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ABSCISSION OF REPRODUCTIVE STRUCTURES IN PIGEONPEA (Cajanus cajan (L.) Millsp.)

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ABSTRACT

The percentage abscission of reproductive structures in dwarf pigeonpea cultivars (UW 10, UW 17 and UW 26) was found to be high (83 - 87%) and was similar to those recorded for tall indeterminate cultivars. Variations in the percentage abscission were observed for inflorescences in different regions in the canopy. These variations differed with the cultivar. Higher abscission rates were recorded for flowers developing at the most proximal node and buds at the distal ends of the inflorescence. Flowers at the anthesis and the post-anthesis stages of development abscised in greatest quantities. Forty-eight percent of the flowers which abscised at either anthesis or post-anthesis stages of development from node three on the inflorescence had at least one of their ovules fertilized. These results are discussed in relation to proposed theories of abscission: inadequate supply of photosynthates, hormonal signals, incomplete development of translocatory tissues and unsuccessful fertilization of ovules.

INTRODUCTION

The research program on pigeonpea breeding at the University of the West Indies resulted in the development of several cultivars which showed many desirable agronomic characteristics, e.g. dwarfness, ease of mechanical harvesting and shelling of pods, profuse flowering and relative daylength insensitivity. However there was little improvement in economic yield over those recorded for the traditional indeterminate cultivars.

One of the major factors suggested for the low harvest index of pigeonpea was the high percentage abscission of its reproductive structures. This phenomenon has been reported for many other legumes, e.g, Glycine max (van Shaick and Probst, 1958), Vicia faba (Gates, Smith and Boulter, 1983), Phaseolus vulgaris (Subhadrabandhu, Adams and Reicosky, 1978). Such high abscission rates were explained in the literature on the basis of (a) an inadequate supply of photosynthates e.g. (Hansen and Shibles, 1978; Wiebold, Ashley and Boerma, 1980; Subhadrabandhu et al., 1978; Sheldrake and Saxena, 1978; Clifford, 1978; Pandey and Singh, 1981; Tayo, 1981); (b) a hormonal signal (van Steveninck, 1958; Huff and Dybing, 1979; Gates et al., 1983); (c) the degree of vascularization (van Steveninck, 1957; Brun and

Betts, 1984) and (d) lack of successful fertilization (Gonzales, 1974; Abernethy et al., 1977; Rowland, Bond and Parker, 1982).

This study purports to establish a pattern of abscission for reproductive structures in pigeonpea in relation to their position in the canopy and on individual racemes and to their developmental stage. It also seeks to determine whether or not flowers which abscised at anthesis and post-anthesis stages of development had been fertilized. The results obtained are discussed with regard to the proposed theories of abscission.

MATERIAL AND METHODS

Pigeonpea plants (cv UW 10, UW 17 and UW 26) were grown in tins containing a 1:1:1 mixture of clay, sand and manure and the tins were spaced at 75 cm x 75 cm. Ten mature plants of each cultivar were selected and their branches were tagged and classified as upper, middle and lower according to their position on the main stem. Each branch was subdivided into three equal sections and the racemes on each section classified as either distal, middle or proximal (Fig. 1). Each node on a raceme was numbered, with node 1 being the most proximal (Fig. 1). At the end of the reproductive phase, the total number of scars and mature pods on each raceme of each branch was recorded. In addition, the number of scars and pods present at each node on terminal racemes of branches was scored.

In a separate experiment, five plants (cv UW 26) were placed into a netted enclosure with nets placed at the base of each plant in order to collect abscised reproductive structures. These were collected daily until the end of the reproductive phase and the numbers abscised at each stage of development were recorded. Seven stages were identified as follows:

Stage 1	- early bud
Stages 2 & 3	- developing buds
Stage 4	- fully developed bud (17 - 20 mm long) Stage of anther dehiscence
Stage 5	- Anthesis (open flower)
Stage 6	- Post anthesis; corolla beginning to wither
Stage 7	- immature pod (>1.5 cm in length)

This experiment was conducted during both the dry (March-May) and wet (Jul-Oct) seasons. An additional ten plants of cv UW 26 were used to obtain a total of 145 ovaries from abscised flowers at stages 5 and 6 of development at node 3 position on the racemes. Each flower developing in this position was tagged at stage 3 of development and was collected if it abscised at stage 5 or stage 6 of development. The ovaries were dissected out and approximately 0.25 mm tissue was excised from both ends to facilitate infiltration of chemicals during fixation. An ethanol/tertiary butanol series was used prior to embedding in paraffin wax.

