CHAPTER 11

Pigeonpea

A. RUPERT SHELDRAKE
Consultant Plant Physiologist, ICRISAT, Patancheru PO, A.P. 502 324,
India

TAXONOMY

The pigeonpea (*Cajanus cajan* (L.) Millsp.) is a member of the subtribe Phaseoleae, family Leguminosae. Although it is often stated to be a monotypic genus, *Cajanus* actually has another species, which grows wild in West Africa. Many species of the closely related genus *Atylosia* successfully cross with pigeonpea. The main morphological difference between the two groups was thought to be the presence of a seed strophiole in *Atylosia* and its absence in *Cajanus*, but in fact seed strophioles are present in over 100 of the 5800 pigeonpea entries in the world collection at ICRISAT Center (van der Maesen, 1980). The presence of this characteristic is governed by two major genes (Reddy *et al.*, 1981).

Pigeonpea originated in India, where the largest diversity exists and most related *Atylosia* spp. occur (van der Maesen, 1980). The little known wild species *Atylosia cajanifolia* Haines, from the Eastern Ghats of India, is very similar to pigeonpea. East Africa, to which the crop was taken over 4000 years ago, is a secondary centre of diversity. The crop reached America with the European conquests.

CULTIVATION

Pigeonpeas are cultivated in many countries in the tropics and subtropics, where their drought tolerance and ability to utilize residual moisture during the dry season make them an important crop in the semi-arid areas.

Total world production in 1975 was estimated to be 1.96 million tonnes. Over 90 per cent is produced in India. Africa accounts for 4 per cent, the most important pigeonpea producing countries being Kenya and Uganda. The Caribbean, Central and South America produce 2 per cent of the total (Sharma, D., et al., 1981).

The plants grow into woody shrubs, generally about 1 to 2 m tall at the time when the first season's pods mature. As a field crop, the plants are normally harvested at this stage, but if left to grow as perennials they develop into small trees which may be 4 m or more in height.

Pigeonpeas are grown in a wide range of cropping systems. These can be broadly divided into long season, full season, and short season classes (Byth et al., 1981). The long season crops are usually sown around the longest day of the year and flower after the shortest day. This is the traditional system in north India and parts of central India. The crop is commonly sown at low density with the onset of the monsoon in June to July, grows vegetatively throughout the monsoon season, flowers around January, and is harvested in March to April. Such long season pigeonpeas are usually intercropped with one or more other species (Laxman Singh and Shrivastava, 1977; Willey et al., 1981). They are generally confined to frost-free areas and are grown on soils of high water holding capacity (Reddy and Virmani, 1981).

Full season crops mature earlier than long season crops, with sowing around the longest day. They flower in decreasing daylengths, and are harvested after the normal sowing time of winter crops. Such full season systems are common in peninsular India, and once again usually involved intercropping with cereals or other crops. Since pigeonpeas are slow growing in their early stages they offer little competition to faster growing, earlier maturing companion crops, and substantially greater combined yields can be obtained per unit area than if the crops are grown separately (Rao and Willey, 1980a; Willey et al., 1981). Such intercropping systems also have advantages from the point of view of yield stability (Rao and Willey, 1980b).

Short season cropping systems either involve early maturing cultivars which are more or less insensitive to photoperiod and which mature relatively quickly regardless of sowing date, or depend on sowing several months after the longest day, when the more rapid flowering under short day conditions enables both photoperiod-sensitive and insensitive cultivars to be used.

In addition, in many tropical countries pigeonpeas are grown as perennial 'backyard' plants. They can also be used as a green manure or forage crop (Gooding, 1962; Whiteman and Norton, 1981).

In India, pigeonpea seeds are usually dried, dehusked, and split to give *dhal*. The young green seeds are eaten as a vegetable in many countries and are canned in Puerto Rico and Trinidad. The stems of pigeonpea are of some importance as a source of firewood and are also used for making baskets, etc. (Pathak, 1970).

STRUCTURE

Leaves

In seedlings the first two leaves are simple and opposite. The subsequent leaves are trifoliate, with lanceolate to elliptic leaflets acute at both ends, and are spirally arranged.

There are over ten times more stomata on the lower than the upper surface of the leaves (Bisen and Sheldrake, 1981). In the lamina there is a distinct palisade layer, below which is a spongy mesophyll with large intercellular spaces (Figure 11.1).
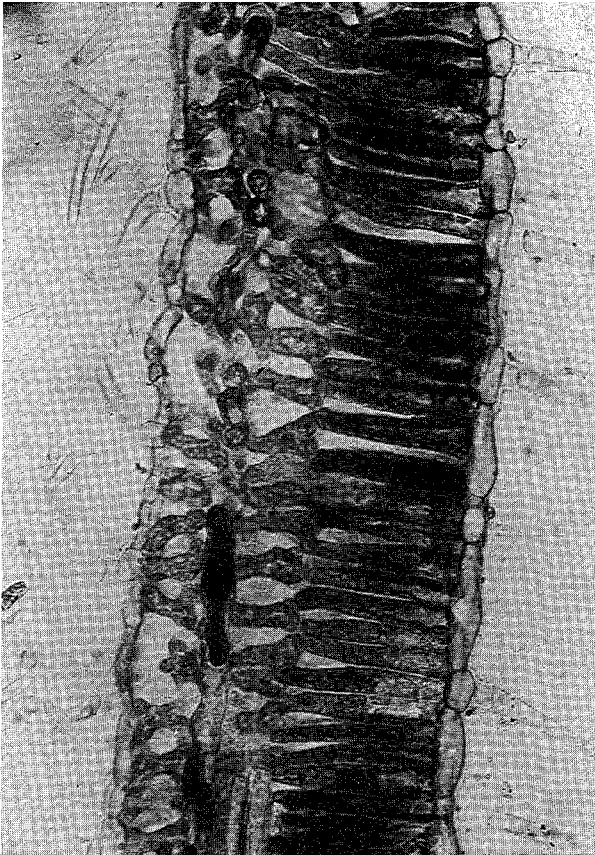

Figure 11.1 Transverse section of a pigeonpea leaf lamina showing palisade tissue (to the right) and spongy mesophyll (cv. ST-1) × 375

The leaves are pubescent, more so on the lower than the upper surface. There are two main types of hair, simple and glandular. The latter are spherical, and contain a yellow oily material which is probably responsible for the fragrance of pigeonpea plants. (For photographs of these and other aspects of pigeonpea anatomy, see the monograph by Bisen and Sheldrake, 1981). An essential oil can be collected by the steam distillation of pigeonpea leaves and other aerial organs: it contains a mixture of compounds including the terpenoid α-copaene (Gupta et al., 1969). The function of this glandular secretion is unknown. It is conceivable that it may have an insect-repellent role. Similar simple and glandular hairs are found on all aerial parts of the plants, except some parts of flowers such as petals and stamens.

Pulvini are present at the base of the petiole and at the base of the leaflets. As a result of their activity, the angles of the leaves and leaflets can be adjusted throughout the day. When the sunlight is intense, and especially when the plants are under water stress, in the exposed parts of the canopy the leaflets tend to take up a position parallel to the incident light, i.e. behave paraheliotropically, thus minimizing the interception of radiation.

At night the leaflets are folded vertically upwards into the 'sleep' position. This positioning is due to the sensitivity of the pulvini to gravity; if the angle of the branch is altered, e.g. by tying a weight to it so that the leaflets are no longer pointing upwards, they return to a vertical position within an hour or two. The functional significance of these 'sleep' movements is unknown.

As the leaves senesce, abscission zones develop both at the base of the petiole and at the base of the leaflets.

Stems

The primary vascular tissue of the stems is organized in strands connecting the nodes; each strand is associated with a ridge on the stem, clearly visible even in old, secondarily thickened stems. Collenchymatous bundle caps underlie the epidermis of the ridges (Bisen and Sheldrake, 1981).

The stem thickens as a result of the activity of the vascular cambium, producing a continuous ring of phloem outside and xylem inside. Within the xylem, the vessels are surrounded by parenchymatous cells and tangential bands of parenchyma run between the rays. Much of the remainder of the xylem tissue between the medullary rays consists of xylem fibres (Bisen and Sheldrake, 1981).

