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The evolutionary diversity of the pulses

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In the very limited sector of the plant kingdom that includes the world's crop plants, three groups stand out as of particular importance, the grasses, the brassicas and the legumes. Of these I am to discuss the legumes, and I will begin by defining their contributions to agriculture. The family Leguminosae has the special characteristic that its members are able to participate in a symbiotic relationship with a group of bacteria that can oxidize atmospheric nitrogen. The symbiosis occurs in outgrowths of plant and bacterial tissue on the roots, the root nodules. The leguminous plant contributes the products of photosynthesis to the bacteria, and the bacteria contribute the products of nitrogen fixation to the plant, in which they are used in the synthesis of living tissue.

The Leguminosae are among the most successful—if not the most successful—families in the plant kingdom, and it may well be that their access to supplies of newly fixed nitrogen is the secret of their success. They have a world-wide distribution, and there is to be found in the family every kind of plant form from the great hardwood timber trees of the tropical rain forests to the herbs of temperate region pastures. The advantage of nitrogen availability is evident on the one hand in the Mora forest in Trinidad, and on the other, on newly excavated road cuttings on English motorways. The soils of the Mora forest will grow little but Mora. The great forest trees maintain a closed nutrient cycle in a heavy rainfall area, and a supply of nitrogen must be of great importance to their economy. On the motorway banks, where top soil has been removed, among the first and most successful colonists are clovers, and their ability to supplement mineral nutrients from the subsoil with nitrogen gained by fixation must contribute substantially to their success. Intermediate between these extremes I have seen small leguminous trees of the genus *Glyricidia* used to re-establish vegetation on eroded hillsides in St Vincent. They grew from stakes planted in bare subsoil, and for success it was necessary to inoculate each planting hole with a watery mash made by crushing well nodulated roots from established trees.

The section of the family that is of agricultural importance is the Papilionoideae, the 'pea family'. Their value to agriculture is twofold. First, they provide nitrogen-rich plant material for consumption by man and by his livestock, and secondly they leave nitrogen-rich residues in the soil, and thereby enhance the productivity of other crop plants grown either with them in mixed stands or following them in a crop rotation. The food and feed they supply is of three kinds, forage (leaf, stem and green pods) for livestock, legumes (green pods and unripe seeds) and pulses (ripe, dry seeds) for human consumption. Forage does not concern us in this symposium, but it is worth noting that leguminous plants contribute substantially to the animal protein consumed by man through the leguminous forage plants that are used in pastures, and hay and silage crops.

The Papilionoideae are classified in ten botanical groups. Of these, six (*Loteae*, *Galegeae*, *Podalyrieae*, *Genisteae*, *Sophoreae* and *Dalbergeae*) are of little agricultural interest, contributing only some minor forage plants, a few dye and drug plants, some cover crops such as lupins and sann hemp, and some tropical timbers. The agricultural value of the four important groups is summarized in Table 1.

Table 1. *The agricultural uses of four groups of the Papilionoideae*

Distribution and chromosome number*	Forage plants	Pulses and legumes
I. *Vicieae*		
7, 8, 14 Mediterranean and temperate Eurasia	Twining or sprawling herbs *Vicia*, *Lathyrus*. Annual tares and vetches	Twining or bushy annual herbs. *Lens* (lentils), *Pisum* (peas), *Cicer* (chick pea), *Lathyrus sativus*. Strong-stemmed upright herbs. *Vicia faba* (broad bean, horse bean)
II. *Hedysareae*		
7, 8, 9, *10*, *11*, 14, 20 Mediterranean and temperate Eurasia. Occasionally America	Twining and sprawling perennial herbs. *Lespedeza*, *Desmodium*. Upright short-lived perennial herbs. *Onobrychis* (Sainfoin)	Sprawling or bushy annual herbs. *Arachis* (groundnut)
IV. *Trifolieae*		
7, *8*, 9, 14, 16 Mediterranean and temperate Eurasia. Occasionally America	Upright perennial herbs. *Trifolium* (clovers), *Medicago* (lucernes) *Melilotus*	
IX. *Phaseoleae*		
10, *11*, 12 World-wide	Pulse species often used for forage	Twining or bushy annual herbs. *Glycine* (soya), *Lablab* (lablab, lubia), *Phaseolus* (numerous species of beans and grams). *Vigna* (cowpea). Strong, woody-stemmed upright bushes. *Cajanus* (pigeon pea).

