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by K. O. Rachie and L. M. Roberts

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GRAIN LEGUMES OF THE LOWLAND TROPICS

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I. Importance and Production

Grain legumes form a major component of lowland tropical cropping systems. Several species are utilized throughout the wet and dry tropics both in monoculture and complex multiple cropping and bush-fallow practices. More than two dozen species are grown to lesser or greater extent depending on the specific uses required of each, but all share similar desirable features. The universal ability to grow vigorously under a wide range of environments and on poor soils without supplemental nitrogen is particularly advantageous in subsistence agriculture in remote areas. The quick growth of some annuals like cowpeas and dry beans, the high consistent productivity of soybeans and peanuts, and the extended fruiting habit of long duration viny species (yam, lima, and velvet beans) and woody perennials (pigeon pea, jack bean, and locust bean) are complementary advantages in complex bush-fallow farming systems.

Legumes have several advantages over other food plants in their simplicity of preparation and multiplicity of edible forms, such as tender green shoots and leaves, unripe whole pods, green peas or beans, and dry seeds. Some species, for example, the Mexican yam bean, produce edible tubers in addition to the fruit, and the winged bean is reputed to be utilizable as seedlings, tender green leaves, green pods, dry seeds, and tubers. The excellent nutritional values of most legumes in terms of proteins, calories, vitamins, and minerals are highly complementary in tropical diets comprised of roots and tubers, plantains, cereals, indigenous vegetables, fruits, and minimal animal proteins. Legume seed proteins are also the least expensive, most easily stored and transported, nonprocessed proteinaceous food concentrate for both rural and urban utilization.

A. The Protein Shortfall

Plant sources contribute about 70% of the world's protein needs, but in many developing countries in the torrid zones this proportion can be even higher, up to 90%. Cereals contribute two-thirds of all plant proteins consumed directly; grain legumes, 18.5%; and other sources (roots, tubers, nuts, fruits, and vegetables), 13.5%. The production of plant proteins from

all sources in 1968 was 153.8 millions of metric tons, or 43.0 kg per capita, but developing countries of the Far East had only 24.1 kg and Africa only 26.0 kg per capita (Tahir, 1970).

1. Nutrition and Climate

Human nutrition often seems to deteriorate proportionately with the decline in elevation and increase in mean annual rainfall. In Nigeria the availability of both protein and caloric energy decreases from the drier north to the subhumid west and humid southeast. In a survey carried out in 1963–1964 by FAO (1966), it was found that both energy (2719 cal per day) and proteins (80 g per day) were adequate in the semiarid northern region, but were below recommended nutritional levels in the west (1909 cal and 40 g protein per day), and in the southeast (1774 cal and 33 g of protein per day). Whereas cereals comprised 64% of caloric intake in the north, roots and tubers made up 53 and 68% of the energy sources in the west and east, respectively.

The effects of unbalanced nutrition in areas where energy sources may be adequate can be more dramatic. In some humid and subhumid intermediate elevations like Uganda (1000–1200 m) where carbohydrates are more than adequate (3000–4000 cal per day), but proteins are inadequate, there may be as many as five malnourishment deaths per 1000 population—primarily in postweaning children.

It might appear that semiarid lowlands and higher elevations with lower population pressures, and where cereals and pulses are more easily cultivated and stored, are better off nutritionally, except that statistics seldom reflect the vulnerability of subhumid and semiarid regions to vagaries of the climate and cyclical famines, which have tended to hold the populations down in the first place. The acute famines in West Africa and Southern Asia in 1972–1973 illustrate this problem. Most vulnerable are those segments of the agricultural society—including nomadic graziers—primarily dependent on domestic animals for their livelihood since they exploit the most arid, and hence, climatically volatile, regions. When a drought continues for more than one season, they begin losing their younger, breeding stock, and recovery may require several years.

2. Constraints

Tropical grain legumes have evolved under high stress conditions or are not genetically capable of responding to favorable growing conditions, and therefore they do not attain reasonable yield levels and good product quality under high temperatures and extreme moisture conditions. In this situation, survival even at low productivity levels is probably more important to both the plant and the peasant cultivator than high yields.

a. Hazards. Among many hazards limiting productivity in the tropics are pests, diseases, moisture extremes, high temperatures, low insolations, inadequate or unbalanced plant nutrients, and poor soil conditions. These problems may be exacerbated by inefficient plants types with low yielding potential, susceptibility to insects, nematodes, and diseases, soils with extreme pH levels, poor physical structure, and depleted fertility, and poorly distributed rainfall. When it is not possible to relieve these constraints through better management, such as pest control, it may be essential for the plant to have resistance or genetic escape mechanisms like the slowing or cessation of growth processes during dry periods, deep rooting habit, indeterminacy, and photoperiod sensitivity.

b. Utilization. Most grain legumes have some specific nutrient deficiencies like the sulfur-bearing amino acids, or contain certain undesirable off-flavors, flatus factors, metabolic inhibitors, alkaloids, and other toxic substances. Nevertheless, some otherwise well-adapted, high-yielding and nutritious species are not utilized as a consequent of ignorance or unfamiliarity with their culture and methods of preparation. For example, soybeans with 2–3 times the yielding potential, 60% more protein and 20 times more oil than indigenous legumes have not been accepted in the African tropics in spite of their repeated introduction since the 1920's. Major deterrents are primarily unfamiliarity with production practices and utilization. However, high world demand for this commodity and urgent need for vegetable oils and animal feedstuffs is providing considerable incentive for increasing tropical soybean production—first, as a cash crop for export and industry, and later for domestic use.

B. World Production

Production of tropical food legumes is highly complex owing to the density and distribution of population, climatic/environmental considerations, large numbers of species involved, and inadequacy of available information. Therefore, a cursory analysis has been made on grain legume production and population in tropical regions based on information in Volumes 24 and 25 of the FAO Production Yearbook (1971–1972) in order to gain perspective on the problems involved and establish priorities in pulse improvement programs. In this analysis the tropics are defined as countries with the greater part of their territories lying between the Tropics of Cancer and Capricorn. Thus, in the Americas, Mexico is included on the North, but Argentina, Chile, and Uruguay are omitted in the south; in Africa, countries north of the Sahara, and South Africa are omitted; and in southern Asia, India is included, but Pakistan, Bangladesh, Taiwan, and Australia are omitted (Rachie, 1973; Rachie and Silvestre, 1974).

1. Populations in the Tropics

In 1970 approximately 1.36 billion people or 36.6% of the world's population lived in the tropics. The vast majority, or about 24%, are in Southern Asia, with India making up nearly two-thirds of the 848.5 million people in that region. Tropical Africa and Latin America contribute almost equally to the remainder—260 million (7.2%) and 240 million (6.7%), respectively.

2. Production Trends

The worldwide production of all grain legumes increased by 49.1% in area and 103.4% in production between 1948–1952 and 1971. This represents a proportionately greater increase than for cereals and roots and tubers during the same period. It is further observed that 111.6 million metric tons of grain produced on 117.5 million hectares was about 23% above the production for 1961–1965. However, a considerable proportion of this increase (almost 60%) is attributable to the rapid expansion of soybean cultivation in North America. Further increases are anticipated in 1972 and 1973. Preliminary estimates for 1973 project soybean production at 52.8 million tons on 38.3 million hectares. This would increase total world grain production by 4.12 million tons (3.7%) to 115.7 million metric tons, allowing for a decline of 412,000 tons of peanuts and dry beans in that year.

Producing Regions. Among tropical regions (all elevations) in the early 1970's, southern Asia contributed 20 million tons of dry grain on 33 million hectares, while tropical Africa and Latin America harvested about 8 million tons each on 12 and 10 million hectares, respectively. Increases in estimated grain legume production in the intermediate/high versus lowland tropics for three separate periods over a 22-year period are presented in Appendix Table I. Production increased by 47.5% in area and 89.7% in tonnage for all elevations between 1948–1952 and 1971. Lowland tropical legumes increased by about two-thirds between 1948–1952 and 1961–1965; and to 190% of 1948–1952 yields by 1971, when production attained 21.6 million metric tons on 33.3 million hectares.

Chick-peas (5.7 million tons) and dry beans (5.5 million tons) constituted two-thirds of total pulse production at intermediate and high elevations whereas peanuts (13.0 million tons in shell; or 8.7 million tons kernels) comprised about 40% of all lowland tropical grain legumes in 1971. Pigeon peas were probably the most important lowland pulse, with nearly two million metric tons of estimated production; although the Asian grams collectively were higher (2.5 million tons) in 1971. Proportionately, soybeans increased more rapidly at intermediate to high elevations record-

ing a 5-fold increased production between 1961–1965 and 1971. At low elevations, cowpeas more than doubled in production between 1948–1952 and 1961–1965 and by 2.5 times by 1971. The Asian grams increased similarly in the lowland tropics by reaching 2.3 times their 1948–1952 production in 1970.

3. *Distribution of Species*

More than a dozen species contribute to the production of grain legumes in tropical regions. Of these, dry beans (*Phaseolus vulgaris*), chick-peas (*Cicer arietinum*), some of the soybeans (*Glycine max*), dry peas (*Pisum* spp.), lentils (*Lens esculenta*), and broad beans (*Vicia faba*) are clearly cool weather and, hence, intermediate-to-high elevation species and are so classified. Similarly, pigeon peas (*Cajanus cajan* Millsp.), cowpeas (*Vigna unguiculata* Walp.), peanuts (*Arachis hypogaea*), and the Asian grams (mung beans, black gram, rice beans, hyacinth bean, moth, and others included in the "dry beans" category for southern Asia) are usually grown at lower elevations. However, soybeans do occur in both ecologies—at least in southern Asia.

Most of the important lowland legumes perform better in the subhumid to semiarid tropics, as evidenced by results and experience in East and West Africa. Among the better known species, pigeon peas seem to occur over a wider range of moisture conditions, while soybeans may have greater tolerance for wet soils than do cowpeas and groundnuts. This implies that grain legumes are not planted as extensively and other protein sources are utilized or available statistics do not accurately reflect the true situation. It is suggested that all three assumptions apply to varying degrees and that per capita intake of proteins is often much lower in humid than in semiarid tropical regions. However, it is also becoming evident that several less familiar species other than those mentioned above are utilized in the humid tropics but are not accounted for in production estimates. Some of these will be described and discussed further in the following sections (see Appendix Table II).

a. Peanut-Producing Regions. Peanuts are more important than all other lowland tropical legumes combined, contributing 13 million tons in shell (about 67% seeds) or about 40% of the total production on the basis of net seed weights. However, peanuts are mainly grown as a cash crop for industrial processing of oil and cake, rather than for direct consumption. Therefore, pigeon peas, cowpeas, and mung beans may contribute more directly to human diets even in areas where the peanut is a major crop.

Several countries, led by India, contributed 54.5% of the world crop and 77.4% of the tropical production in 1971. In southern Asia, India (31.4%), Indonesia (2.6%), and Burma (2.8%) contributed 36.8%; in

Africa, Nigeria (6.0%), Senegal (5.2%), and Sudan (1.9%) made up 13.1%; and, in Latin America, Brazil produced 4.6% of the world crop. Between 1961–1965 and 1971, total production in the Americas increased by 36.6%, in Africa by 7.8%, and in Asia (omitting mainland China and the USSR) by 18.0%.

b. Pigeon Peas. India produced 1.84 million metric tons of dry grain on 2.65 million hectares in 1971 for 93% of the world crop. Other producers were Uganda (2.0%) and Malawi (1.0%) in Africa, Burma (1.4%), and Dominican Republic (1.1%). Considering unreported and "kitchen garden" plants for home use, these statistics may be underestimated by as much as 10–15%, thereby increasing total world production to as much as 2.25 million metric tons.

c. Cowpeas. Africa produced 94.8% of the world crop of 1.14 million metric tons in 1971. Major growing countries were Nigeria (61.2%), Niger (13.1%), Upper Volta (7.4%), and Uganda (5.5%). However, it is quite possible this production was underestimated by 10–15% considering unreported and "kitchen garden" plantings. This would increase world production by as much as 170,000 metric tons to 1.31 million tons.

d. Asian Grams. Mung beans or green gram and close relatives—black gram, yellow gram, rice bean, and moth bean, which have recently been reclassified as *Vigna* species (Verdcourt, 1970) and possibly horse gram (*Dolichos biflorus*), hyacinth, or field bean are presumed reported under "dry beans" in statistical reports. The worldwide tropical production of these species is estimated at 2.7 million metric tons on 8 million hectares, of which probably 80% is grown in India where black gram (mash or urad) production is estimated at 0.44 million tons on 1.5 million hectares, green gram (mung) at 0.30 million tons on 1.4 million hectares and horse gram at 0.39 ton on 1.8 million hectares.

e. Unspecified Commodities. The category "other and unspecified" species may include both common and less familiar species and are estimated at 80% for lowland tropics or 1.6 million tons from 3.3 million hectares. India is the main producer in this category, with an estimated 70% of the total.

II. Botanical

The food legumes are classified in the Order Leguminosae, and predominantly in the large Family Papilionoideae having 480 genera and 12,000 species, which are widely distributed in both tropical and temperate climates. However, a few economic species do occur in the second and third families of this order, Caesalpiniaceae with 152 genera and 2800 species, and Mimosaceae having 56 genera and 2800 species. The distinguishing

features of legumes are the following: (1) Leaves are usually alternate and compound, pinnate or trifoliate. (2) Flowers are predominantly hermaphroditic and usually with five sepals and five petals. (3) Ovary is superior with a single carpel, cavity, and style. (4) Fruit is usually a pod formed by a single carpel and dehisces by both ventral and dorsal sutures into two valves. (5) Seeds consist of two cotyledons and an embryo containing very little endosperm.

Papilionoideae is distinguished from the other two families primarily by the flower petals being imbricate (overlapping) with descending aestivation (order). The upper (adaxial) petal is exterior, usually largest, and forms the standard or vexillum. The two lateral petals are parallel, forming the wings or alae; and the two lowest petals are interior, usually joined by the lower margins to form the keel which encloses the stamens and ovary. There are normally ten stamens, and they may be either monadelphous (all united by filaments) or diadelphous with nine united stamens, the upper or vexillary stamen being free. The anthers have two locules and dehisce lengthwise by slits. The ovary is superior, consisting of one carpel, usually monolocular and sometimes with a false septum; the ovules may be one to many borne on the ventral suture (Purseglove, 1968).

