



# Genetic improvement of peanut in Argentina between 1948 and 2004: Light interception, biomass production and radiation use efficiency



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## ABSTRACT

An important milestone in Argentina peanut (*Arachis hypogaea* L.) breeding was the shift in the 1970s from cultivars with erect growth habit (CEGH) to cultivars with procumbent growth habit (CPGH). CPGH improved seed yield but also lengthened growth cycle. However, there is no information if the change in growth habit (GH) may have involved a phenotype with a canopy architecture that makes a differential capture and use of resources. Field experiments were performed to compute leaf area index (LAI), the fraction of incident photosynthetically active radiation intercepted by the crop (fIPAR), biomass production, radiation use efficiency (RUE) and harvest index (HI). Four cultivars of each GH, released between 1948 and 2004, were evaluated. The LAI was always larger among CPGH than among CEGH. Only the former reached the critical LAI. Likewise, fIPAR of CPGH was higher than that of CEGH throughout the crop cycle. Maximum fIPAR differed between GHs ( $P < 0.001$ ), with interannual mean values of 0.95 for CPGH and 0.77 for CEGH. Final total biomass of CPGH was 37% larger than that of CEGH. RUE values ranged between 1.88 and 2.46 g MJ<sup>-1</sup>, and differed significantly ( $P \leq 0.008$ ) between GHs (CEGH > CPGH), Years (Year 1 > Year 2) and GH × Year (CPGH Year 1 > CPGH Year 2 = CEGH Year 2 = CEGH Year 1). CPGH improved pod yield (+64%), seed yield (+101%), HI of pods (+29) and HI of seeds (+56%) respect to CEGH. Considering the effects of GH on the capacity of cultivars for achieving the critical LAI with current crop management, future research should focus on alternative sowing patterns (e.g., reduced row spacing among CEGH).

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## 1. Introduction

During most of the 20th century, peanut breeders aimed almost exclusively at developing cultivars with enhanced seed yield (Holbrook and Stalker, 2003). Consequently, selection was focused on yield per se and was conducted in trials at sites representative of the target environment, a common practice in extensive grain crops (Betran et al., 2004; Orf et al., 2004). This process produced an increase in the number of reproductive structures, reproductive efficiency (Coffelt et al., 1989; Haro et al., 2013; Seaton et al., 1992)

**Abbreviations:** CEGH, cultivars with erect growth habit; CPGH, cultivars with procumbent growth; DAS, days after sowing; fIPAR, fraction of IPAR intercepted by the crop; GH, growth habit; HI, harvest index; HI<sub>POD</sub>, HI of pods; IPAR, incident PAR; IPAR<sub>i</sub>, intercepted IPAR; LAI, leaf area index; PAR, photosynthetically active radiation; RUE, radiation use efficiency.

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and seed weight (Haro et al., 2013) of new cultivars as compared to the old ones.

Until the mid-1970s, processing and export peanut companies from Argentina required grains with high levels of oil. Farmers achieved this demand by sowing cultivars of erect growth habit (CEGH), representative of the subspecies *fastigiata*, since these cultivars were characterized by producing grains with oil levels close to 48%. These cultivars had a growth cycle of 1209–1365 °C day (ca. 120–135 calendar days), which was computed in a previous study (Haro et al., 2015) using a base temperature of 11 °C (Williams and Boote, 1995). From 1975 onwards, the demands, therefore the objectives, of the export market changed to confectionery peanut, which led breeders to focus on new cultivars with enhanced yields and seed grade. Since that moment, farmers have attempted to produce large volumes of grains. This new phase started with the release of the first CPGH (Virginia 5 INTA), representative of the subspecies *hypogaea*, with significant results in terms of yield with respect to the preceding CEGH (Haro et al., 2013). Introduction of CPGH brought an extended growth cycle

(1667–1697 °C day computed as explained above, ca. 140–145 calendar days), whereas seed oil content remained unchanged (Giandana, 2006). This lengthening of the crop cycle was 31%, comparing GHs averages (Haro et al., 2015), which was caused by an extension from R5 stage onwards (57% of increase of CPGH respect to CEGH). Prior to the R5 stage, CPGH just extended the cycle 13% compared to CEGH, which caused similar time occurrence for R5 stage between GHs. Over the last decades, the demand for improved seed yield was met via the release of CPGH, suggesting that other traits may have accompanied the increase in growth cycle for producing increased seed yields. On the one hand, change in growth habit (GH) may have involved a phenotype with a canopy architecture that makes a differential use of resources with respect to the CEGH. On the other hand, reducing crop duration in order to promote the occurrence of more floral cohorts in environments of high photothermal levels (i.e., high temperature and solar radiation) without yield penalty became the greatest challenge to Argentine peanut breeders.