*Haploid numbers. Common numbers are shown in italic.

Only species with large seeds are of value as pulses and legumes. These are confined to two groups, the *Vicieae* and the *Phaseoleae*, with a single genus, *Arachis* the groundnut, in the *Hedysareae*. Many of the pulse crops are used for forage, but the important forage species are the clovers and lucernes of the group *Trifolieae*. Some minor temperate region forage plants belong in the *Vicieae*. Interest in tropical and subtropical forage plants has developed greatly in recent years, and genera in both the *Hedysareae* and the *Phaseoleae* have been added to the range of crop plants in both America and Australia.

Domestication

Pulse crops were domesticated very early in history, in both the major centres of origin of agriculture. Peas, beans and lentils are among the early domestications in the Old World. Helbaek (1966), discussing the food plants of the earliest agriculture in the Middle East, wrote:

'At Aceramic Hacilar and the somewhat later Jarmo, pea, vetchling and lentil were established. So also the Beidha farmers desired the seeds of this family. The traces are few but unmistakable: one imprint of the large vetch *Vicia narbonense* was found, two of a medic, *Medicago* sp., and dozens of Cock's comb, *Onobrychis cristagalli*.'

The Hacilar and Beidha remains date about 7500 to 6500 BC. Renfrew (1966) described seeds of *Pisum* (Peas), *Vicia* (bean/vetch) and *Lens esculenta* (lentils) from Aceramic Neolithic sites in Thessaly in Greece. The Aceramic Neolithic in Greece cannot yet be dated with confidence, but Renfrew wrote: 'In Thessaly the first notable event is the "arrival" of the Aceramic Neolithic farmers with their almost complete repertoire of cultivated cereals and pulses'. She went on to record the known finds of food crops from Neolithic and Bronze Age sites and concluded: 'It is also interesting to note that the pulses were also grown from the beginning and that the beans in particular became very important during the late Bronze Age.'

In the New World, MacNeish (1964) and Kaplan & MacNeish (1960) have reported the use of common beans (*Phaseolus vulgaris*), runner beans (*Phaseolus coccineus*) and tepary beans (*Phaseolus acutifolius*) throughout prehistory from the beginnings of agriculture in Central America, and lima beans (*Phaseolus lunatus*) likewise from the earliest times from western South America. *Arachis* (groundnut), which is South American in origin, has been found by Engels (1960) in preceramic remains dated about 1000 BC in Peru.

The remaining group of pulses is the Afro-Asian group. This includes the African *Vigna*, or cowpea, and *Cajanus*, or pigeon pea, the Indian species of *Phaseolus* with small seeds, and *Lablab* or lubia, and the Chinese *Glycine*, soya bean. All these species are indigenous in areas to which agriculture was introduced from the Middle East, and it is most probable that they were taken into cultivation by the early colonists as farming peoples spread outwards from the centre of origin of Old World agriculture. The need for such new domestications arose as man moved out of the climatic regions in which he invented farming. As he moved westward he took his crop plants with him throughout the Mediterranean and up into western Europe, as Renfrew noted. When he went south and east, he moved beyond the climatic limits of his temperate crop plants. In Africa he domesticated sorghum, finger millet and bulrush millet to replace wheat and barley, and pigeon pea and cowpea to replace peas and beans. In India he took in rice to replace wheat and barley, and grains of the genera *Phaseolus* and *Lablab* to substitute for peas and beans.

The beginnings of domestication must have been no more than the adoption of wild plants that had some desirable characters. There is an indication of the early stages of the process in Helbaek's (1966) account of the Beidha material, where *Vicia narbonensis*, a *Medicago* and an *Onobrychis* were found. The medic and the *Onobrychis* must have been relegated to the pastures at an early stage and the *Vicia narbonensis* probably soon gave place to *Pisum* and *Vicia faba*. But these were the beginnings. The promising species must have been sorted out very early. Smartt (1969) has shown that in the New World *Phaseolus* species, the cultivars are each conspecific with a readily identified wild species. This seems to be the pattern among the pulses. At least the greater part of the species differentiation took place before domestication. This latter involved changes in the growth habit of the plants, in cropping capacity, in size and quality of seed and seed pods, and in chemical composition.

