:1 ratio.

and 0.445 g seed^{-1} for CEGH and CPGH (Fig. 1f), respectively (62% increase of the latter with respect to the former).

3.2. *Relationships between seed yield and its components*

Breeding had no clear effect on seed number (Fig. 1c), but seed yield was significantly ($P < 0.0001$; $r^2 \geq 0.71$) related to this yield component. Both groups (CEGH and CPGH) explored a similar range of seed numbers (between 671 and 1340 for CEGH, and between 763 and 1405 for CPGH), but parameters of fitted linear models were greater for the procumbent group (seed yield = 60.19 + 0.39 seed number m^{-2}, $r^2 = 0.71$, $P < 0.0001$) than for the erect one (seed yield = −14.78 + 0.29 seed number m^{-2}, $r^2 = 0.86$, $P < 0.0001$). This trend was indicative of a genetically greater seed weight of the former than of the latter (parameter a; $P < 0.001$), but also of a differential sensitivity of seed weight to variation in seed number (parameter b; $P = 0.095$) between growth habit types (CEGH > CPGH, i.e. opposite to parameter b).

Variation in seed weight explained 74% of the variation observed in seed yield ($P < 0.0001$; Fig. 2a), but this trend was forced by a marked clustering of data between growth habits. Seed weight values displayed by CEGH were always smaller than those explored by CPGH. Nevertheless, the relationship between seed yield and seed weight held for each group ($P \leq 0.009$), and fitted models did not differ between them ($P > 0.10$). Within each group, seed weight explained a reduced proportion of the variation in seed yield (25% for CEGH and 31% for CPGH). To assess the magnitude of the effects of variation in seed weight on yield independently of this bias, the relationship in Fig. 2a was redrawn using a normalized scale (Fig. 2b). A single model was fitted to the whole dataset and no differential trend was observed between growth habit groups. This scale highlighted that (i) a large range of variation in seed yield (−0.35–0.50) was associated with a comparatively small variation in seed weight (−0.46–0.14), (ii) the latter was mostly attributed to the shift from the erect to the procumbent habit produced with the release of Virginia 5 INTA in 1975, and (iii) enhanced seed yield of subsequent procumbent cultivars (range between 0 and 0.50 of relative seed yield) could not be attributed to enhanced seed weight (range between 0 and 0.14 of relative seed weight).

No association between seed weight and seed number was observed (Fig. 3a), and increased seed numbers always caused an increase in seed yield (i.e. no evident trade-off between grain yield components). This trend was independent of the growth habit type, but the procumbent group explored larger seed yields (between isoquants of 400 and 500 g m^{-2}) than the erect one (between isoquants of 200 and 300 g m^{-2}). Lack of relationship between seed yield determinants remained when these variables were compared on a normalized scale (Fig. 3b).

3.3. *Numeric and physiological determinants of seed number*

The number of flowers per plant (Fig. 4a), the number of pods per plant (Fig. 4c), and the fertility index (Fig. 4e) were always affected by the growth habit (CPGH > CEGH; $P < 0.001$), and there were differences among cultivars for all these traits ($P < 0.001$). Breeding caused a significant increase ($P < 0.001$) in the number of flowers per plant (Fig. 4a), the number of pods per plant (Fig. 4c), and the fertility index (Fig. 4e). This response, however, was forced markedly by the growth habit (Fig. 4b, d and f), because only the number of flowers per plant had a uniform increase across the period under analysis (Fig. 4a). For this trait, a genetic gain

