Growth, development and nutrient uptake in pigeonpeas (*Cajanus cajan*)

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SUMMARY

The growth and development of two early (Pusa ageti and T-21) and three medium-duration (ST-1, ICP-1 and HY-3C) cultivars of pigeonpea (*Cajanus cajan* (L.) Millsp.) were compared at Hyderabad, India, in 1974 and 1975; in 1976 cv. ICP-1 was studied. The pigeonpeas were grown on a Vertisol and on an Alfisol. The crop growth rate in the first 2 months was low. The maximum rate of 171 kg/ha/day was found in the fourth month of growth of cv. ICP-1 on Alfisol. The early cultivars, one of which (cv. Pusa ageti) was morphologically determinate, and the other (cv. T-21) indeterminate, did not differ in the proportion of dry matter partitioned into seeds. The mean dry weight of the above-ground parts of the medium cultivars on Vertisol in 1975 was 8·45 t/ha, including 2·23 t/ha of fallen plant material. The mean harvest index (ratio of grain dry weight to total plant dry weight) of these cultivars was 0·24 excluding fallen material and 0·17 taking fallen material into account. Starch reserves were present in the stems during the vegetative phase, but disappeared during the reproductive phase. In 1974 the maximum leaf-area index on Vertisol was 3 and on Alfisol 12·7. The net assimilation rate tended to decline throughout the growth period, but in the medium cultivars increased at the end of the reproductive phase, probably because of photosynthesis in pod walls and stems.

In 1974 and 1975 the growth of roots and distribution of nodules in Vertisol was investigated by means of soil cores. Roots extended below 150 cm and root growth continued during the reproductive phase. Most nodules were found within the first 30 cm of soil, but some were found below 120 cm. In cv. T-21, grown in brick chambers 150 cm deep, at the time of harvest about three-quarters of the mass of the roots was found in the first 30 cm, and the shoot:root ratio was around 4:1.

In 1975 the mean uptake of nitrogen by the medium cultivars on Vertisol was 120 kg/ha, including 34 kg/ha in fallen material. In 1976 the uptake of nitrogen by cv. ICP-1 was 89 kg/ha on Vertisol and 79 kg/ha on Alfisol, including 32 and 23 kg/ha respectively in fallen material. Nitrogen uptake continued throughout the growing period. The percentage of nitrogen in stems and leaves declined as the plants developed and there was a net remobilization of nitrogen from these organs. The pattern of uptake and remobilization of phosphorus resembled that of nitrogen. In 1976 the total uptake of phosphorus by cv. ICP-1 on Vertisol was 5·8 kg/ha and on Alfisol 5·0 kg/ha.

The relatively low yields of pigeonpeas result from a restricted partitioning of dry matter into pods, which may be related to the plants' perennial nature.

INTRODUCTION

Pigeonpeas (*Cajanus cajan* (L.) Millsp.) are an important pulse crop in India, which accounts for about 90% of the total world production (Sinha, 1977). They are intrinsically perennial (Derieux,

1971), but in India are generally grown as an annual crop, when the plants develop into woody shrubs 1–2·5 m high (Mahta & Dave, 1931). They are usually sown in June or July, soon after the beginning of the monsoon. In peninsular India, 'early' cultivars are harvested after 4–5 months, 'medium' cultivars after 5–6 months and 'late' cultivars after 6–9 months; these durations are somewhat longer in northern India. The first 3–4

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months of growth take place during the monsoon; the ensuing winter season is generally dry and the pigeonpeas depend for their continued development on moisture stored within the soil.

Little detailed information is available on the growth and development of pigeonpeas in India or, indeed, anywhere else (Akinola, Whiteman & Wallis, 1975). As part of the first phase of a research programme on the physiology of this crop, we carried out descriptive studies of early and medium-duration cultivars grown during the normal season and compared representatives of two morphological types 'indeterminate' and 'determinate' (Reddy & Rao, 1974). We also investigated the uptake of nitrogen and phosphorus throughout the growing season.

MATERIALS AND METHODS

The pigeonpeas were grown at ICRISAT Centre, near Hyderabad, India, on a Vertisol (fine clayey, calcareous, Typic Chromustert) and on an Alfisol (fine loamy, Lithic Ustochrept) fertilized with single superphosphate (50 kg P_2O_5/ha). The soils contained 60–80 mg available nitrate/kg. No nitrogenous fertilizer was supplied. The roots were nodulated with native *Rhizobia*.

In 1974, trials were sown in Vertisol on 26 June and in Alfisol 4 July; in 1975 in Vertisol on 26 June; and in 1976 in Vertisol on 29 June and in Alfisol on 3 July. Two early cultivars, T-21 (indeterminate) and Pusa ageti (determinate) and three medium-duration indeterminate cultivars, ST-1, ICP-1, and HY-3C were grown in 1974 and 1975; in 1976 only cv. ICP-1 was used. These cultivars are among the heaviest yielding available. Two seeds per hill were sown at a spacing of 0.30×0.75 m (except for early cultivars in 1975, which were grown at a spacing of 0.30×0.50 m). The seedlings were thinned to one per hill. The plots were weeded by hand. Insect pests were controlled by sprays of endosulfan at fortnightly intervals. No irrigation was given. The early cultivars were harvested in mid-November and the medium cultivars in late December.

In 1974 all cultivars were sown in a randomized block design on Vertisol (two replications; plot size 9×40 m) and cv. ICP-1 was also grown in two replicated plots (9×20 m) on Alfisol. In 1975 the early cultivars were planted on Vertisol in a randomized block design (four replications; plot size 6×9 m) and the medium cultivars were grown on both soils in randomized block designs (four replications; plot size, 9×10 m). In 1976, cv. ICP-1 was planted in four replicate plots (9×10 m) on each soil type. Monthly rainfall and mean maximum and minimum temperatures during the

1974, 1975 and 1976 growing seasons are given in Table 1.

Growth analysis

Samples of five adjacent plants per plot were taken for growth analysis at approximately weekly intervals in 1974, and approximately monthly in 1975 and 1976. Leaf laminae, petioles, stems, flowers + buds, and pods were separated. The area of the leaf laminae was measured with an automatic leaf area meter. Oven-dry weights of all separated plant parts were recorded.

