

43

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## A HYDRODYNAMICAL MODEL OF POD-SET IN PIGEONPEA (*CAJANUS CAJAN*)

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### SUMMARY

In pigeonpeas (*Cajanus cajan* (L.) Millsp.), most flowers are shed without setting pods. Pod-set is reduced by shading, defoliation and the presence of already developing pods, probably because of the reduced availability of assimilates or other nutrients. In pigeonpeas, unlike most leguminous crops, the average weight per pod of earlier and later formed pods is the same; this indicates that pod-filling is not limited by nutrient supply. Pod-set seems to be controlled in such a way that fewer pods develop than the plants are capable of filling. These processes can be represented by a simple working model, in which the assimilate supply corresponds to water in a reservoir, the axis of a branch or a raceme to a horizontal tube connected to the reservoir, and pods to containers of limited volume at a lower level; the connecting tubes between the axis and the 'pods' have an ascending limb, shorter than the descending limb to the pods, creating a siphon. 'Pods' can 'set' only when the level of water in the reservoir is higher than the threshold of the siphon; during the filling of earlier-set 'pods', the setting of other 'pods' is inhibited by the reduction of pressure within the axis. This model may provide a crude representation of mass flow within the phloem from sources to sinks; it also illustrates some of the hydrodynamical factors involved in competition among sinks.

### INTRODUCTION

Pigeonpeas (*Cajanus cajan* (L.) Millsp.) generally flower profusely, but most of the flowers are shed without setting pods. The factors which lead to the abscission of flowers, and to a lesser extent of young pods, are primarily physiological. Under normal conditions, most pods develop from earlier-formed flowers, but if these flowers are removed, pods are set from later-formed flowers which would otherwise have abscinded, indicating that developing pods have an abscission-promoting effect (Sheldrake, Narayanan and Venkataratnam, 1979). Similar results have been obtained with yellow lupins (van Steveninck, 1957), cowpeas (Ojehomon, 1970) and soybeans (Tayo, 1977).

The simplest explanation for these observations would be in terms of a competition for assimilates or other nutrients. However, in yellow lupins, van Steveninck (1957) found that even in the absence of competition from earlier-formed pods not all the later-formed

flowers were capable of setting pods, suggesting that other factors were also involved; these may have included inadequate vascular connections (van Steveninck, 1957) and damage by insects. With cowpeas, Ojehomon (1972) showed that the removal of developing pods did not prevent the abscission of flowers which opened on the same day, indicating that the abscission-promoting effect was already in operation before flower opening; indeed these flowers had already suffered a retardation of ovule development. Such results are consistent with a nutrient-competition hypothesis, but could also be interpreted in terms of abscission-promoting hormonal influences of developing pods on flowers within the same inflorescence (van Steveninck, 1957, 1958; Ojehomon, 1972); the evidence is equivocal. However, in pigeonpeas, if there are any abscission-promoting hormonal effects of developing pods on subsequently formed flowers, they seem to be relatively minor compared with the effects of nutrient competition, for the following reasons. Firstly, the repeated removal of all flowers from racemes at alternate nodes results in approximately twice the normal number of pods setting on the untreated racemes (Sheldrake et al., 1979); similarly, the repeated removal of all flowers from alternate branches results in a compensatory setting of pods from flowers on the other branches (Narayanan and Sheldrake, unpublished results). Comparable observations have been made with soyabeans (Hicks and Pendleton, 1969). Secondly, in morphologically determinate cultivars of pigeonpeas, fewer racemes per plant are produced than in indeterminate cultivars, but the determinate cultivars have many more pods per raceme (Sheldrake and Narayanan, 1979 a). In these cases, the formation of more pods per raceme is simply explicable in terms of a reduced competition from other racemes, but would be difficult to explain on the hypothesis that the abscission of later-formed flowers is primarily caused by hormonal factors from pods developing in the same raceme.