A. Taxonomy

Papilionaceae is divided into twelve tribes, but nearly all of the economic grain legumes occur in VII, Phaseoleae. However, a few also occur in VII, Cicieae, and peanuts belong to IX, Hedysareae. The Phaseoleae may be herbs—erect, procumbent, or climbing; or subshrubs and even small trees. The leaves are pinnately foliate (rarely pentafoliate) and have a terminal leaflet; stipels are present, hairs are never medifixed, stamens are not broadened at the apex, and the ovary is surrounded by a disc. Hedysareae is distinguished from other tribes by having jointed fruits, constricted between the seeds and breaking transversely into one-seeded portions, and stipels are sometimes present (Hutchinson and Dalziel, 1958).

Key to the Genera of Tropical Grain Legumes

A simplified key to the warm weather lowland tropical legumes has been prepared and modified after Hutchinson and Dalziel (1958) and Purseglove (1968). Members of the pea family *Pisum, Cicer, Vicia, Lens,* and *Lathyrus*) are omitted as being cool season plants and confined mainly to intermediate and higher elevations or as winter crops in the subtropical and temperate regions. In this classification, the old world Asian grams (*Phaseolus mungo, P. aureus, P. radiatus, P. acontifolius, P. angularis,* and *P. calcaretus*) have all been transferred to *Vigna* Savi on the basis

of extensive taxonomic studies on foliage morphology, flower structure, pollen grain sculpture, serological tests and electrophoretic analysis of seed extracts as proposed by Verdcourt (1970). An adaptation of taxonomic keys to these lowland tropical species is outlined below:

A. Fruits ripening underground
- B. Leaves pinnate with four leaflets; leaflets without stipels; stamens monadelphous, flowers axillary and solitary; jointed fruits constricted between seeds ..... *Arachis*
- BB. Leaves trifoliate, not gland dotted; vexillary stamens free from near base upward; style bearded; calyx with short broad teeth ..... *Voandzeia*
  - C. Style glabrous; calyx deeply divided into narrow lobes ..... *Kerstingiella*

AA. Fruits ripening above ground
- B. Leaves trifoliate
  - C. Vexillary stamen free from base upward
    - E. Keel of corolla and style coiled through 360° (1–5 turns); pollen grains with no obvious sculpture; standard with transverse groove at the top of the claw usually without appendages (but sometimes two); fruit not separate ..... *Phaseolus*
    - EE. Keel and style arched or curved but not coiled more than 360°; stipules cordate or appendaged below base; pollen grains strongly reticulated
      - F. Stigma strongly oblique or introrse; roots not tuberous ..... *Vigna*
      - FF. Stigma on inner face of style, subglobose roots tuberous ..... *Pachyrrhizus*
  - D. Style glabrous, has terminal stigma
    - E. Keel and style bent inward at right angles, beaked
      - F. Stigma surrounded by a ring of hairs .... *Dolichos*
  - DD. Style bearded down one side; stigma without ring of hairs ..... *Lablab*
    - F. Stigma may have a ring of hairs, is laterally oblique, hooded or flattened and broad, more or less spatulate but not appendaged; keel not twisted; stems twining or erect ..... *Sphenostylis*
- BB. Trifoliate leaves gland-dotted underneath; lanceolate-oblong
  - C. Flowers yellow or orange, borne in subcapitate axillary racemes; vexillary stamen free from near base upward; ovules more than four; fruit obliquely subtorulose; erect, perenniating shrubs ..... *Cajanus*
- BBB. Trifoliate leaves not gland-dotted underneath
  - C. Vexillary stamen free from near base upward
    - E. Bracts and bracteoles small and inconspicuous caducous:
      - F. Keel longer than the standard petal; fruit hispid usually with stinging hairs; flowers in zigzag racemes, short racemes, or somewhat umbellate ..... *Mucuna*
    - FF. Keel shorter than standard petal

CC. Style glabrous; calyx four lobed, upper lobe entire or shortly two-toothed; nodes of raceme not swollen; standard mainly pubescent; very small flowers ..... *Glycine*

D. Vexillary stamen united in upper part with others, free below

E. Fruit square, four winged, 5–6 seeded; leaves 1–3 foliate, herbaceous climber ..... *Psophocarpus*

EE. Fruit not winged; many seeded; trifoliate

CCC. Nodes of raceme swollen; apex of fruit not hooked; stamens all fertile

D. Calyx lobes unequal in size, upper two rounded and larger than lower three, fruit broad, furrowed along the upper suture ..... *Canavalia*

E. Fruit 1–3 seed; nodes of raceme swollen; woody climber ..... *Dioclea*

B. Comparative Ecology

There are two major classes of tropical grain legumes: (1) Leguminous oilseeds, mainly peanuts and also soybeans, grown primarily in southeast Asia; and (2) pulses—pigeon peas, cowpeas, and mung beans/black gram. A secondary group of crops includes several species with localized use, undetermined potential or unavailable production estimates. Chief among the secondary category are hyacinth bean (*Lablab niger*), horse gram (*Dolichos biflorus*), lima beans (*Phaseolus lunatus*), yam beans (*Sphenostylis stenocarpa*), rice beans (*Vigna umbellata*), moth beans (*Vigna acontifolia*), and velvet beans (*Mucuna* spp.)

In terms of adaptation, these warm weather lowland species could be classified in the following categories (asterisk indicates major species):

I. Semiarid regions—annual precipitation less than 600 mm
1. Short duration cowpeas (*Vigna unguiculata*)*
2. Short duration groundnuts (*Arachis hypogaea*)*
3. Bambarra groundnuts (*Voandzeia subterranea*)
4. Moth bean (*Vigna acutifolia*)
5. Horse gram (*Dolichos biflorus*)
6. Cluster bean (*Cyamopsis tetragonolobus*)

II. Semiarid to subhumid regions—600–900 mm precipitation
1. Groundnuts—medium and long duration*
2. Cowpeas—medium and long duration*
3. Pigeon peas (*Cajanus cajan*)*
4. Mung beans (*Vigna radiata* var. *aureus;* var. *mungo*)*
5. Hyacinth bean (*Lablab niger*)
6. Horsegram (*Dolichos biflorus*)

III. Subhumid to humid regions—900–1500 mm precipitation
1. Pigeon peas—medium and long duration*
2. Cowpeas—medium and long duration*
3. Mung beans—medium and long duration*
4. Lima beans (*Phaseolus lunatus*)
5. Haricot beans (*Phaseolus vulgaris*)
6. Soybeans (*Glycine max*)

IV. Humid and very humid regions—above 1500 mm precipitation
1. Lima beans—climbing types
2. Yam beans (*Sphenostylis stenocarpa*)
3. Rice beans (*Vigna umbellata;* syn. *P. calcaretus*)
4. Velvet beans (*Mucuna pruriens* var. *utilis* and *M. sloanei*)
5. Pigeon peas—medium and long duration*

A precise definition of an ecology is difficult inasmuch as several factors besides mean annual rainfall are involved including: (1) rainfall pattern (bimodal or monomodal), (2) moisture distribution, (3) temperatures and cloud cover, (4) relative humidity, (5) soil moisture holding capacity, (6) soil fertility and physical structure, (7) prevalence of diseases and pests, and (8) interaction of the species genotype with the total environment. The range of genetic diversity within species is often considerable, sometimes exceeding variability between species. Characteristics like resistance to pests and diseases, quick germination, rapid growth, earliness, tolerance of high temperatures, deep rooting, indeterminancy, day-length sensitivity, yielding potential, and other heritable factors have profound influences on fitness for specific ecological situations.

Other aspects must be considered in assessing adaptation. The first is human preference and needs. Often a cultivator will grow a low-yielding, poorly adapted species and cultigen because he prefers its taste, requires the crop for some specific use, or has a cash market for its produce. Moreover, characterization of a particular ecological zone is based on long-term weather records. Therefore, fluctuations in "normal" patterns could result in successful cultivation of otherwise poorly adapted species or cultigens a certain proportion of the time, such as two years out of three seasons out of five. In practice two or more crops are frequently grown in a mixture established after long experience and specific needs, some of which will succeed—although not always the preferred ones. In other situations the grower might wait until the season is underway, or, based on preseason showers, plant more exacting, longer duration species and varieties.

In spite of the broad-range genetic diversity and adaptation within species, certain generalities can be assumed regarding botanical characteristics, tolerance of variable stresses, genotype X environment interactions and utilization. These are outlined for 16 genera and 24 species under four distinct ecological zones of the lowland tropics in Appendix Table III (Rachie, 1973).

III. Peanuts

There are two important leguminous oilseed crops: peanuts (*Arachis hypogea* L.) and soybeans (*Glycine max* Merr.). Peanuts are of major importance in the lowland tropics, comprising an estimated 60% of all

tropical grain legumes. In contrast, soybeans have a very minor role in lowland tropics, primarily in southeastern Asia. In Africa, not more than 50,000 tons of soybeans are produced annually in tropical areas as a consequence of lack of an established demand or preference for them as food and some basic problems of management. Nevertheless, the soybean demonstrates exceptional potential for the lowland tropics, and there is increasing demand for industrial protein sources for both human and animal nutrition in developing tropical countries. It is therefore highly likely that increasing emphasis will be placed on adapting and improving this crop for the lowland tropics.

A. Botanical

There are only about 19 species of *Arachis* indigenous to tropical and subtropical South America from the Amazon through Brazil, Uruguay and Argentina to about 35° south. The cultigen *A. hypogaea* L. has $2n = 40$ chromosomes and is unknown in the wild state; the other species have $2n = 20$ chromosomes, are wild and perennial, being used commercially only for forage. All species ripen their fruits underground (Purseglove, 1968). The Portuguese probably introduced the peanut to the west coast of Africa directly from the Caribbean region early in the sixteenth century, while the Spanish brought it from the west coast of Mexico to the Phillippines from whence it spread to Asia, Madagascar, and East Africa (Rachie and Silvestre, 1974).

1. Ecological

The highest yields of good quality groundnuts are obtained on well drained, light, sandy-loam soils with a pH above 5.0. Dark soils tend to stain the hulls, and heavy, clayey soils may become too waterlogged to allow optimum growth, or too hard for penetration of pegs (gynophores) and digging to harvest the crop. The most favorable climatic conditions are moderate rainfall during the growing season (annually 1000–3000 mm), plenty of sunshine, and reasonably high temperatures. The heaviest demand for moisture is from the beginning of blooming up to 2 weeks before harvest. However, it should be emphasized that peanuts are not well adapted to the more humid tropics (above 1300 mm) owing to the high incidence of diseases and pests, and other factors.

2. Description and Classification

The peanut plant is a low-growing annual with a central upright stem readily separated into bunch and runner types. In bunch or erect types the nuts are closely clustered about the base of the plant, whereas the runner types have nuts scattered along their prostrate branches from base to

tip. Several investigators, notably Gregory *et al.* (1951), Bunting (1955, 1958), Krapovickas and Rigoni (1960), Krapovickas (1968), and Gibbons *et al.* (1972) have contributed to the description and classification of the cultivated forms of *Arachis hypogaea.* Distinction between races based on the distribution and ramifications of vegetative and reproductive branches are described as follows:

A. Subspecies *hypogaea* Waldron: This includes the Virginia types. Inflorescences are simple and never borne on the main axis. The first bud of cotyledon axis is always vegetative, and branches have two vegetative and two reproductive buds alternatively and in succession. The main stem can be viny (runner types) or straight. In the latter form the plant presents a bushy appearance owing to the abundance of successive branches.
   1. Var. *hypogaea:* either viny or erect; the main stem is short (less than 40–50 cm) in viny forms; branches are rarely hairy; duration is rather long.
   2. Var. *hirsuta* Kohler: erect with long main stem (more than 100 cm); branches are very hairy; it is very late; and susceptible to *Cerospora* leaf spots.

B. Subspecies *fastigiata* Waldron: This group has sequential branches of the Spanish and Valencia types, but has few branches and the stem is always erect. Inflorescences always occur on the main stem, the first buds of the cotyledon axis are reproductive, and vegetative and reproductive buds succeed each other in an irregular series.
   1. Var. *fastigiata* type Valencia: the branches arising from the main axis do not have branches or branch only at their extreme ends; the inflorescences are simple; and the pods contain 2, 3, or 4 seeds.
   2. Var. *vulgaris* Harz type Spanish: the branches arising from the main stem do have irregular secondary branching; the inflorescences are complex; and the pods are two seeded.

The variety *hirsuta* is not widely grown, being mainly of botanical interest. Therefore, cultivated sorts can be classified as Virginia, Spanish, and Valencia. Although these have been extensively intercrossed and most advanced cultivars are intermediate, combining characters from all three forms, there appear to be certain associations of characters and categories of utilization, which can be described as follows:

A. Virginia: primarily runners or spreading types; indeterminate requiring 120–150 days growing season; small leaflets and foliage dark green in color; seeds markedly dormant (1–12 months); two seeds per pod; testa is deep russet brown; resistant to *Cercospora* leaf spot and some resist rosette disease; seeds reach maximum oil weight before total dry matter during maturation (Schenk, 1971); fat is higher in unsaturated fatty acids than for Spanish and Valencia varieties (Verhoyen, 1960; Gillier and Silvestre, 1969); protein content is lower than sequentially branched forms. These types have higher productivity potential, but require better growing conditions; they produce large fruits extensively used as an edible form.

B. Spanish-Valencia: sequentially branched, erect, bunch types; determinate, short season (90–110) days); leaflets larger than Virginia types, and foliage is lighter green; seeds are not dormant; pods have 2–6 seeds; Kernels have a wide range

of size and testa color; they are highly susceptible to *Cercospora* leaf spots; and they are higher in protein content and saturated fatty acids than Virginia types. Valencia cultivars can be readily distinguished from Spanish types by having more seeds per pod (usually 3 or 4), and thicker stems with a light reddish or purple tinge.

Virginia varieties produce larger fruits and have higher yielding potential than the Spanish and Valencia types, but are also more exacting in their requirements of moisture, insolation, temperature, and fertility levels. Therefore, production of the large-seeded edible forms is often restricted to the more favorable growing conditions, such as those of Georgia (USA), China, and Senegal (south), or to the irrigated areas of Egypt, Sudan, and Israel.

B. Plant Improvement

Improvement of the peanut has received considerably more attention than most other grain legumes except soybeans by virtue of its high oil content and industrial potential. Therefore, a substantial amount of information and literature is available on the crop. Since much of this knowledge is already available in various sources, including monographs, this section will deal primarily with some of the more recent literature pertinent to the lowland tropics.