In 1976 in the trial on Vertisol, fallen plant parts were collected at weekly intervals from 3×3 m subplots within each plot; the fallen leaves, flowers + buds, and pods were separated from each other and their oven-dry weights were recorded.

At harvest, the air-dry weights of the stems + attached leaves, pods, seeds and fallen plant parts were recorded from each plot (excluding border rows and areas from which samples had been taken for growth analysis). These air-dry weights were corrected to oven-dry weights on the basis of data from a subsample of 10 plants per plot.

In 1974 the lengths of the main stems and the branches were recorded, and also their diameters at their mid points. From these measurements, the approximate surface area of the stem system was calculated assuming that the stems and branches were cylinders with mean diameters equivalent to those at their mid-points.

Roots and nodules

In 1974 and 1975 soil cores were taken from the Vertisol at regular intervals with a mechanically powered auger (diameter 7.6 cm) to a depth of 150 cm. The cores were divided into sections representing depths of 0–15, 15–30, 30–60, 60–90, 90–120 and 120–150 cm. The soil was kept in water overnight, and then the nodules and roots were washed free of soil. The total length of the root fragments and the number of nodules were recorded. The cores were taken over the stems of plants which had been cut immediately beforehand. Three plants per cultivar were sampled on each occasion. In 1974 observations were made on all cultivars except T-21, and in 1975 on cv. ST-1 only.

Chemical analysis

In 1974 samples of the different plant parts from one replicate, and in 1975 pooled samples from two replicates were ground to a powder and analysed for nitrogen by the Kjeldahl method and for phosphorus as described by Koenig & Johnson (1942). In 1974 nitrogen analysis was carried out for cvs T-21 and ICP-1; in 1975 for cvs Pusa ageti, T-21, ST-1; and in 1976 for cv. ICP-1.

Table 1. *Monthly rainfall and mean maximum and minimum temperatures (°C) at ICRISAT centre, Hyderabad, during the pigeonpea growing season (June to December) in 1974, 1975 and 1976*

| | 1974 | | | 1975 | | | 1976 | | |
| | | Temperature | | | Temperature | | | Temperature | |
Month	Rainfall (mm)	Mean maximum	Mean minimum	Rainfall (mm)	Mean maximum	Mean minimum	Rainfall (mm)	Mean maximum	Mean minimum
June	120	36·4	20·4	98	35·6	22·1	86	36·4	21·7
July	89	34·1	21·6	195	33·3	21·3	216	32·5	21·0
August	160	31·0	20·9	139	30·5	21·1	314	28·6	21·9
September	186	31·8	20·2	422	30·8	20·8	57	31·7	20·7
October	279	30·2	17·7	74	30·5	19·0	1	33·5	17·6
November	5	29·1	10·1	15	28·0	11·3	30	30·1	17·6
December	0	28·2	8·2	0	27·8	8·1	0	28·7	15·3

Root growth in brick chambers

In 1976, plants of cv. T-21 were grown in the normal season in clayey and in loamy soil, taken from the surface layers of Vertisol and Alfisol respectively, in brick chambers 1·50 m deep and 0·50 × 0·70 m in cross-section. There were three plants in each of four replicate chambers with clayey and three with loamy soil. At the time of maturity, one wall of each chamber was dismantled and the roots were washed free of soil. The total shoot dry weight (excluding fallen leaves) and the dry weight of the upper 0·30 m of the root system and of the part below 0·30 m were recorded. These samples were analysed for nitrogen.

Data and calculations

In the Tables and Figures below, means over all replications within a trial are shown. In the curves shown in Figs 2, 3, 6 and 7, 'leaves' refers to laminae and petioles, 'stems' to main stems and branches, and 'reproductive structures' to flower buds, flowers, pods, peduncles and pedicels.

Net assimilation rate (increase in dry weight/ unit leaf area/unit time) was calculated on the basis of the average leaf area, assuming that there was a linear increase or decrease of leaf area during the period between sampling times. The dry weight of fallen material was not taken into account in these calculations unless otherwise stated. The harvest index was calculated by the formula: grain dry weight/total plant dry weight.

RESULTS AND DISCUSSION

Accumulation and distribution of dry matter in the shoot system

The mean yields of the medium-duration cultivars grown on Vertisol in 1974, 1975 and 1976 were

1·75, 1·49 and 1·20 t/ha respectively. A similar trend was found in other trials conducted at ICRISAT. The reduced yields in 1976 probably resulted from moisture stress during the reproductive phase caused by the early cessation of the monsoon (Table 1). By contrast, the yields of the early cultivars on Vertisol were highest in 1976, when the monsoon ended early. The protracted monsoon in 1974 and 1975 meant that part of the reproductive phase of these cultivars took place in wet and cloudy weather. The mean yields of the early cultivars in 1974, 1975 and 1976 were 0·80, 0·76 and 0·96 t/ha respectively.