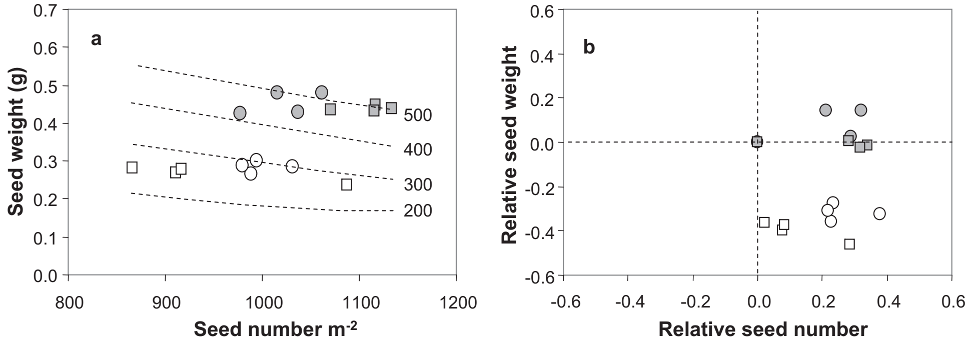

Fig. 3. Seed weight as a function of seed number (a) absolute values, where each point represents an individual replicate, and (b) normalized dimensionless values, where each symbol represents a cultivar mean ($n = 3$). Symbols as in Fig. 1. Dashed lines in (a) represent yield isoquants (g m^{-2}).

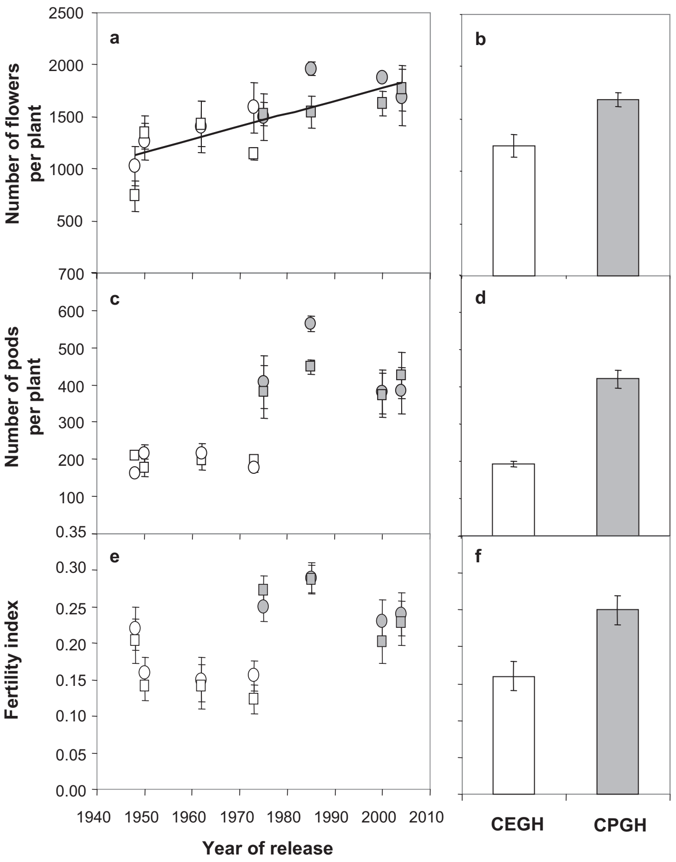

Fig. 4. Evolution of the (a) number of flowers per plant ($Y = -231 + 12.4X$, $r^2 = 0.57$, $P < 0.001$), (c) number of pods per plant, and (e) fertility index of peanut cultivars released in Argentina between 1948 and 2004, where each symbol represents a cultivar mean ($n = 5$). Average (b) number of flowers per plant, (d) number of pods per plant, and (f) fertility index of cultivars with erect (CEGH) and procumbent (CPGH) growth habit. Symbols as in Fig. 1.

of 12.4 flowers pl^{-1} y^{-1} was computed (i.e. mean genetic gain of 0.856% y^{-1}). For the other traits, the positive relationship was forced by the shift from erect to procumbent cultivars. Moreover, a within-group analysis (i.e. separately for CEGH and CPGH) revealed no clear trend for the number of pods per plant (Fig. 4c) and even a weak negative response ($r^2 \geq 0.43$, $P \leq 0.078$) for the fertility index (Fig. 4e).

There were significant differences among cultivars in the number of seeds per pod ($P < 0.0001$) but no breeding effect could be established (data not shown). Cultivars Blanco Santa Fe and Blanco Manfredi 68 (erect growth habit) and all procumbent cultivars had a mean of ca. 1.65 seeds pod^{-1}, whereas cultivars Colorado Manfredi and Colorado Irradiado INTA (erect growth habit) had a mean of 2.63 seeds pod^{-1}.