1. Breeding Methodology

a. Floral Development and Pollination. The peanut flowers over a 4–6-week period beginning about 4–6 weeks after planting. One flower per inflorescence opens on a particular day, others opening successively from one to several days later. The flower bud reaches 6–10 mm in length 24 hours before anthesis, and pollination occurs at sunrise the following morning, coinciding with the time of petal expansion and occurring within the enclosed keel. There are two sterile stamens, four stamens with oblong anthers (dehisce first) and four shorter stamens with smaller globose anthers that elongate and dehisce later. The petals wither 5–6 hours after opening, and the calyx tube is shed, leaving the ovary and base of style forming the fruit.

The fruit elongates by means of intercalary meristem at the base of the sessile ovary forming a peg or carpophore. Cells at the tip of the ovary become lignified and conical in shape to facilitate penetrating the soil via geotropism to a depth of 2–7 cm. The pegs elongate rapidly, reaching a length of 15–16 cm within 7 days after flowering (Ono and Ozaki, 1971). The force exerted by peanut pegs has been measured at about 13 bars, but when grown in compacted soils crop yields are inversely proportional to soil hardness (Underwood *et al.*, 1971). After reaching maximum depth

the ovary swells rapidly and seeds form (Purseglove, 1968). Seeds reach their maximum size 40 days after flowering, but may require 60 days in Spanish types and 80 days or more for full fruit development in Spanish and Virginia types, respectively (Lin *et al.*, 1969).

b. Vicinism. Peanut flowers are almost totally self-pollinating and frequently cleistogamous. However, some outcrossing does occur and has been recorded in Virginia types at between 0.01 and 0.55% in the United States (Culp *et al.*, 1968), 0.20% in Senegal (Mauboussin, 1968), 1.67% in Makulu Red Eastern Africa (Gibbons and Tattersfield, 1969), and up to 6.6% in Spanish types grown in Java (Bolhuis, 1951).

c. Hand Crossing. Emasculation consists of removing the anthers the evening before dehiscence occurs. Crossing with desired pollen donors is carried out the following morning. Since numbers of F_2 seeds produced per cross are comparatively few, the F_1 may be propagated vegetatively from cuttings. However, cuttings must be taken from lateral branches—particularly in alternate branched (Virginia) forms—to assure production of inflorescences.

d. Breeding Techniques. Early breeding consisted mainly of mass selection within indigenous and introduced germplasm pools. This was followed by pure line selection and recombination of desirable parents. More recently wide crossing, crossing F_1's, recurrent selection, and mutation breeding have been utilized to broaden genetic variability, to more rapidly effect breaking of linkages and increase additive gene action. The use of ionizing radiation has been studied in depth by Gregory (1956), Bilquez *et al.* (1964), and Patil (1968), while use of diethyl sulfate and other chemical mutagens was investigated by Shchori and Ashri (1970) and by Ashri (1972).

Preliminary investigations on interspecific crossing within *Arachis* species have recently been reported by Gibbons and Bailey (1967) in the area of disease (*Cercospora arachidicola*) resistance; phylogenetic relationships by Raman and Sree Rangasamy (1972) and Raman (1973), and interspecific cross compatibility between *A. hypogaea* and other *Arachis* species by Smartt and Gregory (1967). A major but not insurmountable problem in interspecific crossing is that the cultivated *A. hypogaea* has $2n = 40$ chromosomes compared with $2n = 20$ chromosomes in the other species.

2. *Genetic Considerations*

Inheritance and gene action have been studied in several important genetic characters. These may be classified into simply inherited characters, cytoplasmic effects and quantitatively inherited characters. In addition there is the problem of linkage and "blocks of genes" which tend to be

passed on to their progeny and through generations as combinations of characters. This makes it difficult to recombine desired characteristics from different groups, for example, earliness of Spanish and Valencia types with rosette resistance from Virginia types, or to transfer nondormancy characteristics from Spanish to Virginia types (Mauboussin, 1966). Therefore, the backcrossing breeding method has not been successfully used in these and similar situations.

a. Character Associations. Several investigators have contributed to information on character interrelationships in recent years. Some of these are summarized below:

1. Pod yield in erect types: positively correlated with pods per plant and number of vegetative nodes per secondary branch and negatively correlated with lateral spread (Sangha and Sandhu, 1970).

2. Pod yield in bunch types: positively correlated with number of primary branches/plant, 100-seed weight and number of pods/plant in that order (Sangha and Sandhu, 1970). Sanjeeviah *et al.* (1970) observed pod yield to be correlated with number of nodes up to 10 cm above the ground ($r = 0.97\%$) and Lin *et al.* (1969) obtained a correlation with high shelling percent.

3. Pod yield in spreading types: correlated with number of pods per plant, 100-seed weight, number of primary and secondary branches and shelling percent (Sangha and Sandhu, 1970; Raman and Sree Rangasamy, 1970).

4. Shelling percent in interspecific crosses: in various crosses between *A. hypogaea, A. glabrata,* and *A. villosa,* positive correlations were observed with pod weight, kernel weight, and percent filled kernels (Ramanathan and Raman, 1968). In another cross between *A. hypogaea* and *A. monticola,* shelling percent was highly correlated with number of primary branches (Raman and Sree Rangasamy, 1970).

5. Other associations with pod yield: Prasad and Srivastava (1968) found pod yield positively correlated with numbers of branches, leaves, nodes, flowering nodes, and pods per plant; and with 100-seed weight.

6. Interrelationships among yield components: Merchant and Munchi (1971) in studies on erect cultivars found positive correlations between leaf length and leaf width, pod length and pod width, pod length and seed length, and between seed length and seed weight. Seed length was negatively correlated with shelling percent. Martin (1969) observed that seed weight was not positively correlated with oil content.

b. Simply Inherited Characters. Economically important genetic factors controlled by one or a few genes include the following: (1) branching habit; (2) number of seeds per pod; (3) cotyledon characters; (4) color of stem, leaf, foliage, and testa; (5) crimping of leaves; (6) absence of

leaf petiole; (7) constriction of the pod; (8) resistance to rosette; (9) early maturity; (10) oil content.

Some simply inherited characters are expressed or modified by genic–cytoplasmic effects and have been studied by Ashri (1964, 1968, 1969). He proposed two plasmons designated "V4" and "others" as interacting with two genes Hb_1 and Hb_2 to produce the runner (trailing) or bunch (erect) growth habits. In "V4" plasmon Hb_1 and Hb_2 produce runners while either recessive condition produces as bunch habit, whereas in "others" plasmon the dominant alleles are additive and possibly complementary. $Hb_1Hb_1Hb_2Hb_2$, $Hb_1Hb_1Hb_2hb_2$, and $Hb_1hb_1Hb_2Hb_2$ produce runners and all other combinations give bunch plants. Ashri further proposed genetic control of growth habit operated through production of anti-gibberellins similar to abscissic acid.

c. Polygenic Inheritance. Several economically important characters are complex and controlled by several genes acting quantitatively. These include seed yield, number of pods per plant, weight of pods, and size of leaves. The environment also interacts directly and profoundly with these characters. Therefore, the most rapid progress in breeding should be realized through population improvement and recurrent selection under favorable growing conditions of moisture, fertility, temperatures, and soil conditions.

d. Heritabilities and Coefficients of Variation. Heritability in some important botanical characters has been studied by several investigators. Asoka-Raj (1969) found high heritability estimates for days to flowering, number of leaves per main stem, pods per plant and 100-pod weight out of 14 characters studied. The coefficients of variation were high for days to flowering, pods per plant, and haulm weight per plant. Majumdar *et al.* (1969) likewise observed high genetic coefficients of variation for number of leaves, number of nodes, number of peg-bearing nodes, number of pod-bearing nodes, and length of pod. Heritability estimates in the broad sense ranged from 49.6% for pod yield to 98.6% for days to maturity. Numbers of branches, leaves, and nodes had particularly high genetic advance potential; whereas numbers of pods and pod yield had low heritability values.

Oil content and shelling percent were both observed to be highly heritable characters; oil content was controlled by two pairs of genes; shelling percent was governed by a single pair of genes without dominance; and 100-seed weight, which is closely correlated with shelling percent but not with oil content, was controlled by five pairs of genes, four of which had isodirectional effects in genetic studies carried out by Martin (1969). In heritability analysis of maturity as measured by light transmittance through the seed oil, Gupton and Emery (1970) obtained higher rates of genetic gain

in later maturing groups and suggested that most rapid gains could be made by selecting for rapid maturation in later pegging segregants.

e. Combining Ability. Recent studies on heterosis and combining ability were carried out by Parker *et al.* (1970) and Wynne *et al.* (1970) in diallel crosses of six lines representing the three major groups Virginia, Spanish, and Valencia. Virginia × Valencia crosses had the highest combining ability. Estimates of general combining ability were significant for 8 out of 17 characters studied, and estimates of specific combining ability showed significance for 16 characters. Specific combining ability was greatest for yield and most fruit characters. Specific combining ability effects were greatest for leaves on mainstem (at 15 days), days to first flower, and petiole length (at 33 days). The greatest portion of genetic variance was associated with general combining ability. Heterosis for vegetative characters was greatest in Virginia × Valencia crosses, and for seed yields in Valencia × Spanish crosses.

3. Breeding Objectives

There are several important breeding objectives being actively pursued in the important peanut growing regions of the world, depending on their relative importance in that locality. Overriding all other considerations is yielding potential and stability of productivity over a reasonably broad range of ecological conditions. The most important specific breeding objectives of present plant improvement programs are briefly summarized below:

1. Yield potential— a highly complex character with very high genotype X environment interactions. Yield and stability of yield must remain at the highest level of priority for all breeders.

2. Oil content— Virginia types have up to 47% or more oil contents, but higher levels of unsaturated fatty acids than Spanish–Valencia types, and crosses between Virginia and Spanish types have recorded oil contents up to 53% in Upper Volta (IRHO, 1972). Oil content is a highly heritable characteristic (Martin, 1969), but also strongly influenced by environment (Holley and Hammons, 1968). In India, higher oil content was recorded in TMV-1 (Virginia) and TMV-2 (Spanish) cultivars grown on upland conditions than under irrigation (Gopalswamy and Veerannah, 1968). Genotype, environment, and stage of maturity directly influence the quantity and fatty acid composition of peanut oil (Worthington and Hammons, 1972; Young *et al.*, 1972). In the latter investigations, concentrations of stearic and oleic acid were higher, and the linoleic, arachidic, and behenic fatty acids were lower in mature than in immature nuts.

3. Protein content and quality—comparatively little attention has been given to improving protein content and quality in the peanut. Crude protein

content commonly ranges between 24 and 35% and is negatively correlated with oil content (Holley and Hammons, 1968). Perhaps the most serious problem in peanut protein is its poor quality and deficiencies not only in the sulfur-bearing amino acids, but in tryptophan and lysine as well (Harvey, 1970).

4. Edible peanut—the confectionary type of nut is mainly found in large seeded (100 seeds = 65 + *g*) Virginia types. These should have constricted pods to eliminate the flattened ends of the seeds, but the constriction should not be too tight to avoid rupturing the locules. They should also have attractive flavor and aroma. Some excellent confectionary varieties include the following: (a) United States types (Virginia): NC 2, NC 4, NC 17, GA 119–20, FLORIGIANT, and FLORUNNER. The latter has a particularly desirable flavor and aroma. (b) African/Indian types (Valencia): Valencia 247 from Madagascar, A 1241 B from Central Africa, and WHITE ACHOLI from India.

5. Earliness—reducing the vegetative cycle in Virginia types by crossing with Spanish–Valencia strains has been an important objective in several breeding programs (Goldin, 1970; IRAT, 1969). Several short-duration types (105 days) have been developed in this way in Israel and Senegal; but combinations of characters have proved somewhat of a block in these efforts.

6. Seed dormancy—dormancy from Virginia types could be very useful in Spanish–Valencia types in tropical regions with bimodal rainfall patterns for growing during the first season, or where dry weather does not otherwise coincide with maturation. Combining seed dormancy with short duration has been of limited success in Senegal, Sudan, and India (Gillier and Silvestre, 1969; Ramachandran *et al.*, 1967), but dormancy has not yet been satisfactorily introduced into Spanish-Valencia types for the more humid regions, nor for the intermediate elevations of the tropics.

7. Drought resistance—while drought resistance is a very valuable attribute in the peanut, there is some difficulty in effectively screening and evaluating this character. Relationships between drought resistance, short internodes, and root volumes were demonstrated in India (IARI, 1970). High pressure osmotic germination tests, relative transpiration rate, high temperature, suction pressure, number of stomata and rapidity of stomata regulation have been used with varying success to measure drouth tolerance. Gautreau (1969) demonstrated that rapidity of stomata regulation is more important than numbers of stomata in drought tolerance. Two drought resistance cultivars developed in Senegal utilizing high osmotic pressure germination tests are 55–437 and 59–127.

8. Resistance to rosette disease—major sources of resistance have been found in later maturing Virginia types in Africa. Two rosette-resistant

strains such as 48–37, 28–206 RR, and 1040, have been developed at Bambey and Niangoloko experiment stations and are well adapted throughout West Africa (Daniel and De Berchoux, 1965). Resistance is physiological, recessive, and governed by two pairs of homologous genes in the presence of a modifier (Dhery and Gillier, 1971; Mauboussin, 1970; IRHO, 1972). Several lines extracted from Mwitunde stock have not proved as satisfactory in resistance as the West African sources (Klesser, 1967).

9. Resistance to *Cercospora*—Virginia types are usually more tolerant of *Cercospora arachidicola* than Spanish–Valencia strains. There also appears to be an association between resistance to rosette and *Cercospora.* West African strains combining moderate resistance to both diseases with regional adaptation include 55–460, 48–37, and 52–14 (Fowler, 1970). The resistance mechanism may result from hypersensitivity or small stomata size. Resistance factors have also been found in wild species of both Rhizomatosae and Extranervessae groups including *A. repens, A. glabrata, A. hagenbeckii* and *A. villosa* (Abdou, 1966; Gibbons and Bailey, 1967).

10. Resistance to rust—resistance to *Puccinia arachidis* is physiological in nature and has been found in several lines including PI 314817, a selection out of PI 298115, NC 13, and others; and in *A. glabrata* (Bromfield and Cevario, 1970; Bromfield and Bailey, 1972; Cook, 1972).

11. Resistance to *Aspergillus flavus*—production of aflatoxin should be controlled by resistance to this fungus. Moderate resistance has been found in Kaboka and Mwitunde (Rao and Tulpule, 1967; Kulkarni, 1967); and a higher level of resistance was found in two Valencia strains from Argentina, PI 337394 and PI 337409 (Mixon and Rogers, 1973). Resistance may result from inability of the pathogen to penetrate the seed coat.