The accumulation and distribution of dry matter in the shoot system of two early and two medium cultivars grown on Vertisol in 1974 are shown in Fig. 1. The curves for cv. HY-3C resembled those for cv. ST-1. In all cultivars, the dry weight of the leaves declined during the latter part of the reproductive phase, owing to senescence and abscission. Growth of the stems continued during the reproductive phase in all cultivars. In the determinate cv. Pusa ageti, there was no increase in height after flower-bud initiation (Fig. 2), but new primary and secondary branches developed; 73 % of the total stem weight at the time of harvest was produced during this period. Other indeterminate cultivars did not show such a trend. The morphologically determinate habit of this cultivar did not confer any advantage in the proportion of dry matter partitioned into reproductive structures, compared with the early indeterminate cv. T-21. The harvest indices of cvs Pusa ageti and T-21 were 0·33 and 0·34 respectively on Vertisol, and 0·32 and 0·36 on Alfisol. In soya beans a comparable lack of difference has been observed in the proportion of dry matter partitioned into seeds of determinate and indeterminate cultivars (Egli & Leggett, 1973). The mean harvest index for the
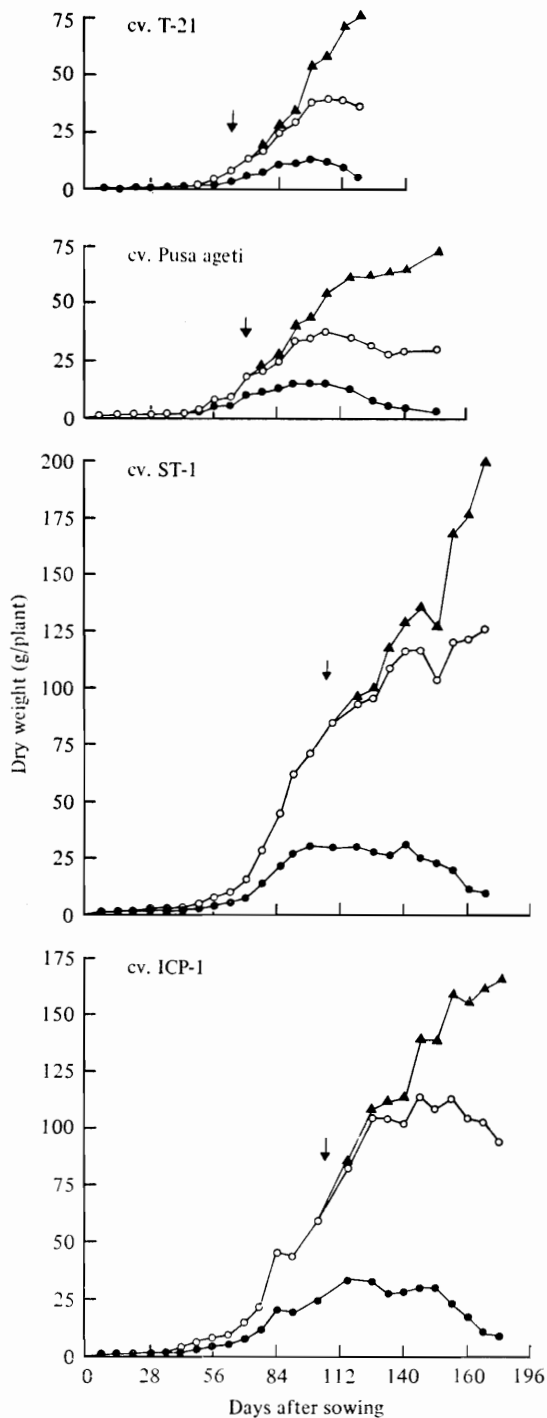
Fig. 1. Accumulation and distribution of dry matter in the leaves (●—●), leaves + stems (○—○), leaves + stems + reproductive structures (▲—▲) of cvs T-21, Pusa ageti, ST-1 and ICP-1 grown on Vertisol in 1974. Arrows indicate the dates of flower bud initiation.
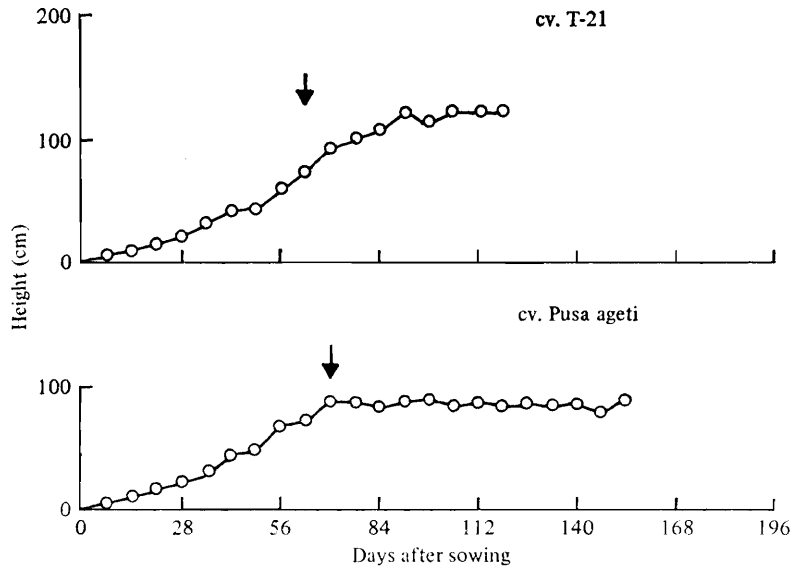
Fig. 2. Plant height of cvs T-21 and Pusa ageti grown on Vertisol in 1974.
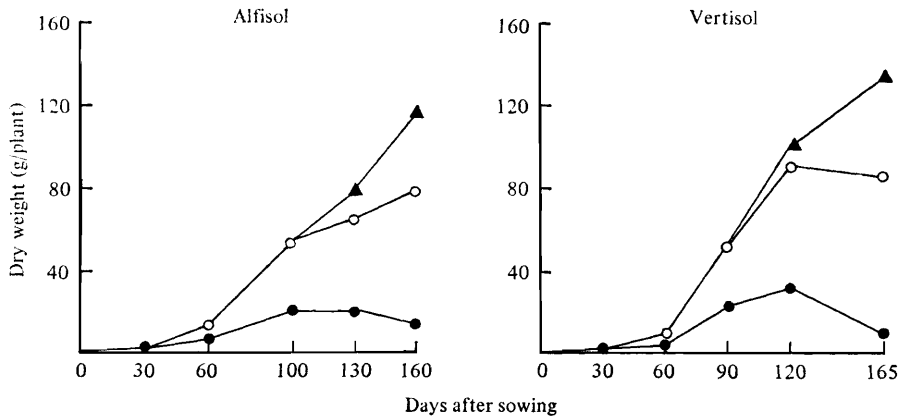Arrows indicate the dates of flower bud initiation.

Fig. 3. Accumulation and distribution of dry matter in the leaves (●—●), leaves+stems (○—○),
leaves+stems+reproductive structure (▲—▲) of cv. ICP-1 grown on Alfisol and Vertisol in 1976.

medium cultivars ST-1, ICP-1 and HY-3C was 0·24 excluding fallen material, and 0·17 taking fallen material into account. The uncorrected harvest index for cv. ICP-1 grown on Vertisol in 1976 was 0·26 and 0·17 after correction for fallen material; on Alfisol the uncorrected and corrected harvest indices were 0·15 and 0·11 respectively.