During the vegetative phase, the xylem parenchyma, including the medullary rays, contain starch (Figure 11.2). These starch reserves can be detected very simply by applying a few drops of iodine solution to the cut ends of stems and branches, which turn blue or black if starch is present. During the reproductive phase this starch disappears; but in plants from which flowers and young pods are continually removed, the starch reserves are not
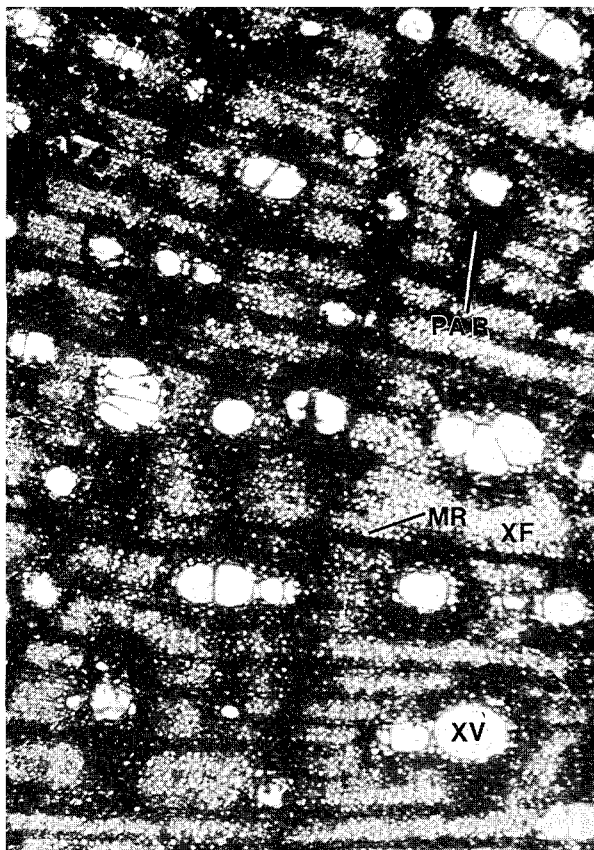
Figure 11.2   Transverse section of the xylem in a woody stem of a pigeonpea (cv. ST-1), showing starch in medullary rays and xylem parenchyma, darkly stained with iodine (× 75). XV, xylem vessel; XF, xylem fibre; MR, medullary ray; PAR, xylem parenchyma

depleted, indicating that they are mobilized as a consequence of pod development.

Within the phloem region and also in the outer parts of the pith are cells containing densely staining material, probably polyphenolic or tannin-like in nature. These cells are joined end to end, forming ducts. Such secretory ducts differentiate at an early stage in primary tissue and are also formed within secondary phloem. They occur not only in stems, but in all other organs, including pods and roots.

When pigeonpea tissues are damaged, droplets of clear fluid exude from the secretory ducts onto the cut surfaces and the exudate turns red on exposure to

air. As a consequence wounds become covered with reddish varnish-like material. This exudate has an extremely astringent taste and may well have a role in protection against pests and/or diseases.

Branching pattern

Cultivars differ greatly in the number and angles of their branches when grown at fairly wide plant-to-plant spacings. At one extreme are those which form rather low wide-spreading bushes (e.g. cv. ICP-7375), and at the other, compact, upright types (e.g. cv. HY-3A). However, in all cultivars branching is greatly reduced in dense plantings and in intercropping systems where the pigeonpeas are shaded by faster-growing companion crops such as sorghum and maize.

Roots

The primary structure of the roots is usually tetrarch. Secondary thickening takes place as a result of cambial activity and the main roots become thick and woody. In the cortex of young roots, mycorrhizae can sometimes be observed within the cells (Bisen and Sheldrake, 1981).

Excavation of the root system reveals that it is usually both deep and wide-spreading, with well developed lateral roots in the superficial layers of the soil. Sampling by means of soil cores in a Vertisol at Hyderabad has shown that roots extended more than 2 m down, but that the most extensive development took place in the upper 60 cm (Sheldrake and Narayanan, 1979a; Natarajan and Willey, 1980a). Root growth continued during the reproductive phase and the total length approximately doubled after the onset of flowering. In the medium duration cv. ST-1, there were about 1500 m of roots beneath each square metre of soil surface by the end of the reproductive phase (Sheldrake and Narayanan, 1979a).

Nodules

Pigeonpeas are nodulated by *Rhizobia* of the cowpea group. The nodules on the roots of plants grown on Vertisol at the ICRISAT Center, Hyderabad are generally small. The majority are on the upper 30 cm of the root system, but some can be found even below 120 cm (Sheldrake and Narayanan, 1979a). The nodules of plants grown on Alfisol are generally larger and better developed than those on Vertisol; plants on Alfisol have also been found to have a higher rate of nitrogen fixation, as estimated by the acetylene reduction technique (Kumar Rao *et al.*, 1981).

The number of nodules on field-grown plants fluctuates throughout the growing season, but shows a clear tendency to decline towards the end of the reproductive phase (Sheldrake and Narayanan, 1979a). Senescent and hollow

nodules are common. Both on the experiment station and in farmers' fields, many have been found to be damaged by the larva of a fly, *Rivellia angulata* (Sithananthan *et al.*, 1981).

The growth of the nodules occurs through the activity of a meristematic zone arching around the apical end and the medulla contains numerous bacterioid-filled cells. Sometimes the latter are highly vacuolated (Bisen and Sheldrake, 1981).

Flowers

In most cultivars, the inflorescences develop as axillary recemes, 4 to 12 cm long, and flowering proceeds acropetally both within the racemes and on the branches (Figure 11.3). Some cultivars are morphologically determinate in the sense that apical buds of main shoots develop into inflorescences, and here the sequence of inflorescence production is basipetal. In a few cultivars, flowering starts at nodes behind the apex and proceeds both acropetally and basipetally. The flowers are yellow, or red, or yellow and red or ivory coloured and are usually around 2 cm in length (for a full description of floral structure and a diagrammatic illustration, see Purseglove, 1968). The majority open between 11 a.m. and 3 p.m. They are visited by bees and other insects.

Most of the flowers are self-pollinated but cross-pollination also occurs and poses a serious problem for the maintenance of pure lines under open pollinated conditions (Sharma and Green, 1975). In some cultivars, in which lobes of the standard petal overlap, the 'wrapped flower' character enforces a high degree of self-pollination (Byth *et al.*, 1981). In other cultivars, the extent of outcrossing varies considerably depending on the location and conditions; for example at Badnapur an averge of 2.9 per cent outcrossing was found, while at Coimbatore the average was 40.2 per cent (ICRISAT, 1980). At one location in Kenya, with a high population of insect pollinators, outcrossing was as high as 94.5 per cent, pointing to the possibility that population breeding methods could be employed under such conditions (Onim, 1981).

Several sources of genetic male sterility have been identified (Reddy *et al.*, 1978), and the use of this character for the possible large-scale production of high-yielding F_1 hybrids is being explored (Green *et al.*, 1979; ICRISAT, 1980).

There is an abscission zone at the base of the pedicel and the majority of the flowers drop off without setting pods (Howard *et al.*, 1919; Datta and Deb, 1970; Ariyanayagam, 1975; Pandey and Singh, 1981).

Pods

For about the first 3 weeks after anthesis the pod wall develops more rapidly than the young seeds, but thereafter it makes little further growth (ICRISAT, 1975).

Figure 11.3   A primary branch of a morphologically
indeterminate pigeonpea cultivar (cv. ICP-1) showing
flowers and developing pods ($\times$ 0.36)

The pods are flattened, with diagonal depressions between seeds, and are beaked. They are green, green with purplish blotches, or purplish, from 3 to 10 cm long and can contain as few as 2 to 3 seeds or as many as 8 to 9 depending on

the cultivar. The seeds are in separate locules, the cross walls of which develop during the first week after anthesis. There is little or no shattering of dried pods in the field.