In maximizing yield, the crop must maximize the acquisition and conversion of a resource into assimilates (i.e., biomass production), as well as the allocation of assimilates to economic yield (i.e., biomass partitioning). For example, when water is not a limiting factor, biomass can be expressed as the product of incident photosynthetically active radiation (IPAR) on the crop, the fraction of IPAR that is intercepted by its canopy (fIPAR) and the efficiency of conversion of radiation to the amount of assimilate partitioned to economic yield components (Charles-Edwards, 1982; Monteith, 1977). fIPAR is a function of leaf area, leaf distribution and leaf orientation relative to the sun. Under well-watered conditions, the GH (i.e., branching pattern and insertion of branches with respect to the main stem) of peanut cultivars defines a canopy architecture that affects light capture and light attenuation within the peanut crop (Boote and Loomis, 1991). Radiation use efficiency (RUE) expresses the crop mass accumulation relative to the amount of light intercepted by the leaves. When growth is not limited by other factors, the most appropriate measure of RUE is obtained by fitting a linear function to the relationship between cumulative biomass and cumulative intercepted IPAR (IPAR<sub>i</sub>). RUE is the slope of this function (Sinclair and Muchow, 1999).

Finally, peanut economic yield depends upon the allocation rate of biomass into reproductive organs, which is represented as a harvest index (HI). Matthews et al. (1988) expressed HI as a function of assimilate partitioning to pods (HI<sub>POD</sub>); this partitioning index has the greatest effect on pod yield under both well-watered conditions (Dwivedi et al., 1998) and terminal drought (Wright et al., 1991). The use of cultivars that combine the ability to intercept more IPAR, use it more efficiently and partition more assimilates to pods, should be advantageous. Accordingly, it is expected that capture and use of environmental resources as solar radiation will be different between GHs, and that those differences be enhanced under the strict crop implantation practices applied in Argentina since the release of the first cultivar, which means a single row spacing of 0.7 m and a stand density of 14 plants m<sup>-2</sup>.

There is no evidence of the trends caused by peanut breeding on resource capture and resource use efficiency. A better understanding of the differences between GHs and how these differences are related to the yield potential of both cultivar types may contribute to the selection process and future yield improvement in peanut. The objective of our study was to compare biomass production, fIPAR, RUE and partitioning of assimilates among peanut cultivars of contrasting growth habit (erect and procumbent) released in Argentina between 1948 and 2004. The present manuscript completes a broader study of the changes involved in the move from CEGH (subspecies *fastigiata*) to CPGH (subspecies *hypogaea*), with previous papers (Haro et al., 2013, 2015) focused on the effects of

differences in phenology, source/sink relationships, seed yield and its components.

## 2. Materials and methods

### 2.1. Experimental design and crop husbandry

Two field experiments were conducted during the 2010–2011 (Year 1) and 2011–2012 (Year 2) 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. A detailed description of cultivars, crop husbandry and measurements can be found in Haro et al. (2013). Briefly, eight cultivars of contrasting GH developed for this region and released between 1948 and 2004 were sown on 19–Oct-2010 (Year 1) and 01–Nov-2011 (Year 2). Seeds were hand-planted at the row spacing (0.7 m apart) and stand density (14 plants m<sup>-2</sup>) traditionally used by farmers. Treatments (cultivars) were arranged in a completely randomized block design with three replicates; plots were four rows wide and 15 m long. The soil was a silty loam Typic Haplustoll (USDA Soil Taxonomy) and experiments received drip irrigation to keep the uppermost 1 m of the soil profile near field capacity throughout the growing season. Weeds and foliar diseases were adequately controlled.

Daily values of incident global solar radiation and air temperature were obtained from a weather station (LI-COR 1200, Lincoln, NE) installed at the experimental field. Mean daily air temperature ( $T_{\text{mean}}$ ) was computed as the average between daily minimum ( $T_{\text{min}}$ ) and daily maximum ( $T_{\text{max}}$ ) temperatures. An optimum temperature ( $T_{\text{opt}}$ ) of 34 °C (Vara Prasad et al., 1999a) was used for computation of the number of days with  $T_{\text{max}} > T_{\text{opt}}$  as indicative of heat stress. Incident solar radiation was converted into IPAR by multiplying by 0.45 (Monteith, 1965).

### 2.2. Measurements

Crop phenology (Boote, 1982) was monitored on three plants tagged at R1 (first flower visible in at least 50% of the plants) per plot. fIPAR measurements and biomass sampling started at R1 in both experiments and continued fortnightly up to maturity at R8. Total biomass (roots excluded) was surveyed fortnightly between R1 and R8 (final harvest). For this purpose, plants within a 0.35 m<sup>2</sup> area of the two central rows were harvested, separated into leaves plus stems (vegetative biomass) and pods (reproductive biomass) when present, and dried at 70 °C until constant weight. Corrected total biomass (in g m<sup>-2</sup>) was calculated as vegetative biomass plus reproductive biomass multiplied by a 1.65 energy correction factor (Duncan et al., 1978). Details of these measurements were given in Haro et al. (2015). From R3 (beginning pod) onwards, the HI of pods (HI<sub>POD</sub>) was calculated as pod weight divided by total biomass weight. At R8, pods were weighed to quantify final pod and seed yields, and the HI of seeds was calculated as seed weight divided by total biomass weight. On each sampling date, leaf area was measured using an LI-3000 leaf area meter (Li-Cor, USA), and leaf area index (LAI) was calculated as the ratio of sampled leaf area to harvested ground area.