Owing to their photoperiodic sensitivity, the development of pigeonpeas is strongly influenced by the date of planting (Derieux, 1971; Akinola & Whiteman, 1974). They grow less and mature sooner when they are planted in the winter season, and their harvest indices are higher. With winter-sown medium cultivars we observed mean harvest indices without and with correction for fallen leaves of 0·33 and 0·26 respectively (A. Narayanan & A. R. Sheldrake, unpublished). Even so, these harvest indices are low compared with a crop such as chickpea (*Cicer arietinum* L.); under Hyderabad conditions the harvest indices of well-adapted chickpea cultivars are around 0·5, or 0·4 after correction for fallen leaves (Anon. 1976a). This greater partitioning of dry matter into seeds enables chickpeas to outyield pigeonpeas, in spite of the fact that their growing season is shorter and the plants are smaller. Therefore the future line of
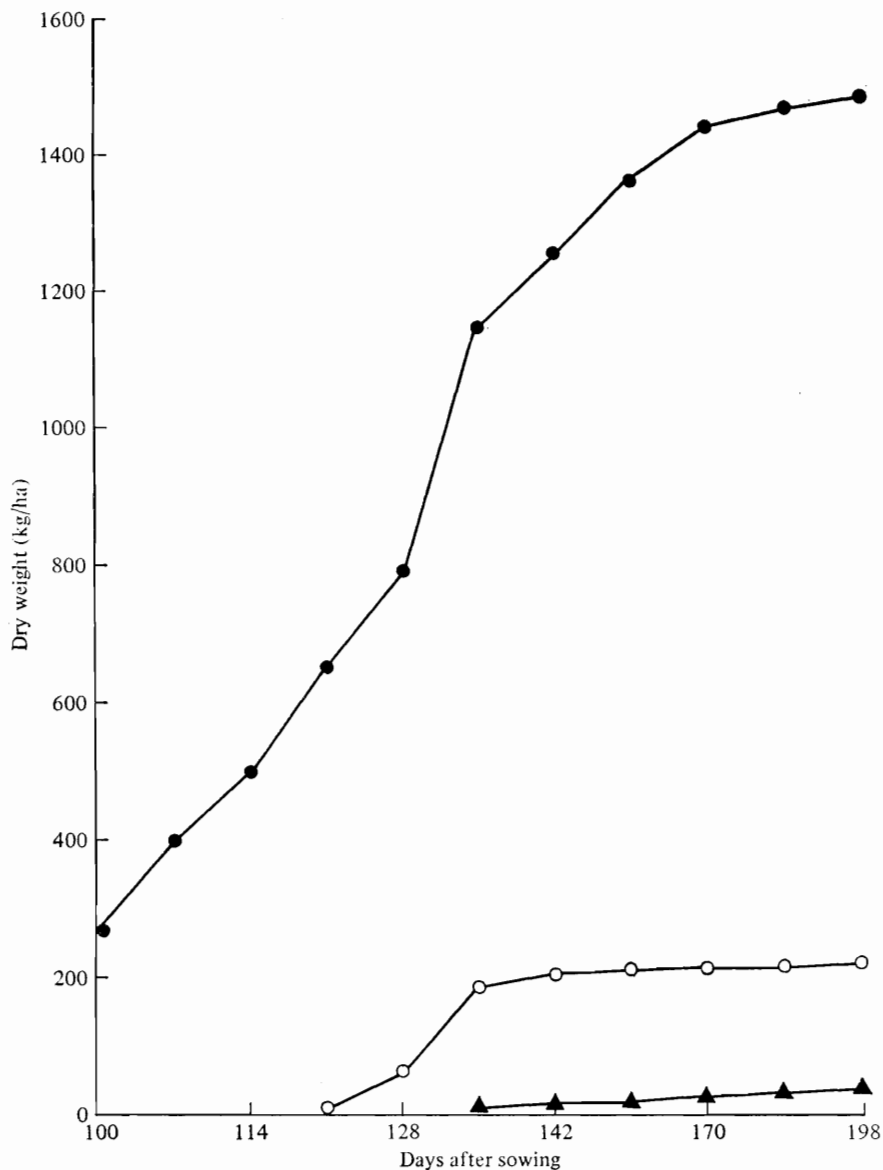
Fig. 4. Cumulative dry weight of fallen plant parts of cv. ICP-1 grown on Vertisol in 1976. ●—●, Leaves; ○—○, flowers+buds; ▲—▲, pods.

work should concentrate on these aspects for yield improvement in pigeonpea.

In 1974 the growth of cv. ICP-1 on Alfisol exceeded that on Vertisol, but in 1976, when there was little rainfall during the latter part of the monsoon (Table 1) growth was better on Vertisol (Fig. 3), which has a higher water-holding capacity.

In 1976 the fallen plant parts were collected at regular intervals from the plants grown on Vertisol. The majority of the dry matter was in fallen leaves

(Fig. 4). By the time of harvest, leaves accounted for 86% of the total fallen material, flowers and flower-buds for 12% and pods for only 2%.

The dry matter in the shoot system and the weight of the fallen material at the time of harvest in 1975 and 1976 is shown in Tables 2 and 3.

Crop growth rate

The crop growth rate (CGR) of all cultivars was low during the first 2 months (Table 4). Even lower

Table 2. *Dry-matter content (t/ha) of the above-ground parts at the time of harvest of cvs ST-1, ICP-1 and HY-3C grown on Vertisol in 1975*

Above-ground parts	Cultivars		
	ST-1	ICP-1	HY-3C
Seed	1·51	1·43	1·53
Pod wall	0·85	0·75	0·91
Stem	4·07	3·93	3·34
Attached leaves	0·25	0·21	0·16
Fallen material	2·23	2·13	2·33
Total	8·91 ± 0·95	8·45 ± 0·33	8·27 ± 1·05

Table 3. *Dry-matter content (t/ha) of the above-ground parts at the time of harvest of cv. ICP-1 grown on Vertisol and Alfisol in 1976*

Above-ground parts	Vertisol	Alfisol
Seed	1·01	0·70
Pod wall	0·43	0·30
Stem	2·13	3·10
Attached leaves	0·29	0·63
Fallen material	2·16	1·71
Total	6·02 ± 0·28	6·44 ± 0·61

Table 5. *Maximum leaf area index of five pigeonpea cvs grown in Vertisol and Alfisol during 1974 and 1976*

Cultivars	1974		1976	
	Vertisol	Alfisol	Vertisol	Alfisol
T-21	1·34	—	—	—
Pusa ageti	1·68	—	—	—
ST-1	3·60	—	—	—
ICP-1	3·68	12·70	3·00	1·90
HY-3C	3·58	—	—	—