In a study on a limited number of cultivars, the extent of ovule and seed abortion has been estimated. In some small seeded cultivars up to 90 per cent of the ovules developed into mature seeds, but in others, especially those with large seeds, more than half of the ovules or young seeds aborted. There was a negative correlation ($r = -0.81$, significant at the 1 per cent probability level) between the percentage realization of the potential seed number and the weight per seed (ICRISAT, 1977).

The pod walls are well supplied with secretory ducts containing tannin-like material. The outer epidermis contains stomata. In addition to the simple hairs and the spherical glandular hairs found on other aerial organs, pods bear large numbers of another kind of hair, seen only occasionally on vegetative organs, with secretory cells towards the base and a long tubular neck (Figure 11.4). These hairs produce a colourless fluid, which can be seen in droplets on their tips. When this exudate is washed off, there is an increased incidence of podfly attack, at least in some cultivars, suggesting that it may play a role in protecting the pods against pests (ICRISAT, 1979).

The pedicels of the flowers contain small vascular bundles surrounded by a ring of fibres (Figure 11.5). During the first week of pod development, secondary thickening begins through the activity of a cambial zone and continues during the second and third weeks to give a considerable increase in the cross-sectional area of the vascular tissue supplying the pods (Bisen and Sheldrake, 1981).

Seeds and germination

The seeds are smooth coated, with a small white hilum, and are usually round or oval. They are white, greyish, brown, red, purplish or speckled in colour. Hundred-seed weights range from 4 to 24 g. The whole seeds contain 18 to 29 per cent protein and 48 to 59 per cent starch (ICRISAT, 1976, p. 113).

Germination is hypogeal. There are no dormancy problems in this crop and germination is generally good except under cool conditions. Studies in controlled environments have shown a broad optimum temperature range (19 to 43 °C) for germination, with the most rapid growth of the seedlings occurring between 29 and 36 °C (de Jabrun et al., 1981).

Not surprisingly, small seeds selected from a given seed lot give rise to smaller seedlings than do large seeds. However, the initial advantage of the latter is lost as the plants grow, and no significant effect of seed grading on the yield of medium duration cultivars has been detected (Saxena et al., 1981). Likewise, small seeded cultivars have smaller seedlings than large seeded
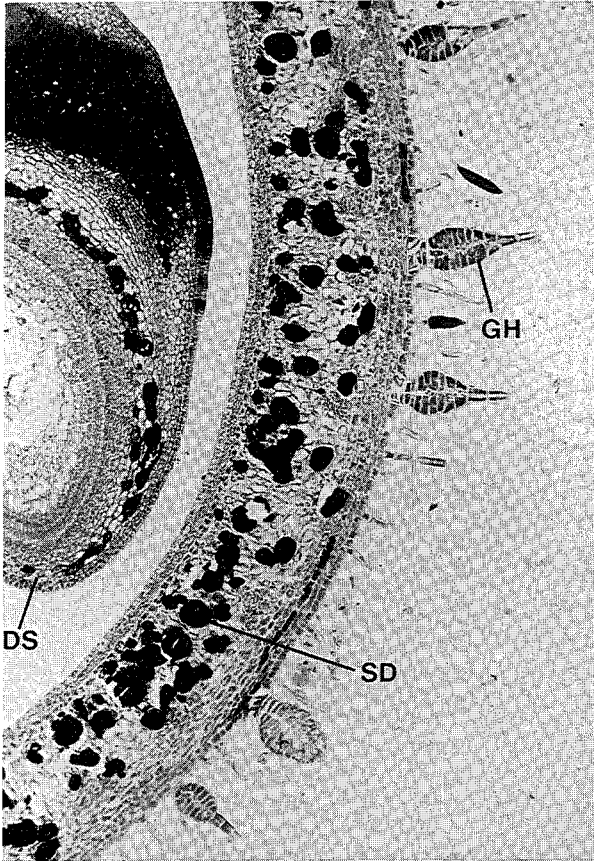
Figure 11.4   Transverse section of an 8-day-old pod wall of a pigeonpea (cv. ST-1) showing glandular hairs and secretory ducts. GH, glandular hair; SD, secretory duct; DS, developing seed

cultivars, but these differences due to seed size become less pronounced as the crop develops (Narayanan *et al.*, 1981b).

FLOWERING

Pigeonpeas are short day plants. Through a combination of photoperiodic and temperature effects, the time to flowering and maturity of pigeonpea cultivars varies according to the date of planting (Derieux *et al.*, 1971; Akinola and Whiteman, 1974a; Hammerton, 1976; Green *et al.*, 1979; Ariyanayagam, 1981). Data from a location in Queensland, Australia, are shown in Figure 11.6. These effects are of great practical significance (Byth *et al.*, 1981, Lawn,
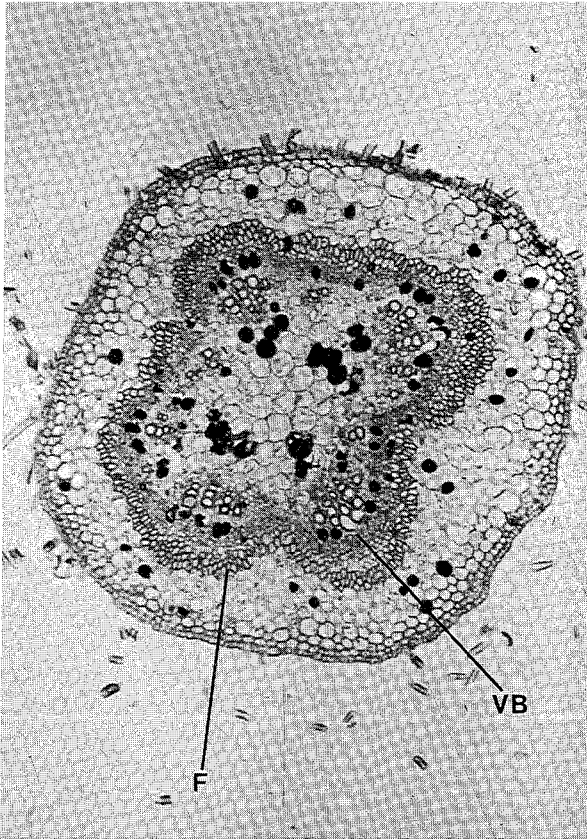
Figure 11.5 Transverse section of the pedicel of a
pigeonpea flower, showing vascular bundles surrounded
by a ring of fibres (cv. ST-1) (× 30). VB, vascular bundle;
F, fibres

1981; Wallis *et al.*, 1981). For example, in peninsular India, with the normal
time of planting at the beginning of the south west monsoon in June or July,
early cultivars mature in 4 to 5 months, medium cultivars in 5 to 6 months and
late cultivars in 6 to 9 months. But when they are grown under short days in the
cool post-rainy (rabi) season, planted around October, they flower sooner and
their development is 'telescoped' in such a way that early cultivars mature in
less than 4 months, medium in 4 to 4.5 months and late in 4.5 to 5 months
(Narayanan and Sheldrake, 1979).

In general, the daylength sensitivity of pigeonpea cultivars is related to their
earliness or lateness, the longer duration cultivars requiring shorter daylenths
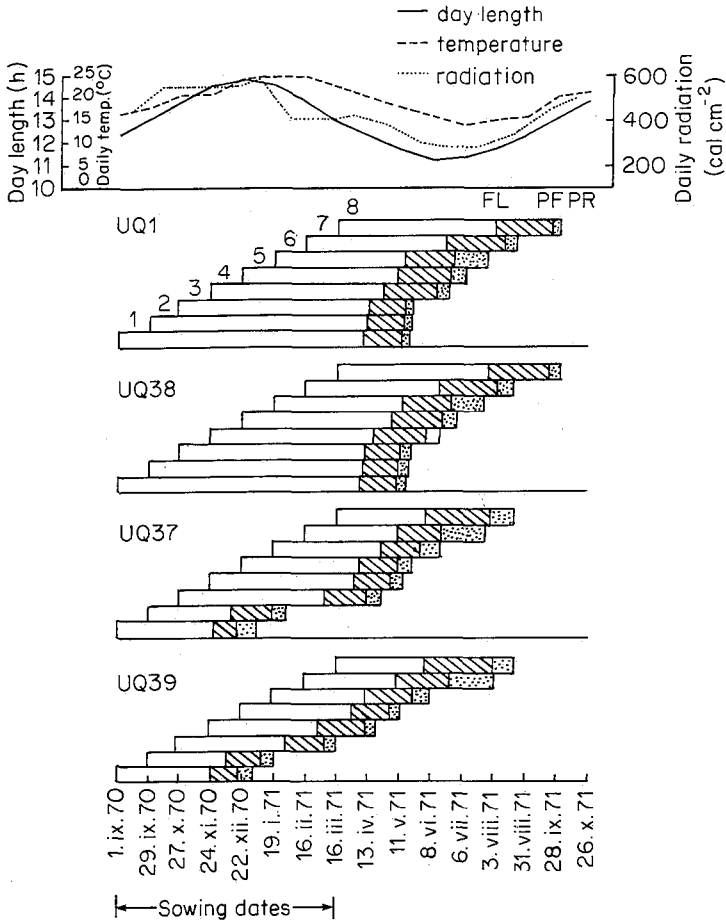(or rather, longer nights) than earlier cultivars (Akinola and Whiteman, 1974a;