fIPAR was estimated from measurements performed above and below the green leaf portion of the canopy at intervals of ca. fifteen days, as described in Haro et al. (2015). Daily values of fIPAR were obtained by linear interpolation, and applied to daily IPAR values for obtaining daily intercepted IPAR (IPAR<sub>i</sub>). RUE (in g MJ<sup>-1</sup>) was estimated as the slope of the relationship between energy-corrected cumulative total biomass (in g m<sup>-2</sup>) and cumulative IPAR<sub>i</sub> (in MJ m<sup>-2</sup>).

Light attenuation within the canopy ( $k$ ) was estimated by means of TBLCURVE (Jandel, 1991) from the exponential function described in Eq. (1):

$$\text{fIPAR} = 1 - \exp(-k \text{LAI}) \quad (1)$$

### 2.3. Statistical analyses

Data of CEGH and CPGH were obtained from eight peanut genotypes (average of four genotypes released from 1948 to 1973 for CEGH and average of four genotypes released from 1975 to 2004 for CPGH).

GH and Year (Y) effects on response variables were evaluated using ANOVA, and significance of differences between means were determined via a  $t$  test (InfoStat V1.1). Linear and sigmoidal 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).

## 3. Results

### 3.1. Growing conditions

The crop growth took place under two environments (i.e., years) where, overall, the monthly mean temperature was higher in the Year 2 than the Year 1 (Table 1). In agreement with this trend, the number of days with  $T_{\text{max}} > 34^\circ\text{C}$  was larger in Year 2 than in Year 1 (Table 1). By contrast, solar radiation levels did not show marked differences between years (Table 1).

### 3.2. Growth habit effects on leaf area index, light capture and light attenuation

In both growing seasons, LAI was similar in both GH groups up to R1 (Fig. 1a), which occurred at approximately 50 days after sowing (DAS). From that moment up to harvest, CPGH generated significantly ( $P \leq 0.01$ ) higher LAI values than CEGH. Differences between GHs were more pronounced in Year 2 than in Year 1 (Fig. 1a). For example, LAI values at 70 DAS were 2.5 and 2.18 for CPGH and CEGH in Year 1, respectively (+15% for the former respect to the latter). In Year 2, LAI values at a similar date were 4.02 and 2.12 for CPGH and CEGH, respectively (+90%). Those differences between GHs accentuated along the cycle, noticeably in Year 2. At R5 (i.e., beginning seed formation), when extended growth cycle of CPGH is only +13% respect to CEGH (Haro et al., 2015), the LAI differed significantly between GHs (Table 2). At this stage, interannual mean values of 4.14 and 2.23 were computed for CPGH and CEGH, respectively (+85%). A significant GH  $\times$  Year non crossover interaction was detected (Table 2), such that CEGH Year 2 < CEGH Year 1 < CPGH Year 1 = CPGH Year 2. Maximum LAI differed significantly between GHs (Table 3), and values of 5.48 and 4.15 (averaged between Years) were determined for CPGH and CEGH, respectively. Interestingly, differences in maximum LAI could not be attributed predominantly to cycle duration, because both GH groups reached this value at a similar calendar date (ca. 110 DAS; Fig. 1a). CPGH attained the critical LAI (i.e., LAI required for fIPAR=0.95) on this date, and crops held it up to harvest (i.e., 40% of the cycle was under maximum light capture levels). Contrary, the critical LAI was never reached among CEGH. LAI reduction took place from ca. 120 DAS (Year 1) and 140 DAS (Year 2) onwards.

The fIPAR of CPGH was higher than that of CEGH throughout the crop cycle. Accordingly, the fIPAR at R5 stage differed significantly between GHs (Table 2), with interannual mean values of 0.78 and 0.43 for CPGH and CEGH, respectively (i.e., 81% increase of

the former with respect to the latter). A significant year effect was detected for fIPAR (Table 2), with the highest values being recorded in Year 1. This trend between years was due to the marked decrease in fIPAR observed among CEGH during Year 2 (Table 2). A significant GH  $\times$  Year non-crossover interaction was detected (Table 2), with CEGH Year 2 < CEGH Year 1 < CPGH Year 2 = CPGH Year 1. A similar ranking was also detected in maximum fIPAR (Table 3). The described difference between years was caused by the already described marked decrease in LAI (Table 3). Maximum fIPAR in Year 2 was achieved earlier among CPGH than among CEGH (100 DAS and 120 DAS, respectively), but this response was not observed in Year 1.

