

Comparisons of Earlier- and Later-formed Pods of Pigeonpeas (*Cajanus cajan* (L.) Millsp.)

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ABSTRACT

On branches of indeterminate cultivars of pigeonpea, flowering begins at the basal nodes and proceeds acropetally; in morphologically determinate cultivars, flowering begins on the apical racemes and proceeds basipetally. In cultivars of both types, within the racemes flowering proceeds acropetally. Under normal conditions more pods are set from earlier-formed flowers than from later-formed flowers, many of which are shed. Consequently the earlier-formed pods are found at the more basal nodes of racemes, and in indeterminate cultivars at the more basal nodes on the branches. The average weight of earlier- and later-formed pods, collected from the basal and apical nodes of the racemes or of the branches, was similar; so was the number of seeds per pod, the weight per seed and the nitrogen content of the seeds. This pattern differs from that found in most herbaceous legumes, where later-formed pods are smaller, and indicates that pigeonpeas set fewer pods than they are capable of filling. This behaviour may be related to the intrinsically perennial nature of pigeonpeas. The comparison of the weights of earlier- and later-formed pods could provide a simple screening procedure for identifying plants with an annual nature among existing cultivars or in breeders' lines.

Key words: *Cajanus cajan* (L.) Millsp., pigeonpea, pod development, seed number, seed weight, nitrogen content.

INTRODUCTION

In most legume crops the earlier-formed pods are larger than the later-formed pods and contain more and/or heavier seeds (Sinha, 1977). The simplest explanation for this phenomenon is that the filling of the later-formed pods is limited by the supply of photoassimilates or other nutrients. In such a situation seed yield may be limited by the ability of the plants to supply developing pods with nutrients, rather than by the number of pods set. On the other hand, if fewer pods than the plants were able to supply with nutrients were set, the earlier- and later-formed pods might be expected to develop to a similar extent. For these reasons, the pattern of pod-set and pod-development could shed light on the factors limiting yield in a given species or a given cultivar.

We investigated these patterns in pigeonpeas (*Cajanus cajan* (L.) Millsp.), an important pulse crop in India and other parts of the semi-arid tropics. The plants grow into woody shrubs which are intrinsically perennial, but are usually cultivated as annuals. Early-maturing cultivars are harvested 4-5 months after planting, medium cultivars after 5-7 months and late cultivars after 7-10 months. Yields are relatively low (Pathak, 1970). Generally less than 20 per cent of the dry matter produced by the plants is partitioned into seeds (Sheldrake and Narayanan, in press). The plants flower profusely, but the majority of the flowers drop off without setting pods (Howard, Howard and Khan, 1919; Mahta and Dave, 1931).

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MATERIALS AND METHODS

Observations were made on pigeonpeas grown in the field in 1974, 1975 and 1976 at ICRISAT Centre, near Hyderabad, India. The plants were grown on two soil types, a vertisol (fine clayey, calcareous, montmorillonitic, hyperthermic, family of Typic Chromustert) and alfisol (fine, clayey, mixed hyperthermic, family of oudic Rhodus-talf). In all cases the soils were fertilized with single superphosphate (at the rate of 50 kg P₂O₅ ha⁻¹) before sowing. Nitrogenous fertilizer was not supplied; the roots were well nodulated by native *Rhizobia*.

The plants were sown at the normal time, in early July, soon after the beginning of the monsoon, at the usual plant-to-plant spacings of 50 × 30 cm for the early cultivars and 75 × 30 cm for the medium and late cultivars. The cultivars were planted in randomized block designs with two replications in 1974 and 1975, and with four replications in 1976. The plot sizes were 9 × 20 m, 4 × 5 m and 9 × 10 m in the 3 years respectively. Irrigation was not supplied. During the growing season the plants were protected against insect pests by sprays of endosulfan.

For the investigation of the pattern of pod-set on the branches at least 30 well-developed, undamaged primary branches of each cultivar were collected at the time of harvest. For each cultivar the pods borne on the basal (most proximal) pod-bearing node (node 1), the second pod-bearing node (node 2), etc. were separated and the pod number, pod d. wt seed number and seed d. wt were recorded. All weights were taken after drying in an oven at 80 °C for at least 2 days.

