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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 $T_c \leq T_a$.

Anatomical study and final pod number

A minimum of six pegs was collected from each pot at the end of each RP treatment, and fixed in FAA (formalin, alcohol, acetic-acid). The distal portion of pegs was embedded in paraffin, and serially cut at 10–12 μm with a Minot-type rotary microtome. Sections were stained with safranin-fast green (Johansen, 1940), and photographed with a Zeiss Axioplan (Oberkochen, Germany) optical microscope.

Plants used for the anatomical analysis of pegs were discarded when sampled at the end of each RP period, and a contiguous plant of the same treatment combination was kept for pod counting at final harvest. At this time, the whole plant plus the soil substrate were removed from the pot, and pod set from each tagged peg was determined.

Statistical analysis

Means of all response variables were computed for main factors and their interactions. Treatment effects were evaluated by ANOVA, and significance of differences between means were determined by a *t* test (InfoStat V1.1). Additionally, the simultaneous effect of WA, Cv and RP on peg viability was analyzed by means of a logistic regression, for which the generalized linear model (GLM) has a binomial component and a Logit link function (McCullagh and Nelder, 1989). For model fit, a value of one (1) was assigned to successful pod set (i.e., at least one seed present in the pod at final harvest), and zero (0) to barren pods. Variables WA and Cv were represented by a dummy variable; a value of one (1) corresponded to well-watered condition and Cv ASEM, a value of zero (0) was for water deficit and Cv Florman. Model fitted to the probability of pod set was described by Eq. (2)

$$\hat{logit}(\pi(x)) = \hat{log}\left(\frac{\pi(x)}{1-\pi(x)}\right) = 4.81 + 0.75\text{Cv} + 1.07\text{WA} - 0.25\text{RP} \quad (2)$$

where $\pi(x)$ is the probability of having a fertile pod, and $1-\pi(x)$ is the probability of having a barren pod. The probability of success ($\pi(x)$) estimated from Logit was computed as in Eq. (3):

$$\pi(x) = \frac{e(\beta_0 + \beta_1 x_1 + \beta_2 x_2)}{1 - e^{(\beta_0+\beta_1 x_1+\beta_2 x_2)}} = \frac{e(4.81 + 0.75\text{Cv} + 1.07\text{WA} - 0.25\text{RP})}{1 - e^{(4.81+0.75\text{Cv}+1.07\text{WA}-0.25\text{RP})}} \quad (3)$$

The derived function of Eq. (2) represents the rate of decline in peg viability (in days^{-1}), and its maximum negative value corresponds to 0.5 pod set.

Results

Degree of water stress

Water availability differed markedly between well-watered and water-deficit treatments (Fig. 1). Plants of the former grew permanently with at least 75% PTW. Those of the latter endured a progressive decline in PTW, which reached levels between 75 and 12% at the end of each partial re-watering event during periods of water restriction (i.e., transient stress). These differences were captured by the SDD. This index augmented with increased duration of water deficit (Fig. 2), and reached cumulated values of 7 °C for the shortest RP period and of 26.1 °C for the longest one (averaged across Cv). Water-stressed plants exhibited severe wilting symptoms (e.g. leaf folding) during these periods. No significant difference was detected between cultivars for SDD values obtained under the same water regime.

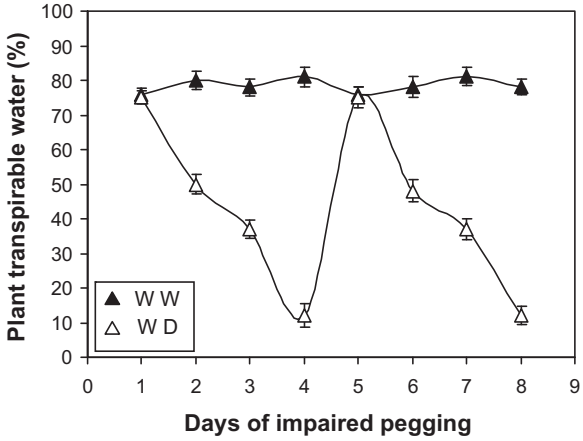

Fig. 1. Evolution of plant transpirable water (in %) in pots of well-watered (WW) and water-deficit (WD) peanut plants. The former were irrigated daily, and the latter were irrigated at 4-day intervals. Data correspond to two consecutive water-deficit cycles, and the overall dynamic is representative of all evaluated periods. Vertical bars represent the standard error of the mean ($n = 3$).