Table 4. *Crop growth rates of cvs T-21, Pusa ageti, ST-1, ICP-1 and HY-3C grown on Vertisol, and cv. ICP-1 grown on Alfisol in 1974*

Days after sowing ...	Crop growth rate (kg/ha/day)						
	7–35	35–63	63–91	91–119	119–147	147–165	165–193
Cultivar							
T-21	1·3	14·5	46·1	68·4	—	—	—
Pusa ageti	1·7	14·2	51·3	39·3	10·3	—	—
ST-1	3·0	16·0	88·9	58·1	68·4	109·4	—
ICP-1	2·3	13·7	59·8	102·6	136·8	44·5	—
ICP-1 (Alfisol)	3·0	16·4	104·3	171·4	68·4	42·8	—
HY-3C	2·5	8·0	42·8	75·2	46·2	17·1	51·3

CGRs of young pigeonpeas have been observed in Australia (Wallis, Whiteman & Akinola, 1974). The maximum CGR of the early cultivars was lower than the medium cultivars. The highest CGR, 171 kg/ha/day, occurred during the fourth month of growth of cv. ICP-1 on Alfisol in 1974 (Table 4). A similar maximum CGR was recorded in the Australian study referred to above; this CGR resembles the maximum reported for soya beans, but is several times less than the maximum recorded for a number of other crops (Evans, 1975).

Although the low CGR of young pigeonpeas is a disadvantage in a crop consisting of a single species, it is not necessarily so in a mixed crop. In India, pigeonpeas are generally intercropped with other species in many different combinations (Pathak, 1970). A common system involves growing medium- or long-duration pigeonpeas with a cereal such as sorghum, which is harvested soon after the monsoon while the pigeonpeas are still in their vegetative phase. In such situations the early growth rate of the pigeonpeas is even lower than in a single species crop, owing to shading by the cereal; however, the pigeonpeas are able to grow rapidly after the companion crop is harvested, and in appropriate combinations yield as well as when sown alone (Anon. 1976b). These results suggest that the pigeonpea breeders should select lines for high CGR in early growth for single species crops and a high CGR in later growth period for mixed crops.
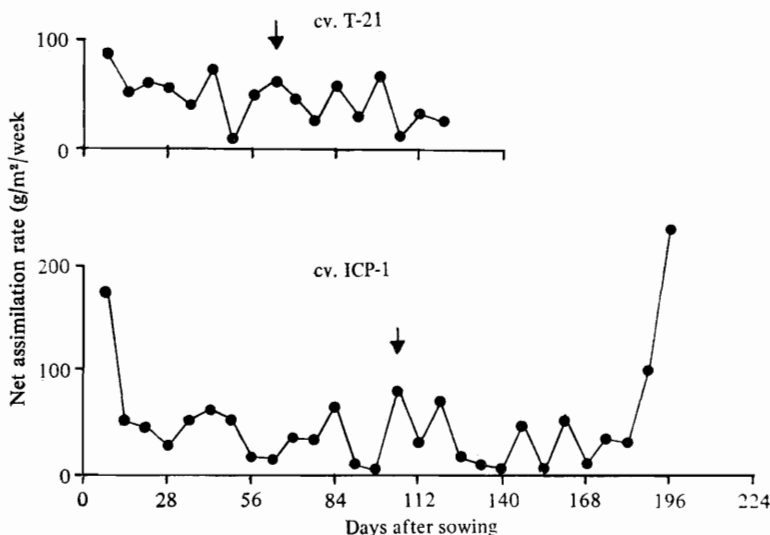
Fig. 5. Net assimilation rate throughout the growing season of cvs T-21, ICP-1 on Vertisol in 1974. Arrows indicate the dates of flower-bud initiation.

Starch reserves

During the vegetative phase there were considerable reserves of starch in the stems, shown by staining with iodine. Microscopical examination revealed that the starch was present in the medullary rays and in the parenchymatous cells around the xylem vessels. During the reproductive phase these starch reserves diminished and little or no starch could be detected at the time of harvest. When pod development was prevented by the repeated removal of all flowers and young pods, there was no decline in the amount of starch in the stems; this result indicates that the starch reserves were mobilized as a consequence of pod development (A. R. Sheldrake, A. Narayanan and N. Venkataratnam, unpublished).

Leaf area

The curves describing the change of leaf area index (LAI) with time closely resemble those for the dry weight of the leaves in Fig. 1. In 1974 the maximum LAI of the early duration cultivars (T-21 and Pusa ageti) was less than that of the medium duration cultivars when grown in Vertisol (Table 5). It may be due to similar spacing $(0.75 \times 0.30$ m) adopted, for both the group of cultivars Cv. ICP-1 grown in Alfisol had a maximum LAI of 12·70 which was about 3·4 times more than that of Vertisol. In Alfisol, the nodulation, drainage and aeration of the soil were better than in Vertisol. Therefore, the plants grew well and put forth more foliage. In 1976 the maximum LAI in Vertisol was almost same as in 1976 for cv. ICP-1 but in Alfisol

the LAI was much lower than in the Vertisol. Also it is evident from Table 5 that the same cultivars had a maximum LAI of 12·70 in 1974 in Alfisol. The reasons for such a drastic reduction is the moisture stress during the reproductive stage caused by early cessation of monsoon (Table 1).

Net assimilation rate

The NAR was calculated for all cultivars grown in 1974. The NAR of early cultivars showed a tendency to decline throughout the growing period. A similar tendency was apparent in the medium cultivars until the end of the reproductive phase, when there was a striking increase in all cases (Fig. 5). These calculations did not involve any correction for fallen leaves. Corrections for fallen leaves were applied to the data for cv. ST-1 which did not affect the pattern of change in NAR, although they somewhat accentuated the increase in NAR towards the end of the growth period.

The increase in NAR need not imply an increase in the photosynthetic efficiency of the leaves; it could be explicable in terms of an increased proportion of photosynthesis occurring in other organs such as pods and stems which are photosynthetically active. In Table 6 the surface area of the stem system in the mid-reproductive phase and at the time of harvest is compared with the leaf area. It shows that by the time of harvest the stem area exceeded the leaf area in all cultivars except T-21.