For investigation of the pattern of pod-set within the racemes, at least 100 racemes whose pods were undamaged by insects were collected from each cultivar. In indeterminate cultivars, unless otherwise stated, these were collected from the more basal pod-bearing nodes of the branches. The pods from the basal (most proximal) node of the peduncle (node 1), the second node (node 2), etc., were separated and data were recorded as described above.

For comparisons of pods at the apical and basal nodes of the branches of indeterminate cultivars, samples of at least 100 pods were taken from each replicate plot. The cultivars were grown in randomized complete block designs with four replications.

Seeds from replicate samples were pooled and ground to a powder for analysis for nitrogen by the micro-Kjeldahl method. The results are expressed as percentages, on a d. wt basis.

RESULTS

The sequence of flowering and of pod-set

In most cultivars of pigeonpea the main stem and branches grow indeterminately during the reproductive phase; flowering begins on racemes borne at nodes at or near the base of the branches and subsequently at more apical nodes. New flowering nodes continue to develop as the branch grows (Fig. 1). Within the racemes flowering also proceeds acropetally. Under normal conditions more pods are set from earlier- than from later-formed flowers, and more pods are borne at the nodes towards the base of the branches and of the racemes

In several representative early and medium cultivars, comparison of the numbers of pods with numbers of scars on the racemes at the time of harvest revealed that only 5–20 per cent of the flowers developed into mature pods. There was some abscission of young pods, but relatively little compared with the abscission of flowers.

Some pigeonpea cultivars form racemes at the apices of the main stem and branches. These are usually described as 'determinate' cultivars (Reddy & Rao, 1974), although the individual racemes develop indeterminately. New racemes continue to be produced



FIG. 1. A primary branch of cv. ICP-1 showing flowers and developing pods. $\times 0.5$.

from axillary shoots. Consequently, the sequence in which flowering begins at the nodes of the main stem and branches of these cultivars is basipetal.

Some cultivars are intermediate between the types described above, with a condensation of nodes at the apical ends of the branches. In such cultivars flowering begins on racemes at sub-apical nodes and proceeds both acropetally and basipetally.

Pods at different nodes of the branches

In determinate cultivars, more pods developed at the apical racemes of the main stem and branches, and fewer pods at the more basal axillary racemes.

In indeterminate cultivars, more pods were formed on racemes towards the base of the branches. The seed number per pod and the weight per seed from the pods formed at the different nodes remained more or less constant. Data for cv. ICP-1 grown on two soil types are shown in Fig. 2. Very similar patterns were found in other cultivars of different duration groups; such patterns were observed in three successive years. The fluctuations in the seed number per pod and weight per seed at the more apical nodes, where there were very few fruits, resulted from the small sample size.

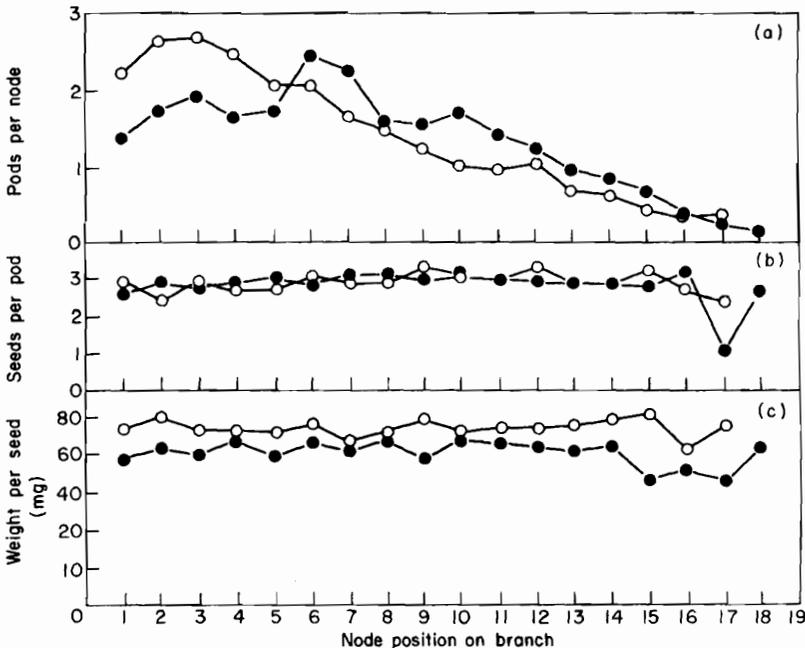


Fig. 2. (a) Number of pods per node (b), number of seeds per pod and (c) weight per seed at different node positions on primary branches of cv. ICP-1 grown on vertisol (●) and on alfisol (○) in 1975.