12. Resistance to other diseases: (a) *Verticillium dahliae*—lines derived from Mwitunde and Schwartz 21 (Frank and Krikun, 1969); (b) *Sclerotium bataticola*—Punjab 1 and TMV 3 (Mathur *et al.*, 1967); (c) *Sclerotium rolfsii* and *Macrophomina phaseoli*—variety 28-204 (Garren, 1964; Bouhot, 1967); (d) *Pseudomonas solanacearum*—Schwartz 21 strains, CES 101, PI 341884, PI 341886 (Bolhuis, 1955; UPCA, 1968; Simbwa-Bunnya, 1972); (e) *Aspergillus niger*—U4-47-7 (EC 21115) from the Sudan (Aulakh and Sandhu, 1970).

C. Plant Protection

The peanut is attacked by several pests and diseases, although damage by foliage- and pod-feeding insects is rather less than for many other tropical grain legumes. However, some insects and diseases are interrelated through spread of virus or by predisposing the plant to invasion of fungi and bacteria.

1. Insect Pests

Insects can attack the peanut throughout its growing cycle and in storage. Several factors influence the severity of attack and susceptibility of the crop. The more common of these pests are included in the accompanying tabulation (Stanton, 1966):

Growth stage	Pests	Region
Seedings	Myriapoda: *Peridontopygae spinosissima* Silv.	Africa
	Coleoptera: several species	All
Stems and leaves	Caterpillars: *Anticursia gemmatalis* Hubn.	USA
	Amsacta albistriga Walk.	India
	Stomopteryx nerteria Meyr.	India
	Prodenia, Leucania, Laphygma, and *Amsacta* species	Africa
	Beetles: *Pontomorus leucoloma*	USA
	Sphenoptera perotetti G.	India
	Capsids: *Halticus minutus* Reut.	Africa
	Thrips: *Hercothrips femoralis* Rem.	Africa
	Aphids: *Aphis craccivora* Koch.	Africa
	Aphis laburni Kalt.	Africa
Flowers	Mylabrid: *Decapotoma affinis* Bilb.	Africa
Pods/stems (in soil)	Termites: *Eutermes parvulus* Sjostedt	Africa
	Rootworm: *Diabrotica undecimpunctata howardi*	USA
Pods and seeds (storage)	Bruchid: *Coredonfuscus* sp.	Africa
	Corya cephalonica Staint.	Africa

Aphids like *Aphis craccivora* are particularly important in their dual role of sucking the plant sap and spreading the rosette virus, whereas the Myriapoda and termites predispose the plant to mildew and other fungi.

a. Controls. Seed treatment helps prevent attack of young seedlings by various pests. Soil insecticides like heptachlor, dieldrin, Thimet, Furadan, and Dyfonate are effective against termites and a broad range of soil-inhabiting grubs (Smith, 1971; Sharma and Shinde, 1970). Several systematic insecticides, such as dimethoate, malathion, and other organophosphates control aphids; and contact insecticides, like gamma BHC, thiodan, and Fenitrothion, control foliage feeders when these build up excessively. However, foliage insecticides are seldom used, nor are they always necessary in many tropical regions.

One of the most effective controls for *Aphis craccivora* is a dense stand of the crop since the insect is attracted to spots of bare soil, where colonization occurs. If wide row spacings are utilized, seeds should be planted thickly within the row to increase ground coverage.

b. Host Plant Resistance. This form of control has recently been explored mainly for foliage-feeding caterpillars. Leuck and Skinner (1971) found Southeastern Runner 56-15 and 40 other lines out of 1700 tested to be partially resistant to fall armyworm (*Spodoptera frugiperda*) in the field. In other studies Leuck and Harvey (1968) observed variation in resistance to the lesser cornstalk borer (*Elasmopalpus lignosellus*) and that seedling survival was highest in PI 259777. However, Smith and Porter (1971) found only low levels of resistance to the southern corn rootworm (*Diabrotica* sp.) in field and greenhouse studies.

2. *Diseases*

There are five major diseases affecting peanuts in tropical regions. In addition there are several secondary pathogens and nematodes that may become important in certain regions or under special circumstances. In some cases the incidence of the disease is dependent on attack by insects or other pests or in physically spreading the disease as in rosette virus. A brief description of these diseases is given below:

1. *Cercospora* leaf spots—The causal organisms are *C. arachidicola Hori C. personata* Ellis and Everh., and, to a lesser extent, *C. canescens* (Fowler, 1970, 1971). These organisms are dark spots surrounded by a yellow ring and are most predominant on the lower and older leaves. Sometimes they can cause complete defoliation. Yield losses may range from 15 to 60% depending on conditions and locality.

2. *Sclerotium rolfsii* Sacc.—this produces a wilt that causes death of branches or the entire plant. Reddish fruiting bodies may be formed on the stem at the ground line. Although widespread it may be most serious in the United States and Australia.

3. *Aspergillus flavus*—this organism attacks the stored seeds with moisture contents of 15–25% and has also been found on living plants. It produces aflatoxin some forms of which are highly toxic causing fatalities in turkeys and possibly also in humans. It has also been found to cause carcinoma of the liver in experimental animals.

4. *Puccinia arachidis*—this pathogen does not yet occur in Africa but is endemic in southeastern Asia, India, and the United States (Van Arsedel and Harrison, 1972). Build up of the disease in the United States occurred when a change was made in fungicides used to control *Cercospora*.

5. Rosette virus—this is the most serious disease of the peanut in Africa and is spread by aphids (*A. craccivora* and *A. laburni*). The whole plant is severely stunted, and the younger leaves are chlorotic and mottled, with successive leaves becoming smaller, curled, distorted, and yellow.

6. Secondary diseases and nematodes:

a. Stem and root rots—these are caused by several secondary pathogens, such as *Rhizoctonia bataticola, Asperigillus niger, Rhizopus nigricans, Macrophomina,* and may cause breaking of gynophores and withering of the plant. *A. niger* and *R. nigricans* are mainly responsible for crown rots. Insects or other injury and drought following germination can predispose the plant to invasion by these pathogens.

b. Miscellaneous virus diseases—several virus diseases are recorded including mottle, foliar spotting, bunchy top, chlorosis and stunt in the United States (Kuhn, 1965; Miller and Troutman, 1966), in India (Sharma, 1966), and in Australia and Senegal (Bouhot, 1968).

c. Nematodes—*Pratylenchus brachyurus* attacks the pods and peg tissues of peanuts in the southeastern United States. VIRGINIA BUNCH 67 and GEORGIA 186–26 were not as susceptible as other varieties tested in Georgia (Minton *et al.,* 1970).

Controls. Diseases are most practically controlled through host plant resistance. However, growing adapted cultivars "in season," sanitation, and control of predisposing pests all contribute to reducing the incidence of diseases. Secondary stem and root rots are often reduced by fungicidal seed dressings or avoided by planting on well drained soils in less humid areas or seasons. Fungicide–insecticide seed dressings have been demonstrated to increase yields by up to 40–50% when germination and seedling growing conditions are unfavorable (IRAT, 1971; Lewin and Natarajan, 1971).

Cerospora leaf spots can be reduced by removing debris from previous crops and by crop rotation (Fowler, 1971; Mazzani and Allievi, 1971) and by spraying with fungicides like Dithane M 45 at the rate of 2.2 kg a.i. (active ingredient)/ha in 400 liters of water whenever regular rainfall has been recorded for 8–10 days (McDonald, 1970a; Corbett and Brown, 1966). The most dramatic recent development in control of *Cercospora* is foliage application of benomyl (Benlate). Applied three times at the rate of 8 oz of 50 WP per acre, it increased yields from about 20% to 10 times that of unprotected plots in Virginia in 1968 and 1969 (Porter, 1970). Miller *et al.* (1970) likewise obtained excellent control in Florida trials in 1968–1969.

The most practical control of rosette disease is probably cultural, although resistant varieties (like IRAT 48–37 and 1040) are becoming available. Vigorous, thick stands without gaps and possibly systemic insecticides are probably the best means of preventing the aphid vectors from building up (Kousalya *et al.,* 1971).

Development of *Aspergillus flavus* in storage can be greatly reduced by the following means: (1) selecting well-adapted varieties and growing to

obtain a good-quality, uniform harvest, (2) avoiding damage to the ripening nuts in the ground by tillage practices and at harvest, (3) cleaning and drying the nuts as rapidly as possible after harvest. It is particularly important to harvest as soon as ripening occurs and to carefully hand or machine sort the pods and seeds, removing blemished and injured ones. A pneumatic sorter has been developed in Senegal to mechanically remove injured pods (Gillier, 1970).

D. Growth Process

Physiological processes in the peanut have been rather intensively studied throughout the growing regions for this crop. Greatest emphasis has been given to the areas of: (1) temperature and light effects, (2) water relationships, (3) mineral nutrition, and (4) hormonal and enzymatic effects. However, it has been difficult to derive definition conclusions in many aspects for various reasons. Field experiments are usually conducted with local varieties of undetermined genetic origins or poorly defined characteristics; a large number of uncontrollable variables interact with genotypes and treatments; and when growth is not retarded by flowering (as in the peanut) the plant often has a compensatory mechanism in response to ecological hazards.

1. Light and Temperature Responses

A. Plant Structure. Investigations at Yaounde, Cameroons, with 516 mm of rain in the 100-day vegetative cycle on the cultivars 55–437 and Minkong planted at 50 × 10 cm (200 th/ha), 25 × 20 cm (200 th/ha), and 40 × 40 cm (62.5 th/ha) showed numbers of leaves developing on the main stem to be positively correlated with mean temperatures; maximum leaf area index was 4.0; net assimilation rate reached a maximum of 0.85–0.90 mg DM/cm^2 per day; the DM content of the leaf blade was 3.0–4.5 mg/cm^2 and was not affected by genotype or growth stage, all parameters being higher than in the drier savannah (Forestier, 1969).

b. Daylength and Light Quality. Initiation of the flowering process is largely unaffected by photoperiodism (Prévot, 1949). However, light quality and intensity does affect floral development. For this reason, elite strains can frequently be grown over a wide range of latitude and seasons. Reduced light and shading tend to inhibit growth and fruit formation particularly during early stages of development (Ono and Ozaki, 1971).

c. Direct Temperature Effects. Peanut seeds will germinate between 15° and 45°C but the optimum is 32–34°C. Optimal growing temperatures are 24–33°C (Catherinet, 1956; Bolhuis and De Groot, 1959). However, ex-

treme differences between day and night temperatures of more than 20°C tend to limit flowering, and night temperatures below 10°C delay maturation (Shear and Miller, 1955).

2. *Assimilating Processes*

a. CO_2 Pathways. Experiments tracing the pathways of CO_2 using ^{14}C have shown that during the vegetative stages, developing leaves assimilated most of the ^{14}C, while fully expanded leaves exported most of their C to developing apices, young expanding leaves, and roots. Immediately following peg formation the developing pods become the main sinks, and at this stage assimilates were mainly translocated from the leaves of a branch to the pods of the same branch (Khan and Akosu, 1971).

b. Protein Synthesis. Accumulation of dry matter in developing seeds begins about 4 weeks and continues for more than 12 weeks. Moisture content declines from the twelfth week, but some protein accumulation continues for two more weeks. Synthesis of proteins is associated with DNA and RNA production during the early part of this period. DNA content reaches its maximum by the eighth and tenth week after pegging in embryonic axes and cotyledons, respectively, and decreases thereafter. Cotyledonary RNA increases for 8 weeks after pegging, decreases from 8–11 weeks corresponding to increased RNase activity, and then increases until maturity, whereas embryonic RNA increases throughout the maturation period (Aldana, 1969; Aldana *et al.*, 1972).

c. Oil Accumulation. The oil content increases rapidly from the fourth to twelfth weeks after pegging, going from about 15 mg per kernel to 360 mg per kernel from the beginning to the end of this period. Toward maturation the carotenoid concentraton decreases markedly, this is attributable to rapid increase in oil (Pattee *et al.*, 1969).

3. *Water Relationships*

Water requirements for peanuts grown on drylands have been estimated as 500–600 mm per season. During the first months of growth, daily requirements increase from 1.5 to 4 mm per day; they reach 5–7 mm during the peak of growth, decrease to 4 mm by the last month of the vegetative cycle, and finally drop to 2 mm daily during ripening (Ilyana, 1959; Ochs and Wormer, 1959; Mantez and Goldin, 1964).

a. Relative Humidity. Experiments carried out in Texas by Lee *et al.* (1972) demonstrated the beneficial effects of high relative humidity at flowering. Plants transferred from 50% RH to 95% RH 50 days after planting had much better flowering, peg growth, formed more ethylene, and had more gibberellins than plants transferred from 95% RH to 50% RH. Low relative humidity (5%) was found less satisfactory for retaining

seed viability in storage than higher relative humidity. Seed remained viable for three years in storage at 30% RH and 4°C in studies carried out by Gavrielit-Gelmond (1970).

b. Drought Resistance. The peanut is highly resistant to drought and is able to extract soil moisture under quite extreme conditions. In the sandy soils of Senegal, yields are reduced when soil moisture reaches 70% of its retention capacity, and the permanent wilting point is estimated at 40% of that level (Dancette, 1970). Nevertheless, moisture deficiency has a direct effect on yields, particulary when it occurs during flowering.

4. Enzyme Activity and Hormones

Seed Dormancy. Dormancy is primarily related to genotype in the peanut. Lin and Chen (1970) found wide differences in seed dormancy in 56 cultivars studied and divided them into four classes: (1) nondormant types, (2) dormant for 2–4 weeks, (3) dormant for 5–8 weeks, and (4) dormant more than 9 weeks. Virginia types tended to have greater dormancy than Spanish cultivars.

Ascorbic acid was found associated with the germination process in studies carried out by Sreeramulu and Rao (1970, 1971). They observed a rapid increase in ascorbic acid from 35 mg in the entire seed to 284 mg in the 5-day-old seedlings of the freshly harvested nondormant TMV 2. In contrast, fresh seed of the dormant variety TMV 3 did not germinate and showed very slight ascorbic acid activity. Sreeramulu and Rao (1971) further observed growth promoting substances to increase from 20–30 days after the pegs touched the ground in both acidic and neutral fractions of both dormant and nondormant seeds. From 30 days onward growth promotors decreased while growth inhibitors increased. In the dormant type (TMV-3) growth inhibitors were higher than the promotors in the acid fraction of the seeds in contrast to the condition in nondormant seeds.