The importance of nutrient supply in determining the extent of pod setting is clearly demonstrated in experiments involving defoliation or shading of the plants. In pigeonpeas, defoliation during the reproductive phase reduces the yield by reducing the number of pods per plant, but has little or no effect on seed number per pod and weight per seed (Hammerton, 1975; Anon, 1978). Shading the plants, throughout the reproductive phase reduces the pod number per plant with no significant effect on seed number per pod or 100-seed weight (Narayanan and Sheldrake, unpublished results). Similarly in lupins (van Steveninck, 1958) and cowpeas (Anon, 1975), defoliation results in reduced pod-set and yield.

In herbaceous legumes such as *Vigna aureus* and chickpeas, later-formed pods are smaller than those which develop earlier in the reproductive phase, indicating that pod-filling is limited by nutrient supply (Sinha, 1977; Sheldrake and Saxena, 1979). By contrast, in pigeonpeas, the average weights of earlier- and later-formed pods are the same; the yield is limited by the number of pods set, rather than by the ability of the plants to fill the pods (Sheldrake and Narayanan, 1979 a). The reason pigeonpeas, unlike most leguminous crops, set fewer pods than they are capable of filling may be related to their intrinsically perennial nature; sufficient vegetative growth and nutrient reserves are maintained during the reproductive phase for the plants subsequent survival (Sheldrake and Narayanan, 1979 b).

The evidence reviewed above shows that in pigeonpeas the number of pods set depends on the supply of assimilates or other nutrients, but 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 nutrient supply below which pod setting does not take place. These relationships can be illustrated by a simple hydrodynamical model.

### THE MODEL

In this working model, the 'source' is represented by water in a reservoir; in the plant the source would depend firstly on the area and photosynthetic activity of the leaves, and secondly on the reserves of starch stored in the stems and roots. During the reproductive phase of the plants the leaf area declines and the starch reserves are depleted (Sheldrake and Narayanan, 1979 b); the resulting decline in nutrient supply is represented by the falling level of water in the reservoir.

The reservoir is connected to a horizontal tube, representing the axis of a branch or of a raceme (Fig. 1).