It therefore seems probable that the increase in

Table 6. *Surface area of leaves and stems of cvs T-21, Pusa ageti, ST-1, ICP-1 and HY-3C grown on Vertisol and of cv. ICP-1 grown on Alfisol in 1974*

Cultivar	Days after sowing	Leaf area (cm²/plant)	Stem area (cm²/plant)	Stem area as % of leaf area
T-21	91	1770	517	29
	126	1060	730	69
Pusa ageti	91	2518	712	28
	161	411	727	177
ST-1	140	4229	2626	62
	175	1559	3166	203
ICP-1	140	3115	1386	44
	175	1843	2029	110
ICP-1 (Alfisol)	140	4764	2679	56
	175	1647	2318	141
HY-3C	140	3882	1021	26
	217	2361	3158	134

Table 7. *Distribution of roots at different depths in soil cores taken at different times during the growing season of cvs Pusa ageti and ST-1 on Vertisol in 1974*

	Pusa ageti			ST-1		
Days after sowing ...	56	70	126	70	133	162
	Root length (m/m² soil surface)					
Depth (cm)						
0–15	135	169	219	294	365	520
15–30	226	167	200	165	296	336
30–60	94	158	123	250	246	363
60–90	42	140	146	144	173	177
90–120	23	46	119	69	105	117
120–150	—	37	86	16	66	6
Total ($\pm$ s.d.)	520 ± 108	717 ± 56	893 ± 125	938 ± 147	1251 ± 348	1519 ± 265

NAR at the end of the reproductive phase of the medium-duration cultivars was at least in part due to photosynthesis in the stems and pods. The absence of a similar increase in NAR of the early cultivars may be because they were maturing at the end of the monsoon season when the overcast skies reduced photosynthetic assimilation; in the post-monsoon season, when the medium cultivars matured, there was no rainfall (Table 1) and little or no cloud-cover.

Root growth

In 1974 and 1975 the root system was sampled by means of soil cores in order to obtain an idea of the development of roots at different depths. Some data for two cultivars grown on Vertisol in 1974 are given in Table 7. The roots extended below 150 cm. Root growth continued during the reproductive phase.

In 1975 the distribution of roots in cores taken within and between rows was compared. The patterns were similar, and resembled those found the previous year. The total length of roots approximately doubled during the reproductive phase.

In both soils approximately three-quarters of the total dry weight of the roots was present in the upper 30 cm ($71 \pm 5\%$ in clayey soil and $75 \pm 9\%$ in loamy soil). The shoot:root ratio at the time of harvest, excluding fallen leaves, was higher in the clayey soil ($4 \cdot 2 \pm 0 \cdot 25$:1) than in the loam ($3 \cdot 5 \pm 0 \cdot 23$:1).

The nitrogen percentage in the lower part of the root system tended to be higher than in the upper part. The overall percentage of nitrogen in the roots grown in clayey soil was 0·92 and in loam 1·07.

Nodulation

On Vertisol most of the nodules were small and many were senescent, even in the early stages of plant growth. The nodules in Alfisol were generally larger and better developed. The poorer development of the nodules on Vertisol during the

Table 8. *Total number of nodules, and distribution of nodules at different depths in soil cores taken at different times during the growing season of cvs Pusa ageti and ST-1 on Vertisol in 1974*

	Cv. Pusa ageti			Cv. ST-1		
Days after sowing ...	37	70	126	37	126	162
	Total number of nodules/soil core ($\pm$ s.d.)					
	$36 \pm 20\cdot3$	$20 \pm 4\cdot1$	$8 \pm 2\cdot9$	$53 \pm 27\cdot3$	$58 \pm 39\cdot5$	$57 \pm 19\cdot7$
	Percentage of nodules at different depths					
Depths						
0–15 cm	82	47	56	74	54	24
15–30 cm	13	20	9	13	14	64
30–60 cm	5	16	17	13	5	10
60–150 cm	0	16	17	0	28	1

vegetative phase may have been due to the poorer aeration and intermittent waterlogging of this clayey soil.

On Vertisol, soil cores were taken at regular intervals to a depth of 150 cm to determine the number and distribution of nodules. The number fluctuated throughout the vegetative and reproductive phases, the only clear tendency was one of decline in the 2 weeks preceeding harvest. Most nodules were found in the upper 30 cm of the soil, but some were found in the deeper zones, even below 120 cm. Data for cvs Pusa ageti and ST-1 are presented in Table 8.

Nitrogen uptake and distribution

In all 3 years the percentage of nitrogen in the leaf laminae and stems, and to a lesser extent in the petioles, declined throughout the growing period. The percentage of nitrogen in the peduncles and pods also declined with time. Results from 1974 are shown in Fig. 6. In cvs T-21 and ICP-1 on Vertisol the net uptake of nitrogen continued throughout the reproductive phase; the overall uptake would have been greater than that indicated in Fig. 6 if the nitrogen in fallen leaves had been included. In cv. ICP-1 the plants on Alfisol took up more nitrogen than on Vertisol; in part, this reflected their greater growth, but there was also a higher percentage of nitrogen in leaves, stems and petioles, perhaps because of the better development of the nodules in this soil. There was little net nitrogen uptake on Alfisol after flowering. This may have been a consequence of moisture stress resulting from the relatively low water-holding capacity of the soil.

The rate of uptake of nitrogen into the shoot system of cv. ICP-1 grown on Vertisol in 1976 was calculated taking into account the nitrogen in the fallen plant parts (Table 9). The maximum occurred during the later part of the vegetative phase (60–90 days after sowing), when the rate of uptake of phosphorus was also at a maximum. However, the CGR was highest in the subsequent month; the new dry matter added during this period contained a lower proportion of nitrogen (Table 9).

The total amount of nitrogen taken up by the shoot systems of cvs ST-1, ICP-1 and HY-3C in 1975 and by cv. ICP-1 in 1976 is shown in Tables 10 and 11. In both years approximately 30 kg N/ha was returned to the soil in the form of fallen leaves. Since the soil had received no nitrogenous fertilizer and contained only little available nitrogen, it is assumed that the majority of the nitrogen taken up by the plants had been fixed by the nodules.

At the time of harvest of cv. ICP-1 grown on Vertisol in 1976, the weight of roots extractable from the upper 30 cm of soil was equivalent to 430 kg N/ha. Assuming that these roots contained three-quarters of the mass of the root system, and that the nitrogen content was approximately 1% nitrogen (assuming similar values to those observed with cv. T-21 grown in brick chambers, as described above), the total root system at the time of harvest would have contained approximately 6 kg N/ha. Assuming the extracted roots represented only half the root system, there would be about 10 kg N/ha in the root system.