The exponential model of Eq. (1) gave an adequate fit to the relationship between LAI and fIPAR, but significant differences ( $P < 0.0001$ ) were detected between GH groups (Table 2). At similar LAI, CPGH reached higher fIPAR than CEGH, which yielded a larger attenuation coefficient ( $k$ , in absolute terms) among the former than among the latter (Fig. 1b). Introduction of the procumbent habit represented an increase in  $k$  of 45% (averaged across years) respect to CEGH. Collectively, enhanced LAI and  $k$  values explained the increase in maximum fIPAR (+22.7%; Table 3) registered among CPGH as compared to CEGH.

Trends described for fIPAR together with differences in total cycle duration affected the amount of cumulative IPAR intercepted by crops (IPAR<sub>i</sub>) of each GH group at final harvest. This trait reached maximum values of 1158 MJ m<sup>-2</sup> and 674.1 MJ m<sup>-2</sup> for CPGH and CEGH, respectively (Fig. 1c); i.e., a 72% increase due to the introduction of the procumbent habit. However, at the time of final harvest of CEGH (128 DAS and 140 DAS in Year 1 and Year 2, respectively), cumulative IPAR<sub>i</sub> reached values of 752.2 MJ m<sup>-2</sup> (average across years) and 518.3 MJ m<sup>-2</sup> (average across years) for CPGH and CEGH, respectively; i.e., a 45% increase of the former with respect to the latter that cannot be attributed to cycle duration.

### 3.3. Biomass production and RUE

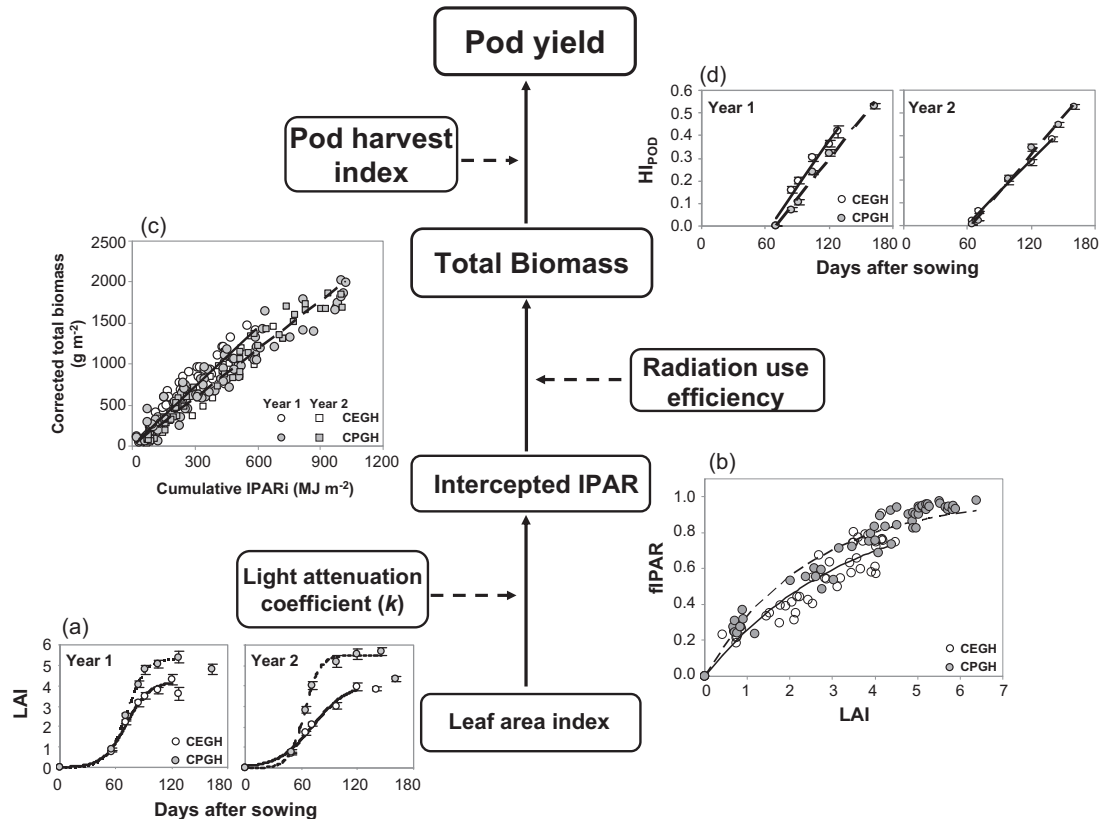
At R5 stage, total biomass differed significantly between GHs (Table 2), with interannual mean values of 522.4 g m<sup>-2</sup> and 294.9 g m<sup>-2</sup> for CPGH and CEGH, respectively (i.e., 77% increase of the former with respect to the latter). A significant year effect was detected for this trait (Table 2), with Year 1 > Year 2. This difference between years was due to a marked decrease in total biomass of the CEGH during Year 2 (Table 2). A significant GH  $\times$  Year non crossover interaction was detected (Table 2), with CEGH Year 2 < CEGH Year 1 < CPGH Year 2 = CPGH Year 1. Final harvest was performed on 134 DAS (mean between years) for CEGH and on 161 DAS (mean between years) for CPGH. At this stage, cumulative total biomass differed between GHs but not between years, and no interaction effect was detected for this trait (Table 3). Averaged across years, final total biomass of CPGH was 37% larger than that of CEGH. Additionally, there was a clear difference between GHs in the evolution of total biomass during the cycle (Fig. 2). In Year 1, no difference was detected between GHs up to 120 DAS, when CEGH reached maximum total biomass. In contrast, significant differences ( $P < 0.05$ ) were detected in this trait between both groups from 64 DAS onwards during Year 2. A similar trend was observed for pod biomass evolution during the cycle in each year (Fig. 2). In Year 2, CPGH produced greater pod biomass than CEGH throughout the growth cycle (Fig. 2b).