Figure 11.6 Effects of sowing date (1–8) on time to 50 per cent flowering (FL), pod-filling (PF), and pod ripening (PR) of two medium (cvs. UQI and UQ 38) and two early maturing (cvs. UQ 37 and UQ 39) pigeonpea cultivars grown at Redland Bay, Queensland. (From Akinola and Whiteman, 1974a)

ICRISAT, 1976). In the extreme case of extra-early cultivars, some have been found to flower under continuous illumination in controlled environments and are effectively day neutral (Turnbull *et al.*, 1981).

The growth duration of a cultivar is one of the most important factors affecting its adaptation to a particular cropping system, climatic environment, and soil type (primarily because of the importance of water retention from the rainy to the post-rainy season). For this reason, it is important to classify cultivars according to their phenology; and ICRISAT breeders have so far

recognized 10 groups on the basis of their duration and photoperiod response (Sharma, D., *et al.*, 1981).

One problem in making such a clasification on the basis of performance at a single location is that the photoperiodic response is affected by temperature; if the temperature sensitivity of cultivars differs, their relative phenologies may change in difference environments. The existence of such differences is suggested by the markedly different rankings of medium and late cultivars in their time to flowering observed in July plantings at Hyderabad and in Puerto Rico, both at a latitude close to 17 °N. For example, the earliest of the cultivars tested in Hyderabad (97 days to flower) was one of the latest in Puerto Rico (116 days); and one of the latest at Hyderabad (137 days) was one of the earliest in Puerto Rico (86 days). Meanwhile, at Kibos in Kenya, almost on the equator, the same cultivars all flowered much sooner, between 61 and 68 days; within this narrow range, the rankings bore little or no similarity to those in Puerto Rico or Hyderabad (Sharma, D., *et al.*, 1981).

An important effect of temperature on flowering seems to be reduction in the requirement for short days under relatively cool conditions. Thus in monthly planting trials carried out at Hyderabad (elevation 500 m) and at Mahabaleshwar (elecation 2000 m) both at the same latitude, under the same long day conditions, cultivars which did not flower at the former flowered under the cooler conditions at the latter (ICRISAT, 1976).

Studies in controlled environments have provided quantitative data on the effects of temperature on the induction of flowering (McPherson, *et al.*, 1980). Under 10 h and 12 h photoperiods, flowering occurred later at mean temperatures of 28 and 20 °C than at 24 °C, suggesting that the latter is close to an optimum (H.G. McPherson and I. Warrington, personal communication). But in interpreting temperature effects on flowering, it is important to bear in mind that floral initiation and the rate of development of the floral primordia may be affected differently. Turnbull *et al.* (1981) found that although floral initiation occurred soonest in the lowest temperature regime they imposed (24 °C by day and 16 °C by night) and was delayed by increasing either day or night temperature, increased temperature promoted the development of the flower buds once they had been initiated.

GROWTH ANALYSIS

Pigeonpeas are grown in such a bewildering variety of cropping systems that the analysis of growth is necessarily system-specific. Of course, even within a given system, as in other crops, the pattern of development is much influenced by planting density. Thus, for example, in a study on an early maturing day netural cultivar grown under irrigated conditions in Queensland, Australia, the leaf area index (LAI) reached a maximum of 4.9 after 49 days at the highest population density, 1×10^6 plants ha^{-1}, but in lower densities of planting

maximum values were reached only after 85 days. The crop growth rate was linearly related to LAI, and was greatest at the highest population density. On the other hand, dry matter and leaf number per plant declined at increasing population densities (Rowden *et al.*, 1981).

An example of the pattern of distribution of dry matter in stems, leaves, and reproductive structures of pigeonpeas grown as a sole crop at Hyderabad in peninsular India is shown in Figure 11.7. The dry weight of the leaves declined during the latter part of the reproductive phase, owing to senescence and
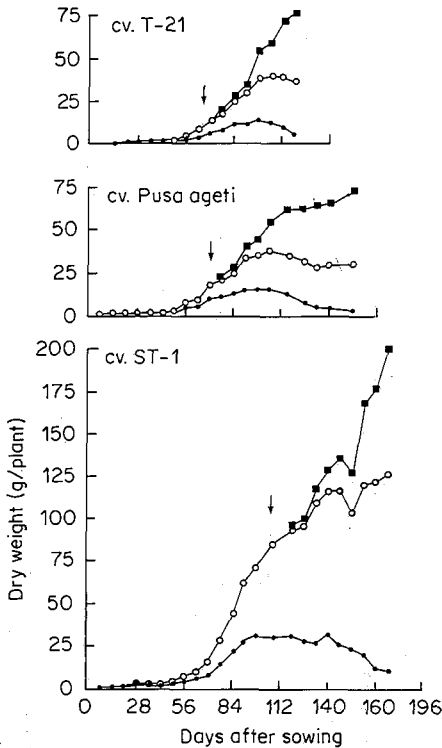
Figure 11.7   Accumulation and distribution of dry matter in the leaves (●—●), leaves + stems (○—○), and stems + reproductive structures (■—■) of an early indeterminate pigeonpea cultivar (T-21), a morphologically determinate cultivar (*Pusa ageti*) and a medium duration indeterminate cultivar (ST-1) grown on Vertisol at Hyderabad (sown on 26-6-74). Arrows indicate the dates on which flowering began. (From Sheldrake and Narayanan, 1979a)

abscission. Growth of the stems continued during the reproductive phase in all cultivars, including the morphologically determinate cultivar *Pusa ageti*. Although there was no increase in height after flower initiation in the latter, new primary and secondary branches continued to develop. The morphoplogically determinate habit of this cultivar did not confer any advantage in the proportion of dry matter partitioned into the seeds, compared with the early indeterminate cv. T-21.

Comparisons of a range of determinate and indeterminate cultivars in different duration groups have shown that the morphologically determinate habit confers no advantage in yield or the partitioning of dry matter into seeds (ICRISAT, 1979). The determinate types in fact have a definite disadvantage when they are not heavily protected by pesticides, since they are more severely attacked by pod borers, mainly caterpillars of *Heliothis armigera*, one of the most important pests of pigeonpea (ICRISAT, 1976). On the other hand, the large clusters of pods exposed above the plant canopy and the generally shorter stature characteristic of these cultivars make them easier to spray with pesticides.

Changes in LAI with time closely parallel the changes in leaf dry weight. The maximum LAI recorded at Hyderabad is 12.7; a similar maximum has been found in Australia (Wallis *et al.*, 1975). However, the maximums LAIs of medium duration cultivars grown in the normal season at Hyderabad usually range from 3 to 6; and in post-rainy season crops, planted around October, LAIs rarely exceed 1, even with high population densities.

Net assimilation rates (NAR) for the cultivars shown in Figure 11.7 showed a declining trend through most of the growth period. They were around 50 g m^{-2} week^{-1} at the time of flowering (Sheldrake and Narayanan, 1979a). In most cultivars there was a marked rise in NAR towards the end of the reproductive phase. This need not imply an increase in the photosynthetic efficiency of the leaves; it seems more likely to be due to an increased proportion of photosynthesis in other organs such as pod walls and stems. As a consequence of leaf fall, by the end of the reproductive phase the surface area of the stems usually exceeds that of the leaves (Sheldrake and Narayanan, 1979a).