Seed number was significantly ($P < 0.001$) related to crop growth rate during the R3–R6.5 phase. A quadratic model gave a fit to this relationship ($r^2 = 0.55$) that was almost identical to that of a linear model ($r^2 = 0.56$), but the latter had a positive ordinate with no biological meaning (data not shown). No statistical difference was detected between independent models fitted to each growth habit group. Nevertheless, data of the procumbent type explored larger $\mathrm{CGR_{R3-R6.5}}$ values (mean $\mathrm{CGR_{R3-R6.5}} = 15.86 \pm 1.89$ g m^{-2} d^{-1}) and were predominantly above the fitted quadratic function (mean residual value = 25.3 ± 42.8 seeds m^{-2}), whereas the opposite was true for data of the erect group (mean $\mathrm{CGR_{R3-R6.5}} = 13.94 \pm 1.26$ g m^{-2} d^{-1}; mean residual value = −25.0 ± 50.8 seeds m^{-2}).

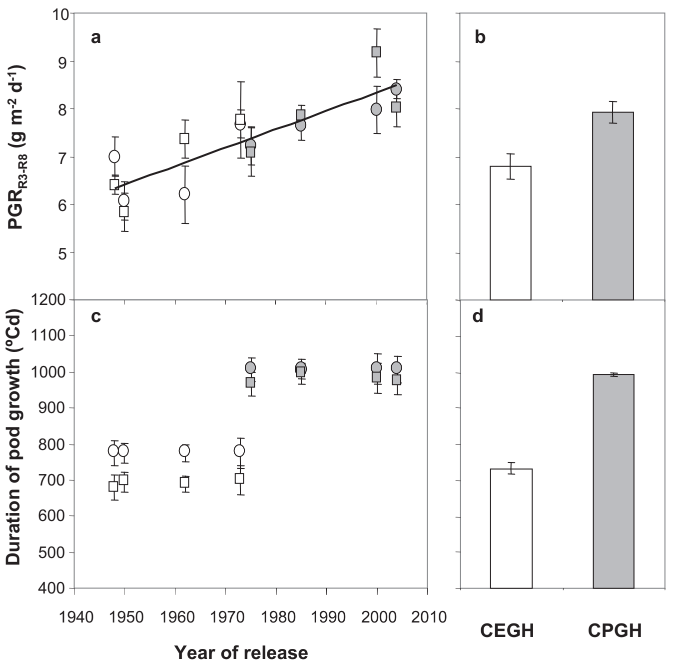

Fig. 5. Evolution of (a) pod growth rate ($Y = -68.60 + 0.0386X$, $r^2 = 0.75$, $P < 0.001$), and (c) duration of pod growth of peanut cultivars released in Argentina between 1948 and 2004, where each symbol represents a cultivar mean ($n = 3$). Average (b) pod growth rate and (d) duration of pod growth of cultivars with erect (CEGH) and procumbent (CPGH) growth habit. Symbols as in Fig. 1.

3.4. Physiological determinants of seed weight

Breeding had a clear effect ($P < 0.001$) on the main determinants of seed weight (Fig. 5). On one hand, mean values were always higher for CPGH than for CEGH (Fig. 5b and d). On the other hand, the general response pattern differed between pod growth rate (Fig. 5a) and duration of pod growth (Fig. 5c). For the former, a positive trend was estimated (mean genetic gain of 0.52% y^{-1}) with no evident effect related to growth habit. Moreover, mean values of Virgina 5 INTA (7.16 ± 0.07 g m^{-2} d^{-1}) released in 1975 were slightly smaller than those of Colorado Irradiado INTA (7.73 ± 0.04 g m^{-2} d^{-1}) released in 1973. For the latter, differences were related exclusively to the growth habit (CPGH > CEGH), because no breeding effect was detected for this trait within each group.

The response of seed weight to pod growth rate between R3 and R8 was driven by the clustering of data caused by contrasting growth habits, with the procumbent group always having higher seed weight values than the erect one (Fig. 6a). Additionally, the latter explored a PGR range between 5.8 and 7.8 g m^{-2} d^{-1}, while this range was between 7.1 and 9.2 g m^{-2} d^{-1} for the former. Similarly, there was a marked clustering of data between growth habits in the response of seed weight to the duration of pod growth (Fig. 6b). Mean duration of the pod growth period was 728 °Cd and 994 °Cd for CEGH and CPGH, respectively. This difference represented a 37% increase in this trait of the latter with respect to the former. In general, the response of seed weight to total biomass production per seed during the seed filling phase (i.e. $\mathrm{SSR_{SF}}$) indicated that biomass production per seed exceeded final seed weight (i.e. excess source for seed filling). This trend did not differ between growth habit groups (Fig. 6c).