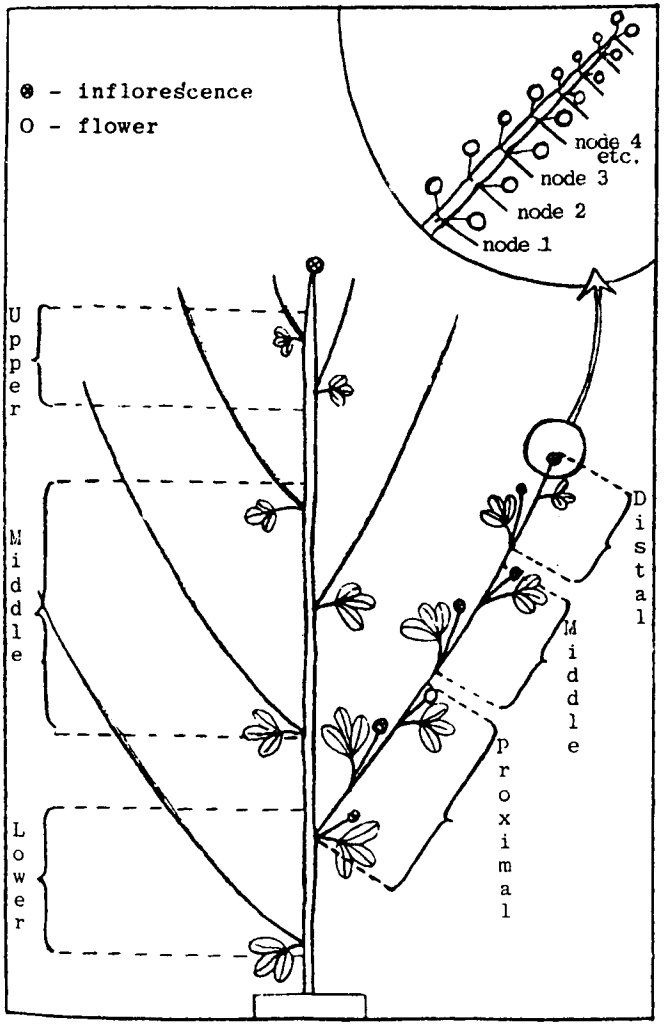

Figure 1. Diagram of pigeonpea plant showing the classification of branches (upper, middle, lower), racemes (distal, middle, proximal) and flowering nodes (starting at the proximal end of the inflorescence) as described in experiment 2.1

Longitudinal serial sections were cut at 20 um and stained using safranin and fast green (Johansen, 1940). They were examined under the microscope and ovaries containing at least one fertilized ovule were scored as fertilized. Unfertilized ovaries were those having no fertilized ovules.

RESULTS AND DISCUSSION

Data (Table 1) showed that the percentage of abscised reproductive structures for pigeonpea (cv UW 10, UW 17 and UW 26) ranged between 81 and 90 percent and were therefore as high as those recorded for other pigeonpea cultivars (Ariyanayagam, 1975; Sheldrake et al., 1978; Pandey and Singh, 1981). The data also showed that there were no significant differences in abscission from branches located at different positions in the canopy for UW 10. However in UW 17, abscission from the lower branches was significantly higher than that from the upper and middle branches, while for UW 26, the lower branches showed significantly higher abscission than the upper branches only.

Data (Table 2) showed significant differences in abscission with position of the racemes on the branches for cvs UW 10 and UW 17. In UW 10, there were significant increases from distal to middle to proximal racemes, while in UW 17, the increase is significant only at the proximal position, no such differences were observed for UW 26.

The variation in results observed for the different cultivars could be due to their genotypic differences since they were all grown under similar environmental conditions. However, the observed increase in abscission with increasing depth into the canopy could be due to decreased penetration of irradiance into the canopy as was suggested by Wiebold et al., (1980) who reported similar findings with soybeans. This would result in decreased photosynthesis and lower availability of assimilates for pod development in those regions. Although Hughes, Keatinge and Scott (1981) reported that productivity in pigeonpea was greatly influenced by the level of radiation intercepted, Edward (1976) found no significant differences in light penetration int the canopy. The quality of light reaching the reproductive structures might be of greater significance than the effect of light in photosynthesis: Myers, Brun and Brenner, (1987) found that application of supplemental red light to soybean flowers resulted in a significant increase in fruit set over the control It was observed that fewer reproductive structures were initiate in lower regions of the canopy of the three pigeonpea cultivars and one of the reasons for this might be that certain wavelength of light are required for flower initiation.

There have been several reports (James, 1984; Ariyanayagam and ames, 1986; Adu-Gyamfi, 1988) indicating the requirement fo "tripping" to achieve successful fertilization. This may be operating differentially within different regions in the canopy

Table 1. Effect of position of branch on abscission of reproductive structures of the UW10, UW17 and UW26 cultivars of pigeonpea (Cajanus cajan (L.) Millsp.).