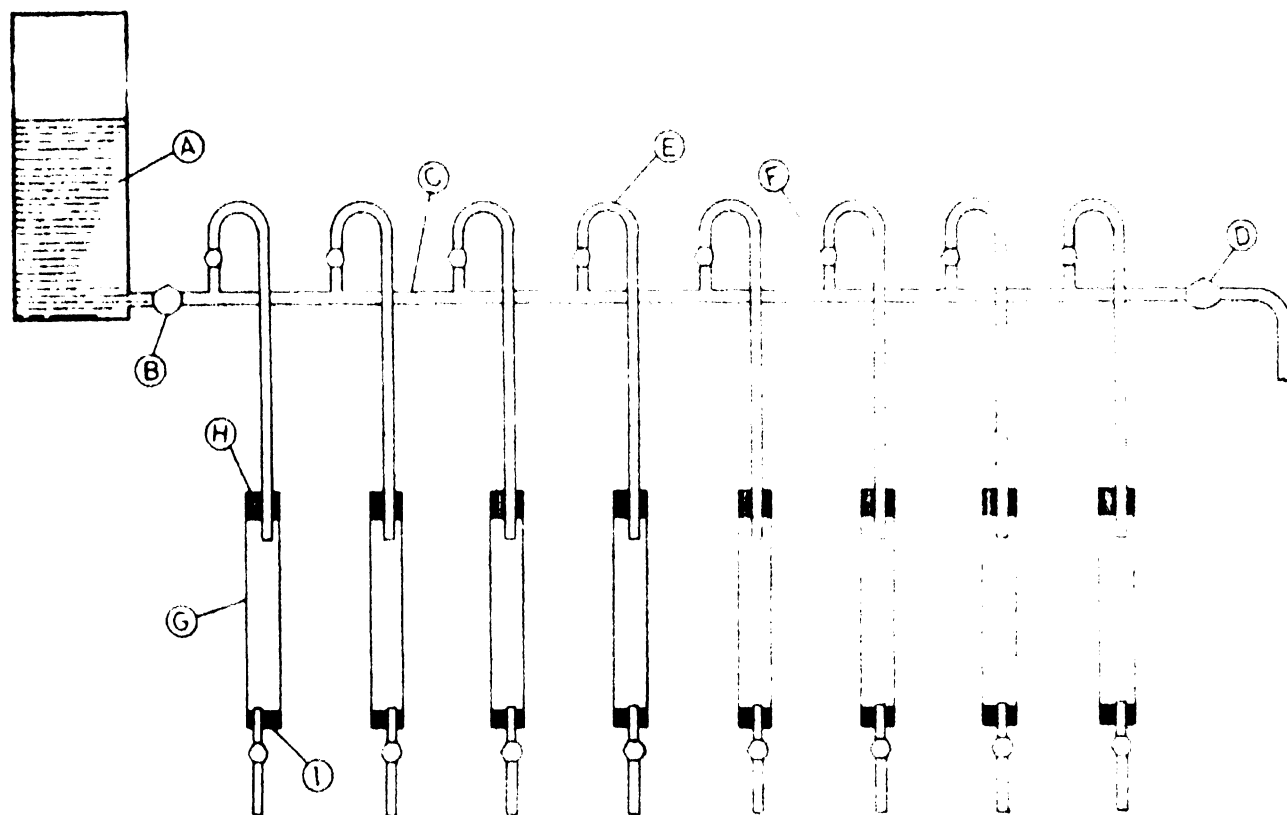


FIG. 1. A hydrodynamical model of pod-set in pigeonpeas.

- 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 level.
- 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.

Pods are sinks, represented by containers of limited capacity. In practice, these can be made of lengths of bicycle inner-tubing, or of wide tubes of glass or transparent plastic stoppered with rubber bungs. A small hole or a hypodermic needle inserted in the upper part of each 'pod' allows the outflow of air as the 'pod' fills with water.

The 'pods' are arranged in sequence, representing successive nodes of a raceme or of a branch. The '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. The rate of flow in these tubes can be regulated by taps or screw-clips.

The beginning of the reproductive phase can be represented by turning on the tap between the reservoir and the axis (or by turning off the tap at the distal end of 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' or 'pods' begin to fill. These processes continue until the water level in the reservoir falls below the threshold of the siphons.

In this model, the filling of the 'pods' is an 'all or none' process. The following factors control the numbers of pods set, and consequently 'yield':

- (i) The initial level of water in the reservoir: A lower level (simulating, for example, the effects of shading or of moisture stress) results in the 'development' of fewer 'pods'.
- (ii) The cross-sectional area of the reservoir: A wide reservoir can fill more 'pods' than can a narrow reservoir with the same initial level of water. The wider reservoir represents a larger plant, with a greater leaf area and/or more stem reserves.
- (iii) The height of the threshold: If this is lowered more 'pods' set. In the limiting case there is no threshold; if the total sink capacity of the 'pods' exceeds the amount of water in the reservoir, 'pod-filling' continues until the reservoir is empty. Under these circumstances, some of the 'pods' fill completely; others, at more distal 'nodes' fill only partially. This simulates the reproductive behaviour of herbaceous legumes such as chickpeas (Sheldrake and Saxena, 1979).
- (iv) The size of the 'pods': If the size of the 'pods' is reduced, more 'pods' are set; conversely if the capacity of the 'pods' is increased, fewer are set. These differences resemble those between small- and large-podded cultivars, which bear many or few pods per plant respectively.
- (v) The diameter of the tubes connecting the 'pods' to the axis: If this diameter is reduced, there is less pressure-drop within the axis when a 'pod' begins to fill. Consequently several 'pods' may begin to fill simultaneously, whereas with a wider diameter the filling of a single 'pod' results in a pressure-drop which inhibits the initiation of 'pod filling' at other 'nodes', and can also lead to the 'abortion' of pods whose siphons were just about to begin functioning. The simultaneous filling of several 'pods' results in higher 'yields'.

because they all continue to fill when the water level falls below the threshold level of the siphons. In the plant, the cross-sectional area of the vascular connections in the pedicel may have analogous effects.

- (vi) Competing sinks: 'Pod set' can be reduced or prevented by opening the tap at the distal end of the axis, representing the flow of assimilates to vegetative sinks.