Pods at different nodes of the racemes

Within the racemes most of the pods were formed at the basal nodes, although in racemes from the lower parts of the branches of indeterminate cultivars there was a tendency for the maximum number of pods to be found not at the most proximal node of the inflorescence, but at the second or third nodes. Most of the flowers at the more apical nodes of the inflorescence were shed without setting fruit. This pattern is illustrated by data for cv. ICP-1 (Fig. 3); similar patterns were found in other indeterminate cultivars.

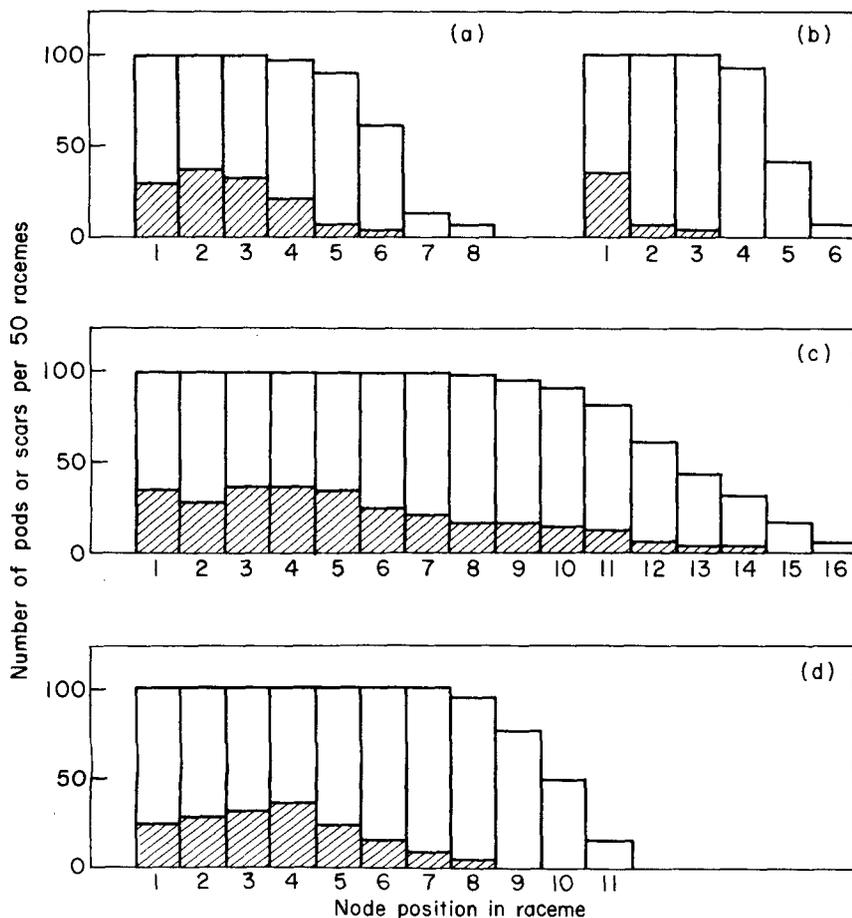


FIG. 3. Number of pods and scars at different node positions within racemes from the (a) basal and (b) apical parts of the branches of cv. ICP-1 and within (c) terminal and (d) axillary racemes of cv. Pusa ageti. □ Scars; ▨ pods.

The determinate cultivars bore fewer racemes per plant than did indeterminate cultivars of comparable duration, but generally produced similar numbers of pods because there were more pods per raceme. Flowering and pod-set continued for a longer time in the determinate cultivars; consequently the maturation of their pods was spread over a longer period than in indeterminate cultivars of comparable duration. The greater number of nodes and pods on the racemes of the determinate cv. *Pusa ageti* (Fig. 3) than in cv. ICP-1 reflect the longer period of flowering and pod development in the former cultivar.