Because of the deep and spreading nature of the root system, quantitative recovery of roots from the soil is extremely difficult and root weights have been omitted from the calculations of NAR.

In intercropping systems in which pigeonpeas are shaded by a faster growing companion crop such as sorghum, the growth rate and LAI are, not surprisingly, much lower than in comparable pigeonpeas grown as a sole crop. However, after the harvest of the intercrop, the amount of light available to the plants is greatly increased (for data on light interception see Natarajan and Willey, 1980b); the growth rate accelerates and the plants partially compensate. For example, in one experiment at Hyderabad with a medium duration

pigeonpea (harvested 173 days after emergence) intercropped with sorghum (harvested 82 days after emergence), at the time of the sorghum harvest the dry weight of the intercropped pigeonpea was only 15 per cent that of a sole crop grown at the same population density; but at harvest it was 41 per cent. Moreover, the proportion of dry matter partitioned into stems was reduced and into pods increased, and the yield was 70 per cent that of the sole crop (Natarajan and Willey, 1980a).

There is no evidence that intercropping leads to an alteration in the pattern of root growth of the pigeonpea or companion crop. The roots of the different species have been found to intermingle freely with each other (Natarajan and Willey, 1980a).

NUTRIENT UPTAKE

Measurements on field grown plants have shown that nitrogen, phosphorus, and potassium uptakes take place throughout the vegetative phase and continue during the reproductive phase (Sheldrake and Narayanan, 1979a; Natarajan and Willey, 1980b). However, throughout the growing season the percentage content of these elements in the various vegetative and reproductive organs declines (Sheldrake and Narayanan, 1979a; Natarajan and Willey, 1980b; Ahlawat, 1981). For example, in pigeonpeas grown in the normal season at Hyderabad, the percentage of nitrogen in the leaves declined from a maximum of around 5 per cent to 1.5 per cent at the time of abscission, and of phosphorus from 0.3 per cent to less than 0.1 per cent showing that over two-thirds of the content of these elements was remobilized during the process of leaf senescence. Calculations have shown that remobilization from the leaves can account for most of the nitrogen in the seeds and for at least half the phosphorus (Sheldrake and Narayanan, 1979a).

Some data for the distribution of dry matter and nutrients in the above ground parts of the plants at the time of harvest of a medium duration cultivar grown in the normal season at Hyderabad are shown in Table 11.1. The amount of nitrogen in the root system was estimated to be about 10 kg ha^{-1} (Sheldrake and Narayanan, 1979a). When added to the 89 kg ha^{-1} in the shoot system, this gives a total uptake of about 100 kg ha^{-1}. Since the crop was grown on soil low in available nitrogen and without nitrogenous fertilizer, much of this was probably fixed in the root nodules. Over 2 tons ha^{-1} or material, mostly fallen leaves, was returned to the surface of the soil, containing over 30 kg ha^{-1} nitrogen.

In further studies at ICRISAT, using a larger range of cultivars, the Microbiology group have recorded total nitrogen uptakes in a range from 69 to 134 kg ha^{-1}, and in one experiment, they estimated that 40 kg ha^{-1} of residual nitrogen was used by a subsequent cereal crop (Kumar Rao et al., 1981). Total nitrogen uptakes reported for pigeonpea crops in other parts of

Table 11.1   Dry weight and nitrogen and phosphorus content of above-ground parts of medium duration pigeonpeas (cv. ICP-1) at the time of harvest. The plants were grown on a Vertisol at ICRISAT Center, Hyderabad in the normal season (sown at the end of June; harvested in mid-December)

Component	Dry matter kg ha^{-1}	Phosphorus		Nitrogen	
		%	kg ha^{-1}	%	kg ha^{-1}
Seed	1007	0.29	2.9	3.45	34.7
Pod wall	428	0.03	0.1	0.68	2.9
Stem	2132	0.05	1.1	0.53	11.3
Attached leaves	290	0.15	0.4	2.93	8.5
Fallen material	2157	0.06	1.3	1.48	31.8
Total	6305	—	5.8	—	89.2

India range from 72 to 216 kg ha^{-1}, and phosphorus uptakes from 10 to 24 kg ha^{-1} (Ahlawat, 1981).

In an extensive series of fertilizer trials carried out at different locations in India, positive yield responses were obtained with starter doses of 20 to 25 kg ha^{-1} nitrogen, and in soils low in available phosphorus there have been significant positive responses to phosphatic fertilization (Kulkarni and Panwar, 1981). The latter result is hardly surprising; but compared with cereal crops, pigeonpea seems to be rather efficient at taking up phosphate from the soil. At ICRISAT Center, Hyderabad, it has been observed on several occasions that pigeonpeas show almost normal growth in soils in which cereal crops show striking symptoms of phosphate deficiency.

SEED YIELD

Pigeonpea is a relatively low-yielding crop. In 1972 the world average yield was 665 kg ha^{-1}, and the Indian averge 681 kg ha^{-1} (Sharma and Green, 1975). At ICRISAT Center, the yields of the best adapted medium duration cultivars, grown as a sole crop without irrigation in the normal season, rarely exceed 2 tonnes ha^{-1}; the mean yield of such cultivars from 1974 to 1976 was 1.5 tons ha^{-1}. Over the same period the mean yield of early cultivars was 0.8 tonnes ha^{-1} (Sheldrake and Narayanan, 1979a). However, in north India, for example at New Delhi, during the same season, early cultivars often give yields of 1.5 to 2 tonnes ha^{-1} and sometimes over 3 tonnes ha^{-1}, and also produce considerably more dry matter than either early or medium cultivars grown in Peninsular India (e.g. Manjhi et al., 1973; Ahlawat, 1981). These differences may be due to the generally warmer conditions in the pigeonpea growing regions of the North during the monsoon season. The growth of pigeonpea is greatly influenced by temperature (Figure 11.8) and, in controlled environment studies with mean temperatures in the

Figure 11.8 Pigeonpea plants (cv. ICP-7220) after growing for 35 days under four different temperature regimes in controlled environment cabinets with a daylength of 12 hours. Day/night temperatures were, from left to right, 24/20, 24/24, 28/24, and 28/28 °C. (Reproduced by courtesy of Dr H. G. McPherson)

range 20 to 28 °C, has been found to have a Q_{10} of about 2.5 (H.G. McPherson, personal communication).

In traditional cropping systems, the highest pigeonpea yields, exceeding 4 tons ha^{-1} (e.g. Singh and Kush, 1981), are obtained with late maturing cultivars, which grow well in frost-free regions of north central and north west India. Recently, however, extraordinarily high yields of as much as 4.5 tonnes ha^{-1} have been obtained with selected lines of early maturing (around 110 days) day netural pigeonpea grown under irrigated conditions in Queensland (Wallis *et al.*, 1981). These results show that the yield potential of pigeonpea in intensive cropping systems is considerably higher than previously thought.

All these yield data refer to the grain formed at the end of the first reproductive period, when the crop is usually harvested. However, if the plants are ratooned they go on to produce a second flush of pods, unless increasing daylengths prevent flowering. In one trial at Hyderabad early cultivars after ratooning gave a second harvest yield which was about the same as the first harvest yield, around 600 kg ha^{-1}. Medium duration cultivars, which had a first harvest yield of 1300 kg ha^{-1}, gave a ratoon yield of 640 kg ha^{-1} (Sharma *et al.*, 1978). In Queensland ratoon yields

as high as 3.5 tons ha^{-1} have been obtained from irrigated day neutral lines (Wallis *et al.*, 1981).

HARVEST INDEX

The harvest index of pigeonpeas grown in traditional cropping systems is generally low. For example in the normal season at Hyderabad in 1974, the mean harvest index for cultivars was 0.34 and for medium cultivars 0.24 (Sheldrake and Narayanan, 1979a). These values exclude fallen leaves; when these were taken into account, the harvest indices were even lower — for medium cultivars between 0.15 and 0.20 — and would be lower still if the root system were included in the calculations.

