Genetic improvement of peanut in Argentina between 1948 and 2004: Links between phenology and grain yield determinants

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A B S T R A C T

In the mid 1970s, there was a shift in peanut cultivars used in Argentina, from cultivars with erect growth habit (CEGH) to those with procumbent growth habit (CPGH), which improved seed yield, but also lengthened growth cycle. However, there is no information on (i) the partitioning of thermal time (TT) requirements between vegetative and reproductive phases, as well as between reproductive sub-phases representative of the seed set and seed-filling periods, and (ii) the effect of developmental changes on growth traits. Field experiments were performed to compute TT, grain yield determinants (i.e., seed number and seed weight), and other related physiological traits. Eight cultivars released between 1948 and 2004 were evaluated. The introduction of CPGH produced a lengthening (31%) of peanut growth cycle (S–R8), which was more pronounced for the reproductive phase (+39% for R1–R8) than for the vegetative phase (+17% for S–R1). This trend held for pod-set (R3–R6.5: +37%) and seed filling (R5–R8: +57%) sub-phases. It also held (CPGH > CEGH) for the rate of flower production (+80%), total flower number (+36%) and number of pods per plant (+117%), and consequently for the fertility index (+56%). The enhanced seed number of CPGH was related to ($r^2 = 0.55$, $P < 0.001$) the variation in crop growth rate during the seed set period ($CGR_{R3–R6.5}$), but not to the duration of this period. Variations in $CGR_{R3–R6.5}$ were partially explained by differences in cumulative IPAR, which were linked to the duration of the R3–R6.5 period as well as to maximum light interception fraction. These trends may have management as well as breeding origins. Introduction of the procumbent habit enhanced seed weight (CPGH > CEGH) and seed-filling duration markedly, but had no effect on seed-filling rate. Seed weight, however, was positively related to this rate ($P < 0.01$) and exhibited a negative trend in response to the duration of the period. Lack of source limitations on seed filling suggest that future breeding efforts should focus on the increase of seed numbers and the reduction of seed filling duration.

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1. Introduction

Peanut (*Arachis hypogaea* L.) breeding in Argentina was initially based on cultivars of erect growth habit (CEGH); representative of the subpecies *fastigiata*. Grains of these cultivars met the demands of the oil industry; the main market for the species. Subsequently; changes in priorities led breeders to focus on new cultivars with enhanced yields and seed grade. As in most species for grain production; the former is commonly the primary objective of a breeding program (Evans, 1993); whereas the latter has been promoted by the peanut industry in the search of grain uniformity for direct human consumption (Holbrook and Stalker, 2003). In this context; the focus of Argentine peanut breeding during the 1970s changed toward the release of cultivars with procumbent growth habit (CPGH) of the subspecies *hypogaea* (Haro et al., 2013). An indirect trait related to these new cultivars was longer cycle than that of their predecessors. This change in crop development (i.e.; thermal time requirements for crop production) introduced in the evolution from CEGH to CPGH has been usually expressed by breeders in terms of calendar days; and represented a higher production risk due to a relatively short frost-free period in the main producing region of the country. An additional disadvantage

was the excessive development of canopies; both within and between the rows; which might contribute to the intensification of foliar and soilborne diseases (Tillman and Stalker, 2009).

Variations in thermal time (TT) requirements per se among cultivars of a given species do not imply changes in yield, except when these variations affect the physiological determinants of grain yield (e.g., crop or plant growth rates, seed set, seed growth). Such changes, therefore, may affect final grain yield depending on the ontogenic stage involved. For instance, a relative modification in the duration of pre-anthesis phases mediated by differences in photoperiod response may affect final grain number among wheat cultivars (Slafer et al., 2001), and further research demonstrated that these effects seemed mediated by changes in carbohydrate consumption that affect floret survival (Ghiglione et al., 2008). Similarly, research works in sunflower (Lopez Pereira et al., 1999), soybean (Kantolic et al., 2007) and maize (Capristo et al., 2007) crops detected that yield improvements were associated with a reduction in the pre-anthesis period and an increase in the duration of the anthesis-maturity period. In Argentine peanut genotypes, the duration of the whole growth cycle has been quantified, but there is no information on its partitioning along the cycle. Our first aim was to assess the partitioning of TT requirements between vegetative and reproductive phases, as well as between reproductive sub-phases representative of the critical windows of seed set and seed filling (Haro et al., 2008) in cultivars released in Argentina between 1948 and 2004. Our second aim was to identify the associations between these TT requirements and grain yield components (i.e., seed number and seed weight). We hypothesize that yield improvement among Argentine peanut cultivars released since 1948 has been mainly due to the lengthening of the seed set and seed weight phases, combined with mild improvements in source activity (i.e., plant and crop growth rates during these phases) partially evaluated in a previous paper (Haro et al., 2013).