Pod set

Reduced WA and increased RP caused a significant ($P \leq 0.001$) decrease in pod set (Fig. 3), and negative effects of pegging restrictions were smaller for Cv ASEM than for Cv Florman ($P < 0.05$). Several aspects of fitted logistic models deserve attention: (i) loss of maximum peg viability (i.e., pod set = 1) started earlier in water-deficit than in well-watered plants, (ii) similarly, decrease of peg viability to pod set = 0.50 took place 5.5 days earlier among the former (21 days for ASEM and 20 days for Florman) than among the latter (27 days for ASEM and 25 days for Florman), (iii) at this stage, the estimated decrease in the rate of pod set ranged between −0.065 days^{-1} (ASEM) and −0.067 days^{-1} (Florman) for well-watered plants and between −0.056 days^{-1} (ASEM) and −0.073 days^{-1} (Florman) for water-stressed plants, and (iv) for plants of all WA × Cv treatment combinations, pod set did not differ from zero after ca. 33 days of impaired pegging. Based on these findings, three main periods were identified in pod set dynamics (Fig. 3): (i) *stage 1*, which extended for 11 (water-deficit plants) or 15 (well-watered plants) days from the start of RP treatments and did not exhibit a decline in maximum pod set, (ii) *stage 2*, which extended from the start of pod set decline (i.e., end of stage 1) until ca. 33 days of RP treatment and was characterized by a decline in peg via-

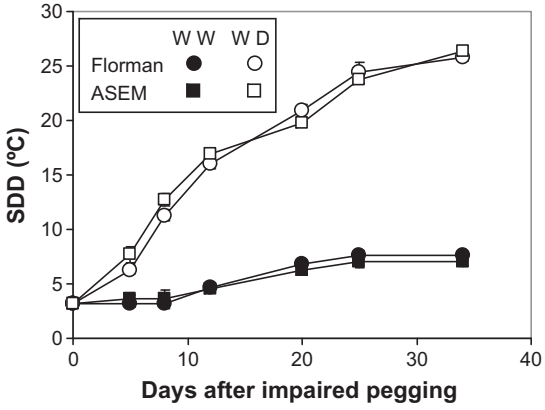

Fig. 2. Cumulative stress degree day index (SDD) of Cv Florman and Cv ASEM growing in well-watered (WW) and water-deficit (WD) conditions, obtained from the start of pegging restriction onwards. Vertical bars represent the standard error of the mean ($n = 3$).

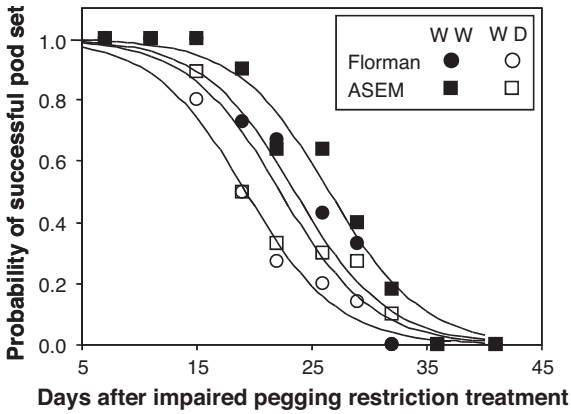

Fig. 3. Probability of successful pod set for different periods of pegging restriction in Cv Florman and Cv ASEM, growing in well-watered (WW) and water-deficit (WD) conditions.

bility, and (iii) *stage 3*, which corresponded to permanent loss of peg viability after 33 days of restricted pegging.

Combined effects of water deficit and impaired pegging on peg anatomy

Before RP periods were imposed, the anatomical structure of distal portions of pegs was the expected one for peanut crops at the R2 stage (Fig. 4). At this time pegs were constituted by (i) an external layer of epidermis cells, followed by spongy parenchymatous cells that occupied a major part of the ovary, (ii) the vascular cylinder, made of ca. 11–13 vascular bundles in radial position, with inner xylem and outer phloem, all accompanied by sclerenchyma-type fibers; a set of 2–3 layers of parenchyma cells was observed around the vascular cylinder, some of them containing tannins, (iii) periclinal divisions in the inner epidermis, (iv) two fertilized ovules and their embryo sacs in a centered-distal position of each peg, and (v) inner integument next to each embryo sac.