Growth habit

All the pulse crops are herbs, with the exception of *Cajanus*, which is a woody shrub. Primitive types and wild species are almost always much-branched, scrambling perennials, with fibrous or even woody stems. They are very commonly photoperiodic in their flowering, and their yield is determined by an annual fruiting episode, limited in duration by the day length response. Gentry (1969) has given an account of the wild forms of *Phaseolus vulgaris* still to be found in Central America. They are annual or short-lived perennial climbing vines, which grow in shrubby secondary vegetation, germinating in the shade and reaching the sun by twining and scrambling over the larger and more woody components of the vegetation. They produce small beans, which must have been a source of food to pre-agricultural peoples. Indeed the wild beans are still collected and eaten by the poorer families.

Smartt (1969) has made a study of the range of plant type in the common bean *Phaseolus vulgaris*, and has shown that there has been a clear evolutionary sequence in the development of the cultivated forms. First, the apical dominance of the main stem was established, and the much-branched scrambling form of the wild ancestor gave place to the single-stemmed or occasionally branched climbing or 'pole' bean. This was well suited to growing in mixed crops with maize, in which the beans gained support and access to light by twining on the maize stems. For growing in pure stand, however, the pole beans suffer the disadvantage that it is necessary to stake them. Moreover, it was no longer an advantage to climb, since there was no competition for light from tall plants. A 'bush' habit then became desirable, and bush beans arose in two genetically distinct ways. A single gene difference governs the difference between indeterminate growth, with the main stem apex growing on as long as the plant persists, and determinate growth in which the main stem apex is terminated by an inflorescence after about five to seven nodes have been produced. Alternatively, bush types have arisen by the development of plants with very short internodes. The apex remains vegetative, but after about ten nodes, elongation ceases and the plant is effectively non-climbing.

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There has been further elaboration on these basic patterns. A determinate plant, for example, may be so weak or 'floppy' as to require staking to keep the pods off the ground. Selection under cultivation has further modified the basic bush pattern to give a fairly stout plant which will stand upright under its crop, at least in a full plant stand. The latest stage in this evolution of habit is the current emphasis on a good upright habit with the crop borne clear of the ground, for mechanical harvesting of green pods for the frozen food trade.

The evolutionary sequence is particularly well illustrated in *Phaseolus vulgaris*, since all the main stages in it are well known and have to be grown in culture and studied genetically. The sequence is characteristic of the pulse crops, and can be observed in a wide range of species. In the lima bean (*Phaseolus lunatus*), the runner bean (*Phaseolus coccineus*) and the tepary bean (*Phaseolus acutifolius*), most of the stages are to be found, though in the lima bean and the runner bean the bush type has not yet become so dominant as in the common bean, *Phaseolus vulgaris*, and in the tepary the determinate type is not known. In the groundnut (*Arachis*) the situation is somewhat different, as the primitive types are creeping, and not scrambling. Nevertheless, the selection pressure under domestication has been towards more compact, bushy types, and the most advanced forms suited to the agronomic circumstances of modern mechanized agriculture are very compact, upright plants with no creeping laterals at all.

Among the Old World pulse crops, changes in habit following domestication are not so widespread. Horse beans (*Vicia*) and pigeon peas (*Cajanus*) are stout upright herbs or subshrubs. Soya beans are also upright herbs, though among the more vegetative types the remains of the twining habit of the related wild species are still to be seen. In the peas (*Pisum*) the demands of large-scale farm cultivation with mechanized harvesting have led to a major change in habit in the past 25 years. The gardener was well suited by the tall, lax, slow-fruiting types that climbed up pea sticks and yielded a picking for the table daily over a substantial period. The farmer growing peas as a dry pulse wanted a type that would ripen all its pods in a short time for efficient harvesting. The processor, harvesting peas green for freezing, must have a variety that will bring all or nearly all its peas to the right stage of development and tenderness at the same time. So the lax and leisurely varieties have given place to dwarf, quick-cropping bush types very like the bush types of the common bean that are likewise grown for processing.

Many of the pulse species are dependent on day length for the initiation of flowering. Tropical species such as the New World *Phaseolus* cultivars tend to flower in short days only, and spread into north temperate regions has depended on the selection of genetically day-neutral types. In the soya bean a range of types exists, responsive to the range of day lengths found throughout the range of the species, from short-day types in the tropics to long-day types adapted to the climatic regime of Manchuria. In breeding it is necessary either to select for response to the day length of the area in which the crop is to be grown, or to breed day length neutral types in which there is a morphologically predetermined pattern of development, irrespective of day length.