Harvest index is unlikely to be of much value in itself as a selection criterion for cultivars showing increased partitioning of dry matter into seed. Apart from anything else, it is strongly influenced by environmental conditions. It is lower in plants grown in dense populations than in wide spacings (Narayanan and Sheldrake, 1979; Rao, I. M. *et al.*, 1981a), and lower in sole cropped pigeonpeas than in comparable intercropped plants. In an experiment at Hyderabad, for example, the harvest index of pigeonpea grown alone was 0.19 compared with 0.32 in an intercrop (Natarajan and Willey, 1980a). Moreover, it is lower in the normal season than in plants grown in the cool post-rainy season, when the plants are smaller and mature sooner (Akinola and Whiteman, 1974a; Narayanan and Sheldrake, 1979). Indeed, in this season, in irrigated plants it can be as high as 0.50 (I.M. Rao and N. Venkataratnam, unpublished data), indicting that under certain conditions the efficiency of partitioning of dry matter into seeds is comparable to that of chickpea and other physiologically annual crops.

YIELD COMPONENTS

Although there are large variations among cultivars in seed size and seed number per pod, within a given cultivar these are remarkably constant; the most important variable determining yield is pod number per plant, or rather pod number per unit area (Hammerton, 1971; Akinola and Whiteman, 1974b; Rao, I. M. *et al.*, 1981a; Rowden *et al.*, 1981).

An analysis of the yield components within racemes and branches shows that earlier formed pods, which in morphologically indeterminate cultivars are produced at the more basal nodes of the branches (Figure 11.3), and later formed pods, at the more apical nodes, contain almost the same number of seeds. Moreover, the seeds are of almost the ame average weight (Figure 11.9; Sheldrake and Narayanan, 1979b). This is in striking contrast to the pattern in annual legumes such as chickpeas, where the earlier formed pods are bigger than the later formed pods, containing more and heavier seeds (Sinha, 1977; Sheldrake and Saxena, 1979).
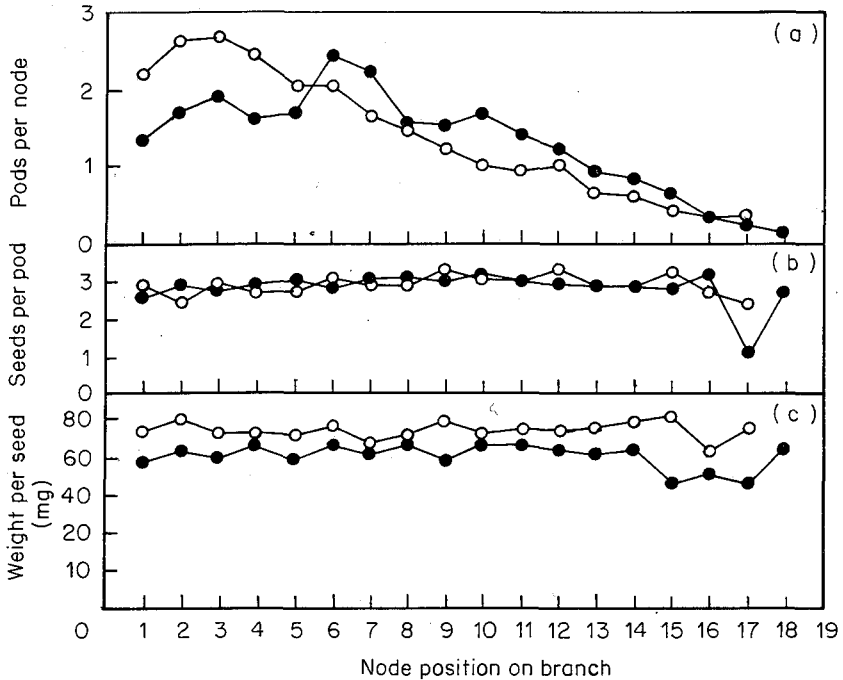
Figure 11.9   (a) Number of pods per node, (b) number of seeds per pod, and (c) weight per seed at different node positions (numbered from the most basal reproductive node) on primary branches of a medium duration pigeonpea (cv. ICP-1) grown on Vertisol (●) and on Alfisol (○) at Hyderabad in the normal season. (From Sheldrake and Narayanan, 1979b)

The fact that in pigeonpeas the later formed pods are so similar to earlier formed pods indicates that the plants set just as many or few pods as they are capable of filling. For if they set *more* pods than they are able to fill completely, then the later formed pods will inevitably contain fewer and/or smaller seeds.

POD SET

The great majority of the flowers of pigeonpeas — often as many as 90 per cent — are shed without setting pods (Pathak, 1970; Ariyanayagam, 1975; Sheldrake, *et al.*, 1979; Tayo, 1980; Pandey and Singh, 1981).

This is not explicable simply in terms of a shortage of assimilates. On the basis of measurements of photosynthetic rates in pigeonpea leaves and using a computer model, Rawson and Constable (1981) have concluded that 'carbon availability within the whole plant at flowering is considerably in excess of that required for pod setting'. They have calculated that if all the carbon fixed after

flowering were put into pods, the yield would be about 1.8 times higher. The fact that a high proportion of assimilates accumulated during the reproductive phase is partitioned into vegetative structures rather than pods is, of course, shown directly by growth analysis (Figure 11.7; Sheldrake and Narayanan, 1979a; Natarajan and Willey, 1980a), and has also been demonstrated by studies of the distribution of ^{14}C photosynthetically assimilated from $^{14}CO_2$ (Cheema and Pandey, 1980).

So why do so many flowers drop off without setting pods? Possible reasons include damage by pests, inadequate pollination, competition from earlier formed pods and other sinks within the plant and intrinsic physiological mechanisms connected with the perennial nature of the plants.

Effects of flower removal

This problem has been invstigated experimentally by removing earlier formed flowers and pods. In field experiments carried out at Hyderabad in the normal season, removal of all flowers and young pods for up to 5 weeks after the beginning of flowering had little or no effect on final yield. The flowering period of the deflowered plants was extended and their senescence delayed; they compensated for the loss of earlier formed flowers by setting pods from later formed flowers (Figure 11.10). The flower removal treatments had relatively little effect on the number of seeds per pod or weight per seed (Sheldrake et al., 1979).

These results are in harmony with the finding of Pandey and Singh (1981) that removal of up to 80 per cent of the flowers throughout the reproductive period had no significant effects on yield or yield components; they conform too with the results of Tayo (1980), who found that pigeonpea could compensate completely for the loss of all developing pods for up to 2 weeks after the beginning of flowering.

The fact that in all these experiments the removal of earlier formed flowers and pods resulted in the setting of pods from later formed flowers that would otherwise have dropped off indicates that the reasons for flower abscission are primarily physiological and cannot be accounted for in terms of pest attack or inadequate pollination.