In India, farmers remove almost all the shoot system of pigeonpeas from the fields at the time of harvest; only fallen material and roots remain to contribute nitrogen to subsequent crops. The data on fallen material and roots, considered above, indicate that the total contribution by the crop of cv. ICP-1 grown on Vertisol in 1976 was approximately 40 kg/ha.

The percentage of nitrogen in the leaves declined from 4–5% to 1·5% at the time of abscission. Thus approximately two-thirds of the nitrogen in the leaves was remobilized into the plant during leaf senescence; in other words the total amount of nitrogen remobilized from the leaves was about
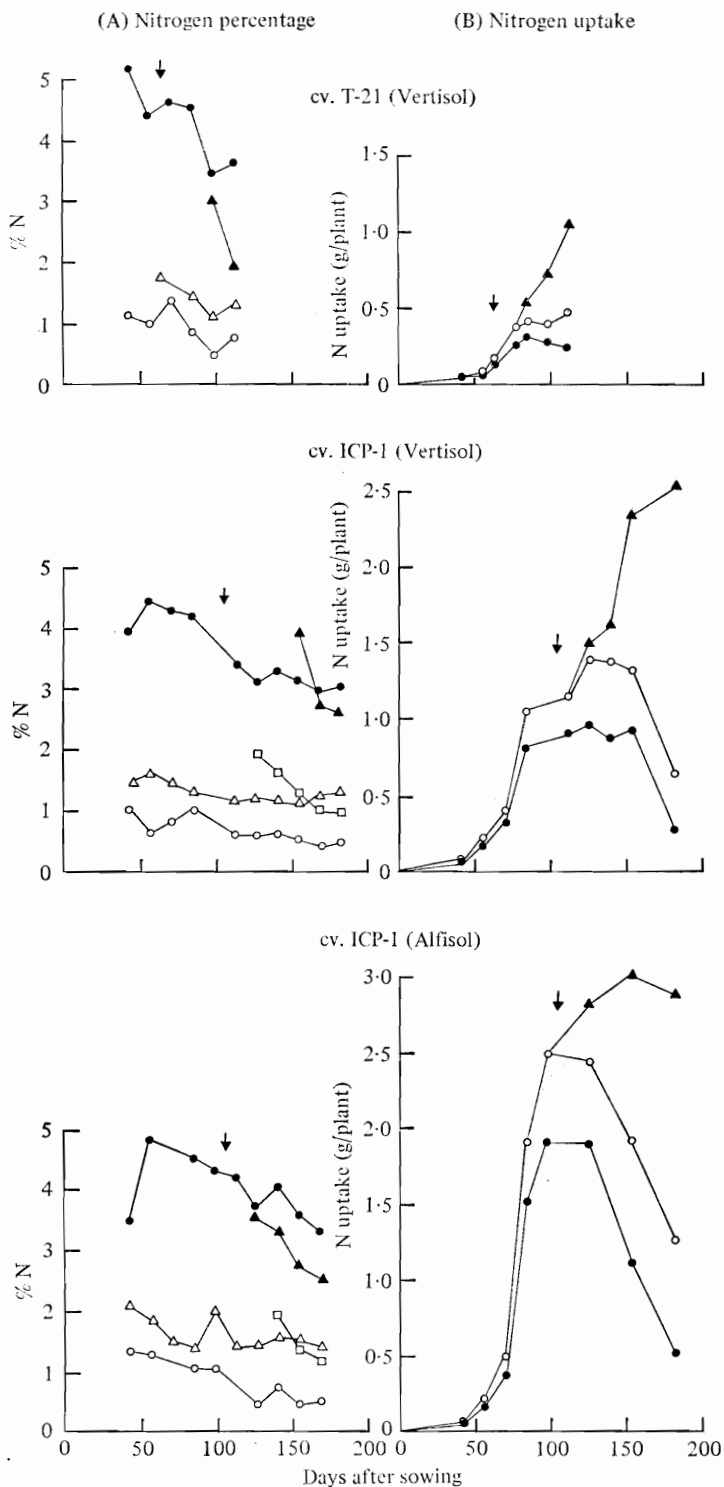
Fig. 6. Nitrogen in cvs T-21 and ICP-1 grown on Vertisol, and cv. ICP-1 grown on Alfisol, in 1974. (A) ●—●, Percentage of nitrogen in leaf laminae; ▲—▲, pods; □—□, peduncles; △—△, petioles; ○—○, stems. (B) Amount of nitrogen in leaves (●—●), in leaves+stems (○—○), and in leaves+ stems+reproductive structures (▲—▲). Arrows indicate dates of flower bud initiation.

Table 9. *Crop growth rate and rates of nitrogen and phosphorus uptake into the shoot system (including fallen plant parts) of cv. ICP-1 grown on Vertisol in 1976*

Days from sowing	CGR (kg/ha/day)	N uptake rate (g/ha/day)	P uptake rate (g/ha/day)	N uptake rate / CGR (g/kg)	P uptake rate / CGR (g/kg)
0–30	1	27	2	27	2·0
30–60	16	376	13	23	0·8
60–90	79	1716	123	22	1·6
90–120	111	1216	62	11	0·6
120–165	61	267	23	4	0·4

Table 10. *Nitrogen content of the above-ground parts at the time of harvest of cvs ST-1, ICP-1 and HY-3C grown on Vertisol in 1975*

	Cultivars					
	ST-1		ICP-1		HY-3C	
Above-ground parts	%	kg/ha	%	kg/ha	%	kg/ha
Seed	3·54	53·4	3·74	53·5	3·50	53·5
Pod wall	1·12	9·5	0·68	5·1	0·55	5·0
Stem	0·44	17·9	0·42	16·5	0·81	27·1
Attached leaves	2·95	7·4	2·83	6·0	2·75	4·3
Fallen material	1·63	36·4	1·50	31·9	1·42	33·1
Total	—	124·6	—	113·0	—	123·0

Table 11. *Nitrogen and phosphorus content of the above-ground parts at the time of harvest of cv. ICP-1 grown on Vertisol and Alfisol in 1976*