The relationship between corrected total biomass and cumulative IPAR<sub>i</sub> was fitted by linear equations (Fig. 1c). Slope values represented RUE, which differed significantly (Table 3) between GHs (CEGH > CPGH), Years (Year 1 > Year 2) and GH  $\times$  Year (CPGH Year 1 > CPGH Year 2 = CEGH Year 2 = CEGH Year 1; Fig. 1c). RUE was

**Table 1**  
Growing conditions.

	Temperature						Solar radiation ( $\text{MJ m}^{-2} \text{d}^{-1}$ )	
	$T_{\text{mean}}$ ( $^{\circ}\text{C}$ )		Mean $T_{\text{max}}$ ( $^{\circ}\text{C}$ )		$T_{\text{max}} > 34^{\circ}\text{C}$ (days)		Year 1	Year 2
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2		
October	18.7	–	25.8	–	–	–	21.7	–
November	21.3	22.5	28.8	29.5	3	5	22.2	22.9
December	25.0	23.3	32.3	30.5	12	6	25.3	24.4
January	24.9	25.2	31.4	32.5	5	11	23.6	25.2
February	22.0	24.4	27.1	30.2	–	6	20.9	20.6
March	20.7	22.1	27.1	28.7	–	4	18.5	18.3
April	–	22.3	–	29.9	–	2	–	16.0

$T_{\text{mean}}$ : mean daily temperature;  $T_{\text{max}}$ : maximum daily temperature.



**Fig. 1.** (a) Evolution of leaf area index (LAI) for cultivars of erect (CEGH) and procumbent (CPGH) growth habit. Each point represents the average of four cultivars and three replicates. Bars are the standard error of the mean; (b) response of the fraction of incident photosynthetically active radiation intercepted by the crop ( $f\text{IPAR}$ ) to the LAI. Solid line corresponds to CEGH ( $Y = 1 - \exp(-0.30 \times \text{LAI})$ ,  $r^2 = 0.87$ ,  $P < 0.001$ ) and dashed line to CPGH ( $Y = 1 - \exp(-0.435 \times \text{LAI})$ ,  $r^2 = 0.94$ ,  $P < 0.001$ ). Each point represents an individual plot in each year; (c) response of corrected total biomass to cumulative intercepted incident photosynthetically active radiation (IPARi). A linear equation of the type  $Y = bX$  was used, where  $b$  represents radiation use efficiency. Lines in figure represent fitted models. Due to significant GH  $\times$  Year effects, solid line corresponds to CEGH Year 1 ( $Y = 2.46X$ ,  $r^2 = 0.86$ ,  $P < 0.001$ ), and dashed line to the remaining GH  $\times$  Year combinations ( $Y = 1.95X$ ,  $r^2 = 0.94$ ,  $P < 0.001$ ). Each point represents an individual plot; (d) evolution of pod harvest index ( $\text{HI}_{\text{pod}}$ ) for CEGH and CPGH. Solid lines correspond to CEGH ( $Y = -0.44 + 0.0068X$ ,  $r^2 = 0.97$ ,  $P < 0.001$ , Year 1;  $Y = -0.27 + 0.0047X$ ,  $r^2 = 0.99$ ,  $P < 0.001$ , Year 2) and dashed lines to CPGH ( $Y = -0.41 + 0.0059X$ ,  $r^2 = 0.99$ ,  $P < 0.001$ , Year 1;  $Y = -0.35 + 0.0055X$ ,  $r^2 = 0.99$ ,  $P < 0.001$ , Year 2). Each point represents the average of four cultivars and three replicates. Bars are the standard error of the mean.

negatively and significantly ( $r^2 = 0.45$ ;  $P = 0.0065$ ) associated with  $k$  values when both GHs were considered, but no significant relationship was reported between these traits when each GH was analyzed individually. Additionally, at final harvest of CEGH (128 DAS and 140 DAS) corrected total biomass reached values of  $1455.4 \text{ g m}^{-2}$  (average across years) and  $1144.1 \text{ g m}^{-2}$  (average across years) for CPGH and CEGH, respectively (i.e., 27% increase of the former with respect to the latter).

#### 3.4. Pod yield, seed yield and HIs

Seed and pod yields were significantly higher among CPGH than among CEGH, and during Year 1 than during Year 2 (Table 2).