In the racemes, as on the branches, there was little or no tendency for later-formed pods at the more apical nodes to be smaller than the earlier-formed pods at the more basal nodes. Data for early, medium and late cultivars grown on two soil types are presented in Table 1. Only in the early cv. T-21 grown on vertisol was there a distinct decline in pod weight at the more apical nodes.

The numbers of seeds per pod and the weights per seed, like the weights per pod, changed very little from node to node in the different cultivars. Overall means for the

TABLE 1. *Weight per pod (mg) at different node positions within racemes of different cultivars grown on a vertisol (V) and an alfisol (A) in 1976, and the mean weight per pod at the two most apical nodes expressed as a fraction of that at the two most basal nodes*

Cultivar	Indeterminate (I) or determinate (D)	Days to flowering	Soil	Node position within raceme							Fraction: apical two nodes basal two nodes
				1	2	3	4	5	6	7	
T-21	I	86	V	299	283	260	186	216	—	—	0.69
			A	307	281	271	267	271	—	—	0.91
<i>Pusa ageti</i>	D	89	V	307	311	302	279	278	362	—	1.03
			A	360	342	366	386	338	322	—	0.94
HY-2	I	105	V	530	525	531	532	—	—	—	1.01
			A	539	505	463	472	—	—	—	0.90
BDN-1	I	112	V	371	371	357	381	382	—	—	1.03
			A	384	387	388	384	356	386	—	0.96
AS-71-37	I	115	V	417	420	417	382	450	—	—	0.99
			A	445	425	430	418	456	—	—	1.00
ICP-6997	I	115	V	577	599	602	633	739	703	—	1.23
			A	510	596	594	753	—	—	—	1.22
ICP-1	I	116	V	389	397	402	441	—	—	—	1.07
			A	396	397	402	362	361	—	—	0.91
ICP-7065	I	147	V	287	291	293	304	296	329	267	1.03
			A	235	249	282	273	294	302	313	1.27
NP(WR)-15	I	155	V	347	344	348	350	358	339	—	1.01
			A	258	265	284	302	319	273	280	1.06
ICP-7035	I	160	V	226	248	228	268	281	275	249	1.11

TABLE 2. *Mean weight per pod, seed number per pod, and weight per seed at the first four nodes of the racemes of ten pigeonpea cultivars grown on two soil types (cultivars and soils as shown in Table 1)*

	Node position in raceme			
	1	2	3	4
Weight per pod (mg)	425	442	427	449
Seeds per pod	3.15	3.17	3.28	3.25
Weight per seed (mg)	99	95	93	95

first four nodes are shown in Table 2. In cv. T-21 grown on vertisol the lighter pods at the more apical nodes had fewer seeds which were also smaller than those at the basal nodes.

Comparisons among cultivars

The observations described so far indicate that there is little or no tendency for the weight of later-formed pods of pigeonpeas to decline relative to the earlier-formed pods. However, data for cv. T-21 (Table 1) suggest that there may be cultivaral differences in this respect. In an attempt to detect such differences, we compared pods collected from the basal racemes with pods collected from the apical racemes on the branches of indeterminate cultivars. If there were a systematic decline in the weight of later-formed pods, the average weight of the pods from the apical racemes should have been less than that of the pods from the basal racemes.

In 1975, samples were collected from 21 medium- and late-duration cultivars grown on vertisol. The average weights per pod from the apical racemes expressed as a fraction of those from the basal racemes ranged from 0.92 ± 0.03 to 1.21 ± 0.06 . The overall mean was 1.04.

In 1976 we compared the pods from apical and basal racemes of 22 cultivars (including seven of those studied in 1975), ranging in duration from extra-early to late, most of which were grown on both alfisol and vertisol. The weight per seed of these cultivars ranged from 60–190 mg. The overall mean weights per seed from the pods at upper and lower nodes were 101 and 102 mg respectively; the mean numbers of seeds per pod were 3.30 and 3.29 respectively and the mean weights per pod were 505 and 506 mg respectively.