Above-ground parts	Nitrogen		Phosphorus	
	%	kg/ha	%	kg/ha
Vertisol				
Seed	3·45	34·7	0·29	2·9
Pod wall	0·68*	2·9	0·03	0·1
Stem	0·53	11·3	0·05	1·1
Attached leaves	2·93	8·5	0·15	0·4
Fallen material	1·48	31·8	0·06	1·3
Total	—	89·2	—	5·8
Alfisol				
Seed	3·38	23·5	0·28	1·9
Pod wall	0·68*	2·0	0·03	0·1
Stem	0·42	13·0	0·04	1·2
Attached leaves	2·88	18·3	0·12	0·8
Fallen material	1·31	22·5	0·06	1·0
Total	—	79·3	—	5·0

* Not analysed in 1976. Value taken from 1975 data.

twice the amount in the fallen leaves. This over-estimates the net remobilization of nitrogen from leaves, because some from earlier-senescing leaves could have been translocated to later-formed leaves. However, even if it is assumed that net remobilization from leaves to other organs was only about half the gross remobilization, on Vertisol about 30 kg/ha, and on Alfisol in 1976 about 20 kg/ha could have been translocated. In 1975 this could have accounted for most, and in 1976 for all, of the nitrogen in the seeds (Tables 10, 11).

Phosphorus uptake and distribution

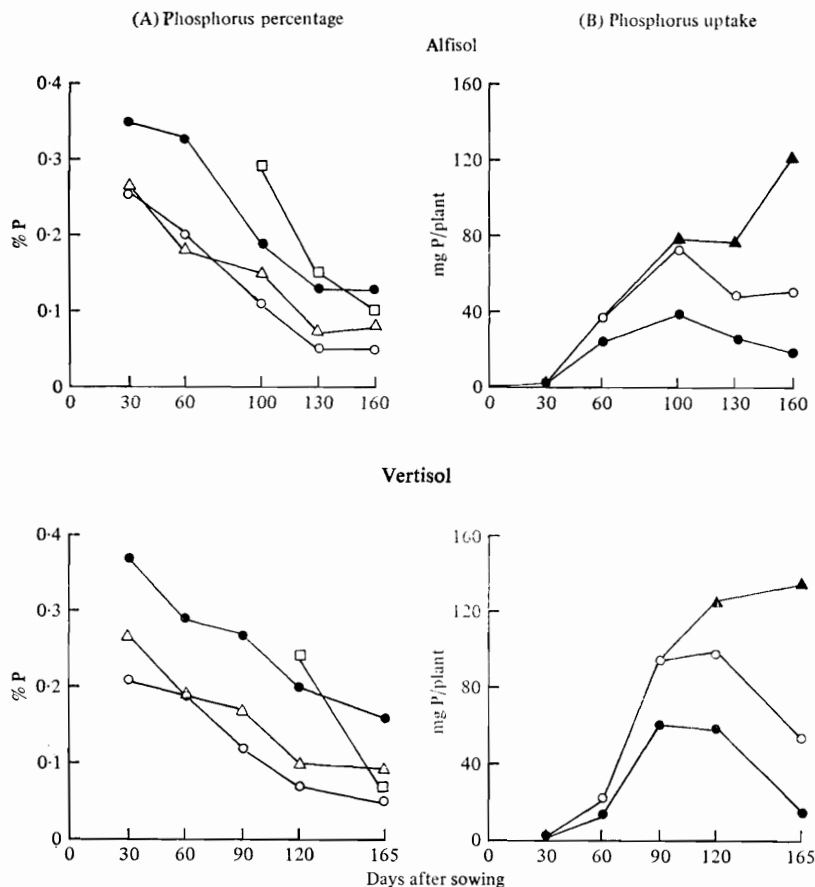The uptake and distribution of phosphorus were studied in cv. ICP-1 grown in 1976 on Vertisol and

Fig. 7. Phosphorus in cv. ICP-1 grown on Alfisol and Vertisol in 1976. (A) ●—●, Percentage of phosphorus in leaf laminae; □—□, peduncles; △—△, petioles; and ○—○ stems. (B) Amount of phosphorus in leaves (●—●), in leaves + stems (○—○), and in leaves + stems + reproductive structures (▲—▲).

Alfisol. On both soils the percentage of phosphorus declined in all organs throughout the growing season (Fig. 7). The uptake of phosphorus by the plants continued during the reproductive phase; the gross uptake would have exceeded that shown in Fig. 7 if the fallen leaves had been taken into account. There was a small net decline in the amount of phosphorus in the stems during the reproductive phase, and a larger decline in the leaves. The decrease in the percentage of phosphorus from over 0·3% in green leaves to less than 0·1% in fallen leaves indicates that there was a considerable remobilization into other organs. By reasoning similar to that applied to nitrogen remobilization, it can be estimated that phosphorus translocated from the leaves could have accounted for about half the phosphorus in the seeds on Vertisol and more than half on Alfisol.

The distribution of phosphorus in the shoot system and the amount in fallen leaves at the time of harvest is shown in Table 11.

The rate of uptake of phosphorus, like that of nitrogen, was at a maximum during the later part of the vegetative phase, and declined during the reproductive phase (Table 9).

Perenniality

In India, pigeonpeas are normally cut and harvested when the pods are mature. But if the plants are left standing, the reproductive phase is followed by a second flush of growth and flowering. In a second harvest taken 2–3 months after the first harvest of the medium cultivars planted in 1974, the mean yield was 30% of that obtained at the first harvest, on both soils.

All the cultivars we investigated were able to survive for at least 2 years on Vertisol and Alfisol

without irrigation. The major cause of mortality was the *Fusarium* wilt disease.

The perennial nature of pigeonpeas means that during their reproductive phase sufficient assimilates and other nutrients must be retained for the survival and continued growth of the vegetative structures. By contrast, annuals such as chickpeas are able to mobilize a higher proportion of their resources into reproductive structures. In chickpeas, yield is limited by the ability of the plants to fill their pods (A. R. Sheldrake and N. P. Saxena, unpublished). Pigeonpeas set fewer pods than they are capable of filling (A. R. Sheldrake and A.

Narayanan, unpublished), probably because pods do not set when the assimilate supply falls below a threshold level (A. R. Sheldrake, unpublished). The relatively small proportion of assimilates partitioned into the reproductive structures of pigeonpeas, reflected in low harvest indices, may be related to their intrinsic perenniality.

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