Pod yield was  $619 \text{ g m}^{-2}$  and  $378 \text{ g m}^{-2}$  (averaged across Years) for CPGH and CEGH, respectively (increase of 64% of the former with respect to the latter), and  $540 \text{ g m}^{-2}$  and  $457 \text{ g m}^{-2}$  (averaged across GHs) during Year 1 and Year 2, respectively (increase of 18% of the former with respect to the latter). A similar trend was observed in seed yield, with CPGH and CEGH producing  $451 \text{ g m}^{-2}$  and  $224 \text{ g m}^{-2}$  (averaged across Years), respectively (increase of 101% of the former with respect to the latter), and  $367 \text{ g m}^{-2}$  and  $308 \text{ g m}^{-2}$  for Year 1 and Year 2 (averaged between GHs), respectively (increase of 19% of the former with respect to the latter). The linear model fitted to the evolution of  $\text{HI}_{\text{pod}}$  summarized the increase in this trait over time (Fig. 1d). A significant ( $P < 0.0001$ ) Year effect was computed for slope of this model

**Table 2**  
Mean values and analysis of variance (*P*-values) of some evaluated traits at R5.

Experiment	Growth habit	LAI	fIPAR	TB (g m <sup>-2</sup> )
Year 1	Erectophyle	2.56 b	0.49 b	349.5 b
	Procumbent	4.08 a	0.78 a	519.2 a
Year 2	Erectophyle	1.89 c	0.37 c	240.2 c
	Procumbent	4.19 a	0.78 a	525.5 a
<i>Source of variation</i>				
GH		<0.0001	<0.0001	<0.0001
Y		<0.0001	0.0181	0.0339
GH × Y		0.0172	0.0317	0.0181
CV (%)		17.0	14.2	20.0

CV: coefficient of variation; fIPAR: fraction of incident photosynthetically active radiation intercepted by the crop; TB: total biomass; GH: growth habit effect; LAI: leaf area index; Y: year effect; GH × Y: interaction effect.

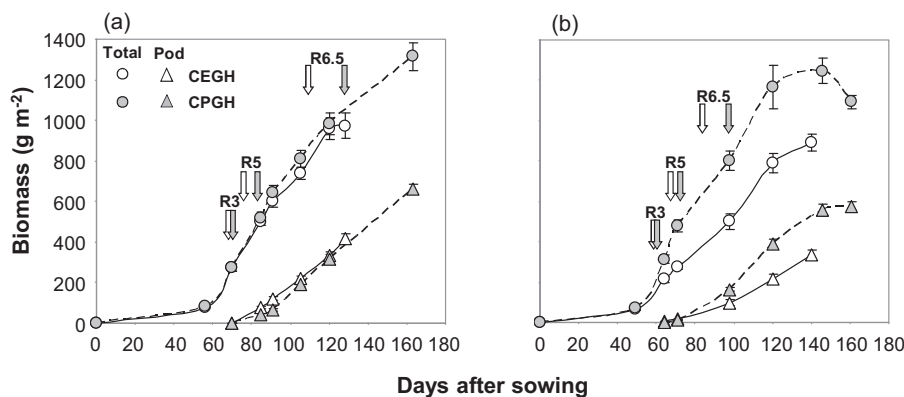
Values followed by different letters within each column indicate differences among means due to a significant ( $P < 0.05$ ) interaction effect.

**Table 3**  
Mean values and analysis of variance (*P*-values) of some evaluated traits.

Experiment	Growth habit	Maximum		<i>k</i>	RUE (g MJ <sup>-1</sup> )	Biomass			Harvest Index	
		LAI	fIPAR			Total (g m <sup>-2</sup> )	Pods (g m <sup>-2</sup> )	Seeds (g m <sup>-2</sup> )	Pods	Seeds
Year 1	Erectophyle	4.32	0.80 b	-0.31	2.46 a	973	417	252	0.42	0.27
	Procumbent	5.39	0.94 a	-0.44	1.88 b	1315	662	481	0.53	0.39
Year 2	Erectophyle	3.97	0.74 c	-0.29	1.99 b	891	338	195	0.38	0.23
	Procumbent	5.57	0.95 a	-0.43	1.97 b	1246	576	421	0.53	0.38
<i>Source of variation</i>										
GH		<0.0001	<0.0001	0.027	0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Y		NS	0.005	NS	0.008	NS	0.0006	0.005	NS	0.039
GH × Y		NS	0.006	NS	0.0001	NS	NS	NS	NS	NS
CV (%)		16.5	10.5	28.1	11.3	13.3	15.9	20.2	10.2	13.2

CV: coefficient of variation; fIPAR: fraction of incident photosynthetically active radiation intercepted by the crop; GH: growth habit effect; *k*: attenuation coefficient; LAI: leaf area index; RUE: radiation use efficiency; Y: year effect; GH × Y: interaction effect.

Values followed by different letters within each column indicate differences among means due to a significant ( $P < 0.05$ ) interaction effect.