Effects of defoliation

In experiments with field-grown pigeonpeas at Hyderabad, plants were partially or completely defoliated throughout the reproductive phase. Not surprisingly, when most or all of the leaves were removed, the yield was reduced. The interesting feature of these results was that the yield reductions were almost entirely due to a decrease in pod number per plant; seed number per pod and 100-seed weight were affected very little (ICRISAT, 1976, 1977).
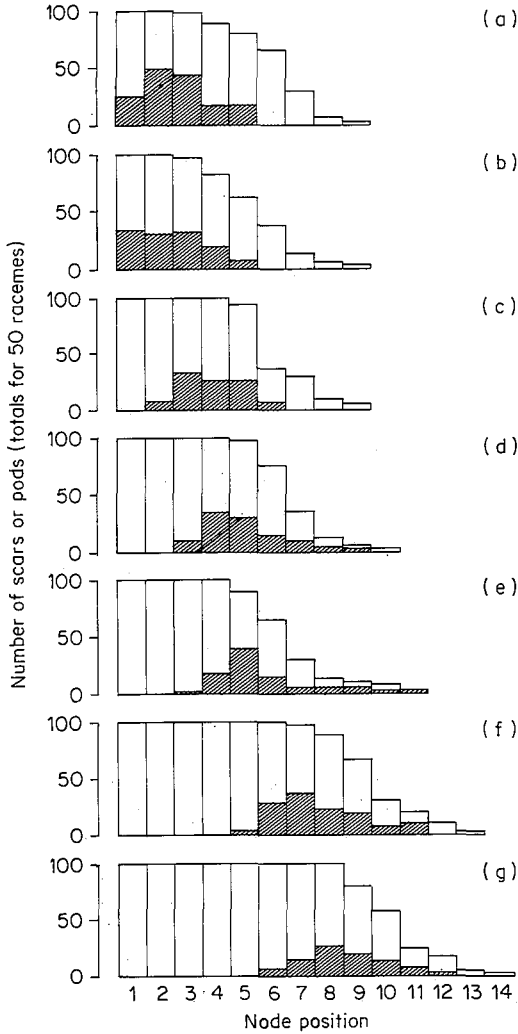
Figure 11.10 Effect of flower removal for
different periods of time on the pattern of pod set
on racemes of a medium duration pigeonpea (cv.
ST-1) grown at Hyderabad in the normal season.
The nodes within the racemes are numbered
from the most basal (proximal) node. Each node
gave rise to two flowers. □ scars; ▨ pods.
Deflowering period: (a) (control), (b) 1 week, (c)
2 weeks, (d) 3 weeks, (e) 4 weeks, (f) 5 weeks,
(g) 6 weeks. (From Sheldrake *et al.*, 1979)

Similar results were obtained in defoliation experiments by Hammerton (1975) and Pandey and Singh (1981).

A model of the physiological factors influencing pod set

The fact that fewer pods develop when the plants are defoliated indicates that pod set depends on the supply of photoassimilates; and the remarkable stability of seed number per pod and of 100-seed weight (under given climatic conditions) shows that pod setting is adjusted in such a way that fewer pods are set than the plants are capable of filling; there seems to be a threshold level of assimilate supply below which pod setting does not take place.

This writer has developed a working hydrodynamical model which illustrates some of the main factors which may be involved in the control of pod set (Sheldrake, 1979). The source is represented by water in a reservoir connected to a horizontal tube, representing the axis of a branch or raceme (Figure 11.11). The pods are sinks, represented by containers of limited capacity arranged in sequence, as if on successive nodes of a branch or raceme. These 'pods' are joined to the axis by tubes with a short ascending and longer descending limb, which create a siphon; the height of the siphon above the axis represents the threshold level of nutrients required for pod set.
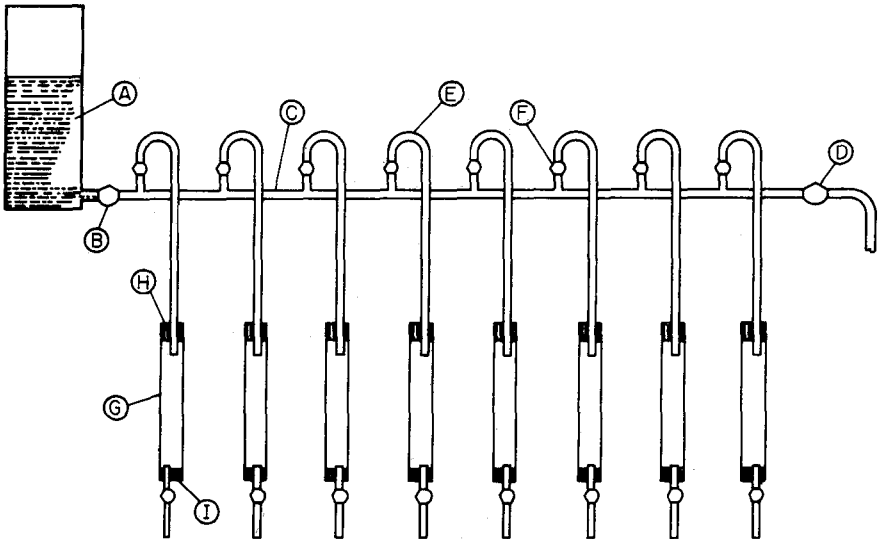

Figure 11.11   A hydrodynamical model of pod set in pigeonpeas (from Sheldrake, 1979): A, reservoir containing water; B, gate valve to axis; C, axis; D, gate valve at end of axis controlling flow into vegetative sinks; E, flexible tube forming a siphon with variable threshold levels; F, gate valve in tube; G, wide receiving tube representing a pod; H, stopper with air outlet; I, stopper with water outlet tube, for emptying pod at the end of an experiment

The beginning of the reproductive phase is represented by turning on the tap between the reservoir and the axis. The water level rises in the ascending limbs of the tubes connecting the axis to the 'pods'; one or more of the 'pods' begins to fill; as a consequence the water pressure within the axis falls and the filling of other 'pods' is inhibited until the first developed 'pods' are full. The level of water in the ascending limbs of the siphons then rises again and another 'pod' begins to fill. These processes continue until the level in the reservoir falls below the threshold of the siphons.

This model is, of course, very crude and could be improved in various ways. I believe that hydrodynamical models of this general type are not only able to represent the relationships between sources and sinks within plants, but that they may also cast some light on the actual mechanisms of source–sink interactions. The movement of assimilates from leaves and from storage tissues takes place in phloem, probably by mass flow down a pressure gradient (Milburn, 1975). Source activity must influence the hydrostatic pressure and pressure gradients within the system, while competition among sinks must be influenced by the cross-sectional area of their functional phloem connections and by the capacity of the sinks. A high flow rate into one sink may reduce flow into competing sinks by lowering the hydrostatic pressure in the connecting phloem strands.

The thresholds for pod set cannot, of course, depend on actual siphons within the plant. It is possible that this threshold effect depends on rates of influx of phloem sap into fertilized flowers, influencing the rate of development of ovules and pods. If these develop fast enough, their strength as sinks will be increased both by their increased size and hence capacity to take up more assimilates, and also through the hormone-mediated induction of more vascular tissue within the pedicel. However, if they develop too slowly, the production of abscission-promoting hormones within them may outweigh the production of abscission- inhibiting and vascular-tissue-promoting hormones (such as auxin), and thus they may drop off (Sheldrake, 1979).

In summary, the control of pod set probably depends both on the supply of assimilates and other nutrients, and also on hormonal factors. The role of the latter may be local, affecting processes such as abscission and vascular differentiation, while the relationships among sources and sinks may depend primarily on the hydrodynamics of the phloem.

PHYSIOLOGICAL ASPECTS OF YIELD IMPROVEMENT

Some of the ways in which physiological research may be able to contribute to the improvement of pigeonpea yield through both breeding and agronomy have been discussed by Lawn (1981), who emphasized the importance of understanding the differential responses of cultivars to different environments, or in other words genotype X environment interactions. An example of such

interaction is in the influence of daylength and temperature on flowering. An ability to predict the phenology of the plants is of great help in choosing which cultivars should be grown in a given environment and cropping system. Of course, breeders and agronomists are already aware of this, but little is yet understood about temperature effects and their influence on adaptation.

Temperature may have differential quantitative effects on growth and yield over and above its influence on flowering and crop duration. This is suggested, for example, by the fact that in the post-rainy season in peninsular India, early cultivars grow and yield much less well than medium or late cultivars, to an extent that cannot be accounted for by their shorter growth duration, which in this season differs little from that of cultivars in the other maturity groups. The reason may be that early cultivars have been selected in the warmer conditions prevailing in the monsoon season and are less well adapted to the cooler conditions of the post-rainy season, when medium and late cultivars normally produce their flowers and pods (Narayanan and Sheldrake, 1979. See also examples of temperature adaptation in common beans, Laing *et al.*, Chapter 9 of this book).

New cropping systems

Physiological research has a role to play in the development of new cropping systems and the selection of cultivars for use within them. The recent development in Queensland of intensive cropping systems using a photoperiod sensitive medium duration cultivar, cv. Royes, provides a good examples of this principle. Investigations on the effects of temperature and daylength have enabled mechanized production systems to be developed which enable high yield to be obtained both in the first harvest and in ratoon crops. The systems take into account the very flexible nature of the plants and involve adjusting sowing dates and spacings in such a way that the plants do not grow too tall and flower as synchronously as possible, making the control of insect pests by pesticide sprays easier to schedule, and facilitating mechanical harvesting (Wallis *et al.*, 1975, 1979, 1981). Physiological research has also played a major part in the development by the same Australian group of very high yielding cropping systems, referred to above, involving early maturing day neutral lines (Wallis *et al.*, 1979, 1981).