As the extent of the RP period increased, changes were observed in the above-described tissues and ovule development, which were accompanied by a decline in seed viability and pod set. These changes were similar under both water regimes, but began earlier in water-deficit than in well-watered plants and earlier in Cv Florman than in Cv ASEM. Observed changes were related to above-described stages of pod set (Fig. 3). Independently of water regime, ovules grew markedly during *stage 1*. The distal one was smaller than the proximal one, and the integument tended to decrease as embryo sacs grew in size. No abnormality was detected in overall layout of previously described tissues, and the general appearance matched that observed at the start of RP treatments (Fig. 4).

Slow disorganization in the arrangement of epidermis cells was detected during *stage 2*, which increased with time until this tissue died and partially disappeared (Fig. 5). A similar process was detected for parenchyma and intercalary meristem cells, except that the latter did not experience a decrease in the amount of tissue of the type observed for the rest (i.e., epidermis and parenchyma). Ovule deterioration also took place during *stage 2*. It started as loss of distal ovules and finished with loss of proximal ovules.

Finally, tissue atrophy continued until generalized death (epidermis, parenchyma, intercalary meristem, vascular bundle) occurred during *stage 3*, yielding an undifferentiated mass of cells (Fig. 6). No traces of ovules could be detected at this stage.

Discussion

Early research developed in peanut crops grown under water deficit highlighted the negative effects on pegging of uppermost soil layer drying (Allen et al., 1976; Boote et al., 1976; Matlock et al., 1961; Ono et al., 1974; Pallas et al., 1979; Underwood et al., 1971), and subsequent studies quantified the pronounced increase in aerial peg biomass when this layer reached a strength of ca. 2.23 MPa (Collino et al., 2000; Haro et al., 2008). Information, however, did not include evidence of peg life cycle from its early development until its death (i.e., abortion) or set (i.e., pods with harvestable seed). Our first important finding was the detection of three stages in the general viability pattern of pegs exposed to prolonged aerial growth, and the identification of WA and Cv effects on the quantitative descriptors of these stages (i.e. duration of maximum peg viability, rate of decline in this trait, and time to permanent loss of viability). We demonstrated that peanut pegs were able to endure a period of aerial growth with no penalty in viability even when PTW was severely reduced. The extent of this period was long (11 days) in comparison with evidence from other crops subjected to water stress during seed set. Decrease in pod survival started after a period of five days of water shortage in soybeans (Liu et al., 2004), and a similar result was obtained with a 5-day water

