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Peg viability and pod set in peanut: Response to impaired pegging and water deficit

Ricardo Javier Haro[a,*], Anita Mantese[b], María Elena Otegui[c]

[a] Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Manfredi, Argentina
[b] Departamento de Recursos Naturales y Ambiente, Facultad de Agronomía, Universidad de Buenos Aires, Argentina
[c] Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura del Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Facultad de Agronomía, Universidad de Buenos Aires, Argentina

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ABSTRACT

Fertilized peanut (*Arachis hypogaea* L.) ovaries develop into aerial gynophores known as *pegs*, which are supposed to endure delayed penetration into the soil (*pegging*) caused by increased surface soil strength promoted by drought. There is no information, however, on the pattern of decay in peg viability in response to impaired pegging duration, which may affect seed yield severely. Two peanut cultivars (Florman and ASEM) were grown in pots under two contrasting water availability levels (WA) imposed at the R2 growth stage (start of peg formation). Pegs of ca. 5 mm were tagged at this stage, and WA extended for 10 different periods (between 7 and 41 days) of restriction to pegging (RP_n). Tagged pegs were used for analysis of histological changes and pod set evaluation. Reduced WA caused a significant ($P \leq 0.001$) decrease in peg viability and pod set, but no negative effect was detected on these traits for at least 11 days of treatment. The extent of maximum peg viability (*stage 1*) was shorter for water deficit (11 days of RP) than for well-watered plants (15 days of RP), and was followed by a phase of linear decrease (maximum rate between −0.056 and −0.073 $days^{-1}$) in peg viability (*stage 2*). The latter finished at ca. 33 days of RP, with permanent loss in peg viability (*stage 3*). Tissue deterioration began at the start of *stage 2*, until complete atrophy was reached at the start of *stage 3*. This trend proceeded faster for water-deficit pots and cultivar Florman.

Introduction

Peanut (*Arachis hypogaea* L.) is a legume species of the Fabaceae family with a distinctive trait among seed crops: it has aerial flowers and subterranean fruits. After pollination, fertilized ovaries of above-ground flowers develop into gynophores, commonly known as *pegs*. The peg is a positively geotropic stalk-like structure, where the cells which elongate comprise the basal tissue of the ovary itself (Coolbear, 1994); embryos are located at the opposite (distal) extreme (Brennan, 1969; Jacobs, 1947). Proembryo development is essential for initiating geotropic peg elongation, because it controls the production of required hormones and meristem activity at the base of the ovary (Brennan, 1969; Jacobs, 1947; Periasamy and Sampoornam, 1984). Pegs force their way through the uppermost soil layer (Badami, 1935). This process, known as *pegging*, is shared with only two other species (*Trifolium subterraneum* L. and *Vigna subterranea* (L.) Verdc), and starts when pegs have a length of 3–4 mm (Amoroso and Amoroso, 1988; Ziv, 1981). Pod growth begins after peg penetration through the soil (Coolbear, 1994; Periasamy and Sampoornam, 1984; Smith, 1950).

Eighty percent of global peanut production takes place in environments prone to water deficit during the crop cycle (Wright and Nageswara Rao, 1994). Consequently, drought is considered the uttermost limiting factor to peanut seed yield (Gibbons, 1980). When water deficit takes place during pegging, reductions in seed yield are mostly linked to decreased pod set, and to a less extent to decreased seed weight (Boote et al., 1976; Haro et al., 2008; Ono et al., 1974; Pallas et al., 1979; Skelton and Shear, 1971; Wright, 1989). This response is due to the direct effects of water deficit on plant growth (Haro et al., 2010) but also to indirect effects linked to topmost soil strength on pegging (Underwood et al., 1971). Lack of rainfall during this stage promotes increased surface soil strength, which impairs pegging and represents an additional factor limiting pod set and final seed numbers (Haro et al., 2008). Mentioned research on the effects of drought, however, did not include the analysis of pod reproductive capacity (i.e., set) in response to impaired pegging.

Pegs that started elongation before or during drought arrest their growth due to the restriction imposed by increased soil strength (Chapman et al., 1993), and many others remain above the

* Corresponding author.
E-mail address: ricardoharo@manfredi.inta.gov.ar (R.J. Haro).

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soil surface until a new rainfall event removes this limitation and allows their penetration into the soil (Haro et al., 2008). Threshold soil strength that triggers a linear increase in pegging failure was established at 2.23 MPa for soils of the peanut production region of Argentina (Haro et al., 2008), in close agreement with findings obtained under artificial soil compaction (Sivakumar and Sarma, 1986; So and Woodhead, 1987). Interestingly, a variable number of pegs resumed growth when the pegging zone was rewetted (Haro et al., 2008). This adaptive trait of peanut to intermittent droughts (Chapman, 1989) indicates that pegs are reproductive organs with the capacity of enduring moderately long limitations to pegging related to the effects water deficits, in contrast to the rapid loss in embryo viability observed in other grain-crop species like maize (Westgate and Boyer, 1986) or soybean (Liu et al., 2004). Nevertheless, there is no information on the variation of peg viability along this latent period and its maximum extent until definitive peg abortion. Similarly, no research documented the histological changes experienced by this reproductive structure. Moreover, studies on the negative effects of surface soil desiccation on pegging (Collino et al., 2001; Underwood et al., 1971), and related physiological responses (Haro et al., 2008, 2010) did not analyze alterations in peg viability, which may vary widely among crops exposed to contrasting levels of deep soil water content that modifies plant water status. Genotypic variation in final pod number among peanut crops exposed to drought and surface soil desiccation (Harris et al., 1988; Wright, 1989) may be also related to differences in peg viability, a trait that deserves attention for breeding crops adapted to the occurrence of water deficit events during pegging.