Seed characteristics

A change that has almost universally followed domestication in crop plants is the elimination of seed dispersal mechanisms. In the pulses seed dispersal is by the sudden shattering of the seed pods as they dry. Primitive types have fibrous pods which dehisce on drying, the two valves of the pod twisting as they become free, and casting the ripe seeds over some distance from the parent plant. This involves substantial losses in harvesting, and types with leathery instead of fibrous pods have been selected which only dehisce on threshing. In the common bean and the runner bean this line of development has been taken further, with great reduction or elimination of fibrous tissue, giving a tender fleshy pod that is eaten as a green vegetable.

All these changes have led to an increase in yield potential. In the small, compact bush types, the proportion of the products of photosynthesis available for seed production is greater than in large, scrambling or creeping plants. There is the countervailing consideration that such plants have no reserves on which to mount a second season's growth, but this is of little significance since the annual habit is in general agriculturally convenient. The elimination of the photoperiodic response releases the farmer from dependence on the pattern of the seasons. And the elimination of seed dispersal ensures that the grain produced can all be harvested. In addition to these yield factors, there is also the very generally observed increase in seed size that has been brought about by selection under domestication. Smartt (1969) estimated that, in the New World species of *Phaseolus*, the cultivated forms produce seeds from four times to ten times the weight of the seeds of their wild relatives.

Chemical composition and nutritive value

Considering first the Leguminosae as a whole, the family produces a wide range of biochemical substances that are not of nutritive value. Dyes from *Indigofera*, fish poisons and insecticides from *Derris* and *Tephrosia*, perfume and flavouring from *Tonka* and fibre from *Crotalaria*, are all products of the Leguminosae. Among the pulses, some races of the sieva beans (*Phaseolus lunatus*) produce cyanogenetic glucosides that can be poisonous, and the common bean (*Phaseolus vulgaris*) contains a trypsin inhibitor. The elimination of such deleterious characters is a task in which the plant breeder must be joined by the biochemist, for the breeder can only breed for characters that he can measure, and these characters can only be measured by biochemical techniques.

The pulses are valued chiefly for their seed proteins, and most of the successful vegetarian diets of the world depend on a balance between a carbohydrate source—a cereal or a root crop—and a high-protein balancer from one or more pulse crops. Kaplan (1967) has pointed out that the good lysine and tryptophan content of the protein of the common bean makes it a satisfactory balancer for maize, zein (the maize protein) being deficient in these two amino acids. In the Old World, a range of Indian pulse crops provides the balance for diets based on wheat in the north, sorghum and finger millet on the dry lands of the peninsula, and rice on the wet lands. In China, Korea and Manchuria, soya bean, with a very favourable amino acid balance, complements wheat and rice.

Two pulse crops, soya bean (*Glycine*) and groundnut (*Arachis*), are two of the world's most important oilseed plants. It is an interesting sidelight on the factors determining success as a crop plant that the Mediterranean countries are increasingly using soya and groundnut oil in place of olive oil. Indeed, the labour costs in harvesting a tree crop like olives are such that one may foresee a time when ancient olive orchards give place to soya beans, planted annually, and combine-harvested.

These are the circumstances in which the pulse-crop breeder must work. He must breed short-term, erect, robust, quick-ripening plants that will meet the demands of 20th century agronomy. He must make use of the resources of biochemistry and breed for amino acid composition and enzyme constitution that will improve the nutritive value of pulses in relation to the carbohydrate sources to which they will be matched.

He has a further opportunity, particularly in relation to the needs of developing countries. The symbiosis whereby the Leguminosae gain nitrogen compounds from the *Rhizobia* in the root nodules is not always an efficient process. Some *Rhizobia* do not fix nitrogen, and many *Rhizobia* are narrowly restricted in the hosts they will infect. Legume nitrogen is the cheapest nitrogen in the world. It costs a developing country neither the capital for a chemical industry nor the foreign exchange for imported fertilizer. Hence the intricate and difficult breeding project of selecting an efficient combination of legume host and rhizobial symbiont for the production of effective root nodules is one of first importance for the tropical world.

I have taken the point of view of the plant breeder, but the breeder does not work alone. I have pointed out his growing need for assistance from the biochemist. Obviously he must collaborate closely with the nutritionist. That there are problems for the agronomist to solve is evident. But I want beyond all these to plead for the help of the humble and undervalued profession of domestic science. If we are to use the world's pulses to improve the world's nutrition, we need also the expertise of the cook and the housekeeper.

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