Dormancy in both apical and dorsal types of seeds can be broken by ethylene gas at 8 ppm and by 2-chloroethylphosphonic acid at 10^{-3} and 5×10^{-4} *M*, increasing germination to 100% in both types of seeds after 48 hours. Gibberellic acid at 5×10^{-4} stimulated ethylene production in apical seeds, increasing germination to 40% above the control (Ketring and Morgan, 1970).

5. Mineral Nutrition

Mineral requirements of the peanut plant have been extensively studied in all major growing regions. Foliar diagnosis has made it possible to determine precisely the requirements of the plant (Prévot and Ollagnier, 1961; Martin, 1965). These can be summarized for each 1000 kg of kernels in shell of yield (see tabulation).

Element	Foliar/stems (kg)	Pods/seeds (kg)
N	10–12	30–35
P_2O_5	1.5–2.0	6
K_2O	10–12	6–10
CaO	8–12	1–2
MgO	8–10	2

a. Nitrogen and Rhizobial Symbiosis. Peanuts utilize considerable nitrogen, which is almost totally provided by the rhizobial system. Therefore, nitrogen fertilizer applications beyond about 19 kg of nitrogen per hectare have not been economic. However, instances of severe nitrogen deficiency have occurred in acidified sandy soils when normal rhizobial populations disappeared (Blondel, 1969). Inoculation can be important in certain regions where peanuts have not been grown previously for some time. However, there is apparently no need to provide rhizobial cultures in most of tropical Africa or Madagascar.

Some strains of peanuts, like Asiriya Mwitunde in India, nodulate better than other strains (Narsaiah *et al.*, 1969). Attempts are also underway to improve the symbiont through mutation breeding utilizing ultraviolet radiation and *N*-methyl-*N*-nitro-*N*-nitrosoguanidine (Raina and Modi, 1969). However, improved mineral nutrition, particularly by supplying adequate amounts of calcium, phosphorus, molybdenum, magnesium, and potassium has shown positive responses under field conditions (Nair *et al.*, 1970, 1971).

b. Phosphorus. This is probably the most important mineral nutrient required by the peanut in much of the tropics. Good response is observed even to applications as low as 11 kg of P_2O_5 per hectare as presently recommended in northern Nigeria. However, in soils markedly deficient in phosphorus, comparatively heavy applications of up to 150 kg of P_2O_5 per hectare every few (3) years have been economic and have a "saturation" effect on the soil complex (Carriere de Belgarric and Bour, 1963; Goldsworthy and Heathcote, 1964).

c. Potash. Peanuts make a heavy drain on soil potash, but seldom respond to this element except in leached ferralitic and intensively cropped soils. Potash deficiency is evident when a high proportion of the pods produce only one seed.

d. Calcium. This element is very important in the formation and development of the seeds and in nodulation. It can be absorbed both by the roots and the gynophores. A deficiency of calcium decreases the shelling percent

and results in a high proportion of "pops" or empty pods. Salinity can inhibit uptake of calcium, as observed in studies carried out by Ramana and Rao (1971). Calcium can be added in the form of lime- gypsum-, or calcium-bearing fertilizers, like single superphosphate. Sometimes gypsum is dusted on the foliage at flowering to increase the uptake of both calcium and sulfur.

e. Sulfur. This element contributes to nodulation and helps prolong flowering. The normal requirement for peanuts is 12–15 kg of sulfur per hectare, and it can be absorbed both by the roots and the foliage. There is usually an adequate quantity of sulfur in sulfur-bearing fertilizers like ammonium sulfate and single superphosphate when used at reasonable levels in the crop rotation to satisfy the requirements of peanuts (Brzozowska and Hanower, 1964; Hanower, 1969; Bromfield, 1973). Sulfur significantly increased the yield of unshelled nuts and the oil, sulfur, and methionine contents of mature seeds in experiments carried out in India by Singh *et al.*, (1970).

f. Iron. In highly calcareous soils iron chlorosis may occur; it has been observed in Negev, Israel, with a soil pH 7.6–8.3 containing up to 21.4% $CaCO_3$. Yields of shelled nuts increased by up to 250% through soil or foliage applications of chelated iron (Fe EDDHA). The most effective treatment was one or two foliar sprays or 10 kg of iron chelate per hectare 3–6 weeks after planting (Hartzook *et al.*, 1971, 1972).

g. Boron. Boron deficiencies cause "hollow heart," blackening of the embryo, and, occasionally, cracking of the stems that may appear to be a secondary effect of drought. The deficiency is correctable by applying 5–10 kg of borax per hectare (Harris and Brolmann, 1966; Gillier, 1969). Excessive boron also causes toxicity by inhibiting the uptake of iron (Gopal, 1970, 1971).

h. Molybdenum. This element acts directly on the rhizobial process, increasing the number and weight of nodules formed, and, therefore, influences nitrogen availability. Deficiencies can be corrected by seed treatment or application of as little as 28 g of molybdenum per hectare (Gillier, 1966; Pillai and Sen, 1970).

i. Manganese Toxicity. Manganese toxicity may occur in acid soils, which change manganese into an exchangeable form, and excess amounts are taken up by the plant. It aggravates the unbalanced soil condition in the absence of calcium. It was first observed in Zaire (Prévot *et al.*, 1955) and sometimes occurs in autoclaved soil (Boyd, 1971).

j. Fertilizer Use in the Tropics. Comparatively little fertilizer is applied directly to the peanut crop itself in the tropics. Rather, the plant has to rely on residual fertility applied to previous or associated crops. In areas, where cash crops like cotton, tobacco, vegetables, or heavily manured

cereals precede the peanut crop, soil nutrients may be more than ample at present levels of production. However, higher yield levels will be necessary in the future for peanuts to compete better with other high-yielding crops. The present nutrition level for a 1-ton crop will hardly be adequate for yields of 4–5 tons/ha.

E. Management

The peanut has made an enormous impact as a cash crop in peasant farming systems. As such it is frequently interplanted with other crops or is included late in rotations with cotton, tobacco, maize, or other cereals. Although possessing the dual advantage of being both a cash and subsistence crop, an estimated 75–90% of the produce is milled for oil and cake, or exported unprocessed. Optimizing husbandry practices will be discussed briefly in the section to follow.

1. Tillage and Planting

Peanuts prefer loose, friable sandy soils and can be planted either on the flat or on ridges. Ridges offer better drainage and facilitate lifting, but impose limitations on the populations that can be grown and may increase difficulties in pegging (particularly narrow ridges). Rows are frequently mechanically cultivated during early growth.

Populations and Spatial Arrangements. Growth habit tends to govern the planting rates. Higher populations and uniform stands generally produce higher yields, in addition to reducing the incidence of rosette virus and suppressing late flowering. Thus, maturation is more uniform and results in better quality. Populations of 250,000 plants per hectare or individual plant spacings of 15 cm × 30 cm and seeding rates of 65–90 kg of shelled nuts per hectare are recommended for hand placement of seeds, or 10 cm × 60 cm for mechanical planting and cultivation for bunch varieties. Spreading or runner types are usually planted at lower populations of about 55,000 plants per hectare at spacings of 30 cm × 60 cm and a seeding rate of 45 kg/ha. In hand planting it is preferable to drop two seeds per hill to assure better stands and permit wider row spacings (Purseglove, 1968). Alternatively, double rows 15 cm apart with 92 cm between pairs of rows has been advantageous in Australia (Wood, 1970).

Seeds for planting should be stored in the shell; just before planting they should be carefully shelled to avoid injury, and treated with a fungicide/insecticide combination. Mercurials or thiram are the preferred fungicides in combination with aldrin or dieldrin.

Early planting is essential for high yields and the young crop must be carefully weeded, as seedling growth is slow. Weeds can greatly re-

duce yields by competing for moisture, nutrients, and light and also cause difficulty in harvesting. Mechanical cultivation and hoeing must be terminated after about 8 weeks to avoid damaging the developing gynophores (pegs).

2. *Weed Control*

Weeds compete for nutrients, moisture, and light and can easily become the major deterrent to increased productivity. In the Sudan, Ishag (1971) found weeds decreased the number of branches per plant and pods per plant, and yields were increased nearly 5-fold by handweeding 30 and 60 days after planting.

Chemical Control. Several preemergence herbicides including trifluralin at 1.1 kg a.i./ha and benefin at 2.2 kg a.i./ha gave excellent control of grasses—mainly *Brachiaria* and *Digitaria* spp. in Australia (Wood, 1970). Prometryne at 1.7–2.2 kg a.i./ha, linuron at 1.7 kg a.i./ha, and nitrofen at about 2.2 kg a.i./ha are promising under a wide range of conditions in India (Sindagi *et al.*, 1972; Patro *et al.*, 1970), Taiwan (Wang *et al.*, 1971), Australia (Wood, 1970), and Ghana (Takyi, 1971).

3. *Harvesting*

Most of the tropical peanut crop is harvested by hand. This consists of pulling and inverting the plants to facilitate drying of the pods in the sun before stripping off the nuts. Harvesting of the optimum time is essential to maximize yields, minimize losses from shedding, and eliminate sprouting in bunch types (Purseglove, 1968; Young *et al.*, 1971). Considerable losses occur if the soil becomes hard before lifting. In most tropical regions peanuts are hand harvested because mechanization is too expensive. However, several shelling machines have been designed for hand or power operation.

Yields. Peanut yields are reasonably high considering the conditions under which they are grown. Worldwide yields are 9.5 Q of unshelled nuts per hectare and up to 23 Q/ha for the United States; but much higher yields—exceeding 4000 kg/ha—have been obtained under favorable conditions. The shelling percent runs to about 80% for bunch types compared with 60–75% for runner (spreading) cultivars.

4. *Combined Technology*

Adoption of a combined improved technology of "package of practices" can increase yields remarkably. Bray (1970) found the mean yields of unshelled nuts in the Sine-Saloum area of Senegal increased from 937 kg/ha in 1960–1963 to 1118 kg/ha in 1964–1967 as a consequence of using an improved variety, treating the seeds, sowing with a drill, obtaining better stands, and applying fertilizers. Application of fertilizers (phosphorus,

potassium, calcium) alone in Sambwa, Tanzania increased yields of unshelled nuts by 20% from 1503 to 1835 kg/ha (Anderson, 1970). At Katherine in northern Australia, Wood (1970) increased yields of unshelled nuts by 270 kg/ha merely by increasing the seeding rate from 55 to 100 kg/ha. In Madras, India, Mohan (1970) obtained higher yields (3221 kg of pods per hectare) by irrigating whenever moisture was down to 60% of field capacity (1.05 atm tension); and, in another trial, yields were increased from 3086 to 3291 kg of pods per hectare by mulching with *Glyricidia* leaves. However, maximized economical production is nearly always achieved by adopting the complete improved technology.

F. Chemical Composition

Peanut seeds contain mainly nondrying oil and protein. Virginia types are usually 38–47% oil, and Spanish types are 47–50% oil. Carbohydrates are about 11.5%, ash is 2.3%, and water is 6.0%. Decorticated cake contains about 10% water, 47% protein, 6–7% fat, 23% carbohydrate, 6.5% fiber, and 6.0% ash. The oil normally contains 53% oleic and 25% linoleic acid, but genotype and environment strongly influence oil quality. The principal proteins are arachin and conarachin. The peanut is also rich in vitamins B and E.

a. Protein Quality. Peanut protein is frequently low in sulfur amino acids and in lysine, but considerable variation has been observed in both methionine (3.7–8.7 mg per gram of seed) and lysine, suggesting that these components might be increased through genetic manipulation (Chopra and Bhatia, 1970; Heinis, 1972).

b. Fatty Acids. Fatty acid composition in 101 local and introduced peanuts were investigated by Worthington and Hammons (1971). They found linoleic acid to range from 14 to 40%, lower in large-seeded Virginia than in Spanish types and positively correlated with levels of palmitic, behenic, and lignoceric acids.

c. Other Constituents. Thiamine (B_1) occurs in raw peanuts, but very little is strongly bound to the proteins, according to Dougherty and Cobb (1970). Some peanut cultivars are comparatively low in intestinal gas-forming sugars in studies carried out by Hymowitz *et al.* (1972). The varieties ARGENTINA, EARLY RUNNER, SPANCROSS, TIFSPAN, and VIRGINIA BUNCH 67 had stachyose contents less than 0.1 g/100 g seed and are believed to be non gas-formers.

G. Potential

The peanut has become a major contributor to the economy of tropical peasant agriculture. It enjoys the dual advantages of being both a cash

and subsistence crop permitting the small holder considerable flexibility in buffering adversities in weather and general growing conditions. That is, he can hold in reserve the quantity required for food, while having a good stable market for the surplus.

Peanuts are comparatively easy to grow and normally do not require sophisticated technology nor massive inputs of fertilizers or plant protection. Moreover, they are well adapted to both hand and mechanized cultivation. They are reasonably free of pests and have few serious diseases. Underground fruiting avoids devastating attacks by pod feeding insects that plague many other tropical grain legumes. Fortunately, there appear to be reasonably effective solutions to some of the major constraints to increased productivity levels in the tropics. These include discoveries in host plant resistance to the most serious diseases; recent developments in systemic fungicides and insecticides; and better understanding of the nutritional and water requirements of the crop. Perhaps the major constraint to expanded use and productivity would be limitations in genetic diversity and moving off the present yield plateau. Nevertheless, the immediate future for peanuts should be very bright.

IV. Pigeon Peas

Origin and Spread. Pigeon pea, red gram, arhar, tur, Congo bean, or gandul (*Cajanus cajan* Millsp.) is probably a native of Africa as a wild species occurs in the Sub-Saharan region. Seeds have been found in Egyptian tombs of the XIIth Dynasty, and it was cultivated there before 2000 BC, when trade relations had been established with both Africa to the south and Arab countries to the east. Pigeon peas were cultivated in Madagascar from a very early period and must have reached India in prehistoric times. Pigeon peas reached the New World shortly after Columbus, perhaps in the 16th century, but were not spread into the Pacific until much later and are recorded to have been introduced into Guam in 1772. However, this crop is now widely spread throughout the lowland tropics and is the most important pulse (non oilseed grain legume) in these regions.

A. Importance

Production. About two million tons of seeds were produced on three million hectares in 1970–1971. Southern Asia—primarily India—produces 95% of the world crop; but statistics for the African tropics may be low by a factor of 2 to 4 times since pigeon peas are extensively grown in compound or kitchen gardens throughout the humid to semiarid low and intermediate elevations. Field plantings are reported mainly from Malawi

and Uganda, but also occur in most other countries throughout central Africa. In the tropical Americas, the pigeon pea is an important vegetable in the form of cooked green peas, but it is also consumed as a dry pulse. Major producing countries are the Dominican Republic, Puerto Rico, and Venezuela, but other Caribbean and Latin American countries grow substantial quantities of this crop (FAO, 1972; Rachie, 1970).