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. A detailed description of cultivars, crop husbandry and measurements can be found in Haro et al. (2013). Briefly, eight cultivars of contrasting growth habit developed for this region and released between 1948 and 2004 were sown on November 10 (Exp1), October 19 (Exp2), November 10 (Exp3) and November 1 (Exp4). This number of genotypes provided 90% coverage of farmer-adopted cultivars over the last 50 years (Haro et al., 2013). Exp1 and Exp2 were aimed at understanding breeding effects at the crop level; for this purpose, seeds were hand-planted at the row spacing (0.7 m apart) and stand density (14 plants m^{-2}) traditionally used by farmers. In these experiments, treatments (cultivars) were arranged in a completely randomized block design with three replicates; plots were four rows wide and 15 m long. Exp3 and Exp4 were performed to analyze traits at the individual plant level; plants were grown with almost no interference among them (ca. 1.5 m between individuals) and treatments were arranged in a completely randomized block design with five replicates (i.e., each experimental unit had one plant). 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 mean air temperature were obtained from a weather station (LI-COR 1200, Lincoln, NE) installed at the experimental field. Solar radiation was converted into photosynthetically active radiation (PAR) by multiplying by 0.45 (Monteith, 1965), and accumulated TT was computed using mean daily air temperatures and a base temperature of 11 °C (Williams and Boote, 1995), from sowing (S) onwards.

2.2. Measurements

In Exp1 and Exp2, crop phenology (Boote, 1982) was observed on three plants tagged at R1 (first flower visible in at least 50% of the plants) in each plot. Light interception measurements and biomass sampling started at beginning pod (R3) and continued fortnightly. Light interception was assessed in each plot from 10 PAR measurements above the canopy (IPAR$_a$) and 10 PAR measurements immediately below the lowest green leaves (IPAR$_b$). Measurements were taken with a line-quantum sensor (AccuPAR radiometer; Decagon Devices, Inc., Pullman, WA) at between 1100 and 1400 h on clear days. For IPAR$_b$ measurements, the sensor was fitted diagonally between the centers of two consecutive inter-row spaces. Fraction of IPAR (fIPAR) was computed as in the following equation:

$$fIPAR = 1 - \left(\frac{IPAR_b}{IPAR_a} \right) \tag{1}$$

Values of fIPAR obtained with spot measurements performed at solar noon were adjusted for the diurnal variation in fIPAR using the relationship derived by Muchow (1985), which was previously applied in works on peanut (Bell et al., 1992; Haro et al., 2007). This correction was made to avoid the underestimation of IPAR computations at early stages of crop growth (Kemanian et al., 2004).

Shoot biomass was surveyed fortnightly between R1 and R8 (final harvest). For this purpose, plants within a 0.35 m^2 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. Crop growth rate (CGR, in g m^{-2} d^{-1}) was estimated by linear interpolation for different periods along the cycle. At R8, total number of pods with seeds and total seed number were counted manually, and seeds were weighed for seed yield determination. The R8 stage was reached when 40% of the pods displayed a maturity darkening of the endocarp (Miller and Burns, 1971). Seed weight was computed as the quotient between seed yield and seed number. Seed filling rate (in mg °C d^{-1}) during active seed filling was estimated as the quotient between final seed weight and the TT between R5 (beginning seed growth) and R8.

In Exp3 and Exp4, the numerical determinants of final seed number (flowers per plant, pods per plant and seeds per pod) were evaluated. The number of flowers per plant was surveyed daily between R1 and R8 (newly produced peanut flowers senesce in less than 24 h, and consequently do not cause a bias in successive counts), and a cumulative value computed during the same period. A trilinear with plateau model was fitted to the cumulative data (Eqs. (2)–(4)), which distinguishes three phases of flower production: (i) an early one at low rate (lag phase), (ii) a second one at maximum rate (phase of active flower production), and (iii) a third one where maximum flower number is reached and the rate is null.

$$\text{Total flower number} = a \times X, \quad \text{for} \quad X < b \tag{2}$$

$$\text{Total flower number} = (a \times b) + (c \times (X - b)), \quad \text{for} \quad d > X \geq b \tag{3}$$

$$\text{Total flower number} = (a \times b) + (c \times (d - b)), \quad \text{for} \quad X \geq d \tag{4}$$

where (i) b and d represent the start and end of the period of active flower production (in days after sowing), respectively, (ii) $(d - b)$ represents the duration of the period of active flower production (in days), and (iii) a (lag phase) and c (active phase) represent the daily rate of flower production (in flowers d^{-1}).