In north India, a promising system currently being studied in irrigated areas involved the sowing of early cultivars in April or May, a month or two before the normal time of planting. This both gives considerable yield advantages and also enable the pigeonpeas to be harvested earlier, in good time for the planting of a post-rainy season crop such as wheat (Panwar and Yadav, 1981). The identification of more or less day neutral cultivars well adapted to high temperatures may enable this new system to be exploited even more effectively.

The growing of pigeonpeas in the cool post-rainy season has recently received much attention in India (Mishra and Mishra, 1978; Narayanan and Sheldrake, 1979; Sharma, R. P. R., et al., 1981; Narayanan et al., 1981a), Australia (Akinola and Whiteman, 1974a) and the West Indies (Spence and Williams, 1972; Hughes et al., 1981). Under these short day conditions, the reduced duration and growth of the plants enables them to be grown at high population densities and to be managed more like an ordinary annual crop than is possible with the tall woody shrubs produced by planting around the time of the longest day.

A perennial extension of this system is currently being explored at ICRISAT. Pigeonpeas grown at high population density in the post-rainy season are harvested by ratooning and left in the field. Many of them survive the hot dry summer, and develop rapidly when the rains begin, giving another crop of pods at the end of the rainy season. This system could be of advantage in large areas of peninsular India with heavy black soils, which are often left fallow during the monsoon season, largely because of the uncertain onset of the rains and the difficulty of working the land when it is wet. Carrying over a pigeonpea crop from the previous post-rainy season avoids these problems and enables the land to be used productively in the monsoon. Such a system has only recently become feasible with the identification of cultivars resistant to the sterility mosaic and wilt diseases (Nene et al., 1981), which otherwise tend to build up and devastate the crop.

The perennial nature of pigeonpeas can be exploited in other cropping systems by ratooning, as mentioned above, but here too diseases can be a major problem. There are considerable cultivaral differences in ratoonability and disease susceptibility after ratooning (ICRISAT, 1976; Sharma et al., 1978).

The intercropping of pigeonpeas is a traditional cultural practice, but has only recently become the subject of scientific study. One important problem is to identify plant types (of appropriate phenology) which are well suited to such systems. Experiments carried out over several years have shown that the performance of cultivars in a sole crop is not highly correlated with their performance as an intercrop. A statistical analysis showed that only 40 to 51 per cent of the variation in intercrop yields could be accounted for in terms of variation in sole crop yields, indicating that intercropping performance depends on some plant characters not associated with sole crop yield. One such character may be the ability to spread out after the removal of the intercrop, and the data suggest that cultivars which produce more and longer branches and which are spreading rather than upright in habit are better suited to intercropping (Rao, M. R. et al., 1981).

Tolerance of adverse conditions

The identification of cultivars tolerant of adverse conditions can play an important role in increasing both yield and the stability of yield.

Some of the regions in which pigeonpeas are grown, or in which they could be grown, are affected by soil salinity. The identification and selection of cultivars tolerant to moderately saline conditions would therefore be of value and preliminary observations at ICRISAT have shown that there are considerable cultivaral differences in salt tolerance. Simple screening procedures are at present being worked out (Rao, I. M. et al., 1981b).

In the semi-arid tropics, heavy rainfall during the wet season can result in waterlogging, especially in the poorly drained soils on which pigeonpeas are often grown (Reddy and Virmani, 1981). There are striking cultivaral differences in waterlogging tolerance (ICRISAT, 1976) and screening methods for selecting tolerant cultivars and breeders' lines are now under development at ICRISAT.

Studies on the ability of plants to compensate for damage to leaves, flowers, and pods have already yielded results of relevance to pest management. However, little attention has so far been paid to anatomical and physiological aspects of disease and pest resistance; this is an area in which cooperative research between physiologists, biochemists, entomologists,, and pathologists could well be of value.

Studies on drought tolerance in this crop have so far been extremely limited (e.g. Sinha, 1981). One problem in taking up this kind of research is in defining what kind of tolerance is needed. In the normal growing season, pigeonpeas may be subjected to intermittent water stress during the rainy season, but in the post-rainy season, when medium and late cultivars enter their reproductive phase, they depend almost entirely on residual soil moisture. Under these conditions, moisture stress is of a different kind, no longer intermittent but inexorable and progressive. The same is true for pigeonpeas grown as a post-rainy season crop without irrigation.

Presumably, routine yield tests carried out under rain-fed conditions already tend to favour the selection of drought tolerant cultivars; in fact field screening seems to be the most reliable way of obtaining an integrated measure of drought tolerance. No doubt many factors are involved, including the depth and activity of the root system, the anatomy and morphology of the shoot system, the pulvinar movements of the leaves, the pattern of stomatal opening, and the ability of the plants to undergo osmotic adjustment (Lawn, 1981). The study of any of these in isolation seems unlikely to lead to a reliable method for predicting the relative drought tolerance of cultivars under field conditions.

The improvement of yield potential

An important physiological limitation to yield in pigeonpeas appears to be that the plants have an inbuilt mechanism (which can be modelled hydrodynamically, as discussed above) preventing them from setting enough pods to exploit the available supply of assimilates to the full. This suggests that yield could be improved by attempting to develop lines in which pod set is increased, and

which therefore partition a higher proportion of available assimilates into seeds. Until some advance has been made in this direction, attempts to select and breed for higher photosynthetic efficiency seem likely to be of limited value, quite apart from the practical difficulties of obtaining reliable measurements under standardized conditions on the basis of which cultivars can be ranked (for a discussion of some of these problems, see Rawson and Constable, 1981).

The mechanism limiting pod set seems to be related to the plants' intrinsically perennial nature; probably most, if not all, polycarpic species have some comparable mechanism. Presumably its function is to retain a sufficient supply of assimilates and other nutrients to maintain the functioning of the roots, to tide the plants over unfavourable seasons, and to provide reserves for new growth.

The yield potential of pigeonpeas would almost certainly be raised if their physiology could be transformed from that of perennials to that of annuals. This would involve a lowering of the threshold for pod set; the resulting plants would consequently produce more pods than they could fill completely, and the later formed pods would therefore contain fewer and/or smaller seeds than the earlier formed pods. The ratio of weights of early formed to later formed pods can in fact be used as a simple assay system for physiological annuality. In all cultivars tested so far, this ratio has been close to 1:1 (Sheldrake and Narayanan, 1979b), indicating their intrinsic perenniality. This is, of course, also shown by their survival after the maturation of the pods.

In the absence of any truly annual types among the existing cultivars, there are three possible ways in which this change might be achieved:

(1) gradually, by crossing high yielding cultivars with each other in the hope that various threshold lowering characteristics can be combined and accumulated, thus producing lines which progressively approximate to a physiologically annual condition. Such types might in due course emerge from existing breeding programmes in which yield is used as a primary selection criterion.

(2) by crossing pigeonpeas with annual species of related genera. Unfortunately it has not so far been possible to obtain progeny from crosses with the putatively annual species, but little effort has yet been expended in this direction. - ·

(3) by induced mutation. There seems to be no basis for estimating the chances of success of this method; for example, no-one knows how many genetic changes might be involved in the transition from the perennial to annual type. However, it seems worth giving it a try; and progeny of plants grown from seed treated with chemical mutagens or mutagenic radiation are at present being screened at ICRISAT.

The transition from perenniality to annuality (or, more generally, from polycarpy to monocarpy) has occurred countless times in the evolution of the

flowering plants. Many genera contain both annual and perennial species; for example, in *Cicer*, the chickpea genus, there are 31 perennials and 8 annuals (van der Maesen, 1972). so the goal of producing physiologically annual pigeonpea cultivars does not appear to be unreasonable and provides a hopeful prospect for increasing the yield potential of the crop.

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