4. Discussion

The introduction of the procumbent habit had two clear effects on peanut seed yield of Argentine varieties. One was the dramatic

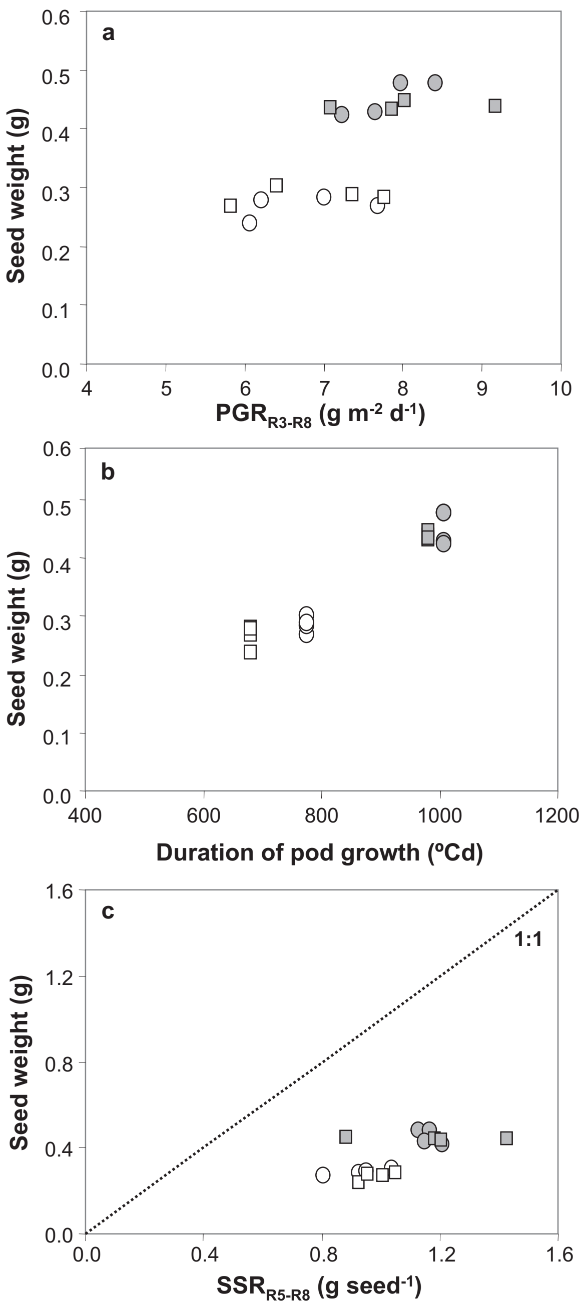

Fig. 6. Response of seed weight to (a) pod growth rate (PGR), (b) duration of pod growth, and (c) the source–sink ratio (SSR: quotient between crop growth during this phase and final seed number) between R5 and R8. The dotted line in (c) indicates the 1:1 ratio. Each symbol represents a cultivar mean ($n = 3$). Symbols as in Fig. 1.