The objective of our research was to study the variation in pod set capacity among a population of pegs, obtained from plants of two peanut cultivars grown under two contrasting water regimes and exposed to different periods of impaired pegging. Histological changes were evaluated in these pegs. We hypothesized that (i) loss in peg viability would start sooner in water-deficit plants than in the well-watered ones, but all would be able to endure a period of restriction to pegging with no negative effects on seed viability, and (ii) after this 'latent' period, loss of peg viability would be related to the extent of the period of impaired pegging, but the magnitude of the decrease would be enhanced under reduced plant water status caused by water deficit. We expected to detect genotypic differences for these traits between two peanut cultivars of contrasting breeding eras (old Florman and newer ASEM), widely used in the Argentine peanut-growing area (more than 60% of it) and characterized by a distinct pod set under water deficit conditions (Haro et al., 2007, 2008).

Materials and methods

Plant material and experimental design

The experiment took place during 2005–2006 in the experimental station of the National Institute of Agricultural Technology (INTA) located at Manfredi (31°49′S, 63°46′W), Argentina. Plants of Runner type peanut cultivars Florman INTA and ASEM 485 INTA (hereafter Florman and ASEM) were grown from seed in 7850 cm^3 pots in the field. Sowing took place on 10 November, at a rate of three seeds per pot, which were thinned to one plant per pot immediately after seedling emergence. A total of 480 pots were distributed at a distance of 50 cm among them. Pots were filled with soil of the type found in the peanut growing region of Argentina (Typic Haplustoll), for which water retention curves and the relationship between soil water availability and soil strength were described in previous papers (Haro et al., 2008, 2010). Pots were kept free of weeds by manual weeding. Foliar diseases were prevented by frequent application of 125 ml ha^{-1} tebuconazole (α-[2-(4-chlorophenyl)ethyl]-α-(1,1-dimethylethyl)-1*H*-1,2,4-triazole-1-ethanol).

Table 1
Detail of treatments.

Water regime	Cultivar	Periods of restriction to pegging (days)
WW[a]	Florman	7, 11, 15, 19, 22, 26, 29, 32, 36, 41
	ASEM	7, 11, 15, 19, 22, 26, 29, 32, 36, 41
WD[a]	Florman	7, 11, 15, 19, 22, 26, 29, 32, 36, 41
	ASEM	7, 11, 15, 19, 22, 26, 29, 32, 36, 41

[a] WW: well-watered plants; WD: water-deficit plants.

Treatments (Table 1) included a combination of two cultivars (Cv), two levels of water availability (WA) and 10 periods of restriction to pegging (RP_n). The experimental design was a split plot, with WA (well watered and water deficit) in the main plot, and all Cv × RP combinations in the subplots. There were six replicates, with twelve pots per each WA × Cv × RP combination (six for peg sampling at the end of each RP period, and six for pod sampling at final harvest). Pegs were all identified on a single date (day 0). Those of approximately 5 mm were selected, which corresponded to approximately the R2 growth stage (i.e., beginning peg; Boote, 1982). At this time, plastic twist-ties were wrapped around the branch, next to the peg of interest, and a minimum of one peg was identified in each plant. On day 0, a plastic sheet was placed directly on the soil surface (i.e., immediately beneath the lowermost branches of the plant) of all pots for preventing pegging. This sheet was removed at the end of each RP period. Final harvest took place on 26 April 2006 (i.e., 167 days after sowing).

Growth conditions and measurements

The water-deficit condition was imposed on randomly selected pots. It was obtained by arresting irrigation at the beginning of each RP treatment. Plant transpirable water content (PTW) of each pot was monitored with a dielectric sensor (ECH_2O Dielectric Aquameter, Decagon Devices, Pullman, WA, USA), calibrated according to manufacturer instructions and connected to a millivolt logger (Cavadevices, Argentina). Well-watered pots were irrigated daily to keep soil water content near field capacity (i.e., at −0.03 MPa soil water potential) all along the experiment. Water content of water-deficit pots was kept between 75% and 10–15% PTW during the corresponding RP period by means of periodic irrigations. On cloudy and rainy days, water-deficit pots were protected by rain-out shelters to avoid the confounding effect of rainfall on water provision to pots. All pots were irrigated daily from the end of each RP period onwards, in order to allow pegging of surviving tagged pegs.

Canopy temperature was surveyed during treatment period by means of a Horiba IT 330 infrared thermometer (Horiba, Japan), sensitive to thermal radiation in the 6–12 μm waveband. This instrument was hand-held in such a position that the crop was viewed from both east and west directions at an oblique angle so that plants, but no soil could be seen. Temperatures were checked daily at noon using a portable blackbody standard that could be read in the nearest 0.1 °C. Canopy and air temperature differences were used to calculate cumulated stress degree day values (SDD; in °C) for each RP period using Eq. (1) (Jackson et al., 1977):

$$\mathrm{SDD} = \sum_{n=1}^{N} (T_c - T_a) \quad (1)$$

where T_c is canopy temperature (in °C) of each water regime, T_a is air temperature (in °C), and n the number of measurements. The degree of stress was considered zero when $T_c \leq T_a$.