The average weight per pod from the upper nodes expressed as a fraction of that from the lower nodes ranged from 0.90 ± 0.05 to 1.24 ± 0.04 . Only in four cultivars, including cv. T-21, was the fraction less than 0.95, suggesting that there may have been a slight decline in the weight of the later-formed pods, but in the remaining cultivars there was no such suggestion. In cv. T-21 the fraction was 0.92.

Nitrogen content of the seeds from earlier- and later-formed pods

The seeds from pods collected from the apical and basal nodes within the racemes, and from racemes at the basal and apical parts of the branches of nine medium and late cultivars were analysed for nitrogen. There was little or no effect of pod-position on the percentage of nitrogen in the seeds (Table 3).

TABLE 3. *Percentage of nitrogen in the seeds from pods collected from the basal and apical nodes of racemes, and from racemes at the basal and apical nodes of the branches of nine pigeonpea cultivars grown on vertisol and on alfisol at Hyderabad in 1976*

Cultivar	Within racemes: vertisol		On branches			
	Basal	Apical	Vertisol		Alfisol	
			Basal	Apical	Basal	Apical
ICP-1	3.50	3.49	3.50	3.46	3.31	3.14
AS-71-37	3.37	3.48	3.30	3.50	3.31	3.36
BDN-1	3.60	3.44	3.64	3.65	3.28	3.33
ICP-6997	3.37	3.14	3.31	3.14	—	—
HY-2	3.61	3.40	3.33	3.53	3.10	3.14
HY-3A	3.29	3.24	3.22	3.15	3.50	3.42
ICP-7375	3.52	3.77	3.59	3.65	3.52	3.65
ICP-7065	3.60	3.20	3.83	3.49	3.39	3.65
NP(WR)-15	3.46	3.32	3.61	3.78	3.53	3.60
Mean	3.48	3.38	3.48	3.48	3.37	3.41

DISCUSSION

The similarity in the average weights of the earlier- and later-formed pods indicates that the development of the later-formed pods was not limited by nutrient supply; this in turn indicates that the yield was primarily limited by the number of pods set.

The failure of more flowers to set pods seems to be related primarily to internal physiological balances within the plant. If earlier-formed flowers and young pods are removed, pods are set from later-formed flowers which would otherwise have abscinded (Sheldrake, Narayanan and Venkataratnam, in prep.). These results are most simply explicable in terms of competition by developing pods for assimilates or other nutrients. In general, the overall number of pods per plant is strongly influenced by the supply of

assimilates, but the constancy of the weight per pod (under a given set of environmental conditions) suggests that pod-set does not take place when the nutrient supply falls below a threshold level (Sheldrake, in press). If more pods were set than could be filled, the later-formed pods would be smaller than the earlier-formed pods, as in herbaceous legumes such as *Vigna aureus* (Roxb.) Hepper (Sinha, 1977) and *Cicer arietinum* L. (Sheldrake and Saxena, 1979).

This difference may be related to the fact that pigeonpeas are intrinsically perennial. The reproductive phase of annuals, and indeed of monocarpic plants in general, ends in death. All the plants' energies and nutrient reserves can be mobilized towards the production of fruit. Such a fatal strategy could not, by definition, be adopted by perennials, especially in environments in which an unfavourable season follows the reproductive phase. In India, the reproductive phase of pigeonpeas is followed by the hot, dry summer when the plants depend on their deep root system for survival.

Any marked improvement of pigeonpeas as an annual crop seems likely to depend on the development of genuinely annual cultivars which produce more and/or heavier pods. The yield of such cultivars should be limited not by the process of pod-setting but by the ability of the plants to fill the pods. The average weight of their later-formed pods should therefore be less than that of the earlier-formed pods.

The method of comparing the average weights of pods from the apical and basal nodes of the branches of indeterminate cultivars (or from the terminal and axillary racemes of determinate cultivars) is simple enough to be used for screening large numbers of cultivars. The World Collection of pigeonpea germplasm at this Institute has more than 5000 entries; it is possible that among them annual types already exist. This method seems more likely to give reliable results than looking for annuality *per se*, since the death of plant after the reproductive phase is influenced by many external factors such as pests, diseases and soil moisture. The identification of such plants in the germplasm collection or in breeders' lines could provide a starting point for the development of higher-yielding pigeonpeas.

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