increase in this trait (+52%) between cultivars of the same era (erect Colorado Irradiado INTA released in 1973 and procumbent Virginia 5 INTA released in 1975), which consequently cannot be attributed to a substantial change in (i) crop husbandry and biotic agents (Austin, 1993; Duvick et al., 2004), or (ii) the target population of environments that affected the genotype-by-environment interaction (De la Vega and Chapman, 2006). The second effect was an improved genetic gain, which was null for the period between 1948 and 1973 but increased at a rate of 2.01 $\text{g m}^{-2}\,\text{y}^{-1}$ since 1975. This rate is slightly higher than previous estimates for runner type Virginia cultivars in the US, which ranged between 1.47 $\text{g m}^{-2}\,\text{y}^{-1}$ for the 1944–1985 period (Mozingo et al., 1987) and 1.8 $\text{g m}^{-2}\,\text{y}^{-1}$ for the 1948–1989 period (Wells et al., 1991). Such differences may be related to the period under analysis (between the 1940s and 1980s for the US and between the 1970s and 2000s for Argentina) together with overall growing conditions and management practices (e.g. no mention to irrigation was made in previous studies and maximum seed yield never reached 5 t ha^{-1} as in current research). The latter usually modified genetic gain estimates, from maximum values under potential growing conditions to minimum ones under low-input environments (Luque et al., 2006). Interestingly, a similar trend to that found in current research for peanut can be found for soybean breeding in the US, for which the genetic gain was very low or null up to 1976 and increased at a rate of 20–30 $\text{kg ha}^{-1}\,\text{y}^{-1}$ thereafter (Specht et al., 1999).

As expected for most grain crops (Egli, 1998; Borrás et al., 2004; Gambín and Borrás, 2010), variations in seed yield were well explained by variations in seed number, but the underlying cause of this response could not be attributed to breeding effects. Both growth habit groups explored the same range of seed numbers and differed only in the ordinate of fitted linear model (i.e. in seed weight). Peanut breeding in Argentina produced no genetic gain in seed number throughout the study period, except for the 10% increase caused by the introduction of the procumbent habit. By contrast, genetic gains in seed weight followed the same trend described for seed yield: no change among erect cultivars, a drastic rise with the shift from erect to procumbent growth habit, and a modest but steady genetic gain for the latter. The described trends deserve several considerations. On one hand, the lack of genetic gain in seed yield during early peanut breeding in Argentina (1948–1973) may be indicative of a predominant breeding focus on defensive and seed quality traits, as observed for sunflower breeding up to 1995 in this country (López Pereira et al., 1999) and soybean breeding up to the 1980s in the US (Salado Navarro et al., 1993; Specht et al., 1999). On the other hand, the drastic rise in seed yield and seed yield components caused exclusively by the introduction of the procumbent habit may be indicative not only of a narrow genetic base in old erect cultivars but also of the use of management practices that did not allow for the expression of their potential seed yield. An example of such practices is the incorrect use of an invariable stand density × row width combination, which may translate into reduced ground cover and CGR with the concomitant negative effects on seed numbers (Haro et al., 2007) for genotypes with low phenotypic plasticity, a trend that cannot be compensated by increased weight of their genetically small seeds. Differences between groups in $\text{CGR}_{\text{R3–R6.5}}$ (CPGH > CEGH) support this contention, and highlight the need of further research on this topic. For instance in soybeans, a study including a reduced set of old (two varieties released between 1938 and 1948) and new (two varieties released after 2005) MG II cultivars and four stand densities (between 4.9 and 44.5 pl m^{-2}) suggested that breeding in the US enhanced radiation use efficiency more than light capture (De Bruin and Pedersen, 2009a). This trend, however, should be tested across different row spacings and maturity groups, because increased tolerance to lodging attributed to reduced plant height observed among 45 soybean cultivars of MGs 0 and 00 released in China between 1950 and 2006 suggested an improved tolerance to crowding (Jin et al., 2010).

Independently of previous considerations on possible non-genetic restrictions for improving peanut seed yield among erect Argentine varieties, introduction of large-seeded runner types had an additional benefit: enhanced market quality (and therefore price) associated with increased seed size (Mozingo et al., 1987). Interestingly, no trade-off was detected between seed number and seed weight (Fig. 3), which was confirmed by evidence of no source limitation to seed filling across all genotypes (Fig. 6c). Lack of a trade-off matched evidences from other crops, as soybeans (De Bruin and Pedersen, 2009b; Jin et al., 2010) and maize (Luque et al., 2006). This fact emphasizes the importance of boosting seed numbers for improving seed yield. Consequently, attention should be paid to its numeric (flower production, pod set, seeds produced per pod) and physiological determinants (availability of assimilates during the seed set period). The sustained increase observed in flower production was not correlated with a similar pattern in the number of pods, except for a drastic rise in the latter caused by the introduction of the procumbent habit. These trends caused an increase in the fertility index of CPGH as compared to CEGH, which was consistent with findings reported by Smith (1954). There are, however, some pending issues that deserve attention. One is the moderate negative trend of the fertility index within each growth habit group. Another one is the increase in the number of seeds per pod (3 seeds pod^{-1}) only among a few erect cultivars. These responses draw attention on the importance of preserving genotypic variation in the selection process, together with adequate phenotyping and incorporation of molecular tools for accumulation of traits of interest within elite germplasm.