Position of branches	UW10 Mean % abscission	UW17 Mean % abscission	UW26 Mean % abscission
Upper	$^{a}85.0$	$^{a}85.5$	$^{a}81.3$
Middle	$^{a}85.1$	$^{a}84.6$	$^{ab}83.3$
Lower	$^{a}85.2$	$^{b}90.2$	$^{b}87.1$
Degree of significance for branch levels ($p \leq 0.05$)	1.s.d. = $\pm$4.7	1.s.d. = $\pm$4.6	1.s.d. = $\pm$4.1
S.E.	$\pm$1.6	$\pm$1.5	$\pm$1.4

(Values with a letter in common within a cultivar are not significantly different)

Table 2. Effect of position of raceme on abscission of reproductive structures of the UW10, UW17 and UW26 cultivars of pigeonpea (Cajanus cajan (L.) Millsp.).

Position of racemes	UW10 Mean % abscission	UW17 Mean % abscission	UW26 Mean % abscission
Distal	$^{a}80.2$	$^{a}82.8$	$^{a}83.6$
Middle	$^{b}87.2$	$^{b}82.6$	$^{a}85.7$
Proximal	$^{c}92.3$	$^{b}90.5$	$^{a}86.2$
Degree of significance for raceme levels ($p \leq 0.05$)	1.s.d. = $\pm$3.6	1.s.d. = $\pm$4.5	1.s.d. = $\pm$5.1
S.E.	$\pm$1.2	$\pm$1.5	$\pm$1.7

(Values with a letter in common within a cultivar are not significantly different)

in that, insects are more likely to visit flowers located at distal or terminal positions. Additionally, the distribution of assimilates may also be different in different regions of the canopy. Photosynthates in leaves of the upper regions in the canopy may be directed to developing pods, while in the lower region, they may be directed to the stems for structural and storage purposes. This would be of particular significance in pigeonpea which is a perennial.

Flowers developing at the most proximal node on a raceme showed a greater tendency to abscise than those developing at nodes 2, 3 and 4 where greatest pod set was observed. (Fig. 2). This tendency to abscise continued to increase beyond node 5 and flowers initiated at and beyond node 10 did not develop beyond the early bud stage. Sheldrake and Narayan (1978) also observed that node 1 was not the position of least abscission as might have been expected from the literature. At this position, it is hardly likely that photosynthates could be limiting, neither can the abscission be accounted for by the hormonal signal theory which could account for abscission at the more distal nodes. One likely explanation is that the signal for the development of translocatory tissues to facilitate flow of assimilates to developing pods may not be synchronized until the production of later formed flowers.

Highest percentage abscission occurred at stages 5 (84%, Fig. 4) and 6 (76%, Fig. 3). Both these stages follow the stage of anther dehiscence and these results concur with the suggestion of Brun and Betts (1984) that abscission is determined at or very near the day of anthesis. The most plausible explanation for the abscission of flowers at these developmental stages would be the lack of successful pollination or fertilization. Gooding (1965) suggested that fertilization failure in pigeonpea was due to self-incompatibility. However both the application of ethyl amino caproic acid (EACA) (Adu- Gyamfi,1988), which has been reported as breaking down incompatibility systems, and outcrossing with closely related genera, (James, 1984) have resulted in only marginal increases in yield.

The result that at least 48% of abscised flowers at stages 5 and 6 of development had at least one ovule fertilized indicates that other factors may override the requirement of successful fertilization for pod set. More recent data suggested that there may be a requirement for a critical number of ovules to be fertilized before pod set can occur.