1. Morphology

The pigeon pea plant is a woody, short-lived perennial shrub which can be grown either as an annual or a perennial (some bushes survive more than 10–12 years). It has a deep taproot with longer laterals in the spreading than in erect types. The narrowly lanceolate and finely pubescent trifoliate leaves are borne in a spiral arrangement with a $\frac{2}{5}$ phyllotaxis on the main axis and on branches. Some cultivars tend to produce long undivided primary branches on a shorter main axis with leaves carried the entire length and which fruit along the terminal one third to half the length. In other strains there is profuse secondary and tertiary branching, but some genotypes branch very little, producing leaves and fruits directly on the main axis, being similar in structure to the modern soybean. There are both erect (acutely angled branches–less than 30°) and spreading types (60° branching).

Inflorescences are smaller than cowpeas and predominantly terminal (basipetalous) or mainly axillary (acropetalous) and racemes can be 4–12 cm long. The flowers are about 2.5 cm in length, yellow or with the dorsal side of the standard red, purple, deep orange, or yellow with red or purple veins. The pods are somewhat flattened and 2–8 seeded (commonly 4) and 4–10 cm $\times$ 0.6–1.5 cm in length and width. Unripe pods may be solid green (recessive), purple or maroon, or green blotched with purple or maroon. Seeds vary in size, are usually globular in shape, may be white, grayish, red, brown, dark purplish or speckled in color, have a small white hilum and commonly weigh 7–15 g/100 seeds. Seeds germinate hypogeally, but dormancy may occur in some species (Purseglove, 1968).

Related Wild Species. The most closely related wild forms are probably *Atylosia* species, especially the erectoid forms. Morphological, taxonomic, and cytological evidence, as well as homology of genetic characters and a high degree of fertility of the intergenetic hybrids indicates a close affinity between *Cajanus* and *Atylosia*—particularly the erectoids, *A. sericea* and *A. scarabaeoides* W. and A. (Deodikar and Thakar, 1956; Kumar *et al.*, 1958; Roy and De, 1965). They suggest that structural changes in the chromosomes may have played a major role in the differentiation of the two species. In crosses between *C. cajan* and *A. lineata* these structural changes

appeared to be responsible for partial seed abortion, low percentage of germinating pollen and chromosomal abnormalities (quadrivalents, bridges, and fragments at meiosis) in the intergenetic hybrid. However, in view of the comparative ease in crossing and similarity in chromosome number ($2n = 22$) Roy and De (1965) suggest incorporating *Atylosia* into *Cajanus* with appropriate cytotaxonomic revision of the latter.

2. *Adaptation*

Pigeon peas are widely adaptable to climate and soil conditions, but perform better when annual precipitation exceeds 500 mm, the soils are not markedly deficient in lime, and waterlogging does not occur. They have a very deep tap root and are highly drought and heat resistant (Gooding, 1962). However, the plant also grows in subhumid ecologies where ripening can occur during the dry season. Thus, it may span the range of lowland tropical conditions better than most other legumes.

Most pigeon peas are highly photoperiod sensitive, although some lines have been shown to be highly insensitive. The range of maturities is from 90 to 250 + days depending on genotype, time of planting and other factors when grown at low elevations in the tropics. Since early growth is very slow, pigeon peas are frequently mixed with other crops—mainly short-term, hot weather cereals or other grain legumes—and continue to grow and fruit after the shorter duration companion crop has ripened and been harvested. Competition with weeds (and companion crops) is very poor during the first 4–6 weeks, but is excellent once a canopy has been established and a leaf litter builds up which not only suppresses weeds but also reduces erosion. High yields can be obtained when there are good rains during the first 2 months, but no further precipitation occurs during the remaining 2–4 months before harvest.

B. Plant Improvement

Pigeon peas are comparatively highly outcrossed from 3 to 40%, averaging about 20%. Wilsie and Takahashi (1934) observed 14.0 to 15.9% outcrossing between adjacent rows of contrasting varieties, Deshmukh and Rekhi (1962) found 25.0% natural crossing in central India; and Abrams (1967) found 5.8% natural crossing between rows 8 feet apart in Puerto Rico. Selfing may be accomplished by bagging terminal racemes with thin cloth bags or mesh (plastic or metal) "sleeves" which permit light and air penetration, but exclude larger insectivorous pollinators; or by sealing the petals with melted candle wax (Kelkar and Pandya, 1934). Higher levels of "controlled" natural outcrossing can be attained by using genetic male sterility or sprays of male gametocides. Kaul and Singh (1967) obtained

100% pollen sterility with minimum yield reduction by a foliar spray of a 1% solution of FW 450 applied prior to floral bud initiation. Thrips (*Taeniothrips* spp.) are believed to be responsible for both selfing and some outcrossing as well (Prasad and Narasimhamurthy, 1963; Sen and Sur, 1964).

Hand Pollination. Hand manipulation can be difficult under certain conditions and a high proportion of flowers shed before setting fruit. Blooming occurs over several weeks and flowers normally open between 11 AM and 3 PM and remain open for about 6 hours. It is important to emasculate before 3 AM on the day before the flowers open as pollen is shed later that morning (the day before opening). Rain reduces fertilization. There appear to be few if any barriers to wide crossing within and between species in *Cajanus*.

1. Plant Types

Early botanists recognized two basic plant types: var. *flavus* DC—the tur varieties of peninsular India which are shorter and earlier, have predominantly yellow flowers, green pods, light-colored seeds, and are usually 3-seeded; and the second basic type, var. *bicolor* DC—the arhar varieties of Northern India, are large, bushy, late-maturing perennials with red or purple or darkly veined flowers and hairy maroon or purple unripe pods with 4–5 dark colored or speckled seeds when ripe. However, most permutations of these characters have been observed in the world collection and in breeding lines, as there appear to be few if any barriers to recombination save the physical ones of time and space.

Perhaps a more useful classification of the cultivated species was developed by Akinola and Whiteman (1972) in studies on 95 accessions of *Cajanus*. They used 31 attributes including plant and leaf morphology, growth, flowering patterns, disease tolerance and components of seed yields to form 15 classes and three major groups according to a hierarchial program (MULTCLAS) and Euclidean system. The group categorization included:

Group A—inflorescence basipetalous, comparatively early maturity and pod ripening was both extensive and intensive

Group B—these types were early in maturity and pod ripening was extensive

Group C—maturity was very late and pod ripening was intensive

Fifty widely diverse plant types were studied by Sharma *et al.* (1971) and classified into five categories based on studies of growth habit and yields: (1) tall and compact, (2) tall open, (3) medium tall compact, (4) medium tall open, (5) dwarf bushy. Early and intermediate maturing types tended to be in groups (4) and (5), whereas late cultivars occurred

mainly in group (1). Seed yields were found positively correlated with spread of the plant, number of secondary branches, effective pod-bearing length of branch and pod number.

2. *Breeding Methods*

The most widely used method of improving and genetically manipulating *Cajanus* is by simple and mass selection in collections and pools of genetic stocks. However, considerable controlled outcrossing and hand-manipulated pollinations with or without selfing or isolation are done. Other techniques include using mutagenic agents like ionizing radiation and chemicals such as EMS, HNO_3, HCl, and chloral hydrate, polyploidizing agents (colchicine), and wide crossing. Objectives in breeding include characters like (1) high-yielding potential; (2) earliness; (3) perenniality of determinancy; (4) resistance to drought; (5) clustering of fruits (for convenience in harvest); (6) resistance to diseases like wilt (*Fusarium udum*), leaf spots, and stem rots, viruses and nematodes; (7) resistance to insects, such as leaf feeders and pod borers; (8) better quality seeds and improved cooking quality.

a. Mutation Breeding. The effect of ionizing radiation has been studied in Puerto Rico by Abrams and Vélez Fortuño (1961, 1962). They obtained a wide range of genetic variation in the R_2 of seeds treated with gamma rays or neutrons in the early-flowering KAKI and late-maturing SARAGATEADO cultivars. Most lines tended to be taller and included both earlier and later and higher yielding types than their parents. The effects of mutagenic chemicals on pigeon peas in India were reported by Deshmukh and Phirke (1962) and Phirke (1966). Seeds of EB3 and EB38 treated with HNO_3, HCl, and chloral hydrate proved to be diploids.Their progenies showed variation in plant height, pod size, yield, and grain weight, but crossed successfully with untreated normals. A new flattened pod character was discovered and proved to be a point mutation.

b. Polyploidy. Both natural occurring and induced polyploids—tetraploids ($n = 22$) and hexaploids ($n = 33$)—have been studied by investigators in India (Pathak and Yadava, 1951; Bhattacharjee, 1956; Joshi, 1966; Dafe, 1966; Shrivastava *et al.*, 1972). They observed total sterility in the hexaploid forms and varying levels of sterility in the tetraploids. The tetraploids were usually later in maturity and shorter in height, had longer and thicker leaves, more branches, and thicker stems, and were more erect. Flowers, stoma, pollen grains, pod and seed sizes were generally larger, and leaves and seeds contained more nitrogen than their parents. Varying levels of multivalence were observed in cytological examination. Since considerable variation in fertility occurred in both natural and induced auto-

tetraploids it should be possible to increase fertility through appropriate breeding methods like recurrent selection.

Wide Crossing. "Intergeneric" crossing between *Cajanus* and *Atylosia* has been reported from India (Deodikar and Thakar, 1956; Kumar *et al.*, 1958; Roy and De, 1965; Sikdar and De, 1967). *A. lineata, A. sericea,* and *A. scarafaeoides* have been utilized to introduce and enhance combining ability, perennial growth habit, tolerance of drought and resistance to pests and diseases. In particular, *A. lineata* and *A. sericea* have shown resistance to the pod borer (*Exelastic atomosa*) and wilt (*Fusarium udum*). Since these crosses have been comparatively easily made, it is proposed to combine *Atylosia* with *Cajanus.*

3. *Genetics*

There is comparatively limited information on heterosis, inheritance, associations of morphological characters, linkage groups, nature of gene action, and cytology in *Cajanus.* Heterotic effects were reported in ten F_1 hybrids grown at Bijapur, India (Solomon *et al.*, 1957). They obtained grain yield increases up to 24.5% over the mean of the parents, but the best-yielding hybrid was less productive than the best parental type in this study.

a. Character Associations and Heritability. Studies of five hybrids between four pigeon pea cultivars demonstrated that seed yields were highly positively correlated with number of pods per plant, to a lesser extent with plant height and 100-seed weight, and negatively with days to flowering. However, there was very little variation in seeds per pod compared with seed weight, plant height, and flowering date. Pods per plant had a low heritability: 45.3% in the F_2 and 52.1% in the F_3; but flowering date, plant height, and seed weights were highly heritable (Muñoz and Abrams, 1971). In other studies carried out in India, Sharma *et al.* (1971) found seed yields to be positively correlated with plant spread, number of secondary branches, effective pod bearing length of the branch and pod number. Beohar and Nigam (1972) confirmed these results and also found a positive correlation between number of branches and number of pods per plant; but number of pods per plant were negatively correlated with pod length.

b. Genotype × Environment Interactions. The nature and magnitude of variance components for yield, date of flowering, plant height, and seed weight were studied in 20 cultivars grown in southern and northwestern Puerto Rico over a three-year period by Abrams *et al.* (1969). They found the variety and variety × year components to be significant for all characters with the latter being greater than the variety component. The variety × locality × year interaction was also highly significant for all characters except yield, but was smaller in magnitude than the varietal components. How-

ever, the variety × locality component was negative and nonsignificant except for date of flowering. It is suggested that the two locations may have been quite similar ecologically (since Puerto Rico is a comparatively small island) insofar as interacting with the genotypes in this study.

c. Inheritance. Several botanical characters have been studied for their inheritance, and linkages with other factors have been determined. Some of these are listed in summary form in Appendices Tables IV and V.

C. Plant Protection

1. Insect Pests

Catepillars of *Heliothis armigera* Hubn., plume moth *Exelastis atomosa*, the pod fly *Agromyza obtusa M.*, and pulse beetle *Bruchus* sp. are serious pests of pigeon peas in India; whereas *Heliothis* sp., *Maruca testulalis*, and *Laspeyresia pychora* occur in Africa; the pod borer *Elasmopalpus rubedinellus* (Zell.), *Ancylostomia stercorea* (Zell.), and *Heliothis virescens* (*F.*) are serious pests in the West Indies; and in Peru, Korytkowski and Torres (1966) reported fourteen pests attacking this crop. In India, yield losses from pod-feeding insects (pod fly, plume moth, and pulse beetle) were studied in eight cultivars by Rawat and Jakhmola (1967). They observed greatest seed yield reduction in the cultivar Jabalpur Local (34.9%) and lowest in Type 148 (5.5%). However, Bindra and Jakhmola (1967) observed no varietal differences among eleven cultivars in tolerance to the same three pests. Nymphs and adults of hemipterous pests (coreids), like *Clavigralla gibbosa* Spin. in India, suck the cell sap from green pods and seeds, causing shriveling and reduced germination (Choudhary, 1969).

Chemical Controls. Insecticidal sprays of such materials as malathion, BHC, thiodan, dimethoate, Gardona, and Furadan (seed or seed furrow treatment) are among the most effective insecticides used in India and Africa (Thevasagayam and Canagasingham, 1960; IITA, 1973). Under intensive management, chemical insecticides are probably the only practical controls and are the most important management input for pigeon pea pests in the tropics at the present time. However, possibilities for biological and cultural controls deserve much greater attention than is presently accorded. The most ideal control would be host plant resistance or tolerance as the major form of augmenting other controls when the problem is highly intractable such as pod feeding pests.

2. Diseases

a. Fungi. Pigeon peas are often less susceptible to diseases than many other grain legumes in the lowland tropics. In India, the most serious fungus disease is a wilt caused by *Fusarium udum* Butl. However, there

appears to be good host plant resistance to different isolates of the fungus in C.11, C36, and NPWR.15 (Subramanian, 1963a; Ramanujam, 1972). In these and other investigations Subramanian (1963b) inoculated plants of both the wilt-resistant NP.15 and the susceptible NP.24 and found greater tolerance associated with a smaller reduction in contents of chlorophyll, ascorbic acid, iron:manganese ratio and total carbohydrates and less rapid decrease in transpiration. Inoculated NP.24 showed a marked increase in free reducing sugars.