Finally, while seed yield of the main cereal crops is mostly determined by resource availability (water, nitrogen, irradiance) during the seed set period (Otegui et al., 1995; Uhart and Andrade, 1995; Egli, 1998; Sinclair and Jamieson, 2006), seed yield of a legume crop like soybean also responds strongly to growing conditions during the seed-filling phase (Mathew et al., 2000; Borrás et al., 2004). As in soybean, peanut seed yield depends upon seed (Haro et al., 2007) and pod numbers (Bagnall and King, 1991), but variations in seed weight of a given genotype can also affect seed yield significantly (Hang et al., 1984). The analysis of the physiological determinants of seed weight (PGR and duration of pod growth) demonstrated that this trait was more affected by the extension of the pod growth period than by PGR, supporting previous evidence on the benefit of direct selection for the former in view of improving seed yield of different crops (Williams, 2000; Egli, 2004). For instance, late maturity soybean genotypes with long seed-filling periods had higher yield than early maturity genotypes (Liu et al., 2005). This apparent cause (seed filling duration) and effect (seed weight), however, should be taken with care, because seed filling duration is strongly dependent on the rate of water loss from the grain (Gambín et al., 2007), which depends upon maximum water content (Borrás et al., 2004; Borrás and Gambín, 2010) and consequently on a strongly genetically control trait as potential seed size (Sadras, 2007). In other words, cultivars with similar cycle duration up to the start of pod growth may differ strongly in seed filling duration depending upon their potential seed size (CPGH > CEGH). In Argentina, peanut breeders should consider prolonging the pod growth period at the expense of reducing the length of vegetative phases. This ideotype would have the advantage of exploring enhanced photothermal conditions during the critical period for seed set and avoiding negative effects associated with late seed filling during adverse fall conditions (Haro et al., 2007). The high source–sink relationships established in this work for the seed-filling phase (post R5) are indicators of an excess of assimilate availability with respect to sink size (i.e. seed number), which suggests no serious limitations to selection for (i) higher seed numbers that will reduce assimilate availability per seed, and/or (ii) enhanced seed weight for taking advantage of current available source per seed. For achieving these goals, however, future selection of peanut varieties should take into account important evidence obtained in this research regarding the response of physiological traits to the traditional selection process based on seed yield, seed quality and defensive traits. We observed (i) traits that can be bred for independently of the growth habit (e.g. flowers per plant, pod growth rate), (ii) traits in which the genetic gain is linked to growth habit with scarce variation among cultivars of the same group (e.g. pods per plant, duration of pod growth), and (iii) traits for which we detected variation between and within growth habits (e.g. seeds per pod, fertility index).

5. Conclusions

In Argentina, increased peanut yield through genetic improvement was mainly driven by enhanced seed weight and to a lesser extent by enhanced seed number. The shift from CEGH to CPGH caused a moderate 10% increase in seed number and a marked average increase in seed weight (61%), with a steady genetic gain of 0.0013 g $seed^{-1}$ y^{-1} among procumbent varieties. Observed variation in seed number was a consequence of increases in availability of assimilates during the seed set phase. At the individual plant level we detected an increase in flower production and floret fertility index, which in turn caused enhanced pod number. Regarding seed weight, increases were mainly related to the extension of the pod growth period, which was linked to the introduction of the procumbent habit in 1975. No trade-off was detected between seed number and seed weight, suggesting that both can still be enhanced with no penalty on seed yield. As a consequence, increase in yield might be achieved by selecting peanut genotypes with increased flower number, high fertility efficiency, increases in $CGR_{R3-R6.5}$, and longer duration of the pod growth period at the expense of shorter vegetative phases, such as fewer days to first flowering. In doing so, however, careful attention should be paid to the genetic architecture controlling each trait. The evidence found in this research suggests important differences among the evaluated traits that have not been taken into account up to now.

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