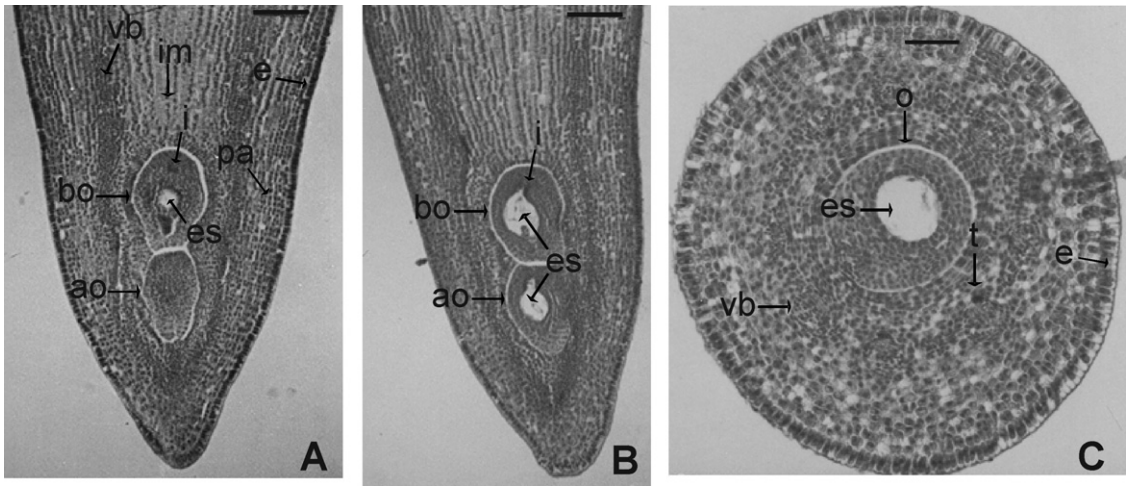

Fig. 4. Lengthwise (A and B) and transversal (C) sections of peanut pegs at time of tagging (ca. R2), representative of the period of maximum probability of seed set (*stage 1*). Figures correspond to different times along this period: the start (A) and end (B) of pegging restriction. (C) Corresponds to a typical peg along this stage. Abbreviations: ao, apical ovule; bo, basal ovule; e, epidermal cells; es, embryo sac; i, inner integument; im, intercalary meristem cells; o, ovule; pa, parenchyma cells; t, tannin cells; vb, vascular bundles. Bars in (A) and (B) = 180 μm; bars in (C) = 110 μm.

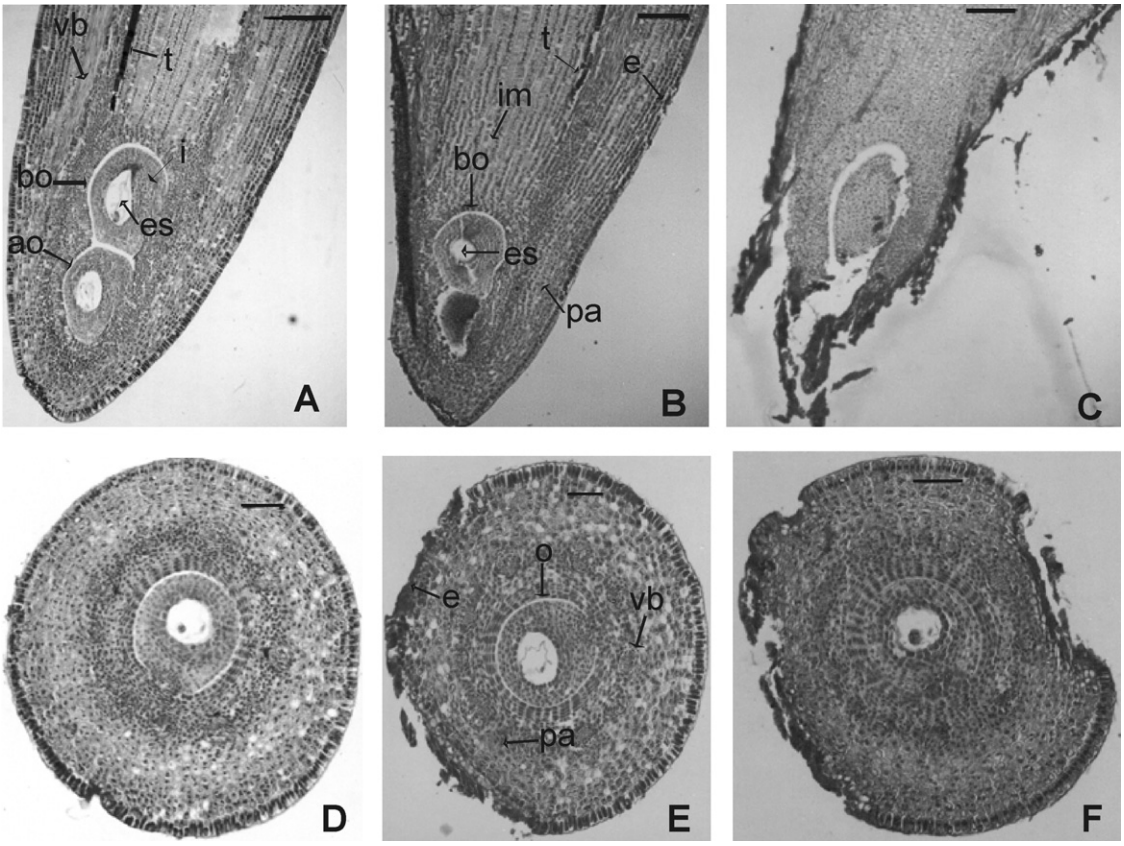

Fig. 5. Lengthwise (A–C) and transversal (D–F) sections of peanut pegs representative of the second phase of seed viability stages (*stage 2*). Figures correspond to different times along this period: the start (A and D), ca. 8 days after the start (B and E), and ca. 20 days after the start (C and F) of pegging restriction. Abbreviations: ao, apical ovule; bo, basal ovule; e, epidermal cells; es, embryo sac; i, inner integument; im, intercalary meristem ce; o, ovule; pa, parenchyma cells; t, tannins cells; vb, vascular bundles. Bars in (A), (B) and (C) = 180 μm; bars in (D), (E) and (F) = 110 μm.