Other important fungus diseases of *Cajanus* in various parts of Africa and Madagascar include root and stem rots caused by *Macrophomina phaseoli* and *Phaeolus manihotis*. Collar and stem rots caused by *Physalospora cajanae* and rust caused by *Uromyces* sp. are important disease in the Caribbean and South America. Leaf spots by *Cercospora* sp. and *Colletotrichum cajanae* and downy mildew caused by *Leveillula taurica* occur in some areas with largely undetermined consequences.

b. Viruses. Very few viruses have been reported on pigeon peas except for the sterility virus in India and witches broom apparently caused by a microplasma in the Caribbean. Sterility "disease" is characterized by: (1) reduction in leaf size, (2) bushy growth habit, (3) light yellowish-green foliage, and (4) suppression of flowers and fruits (Alam, 1933). More recent investigations on this or another form of virus-induced sterility indicate that it may be transmitted by nematodes since it was not transmissible by sucking insects nor with dodder, and the incidence of infected plants was greatly reduced in DD or Nemagon fumigated soil and appeared to be related to populations of *Rotylenchus reniformis* and *Tylenchorhyachus* sp. in the rhizosphere (Narayanaswamy and Ramakrishnan, 1966). Search for varietal resistance to sterility mosaic within a limited range of genetic diversity at Coimbatore, India did not produce resistance (Kandaswamy and Ramakrishnan, 1960).

3. Disease and Pest Control

The options for controlling or reducing losses by diseases are fewer than for insect pests. Application of fungal sprays to the foliage is seldom as economical nor practical as for chemical insecticides. The latter are sometimes the most important and essential management input in the growing of tropical legumes.

The most practical approaches to disease control are through (1) resistant varieties, (2) cultural practices, and (3) seed treatments. While resistant varieties provide the most practical control mechanisms, proper management in terms of crop rotations, sanitation, planting dates, and control of disease vectors (insects and nematodes) can greatly reduce the incidence of disease and its consequences even in susceptible species and cultivars.

Seedling diseases are often reduced by fungicidal seed dressings—a highly economic and convenient practice. To these can be added the newer systemic fungicides (Benlate, Demosan, and others), which greatly improve the effectiveness and extend the period of protection. Similarly, seed dressing contact insecticides like dieldrin or aldrin and the systemics like Furadan, phorate and Lanlate show considerable potential. Furadan seed treatments (1% active ingredient) at Ibadan have given up to 6 weeks of protection from root and foliage insects in addition to its possible nematocidal properties (IITA, 1973).

D. Physiology and Management

There are comparatively few definitive physiological investigations in *Cajanus*, although agronomic studies have been reported from all the major growing regions. While the range in genetic diversity is very great and the influence of environmental factors is considerable in this species, some generalizations can be made.

1. Growth Characteristics

Seedling growth in *Cajanus* is very slow for the first 30 to 50 days. The seedling plant is very slender and fragile, tending to grow upward more rapidly rather than spreading out. This characteristic may be desirable in predominantly mixed cultivation, but can be a handicap in monoculture. However, root development is both extensive and deep, enabling the plant to tap moisture and nutrients at greater depths than the more herbaceous tropical legumes. In comparisons of root development in soybeans, cowpeas, and pigeon peas at Ibadan, only the latter could penetrate the compacted gravel layer underlying these soils at depths ranging from a few centimeters to 1 meter.

The erect, self-supporting *Cajanus* plant, with comparatively small, lanceolate leaves, should confer high levels of photosynthetic efficiency in comparison with other legumes. In fact, some preliminary findings suggests leaf area indexes of 7.0 and higher to be optimal compared with LAI's of 3.0 and 4.0 for other large-leaved tropical pulses.

a. Drought Tolerance. Once established, pigeon peas grow exceptionally well on residual moisture. In southern Nigeria on upland soils the crop has been observed to grow vigorously and fruit profusely 75 days after cessation of rains (plantings established with 50–60 days of rains). The only other short-term field crop with similar capabilities in this area is cassava. Moreover, perennial types tend to be deciduous following fruiting in the dry season and will bear new leaves and resume growth with the return of rains even after several months of dry weather.

b. Light and Temperature Response. Very little is known about light and temperature response in *Cajanus*. Most cultivars are probably responsive to variations and interactions of both factors. However, daylength-insensitive genotypes are available and breeding efforts at IITA (7 N latitude) have produced several strains with "normal," predictable maturities and heights when planted in all seasons (IITA, 1973). Other investigators have demonstrated genotype × environment interactions in *Cajanus* (Derieux, 1971). In Trinidad, Spence and Williams (1972) utilized short days through December plantings and high populations (165,000 plants per hectare) to reduce mature plant growth to about 1 meter and increase determinancy, thereby facilitating mechanical harvesting.

2. *Mineral Nutrition*

It is often difficult to demonstrate response of pigeon peas to fertilizers or rhizobial inoculation in most tropical soils having a reasonable pH and good drainage (Pietri *et al.*, 1971). However, moderate applications of phosphate and potash could be expected to produce economic returns on soils deficient in those elements. Increases in dry matter and absorption of mineral nutrients occurs continuously in the plant, reaching peak assimilation/accumulation rates between flowering and seed set. At all stages of growth, calcium and magnesium are greater in the leaves than other organs, and seeds are richer in nitrogen, phosphorus, and potassium than other tissues. The nutrients exported in a crop producing 1630 pounds of dry matter per acre were: N = 29 lb; P = 9 lb; K = 10 lb; Ca = 12 lb; and Mg = 5 lb (Mehta and Khatri, 1962).

Most studies indicate phosphorus to be the first limiting element under tropical conditions and recommend applying 20–80 kg of P_2O_5 per hectare (Khan and Mathur, 1962; Bhatawadekar *et al.*, 1966). In India yields were increased by 13.5% in Madras by applications of 5 tons of compost plus 22.5 kg of P_2O_5 per hectare (Veeraswamy *et al.*, 1972a), and at Delhi from 1.29 to 2.76 tons of dry seed per hectare by applications of up to 100 kg of P_2O_5 per hectare (Chowdhury and Bhatia, 1971a). Moreover, several elements appear to be essential for satisfactory nodulation and production of rhizobial nitrogen. Nichols (1965) demonstrated that deficiencies of calcium, phosphorus, and magnesium had a direct and greater effect on reducing plant growth and nodulation than nitrogen, potassium, or iron deficiencies.

Singh and Archana (1964) investigated requirements for molybdenum observing the beneficial effect of molybdenum at 0, 1.25 and 2.5 ppm in pot culture on elongation of roots and shoots, dry matter accumulation, and free amino acid levels. The highest molybdenum treatments maximized accumulations of arginine, glycine, serine, asparagine, histidine, and lysine

but decreased β-alanine in the shoots by day 41 after germination. Sulfur applied at 100 ppm alone or in combination with phosphorus was observed to increase the number, dry weight, and nitrogen content of *Cajanus* root nodules, and increased the methionine content and dry weight of plants in pot trials by Oke (1969).

Symbiotic Nitrogen Fixation. Pigeon peas utilize the same rhizobial complex as the cowpea group, but considerable variability in the bacterial strain and in the host × symbiont relationship does occur (Ramaswami and Nair, 1965). Nitrogen fixation and transfer of nitrogen to other parts of the plant can be quite efficient according to experiments carried out in Nigeria by Oke (1967). He found fixation to reach a maximum of 14.5 mg per day per plant in *Cajanus* compared with 10.3 and 4.6 mg per day per plant for *Centrosema* and *Stylosanthes*. Younger plants were more effective than older ones in the fixation process. The beneficial effects of phosphorus, potassium, calcium, magnesium, molybdenum, and sulfur on nodulation as well as plant growth have been previously mentioned. However, nitrogen applications above 20 lb/acre tended to decrease yields of *Cajanus* in mixed cropping with millet in India—perhaps, in part, by increasing competition of the millet (Bhatawadekar *et al.*, 1966).

3. *Enzyme Activity and Hormones*

The occurrence and activity of urease in *Cajanus* were demonstrated by Malhotra and Rani (1969). They recorded a specific activity of 1500 ± units per milligram of protein, and observed it to be inhibited at high substrate concentrations in Tris·acetic acid buffers and by alkali metal and nitrate ions. They concluded the activity of urease on urea and its derivatives to be complex and that the substrate binds to the enzyme through hydrogen bonding involving urea protons.

Acid phosphatase activity was observed only in the nucleus and nucleoli of radicle cells of germinating seedlings by Kathju and Tewari (1968). They considered this finding unique since the autonomous cytoplasm inclusions—lysosomes and mitochondria—assumed to be the only centers of activity had none of the enzyme.

Seed treatments with up to 0.5% solutions of B-nine (*N*-dimethylaminosuccinamic acid) were observed to inhibit shoot growth of *Cajanus* proportionately to the levels applied by as much as 70% in length and weight at the highest treatment levels in experiments conducted by Mishra and Mohanty (1966).

4. *Management*

Pigeon peas are used both in short- and long-term cropping systems for food, forage, cover, or multiple purposes. [illegible]

and Africa they may be used as hedges in family kitchen gardens and to support climbing vegetable and pulse plants (Grubben, 1970). In field plantings pigeon peas are often intermixed with other crops like maize, sorghum, or millet and are left to mature on residual moisture after the cereal is harvested. Therefore, row spacings vary widely depending on the companion crop and cultivar used. In mixed cropping pigeon peas may be planted after every 2–4 rows of the main crop; but in pure stands, spacings normally vary from 30 to 90 cm in the row and 90 to 300 cm between rows. As a forage crop, defoliating and slashing back to 90 cm stubble, heights at 3–5-month intervals produced highest vegetative dry matter yields.

Population Experiments. Long-season types usually respond best to low populations of 7000–10,000 plants per hectare. Mukherjee (1960) obtained highest dry grain yields of 3530 kg/ha at spacings of 2 ft × 2 ft (about 27,200 plants/ha) and highest seed yield per plant at spacings of 4 ft × 4 ft (6800 plants per hectare). Hammerton (1971) investigated the effects of planting date and plant populations ranging from 4300 to 47,900 plants per hectare (0.21–2.32 m^2/plant) on green pod and seed yields and components of yield in two dwarf cultivars grown in Trinidad. There was no effect of planting date on yield nor its components, but a marked effect of plant populations. Increase in area per plant decreased pod yield per hectare, but increased pod yield per plant. The highest populations produced highest green pod yields of 8000 kg/ha, increased plant height at flowering and harvest but had no effect on the yield components (seeds per pod, mean pod and seed weights, and seed:pod ratio).

Exceptionally high plant populations (165,000 plants per hectare) of determinate dwarf cultivars planted under short days in December in Trinidad were shown to give satisfactory seed yields (2.5 tons/ha), reduce plant height at harvest to about 1 meter and greatly facilitate mechanical harvest. Yields were comparable to those obtained from longer-duration cultivars planted at 6600 plants per hectare (Spence and Williams, 1972).

5. *Utilization and Composition*

The green pea makes an excellent vegetable constituting 45% of the weight of the whole pod. In this form it is about two-thirds water (normally harvested when alcohol-soluble solids reach 25%), 20% carbohydrates, 7.0% protein, 3.5% fiber, 1.5% fat, and 1.3% ash. Dry, ripe seeds contain about 10% water, 23% protein, 56% carbohydrate, 8.1% fiber, and 3.8% ash. The protein is of reasonably good quality, but, like most grain legumes, is somewhat deficient in sulfur amino acids and tryptophan. However, the seeds are comparatively low in metabolic inhibitors and flatus sugars; and the testa is free of lipoxidase, which can cause off-flavors in soybeans and

other legumes. Normally the seeds are split and testas are removed in the preparation of Indian dhal, but since the cotyledons contain most of the important nutrients—primarily proteins, phosphorus, copper, and iron—removal of the seed coat and testa during milling does not substantially lower the food value of this pulse (S. Singh *et al.*, 1968; Kurien and Parpia, 1968). However, storage pests, birds, and rodents do cause substantial losses prior to milling (Khare *et al.*, 1966).

Nutritional Values. A trypsin inhibitor in *Cajanus* has been isolated and characterized by Tawde (1961). It was found quite active over pH range of 2.5–10.1 and was fairly heat stable. The deficiency of *Cajanus* seeds and meal in sulfur amino acids and tryptophan has been well established. However, it has also been shown to have a high biological value—comparable with black gram—when fed to mice at a 20% protein level (Daniel and De Berchoux, 1965; Ahsan *et al.*, 1968). Braham *et al.* (1965) showed that 20-minute autoclaved meal at 121°C supplemented with 0.1% tryptophan and 0.3% methionine was comparable to casein in rat diets fed at10% protein level.

E. Potential

The pigeon pea has exceptional potential for use over a wide range of tropical conditions, from subhumid to semiarid regions. It is particularly valuable in mixed cropping and in bush-fallow systems of agriculture where a perennial crop of three to four years is desirable. It can be used both as field and garden crops for producing green seeds as a vegetable, dry seeds as a pulse, green leaves for cooking and for forage or as a cover crop. Green pod yields of 1000–8000 kg/ha (conversion ratio of green pods to dry peas is 3.3:1) have been recorded; and good dry peas yields of 500–1000 kg/ha are realizable. However, favorable growing conditions can result in high yields of 1600–2500 kg/ha; while an exceptional yield of 5000 kg/ha of dry seeds was reported from India (RPIP, 1967), and Akinola and Whiteman (1972) obtained highest dry seed yields per year (7600 kg/ha) based on two major harvests from a single planting of cultivar UQ 50.

V. Cowpeas

The cowpea (*Vigna unguiculata* Walp.), also known as southern pea, blackeye pea, beans (West Africa), lubia, niebe, coupé, or frijóle appears to have originated in West Africa, very likely in Nigeria, where a profusion of wild and weedy species abound in both savannah and forested zones.

It exists as herbaceous, erect, semiupright, prostrate spreading, and twining-climbing forms. The cowpea was gathered or cultivated in prehistoric times in tropical Africa and must have reached Egypt, Arabia, and India very early, since it is known from Sanskritic times. The early Greeks and Romans knew of it, and it was introduced by the Spaniards into the West Indies in the 16th century, reaching the United States about 1700.

A. Description and Importance

The cowpea and its closely related weedy and wild relative have $2n = 22$ and $2n = 24$ chromosomes, but 22 is the more common condition. Outcrossing is low, depending on season and activities of pollen vectors. In subhumid parts of West Africa, the first rains are often characterized by a high level of bee activity resulting in outcrossing to the extent of 10% or more, whereas in the second rains insect activity is reduced and outcrossing may be less than 1%. Seed germination is epigeal, quick (48–72 hours), and usually very high.