This model could be improved in various ways. For example, a continued flow of water into the reservoir would represent continuing photosynthesis; after pod-filling had stopped because the water level fell below the threshold, the continued influx would raise the level above the threshold again, and pods would again be set, crudely simulating the 'second flush' of flowering and pod-setting which occurs in most pigeonpea cultivars after the first reproductive phase comes to an end (Sheldrake and Narayanan, 1979 b). It would be better still if feed-back from the 'vegetative sinks' controlled the rate of flow into the reservoir; this would represent the influence of continued leaf development on assimilate supply.

Another improvement would be a gradual increase in the diameter of the tube leading to a 'pod' during the process of 'pod-filling'; this would model the progressive increase in the cross-sectional area of the vascular tissue in the pedicel during pod development (S. S. Bisen and A. R. Sheldrake, unpublished results). The sequential opening of flowers in the pigeonpea could be modelled by the sequential opening of the connections to the 'pods', the connections could be closed again if the 'pods' did not begin to fill within a defined period, simulating flower abortion and abscission.

#### DISCUSSION

This simple model illustrates several features of pod development in pigeonpeas, and in particular shows how the 'all or none' pattern of pod-set could depend upon a threshold level of nutrient supply. The presence of such a threshold may be related to the perennial nature of these plants (Sheldrake and Narayanan, 1979 a). In chickpeas, which are annuals, yield is limited by the ability of the plants to fill the pods rather than by the numbers of pods set (Sheldrake and Saxena, 1979), suggesting that pod-set does not depend on a threshold level of nutrients, or that this threshold is low. It seems possible that this difference between pigeonpeas and chickpeas may reflect a fundamental physiological difference between polycarpic and monocarpic plants: the former may be characterised by relatively high nutrient thresholds for fruit-set, whereas the latter may have relatively low thresholds, or none at all.

A hydrodynamical model may be able to represent not only the overall relationships between sources and sinks within the plant, but also something of the mechanism of source-sink interactions. The movement of assimilates and other nutrients from leaves and from storage tissues occurs in the phloem. Phloem translocation takes place from sources to sinks, and probably involves a mass flow down a pressure gradient (Milburn, 1975). Source activity must influence the hydrostatic pressure and the pressure-gradients within the system; competition between sinks must be influenced by the cross-sectional area of the functional phloem connections to the different sinks and by the capacity of the sinks. A high flow rate into one sink may reduce flow rates into competing sinks by

lowering the hydrostatic pressure in the connecting phloem strands.

The cross-sectional area of the vascular connections to a developing organ increases as a result of vascular differentiation. Vascular differentiation is regulated by basipetally moving auxin and gibberellin (Sachs, 1969; Hess and Sachs, 1972; Siebers and Ladage, 1973). These hormones are produced in developing organs themselves (Sheldrake, 1973). Hence the growth and development of a sink increases its own strength as a sink not only by providing a greater sink capacity, but also through the induction of more vascular connections. Such sinks may be of indefinite growth, like vegetative shoots, or finite, like fruits; in both cases competition among them depends on processes of positive feed-back.

Sinks which fail in this competition may either persist, like axillary buds under apical dominance, or they may be lost, like flowers and young pods of pigeonpeas. The shedding of these organs depends on the development of an abscission zone. Abscission is influenced by ethylene and other hormones (Addicott, 1970; Cooper and Henry, 1973). The threshold level, represented by the siphons in Figure 1, may be primarily related to the sensitivity of the abscission zone to such factors. Whether or not a given flower or young fruit abscinds may depend on the relative rates of production of abscission-promoting and abscission-inhibiting hormones within the flower or fruit. It is possible, for example, that an insufficient influx of phloem fluid may retard the rates of development of the embryonic tissues relative to the death of the nutritive tissues within the ovules. Different hormones may be produced during these processes (Sheldrake, 1973); thus a change in the relative rates of the death of nutritive tissues and the growth and differentiation of embryonic tissues may change the balance of hormones produced, and could result in a hormonal balance which has an abscission-promoting effect.

These speculations illustrate that it is not necessary to consider that the control of pod-set must depend *either* on nutrient supplies *or* on hormonal factors; both are probably involved, but the role of the latter may be local, influencing processes such as abscission and vascular differentiation, while the relationships between sources and sinks, and competition among sinks, may depend primarily on the hydrodynamics of the phloem.

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