deficit treatment imposed at silking in maize (Setter et al., 2001). For the latter, kernel set was particularly sensitive to water deficit even when plants were re-watered as soon as 24 h after ovary fertilization (Westgate and Boyer, 1986). Our findings recognized the peanut peg as a reproductive structure with a comparatively high resistance to water stress. This characteristic, together with peanut capacity for holding high leaf water potentials (Stirling et al., 1989) and reducing the amount of direct solar radiation by leaf folding (Matthews et al., 1988), confer this species several adaptive advantages for environments prone to water deficits, especially during pod set.

We quantified the decay in pod set associated with loss of peg viability due to variable periods of aerial growth and contrasting water regimes. This type of information is frequently available for the analysis of changes in germination capacity of mature seeds in response to storage conditions (Ellis et al., 1982; Ellis and Roberts, 1981; Fabrizius et al., 1999), but is rarely reported for seed survival during early stages of development (i.e. for the critical period of seed set). The classic approach to the analysis of the response of seed set to abiotic stress consisted in the application of a constraint (e.g. shading, water deficit) during a constant period of time (Cantagallo et al., 1997; Fischer, 1985; Fischer and Palmer, 1984), a methodology that gives no information on the variation in embryo longevity in response to stress. We determined that (i) peanut pegs held up to 50% of their reproductive capacity even after ca. 26 days of pegging restriction among well-watered plants, and (ii) this capacity declined earlier for plants subjected to water deficits characterized by a SDD index of 23.1 °C (ca. 21 days for reaching 50% reproductive capacity). Interestingly, genotypic differences were detected in the general pattern of decline in peg viability. A permanent delay was observed for Cv ASEM as compared to Cv Florman, which may be linked to the enhanced biomass partitioning to reproductive structures registered for the former in previous studies (Haro et al., 2008, 2010). These attributes, together with a more synchronous flowering pattern, may be responsible of the improved seed number and grain yield registered for Cv ASEM grown under water deficit (Haro et al., 2010).

Pegging usually takes place very fast in peanut crops growing with no water restriction (Haro et al., 2008), and ovary walls start significant growth and differentiation after peg penetration into the soil and not during aerial peg expansion (Periasamy and Sampoornam, 1984). In our research, however, distinctive aspects of peg anatomy during its aerial growth included larger size of proximal than of distal ovules. This trait can be attributed to difference in proximity to the source of assimilates between ovules, which may cause an anticipated and enhanced amount of resources for the sink closer to the source (Mena-Alí and Rocha, 2005). Our results confirmed previous findings that reported anticipated growth (1–2 days) of the proximal ovule as compared to the distal one (Patte and Mohapatra, 1987; Smith, 1956). During early growth stages, difference in ovule growth was accompanied by a similar trend in growth of embryo sacs, which nourished from starch grains located in endosperm cells placed within these sacs (Reed, 1924; Smith, 1956). Marked embryo growth during *stage 1* was accompanied by the already reported degeneration of associated endosperm cells (Periasamy and Sampoornam, 1984). Similarly, we verified the expected cell organization of epidermis, parenchyma, intercalary meristem and vascular bundle tissues, but we could not confirm presence of stomata reported in previous studies (Webb and Hansen, 1989).