**Fig. 2.** Evolution of cumulative total and pod biomass in (a) Year 1, and (b) Year 2. Each symbol represents the average of four cultivars and three replicates. Arrows indicate the occurrence of different R stages (Boote, 1982), gray for CPGH and white for CEGH. Bars are the standard error of the mean.

(Year 1 > Year 2), but no GH effect was detected (mean value of 0.0057 HI<sub>POD</sub> day<sup>-1</sup>). There was, however, a significant GH × Year interaction effect ( $P < 0.0001$ ), where 0.0069 HI<sub>POD</sub> day<sup>-1</sup> in CEGH Year 1 > 0.0059 HI<sub>POD</sub> day<sup>-1</sup> in CPGH Year 1 = 0.0055 HI<sub>POD</sub> day<sup>-1</sup> in CPGH Year 2 > 0.0046 HI<sub>POD</sub> day<sup>-1</sup> in CEGH Year 2. At final harvest, HI<sub>POD</sub> was significantly higher among CPGH than among CEGH (Table 2), with values of 0.53 and 0.41 (averaged between Years), respectively (increase of 29% of the former with respect to the latter). HI of seeds was significantly higher among CPGH than among CEGH (Table 2), with values of 0.39 and 0.25 (averaged between Years), respectively (increase of 56% of the former with respect to the latter). Moreover, a significant (Table 2) Year effect was computed, with Year 1 and Year 2 exhibiting HI of seeds of 0.33 and 0.31, respectively (increase of 6% of the former with respect to the latter).

#### 4. Discussion

In the present study we provided a detailed analysis of light capture and biomass production in two groups of peanut cultivars with contrasting growth habits. No trend was detected within each growth habit group for traits evaluated in current work (data not shown). A summary of all established relationships conducive to final seed yield was given in Fig. 1. Substitution of CEGH by CPGH in the mid-1970s brought an increased LAI, with the concomitant anticipated canopy closure and enhanced light interception (Gardner and Auma, 1989). This trend seemed independent of differences in cycle duration. The environments (i.e., years) did not alter the superiority in LAI of CPGH over CEGH; but those differences varied in magnitude throughout the growth cycle depending on the year (e.g., a noticeable relative reduction in LAI of CEGH

respect to CPGH in Year 2). This trend might be attributed to differential genotypic sensitivity to unusual extreme temperature events during Year 2 (Table 1) that were not registered in similar magnitude in Year 1 (Bagnall et al., 1988; Ketring, 1984), a response that deserves attention in future research.

At R5 stage, when thermal requirements are similar between GHs (Haro et al., 2015), introduction of the procumbent habit increased LAI, fIPAR and total biomass (85%, 81% and 77% respectively; Table 2). A similar response to this change was evident among traits involved in seed set and final seed numbers (yield main determinant). These traits are mainly expressed during the R3–R6.5 period (Haro et al., 2007); i.e., they are strongly affected by the pre R5 stage. During this period increases in flower number per plant, pod number per plant and fertility index (pod number/total flower number) were observed for CPGH (Haro et al., 2015). This, in turn, increased seed number (Haro et al., 2013). At final harvest of CEGH (128 DAS and 140 DAS for Year 1 and Year 2, respectively), an increase of 45% for cumulative IPAR and 27% for corrected total biomass was detected among CPGH as compared to CEGH, which could be attributed chiefly to the GH change.

Together with the aforementioned common effects of LAI on radiation interception, GH is also an additional factor that should be carefully considered in this species (Collino et al., 2001). CEGH have a branching pattern with greater insertion angles in the main stem (i.e., erectophile branches) compared to procumbent cultivars (i.e., planophile branches). At a similar LAI, this characteristic of CEGH reduces their capacity to intercept radiation, a condition reflected in their reduced  $k$  (Fig. 1b). Values of  $k$  obtained in this study were similar to those reported in the literature for peanut (Bell et al., 1992, 1994; Gardner and Auma, 1989), and the enhanced (in absolute terms)  $k$  value of CPGH indicates very rapid canopy closure and suggests poor light distribution within the canopy, which develops large amounts of excess leaf area (Bell et al., 1993). By contrast, the low (in absolute terms)  $k$  value of CEGH allowed an improved light penetration into the canopy, thus illuminating more leaf area at low IPAR intensity, thus causing canopy carbon exchange rates to increase (Kiniry et al., 2005). RUE values (Table 3) reflected mentioned effects of crop architecture on light distribution. Though figures computed for this trait (between 1.88 and 2.46 g MJ<sup>-1</sup> of IPARI; Table 3) were within the range usually indicated for this species (Kiniry et al., 2005; Sinclair and Muchow, 1998), mentioned estimates were always larger for CEGH than for CPGH. RUE was negatively associated with the coefficient  $k$ , which is in agreement with previous studies (Collino et al., 2001; Bell et al., 1993). This negative association highlights a compensation effect that may hinder the benefits of altering canopy architecture through management practices (e.g., row spacing, stand density), a response that deserves attention before adoption in breeding programs and farmers' fields (Maddoni et al., 2006).