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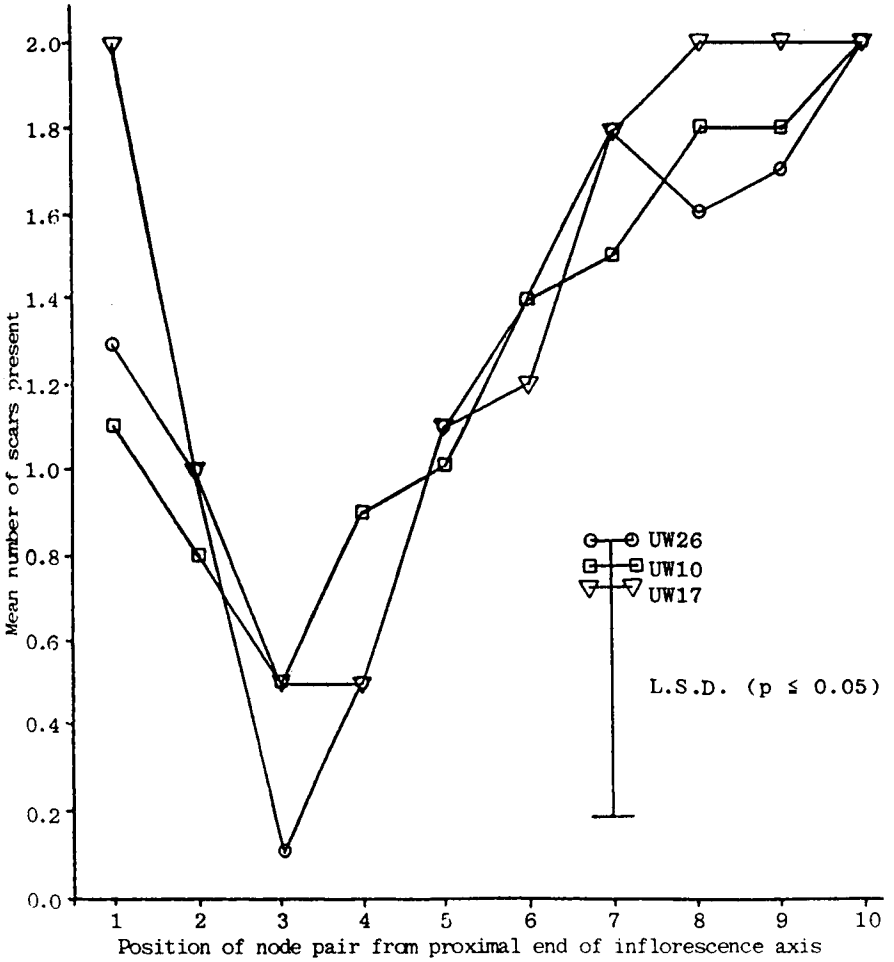
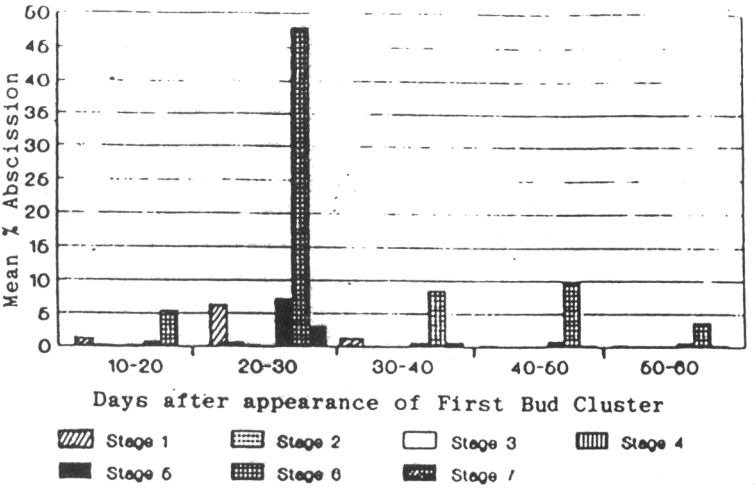
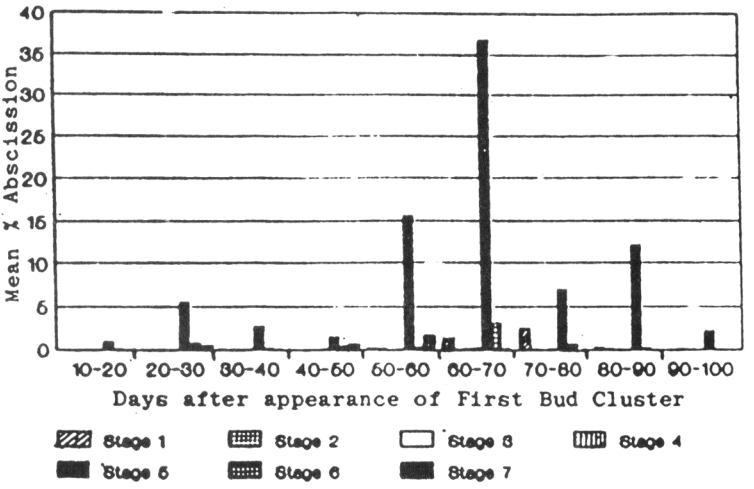


FIGURE 2: Graph showing the mean number of scars located at node pairs along the inflorescence axes of terminal racemes of the UW10 (□), UW17 (▽) and UW26 (○) cultivars of pigeonpea



$$\text{Mean \% Abscission at each stage} = \frac{\text{Mean no. of reproductive structures abscised at the particular stage}}{\text{Total no. of reproductive structure abscised at the end of the flowerir period}}$$

FIGURE 3. Percentage abscission of reproductive stag 1 - 7 of UW26 pigeonpea cultivar at 10-day periods during flowering period 1 (March - May 1987) of experiment 2.2



$$\text{Mean \% Abscission at each stage} = \frac{\text{Mean no. of reproductive structures abscised at the particular stage}}{\text{Total no. of reproductive structures abscised at the end of the flowering period}}$$

FIGURE 4 : Mean percentage abscission of reproductive stages 1 - 7 of UW26 pigeonpea cultivar at 10-day periods during flowering period 2 (July - October 1987) of experiment 2.2

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