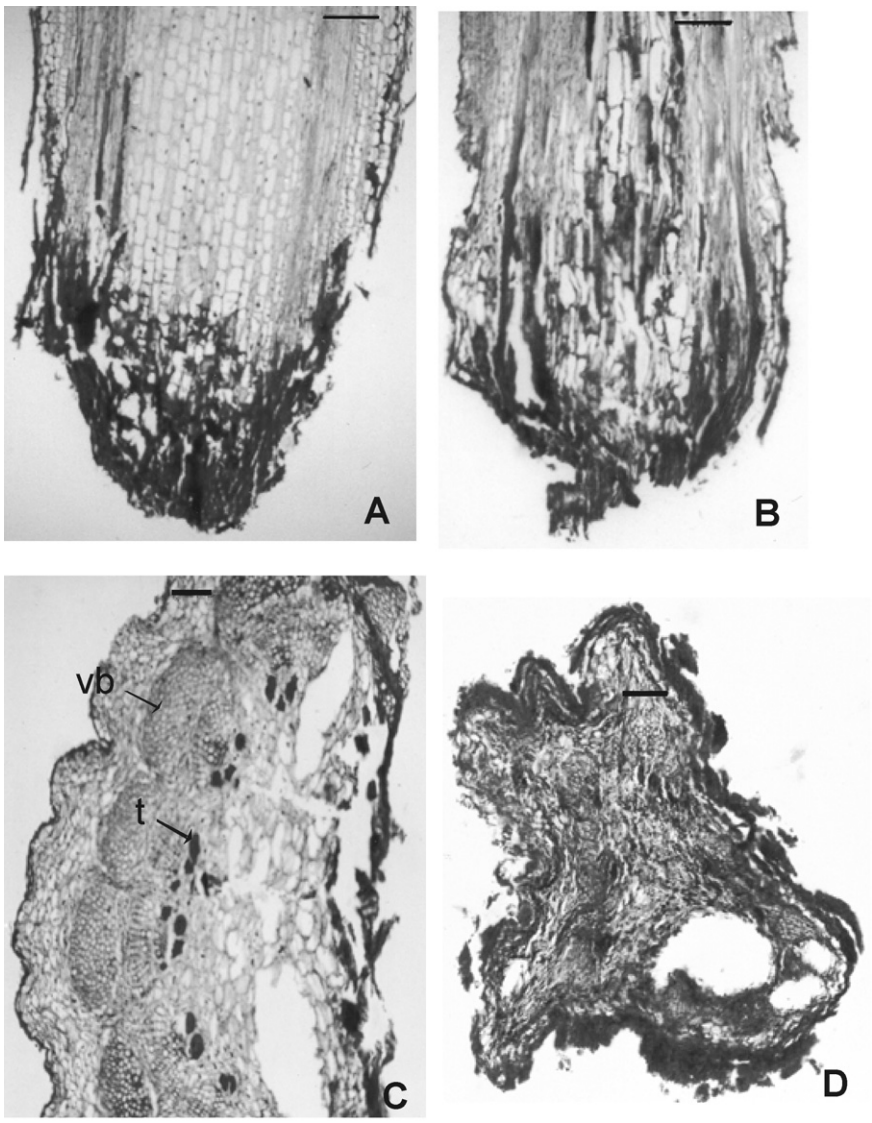

Fig. 6. Lengthwise (A and B) and transversal (C and D) sections of peanut pegs representative of the period of permanent loss of peg viability (*stage 3*). Figures correspond to different times along this period: ca. 33 days (A and C) and ca. 41 days (B and D) since the start of pegging restriction. Abbreviations: t, tannin cells; vb, vascular bundles. Bars in (A) and (B) = 180 μm; bars in (C) and (D) = 110 μm.

Peg anatomical characteristics were altered by prolonged exposure to water deficit and impaired pegging. Response to negative growing conditions started as non random ovule deterioration because the first to fail was the distal one, i.e. opposite to the above-described proximity to the source of assimilates (Mena-Alí and Rocha, 2005). The other tissues (parenchyma, epidermis, etc.) followed a similar decline, but the response was more pronounced for water-deficit than for well-watered plants, until generalized cell death (including embryo degeneration) and permanent loss of peg viability (i.e. pod set = 0) took place. This condition was met earlier for water-deficit (ca. 33 days) than for well-watered (ca. 35 days) plants.

Conclusions

Peanut pegs can preserve the reproductive capacity of their early developing embryos for longer periods than reported for other important seed crops, even when exposed to stressful environmental conditions. The decay in embryo longevity of pegs exposed to different periods of impaired pegging (a common constraint to peanut crops) and its response to water availability was quantified. Differences between cultivars were detected for this trait, which represent relevant information for interpretation of their differential pegging capacity. All these findings, combined with previous knowledge on the effects of surface soil strength on pegging capacity, will be useful for breeding purposes and for improving crop simulation models currently available for this species.

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