Final crop biomass (total and pod biomass) was always higher among CPGH than among CEGH (37% and 64%, respectively; Table 3), partially as a consequence of the extended crop cycle of the former (+31%; Haro et al., 2015). Similar findings were reported by Bell et al. (1993) whom described similar biomass production between GHs at the time of final harvest of short-cycled CEGH, but a marked increase in total biomass (+47%) when CPGH were harvested. However, biomass production differences between GHs in the present research were evident during most part of the cycle in Year 2 (Fig. 2b), when the higher occurrence of extreme temperatures exposed the crops to a different scenario. Whereas biomass production evolution of CPGH was similar in both experiments (Year 1 and Year 2), a different trend was detected between years for this trait among CEGH (Year 1 > Year 2). Accordingly, previous studies showed clear evidences of biomass reduction in peanut crops growing at high temperatures (Golombek and Johansen, 1997; Ketring, 1984; Vara Prasad et al., 1999a,b, 2000b) and at low

temperatures (Bell et al., 1992, 1994). Other studies indicated the sensitivity of this species to high temperature (Greenberg et al., 1992; Wheeler et al., 1997), though whether these are associated with differences in botanical type (Vara Prasad et al., 1999a) rather than with tolerance or susceptibility per se needs to be examined (Vara Prasad et al., 2000b).

In agreement with previous studies (Craufurd et al., 2002; Hammer et al., 1995), we verified that the increase in HI<sub>POD</sub> was linear over time (Fig. 1d), and registered daily rates of HI<sub>POD</sub> were consistent with those reported for peanut in the literature (Bennett et al., 1993; Craufurd et al., 2002; Hammer et al., 1995; Stirling and Black, 1991). Final HI<sub>POD</sub> and HI of seeds were lower for CEGH than for CPGH (Table 3) due to the anticipated maturity of the former. Hence, yield improvements since the release of CPGH in 1975 have been associated with maintenance of high levels of partitioning to pods until harvest (HI<sub>POD</sub> of 0.53), due to improvements in size and activity of the source, lengthening of the crop cycle and increase in the potential seed size (Haro et al., 2013). This seed size difference between GHs cannot be overcome because of the genetically determined seed size and shorter seed filling period irrespective of the high source-sink relationships established for the seed-filling phase (post-R5) in CEGH (Haro et al., 2015). Other responses may be triggered under an environment with frequent events of above optimum temperatures (Year 2), in which cultivars must hold high stability in HI<sub>POD</sub>. Contrasting responses in HI<sub>POD</sub> under adverse temperature events should be taken into account in peanut breeding programs when searching for cultivars with adaptive capacity to climate change. Indeed, increasingly frequent temperature rises are expected and these rises may have adverse effects on reproductive processes and yield of crops in several regions of the world (Boote et al., 2005). We assume that these negative responses in CEGH observed in Year 2 would be associated with negative effects of high temperatures reported in the literature, which indicate that short or prolonged periods of high temperature during reproductive development of peanut are known to cause significant yield losses (Ketring, 1984; Vara Prasad et al., 2000b; Wheeler et al., 1997). Hammer et al. (1995) indicated a reduction of HI in the Cv Early Bunch exposed to temperatures above 28 °C. Likewise, high temperatures during pre-flowering and flowering periods significantly reduced the fruit-set in peanut (Vara Prasad et al., 1999a,b, 2000a,b, 2001) and, therefore, HI. The analysis of responses to above-optimum temperature (i.e. heat shock effects) should include the evaluation of contrasting behaviors in terms of fertility index (number of pods/number of flowers) between GHs (CPGH > CEGH), which have been previously determined for Argentine cultivars (Haro et al., 2013).

## 5. Conclusions

In the current research we demonstrated that the historical substitution of CEGH by CPGH in Argentine peanut production systems represented a marked increase in LAI, light attenuation within the canopy and fIPAR that produced a concomitant increase in cumulative IPARI, total biomass, and final HI<sub>POD</sub>. These trends, together with breeding effects on crop cycle duration (CPGH > CEGH; Haro et al., 2015) that mainly lengthen the seed-filling period (i.e., post-R5), contributed to improved pod and seed yields. Considering the effects of GH on the capacity of cultivars for achieving the critical LAI with current crop management, future research should focus on alternative sowing patterns. For instance, CEGH are expected to improve fIPAR by reducing row spacing from current 0.70 m to 0.35–0.52 m, a common practice in soybean crops grown in the same area. On the one hand, the proposed modification in the sowing pattern would bring an increase of the attenuation coefficient ( $k$ ), indicative of anticipated ground cover and the already

mentioned improved fIPAR. On the other hand, these positive effects may be partially compensated by a decrease in RUE due to the expected negative response of this trait to an enhanced *k*. In summary, the development of experiments focusing on crop architecture is critical for supporting future peanut breeding as well as management.

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