Adaptation and Production

The cowpea is a predominantly hot-weather crop well adapted to the semiarid and forest-margin tropics. It is frequently mixed with other crops like maize, sorghum, millet, and cassava, but it is sometimes grown as a pure crop. Cowpeas are grown on a wide range of soil types from sands to heavy, expandable clays. Most cultivars do not tolerate waterlogging as well as soybeans. However, some forms like yard-long bean both tolerate and require higher rainfall than other cowpeas. Some varieties are day-length insensitive, while others require short days to mature within a reasonable time. Maturities may range from less than 60 days up to 7 or 8 months depending on genotype, and environment. Cowpeas tend to grow and spread very quickly thereby forming a quick cover to prevent soil erosion.

Producing Areas. Cowpeas are grown extensively throughout the lowland tropics of Africa in a broad belt along the southern fringe of the Sahara, and in eastern Africa from Ethiopia to South Africa. They are mainly confined to the hot semiarid to subhumid areas with significant production in Nigeria, Niger, Upper Volta, Uganda, and Senegal. Nigeria alone produces about 61% of the world crop or about 760 thousand tons annually. They are also extensively grown in India, southeastern Asia, Australia, the Caribbean, lowlands and coastal areas of South and Central America, and in the southern United States (primarily in the southeast, with some production in California). Frequently, the production of cowpeas is included under the general category "dry beans."

B. Plant Improvement

Yields of cowpeas in West Africa are very low as a consequence of several constraints including:

1. The climate: Insufficient, poorly distributed or excessive moisture; low insolations; and extremes of temperature.

2. The soil: Poor physical structure, low water holding capacity, deficiency of organic matter; extremes of pH; low or unbalanced fertility; and unfavorable microbiological conditions.

3. Plant protection: Large numbers of insect pests at all stages of growth; and a complex of diseases including fungi, bacteria, viruses, and nematodes.

4. Weeds: Uncontrolled weed growth competition for moisture, nutrients, light, and space.

5. Cultural practices: Land preparation, planting methods, planting dates, populations, spatial arrangements, and fertilizer applications (mainly phosphorus amd potassium).

6. Genetics: Low productivity efficiency; limited range of adaptation; agronomic deficiencies (shattering and lodging); susceptibility to pests and diseases; and poor acceptability and nutrient values.

1. Breeding Objectives

A strategy for breeding cowpeas has been described by Ebong (1970a,b). He stressed the importance of assembling and maintaining collections of genetically diverse materials and breeding for (1) high yield, (2) acceptable quality, (3) day neutrality, (4) erect growth habit, (5) long peduncles (above foliage), and (6) resistance to diseases (anthracnose, seedling blights, stem rot, viruses, and leaf spots). In francophone Africa, research on cowpeas was started in 1953 when variety trials, fertilizer experiments, and populations were studied and germplasm was collected (734 accessions; working collection is 222 entries). Most intensive efforts on "niebe" were made during 1962–1966 (Sène and N'Diaye, 1970). Bambey, Senegal has been the center for hybridization and breeding with emphasis on erect, determinate plant types, while observations and selection are being carried out in Niger, Upper Volta, North Cameroons, and Dahomey (Silvestre, 1970b).

In India, emphasis has been given to both pulse and forage types. Forage varieties like FOS-10, K. 397, and FOS-1 were found high yielding in green matter and useful as a dairy feed (Ralwani *et al.*, 1970). Other pulse breeding programs from Punjab to Madras have concentrated on the dry-seeded pulse types with drought resistance and maturity within 100 days (H. B. Singh *et al.*, 1968; Veeraswamy *et al.*, 1972b). Cowpeas have also

received attention in the Philippines and Indonesia, where both vegetable (*V. sesquipedalis*) and pulse types are grown, in the Caribbean and Central America (Aguirre and Palencia, 1968), and even in Russia (Medvedev, 1949).

2. *Improvement Methodology*

Breeding of cowpeas has largely followed conventional lines. Assembling, introducing, and testing germplasm constitute the all-important first link in this effort. Recombination of desirable characters through pedigree, backcross, and multiple crossing has been the major breeding technique employed. More recently, bulk-pedigree, single-seed descent, mutation breeding, and various population improvement systems have been considered. Wide crossing and mutation breeding have not been attempted seriously considering the vast array of genetic diversity already available.

3. *Assembling and Evaluating Germplasm*

Partial germplasm collections have been assembled by breeding programs in several countries (India, the United States, Nigeria, and others). These have recently been coordinated by the International Institute of Tropical Agriculture located at Ibadan, Nigeria. About 6800 different accessions had been assembled or collected by mid-1974. These will be grown out in total and partially in uniform nurseries to evaluate and catalog their important botanical characters. Records will be maintained on electronic cards for computer analysis and information retrieval.

Genetic Variability. A collection of 1072 lines was evaluated in Jhansi, India, by Kohli *et al.* (1971), and Mehra *et al.* (1969). Variability in several characters was studied and appeared to be related to geographical source. Greatest range in number of days to flowering (42.7–77.6 days) was observed in Indian cultigens; African lines had the greatest range in dry matter per plant (14.2–74.6 g). African sources had the highest green forage weight, plant heights, and main branch lengths. Far-Eastern accessions had greater stem girths, high primary branch numbers (almost equal to African cultigens), but lowest dry matter content (11.1 g per plant). Metroglyph analysis on the analysis of characters produced groupings of 11 distinct plant types.

4. *Mutation Breeding*

Increasing variability through mutation breeding has been explored to a limited extent. Uprety (1968) obtained a significant stimulation in plant growth and increase in protein nitrogen and proteinase activity in plants grown from seeds irradiated with 4 kr of gamma rays. Irradiation also accelerated flower initiation by 8 days. Irradiation greater than 4 kr ad-

versely affected these characters, but 2 kr of gamma irradiation had no effect. Ojomo and Chheda (1971) found significant reduction in survival at irradiation levels of 20 kr of X-rays and 12.2×10^{12} thermal neutrons/cm^2. However, chromosomal disorders, leaf spots, and gross foliage distortion tended to disappear as growth advanced. Čekalin and Zelenskaja (1970) induced sterility by mutagenic treatments.

Chemical mutagens—dimethyl sulfate (DMS), ethyl methane sulfonate (EMS), and *N*-nitrosomethylurea (NMU)—were studied by Sharma (1969). He observed reduction in fertility in the M_1 plants and obtained a late, giant-type mutant with large leaves, peduncles, and fruits. It also had thick, occasionally fasciated stems, large seeds with uniform black or mottled testas, trailing growth habit, and was very late. These mutants constituted 11.3% of all mutants recorded, maintained high fertility, and were high yielding. From these observations the author suggested the presence of a mutator gene with a wide range of activity causing other genes to mutate with differential but specific activity. Yield of mutants were about equal for DMS and EMS; but NMU was about twice as effective (18.2% mutations).

5. *Developing Elite Strains*

Hand Crossing. Improvement in tropical cowpea varieties has been accomplished mainly through selection and recombination followed by simple or mass selection in segregating generations. Genetic recombination in cowpeas is possibly the easiest among the self-pollinated legumes. The flowers are large, the keel is not twisted, emasculation is quick, and seed setting can be very high (up to 50% or more) when conditions are favorable. Reasonably high humidity and moderate temperatures appear to favor setting in hand-manipulated flowers; but there is a strong genetic component as well since some parents are much easier to cross than others.

Naphthalacetic acid in talc dusted into emasculated flowers reduced blossom drop and resulted in 30% setting in hand crosses (Barker, 1970). It is also highly desirable to do the crossing in the greenhouse or where pollinating insects are excluded; and to avoid high winds, rain, moisture stress, and high temperatures which cause heavy flower and bud drop (IITA, 1973). However, wide crossing with wild or other cultivated species of *Vigna* has been largely unsuccessful as either pollen germination fails or union of gametes does not occur. Sometimes when apparent fertilization takes place the embryos collapse soon afterward.

6. *Genetic Aspects*

Genetic investigations have been comparatively limited in *Vigna* species. However, the work that has been done on inheritance, heritability, charac-

ter correlations, nature of gene action, and combining ability has been very useful in support of plant improvement activities. Perhaps the most limited area of research is in evolutionary relationships, wide crossing and cytology, although Mukherjee (1968) has made a pachytene analysis and described the eleven chromosome pairs.

a. Inheritance of Characters. The mode of inheritance of several simply inherited characters in cowpeas is briefly described in Appendix 6; and 14 linkage groups are listed in Appendix Table VII.

b. Variability and Correlations. The major components of dry seed yield are pods per plant, seeds per pod, and 100-seed weight. Genetic variance studies have demonstrated a very wide range in variability of these characters, particularly for pods per plant. Variance estimates were also high for secondary characters like branches per plant, bunches (clusters) of pods per plant, days to maturity, peduncle length, pod length, and weight of nodules per plant; but they were lower for days to flowering and number of seeds per pod (Doku, 1970; Singh and Mehndiratta, 1969; Trehan *et al.*, 1970).

Heritability estimates were high for 100-seed weight, but medium for most of the other important primary and secondary yield components, except for days to flowering, which was low. Sène (1968) found 100-seed weight to have a broad sense heritability of 0.80, and to appear to be controlled by six pairs of genes acting additively in the cross N58-25 × N58-40 with 100-seed weights of 8–9 g and 19–20 g per 100 seeds, respectively.

Correlation and regression analyses in varying numbers of cowpea cultivars have been carried out by Singh and Mehndiratta (1969, 1970), Doku (1970), Trehan *et al.* (1970), and Janoria and Ali (1970). Genotypic correlations were generally higher than phenotypic correlations. These results can be summarized as follows:

1. Seed yield: highly and positively correlated with pods per plant, pod clusters per plant, seeds per pod, 100-seed weight, number of inflorescences per plant, days to maturity, and peduncle length.
2. Weight of 100 seeds: positively correlated with pod length; but negatively correlated with numbers of inflorescences per plant, pods per plant and seeds per pod.
3. Number of pods per plant: highly correlated with pod clusters per plant; and to a lesser extent with seeds per pod.
4. Days to flowering: correlated with days to maturity.

Partial regression analysis carried out by Janoria and Ali (1970) showed that pods per plant, seeds per pod, and 100-seed weight accounted for 83% of the variation in yield, whereas pods per plant and 100-seed weight accounted for 64% of the variation in this character. Singh and Mehndiratta (1970) found these three components of yield together accounted

for 68% of the yield variation in path coefficient analysis; and that selection based on discriminant function involving the three components was 33% more efficient than selecting directly for yield.

c. Combining Ability. Studies on combining ability in a diallel cross of four cowpea cultivars were carried out by Kheradnam and Niknejad (1971) in Iran. They found general and specific combining ability effects were significant for yield per plant, pod clusters per plant, number of seeds per 25 pods, seed weight and flowering date, but not significant for branches per plant. The ratio of general to specific combining ability was close to one for yield and pod clusters per plant, but general combining ability was more important for seed weight, days to flowering, and seeds per 25 pods.

C. Insect Pests

Insects attacking cowpeas in all stages of growth and in storage are probably the major limiting factor in cowpea production in the low humid tropics. Effective control of insect pests in these circumstances often returns 10–30 times the productivity of unprotected crops (IITA, 1973). In Africa and Asia about 15 major and more than 100 minor species attack the cowpea crop. Among these the most serious control problems involve the following:

Stage of growth	Insect species
1. Early seedling growth, foliage, flowers, and pods	*Empoasca fascialis* *Taeniothrips sjostedti* *Sericothrips occipetalis*
2. Green foliage (chewing, rasping)	*Ootheca mutabilis* *Zonocerus* spp. *Spodoptera* spp.
3. Flowers and floral buds	Thrips (same as above)
4. Floral buds and pods	*Hemiptera* spp. Coreid spp. *Maruca testulelis* *Laspeyresia ptychora* *Melanagromyza vignalis* *Heliothis* spp.
5. Stored seeds	*Bruchideae* *Laspeyresia* Others

Other species in addition to those mentioned above and important in the drier regions of West Africa have been noted by Delassus (1970): (1) *Melangromyza phaseoli*—the bean fly attacks the young developing

shoot. (2) *Sphenoptera* sp. (Buprestide)—also attacks the young stems; (3) Hemiptera/coreid species puncturing the floral buds and developing pods include: *Anoplocnemis, Acanthomia,* and *Tassidedes;* (4) pod and seed borers—including *Piezotrachelus varium, Dendorix* sp., and *Lampides* sp.

In the Americas the cowpea curculia (*Chalsodermus aeneus* Boh.) is a very serious pest in the southeastern United States; and the bean leaf beetle (*Cerotoma ruficornis* Oliv.) is a vector for cowpea mosaic in the Caribbean. Otherwise, *Phaseolus* bean pests can also be significant problems on cowpeas.

1. Losses from Insects

Direct losses in grain yields resulting from uncontrolled insect attack have been estimated in experiments carried out in Ibadan by Dr. W. K. Whitney (IITA, 1973). Individually, these losses may be as high as in the following cases.

Insect	Yield reduction (%)
1. Thrips	50
2. Maruca—flower damage	20
3. Maruca—pod damage	20
4. Hemiptera—seed damage	35
5. Laspeyresia—seed damage	50

Collectively these estimates exceed 100%, and productivity is virtually nil without some control in certain seasons in the humid tropics.

2. Chemical Insecticides

The basic approach to insect problems of cowpeas has been through chemical insecticides. The best of these from several points of view are endosulfan (Thiodan 50 WP) at 0.15% a.i. in water or 0.9 kg a.i./ha; lindane 50% WP (Gammalin) at 0.14% a.i. concentration or 0.6 kg a.i./ha (if emulsifiable compound is used, concentration should not exceed 0.5% concentration); azinophosmethyl 25% WP (Gusathion M) at 0.14% a.i. concentration or 0.6 kg a.i./ha; dimethoate 30% EC (Rogor 40) at 0.03% a.i. concentration or 0.2 kg a.i./ha; and Gardona 75% WP at 0.07 to 0.14% a.i. concentration or 0.3 to 0.6 kg a.i./ha. Combinations of Thiodan and Rogor 40 applied six to eight times during the growth cycle provides a high level of control, but often as few as two or three sprays are highly profitable under commercial practice. Gardona alone or

mixed with Thiodan may be more effective against pod-boring species during the postflowering period (IITA, 1973).

Some newer insecticides show considerable promise, including methomyl 90% (Lannate), Orthene 75 SP, Dupont 1410 20% EC and Carbofuran 75% WP (Furadan). Carbofuran and methomyl applied to the seed as a pelleting treatment at 0.5 to 2.0 g per 100 g of seeds or in the seed furrow at 1 kg a.i./ha have been shown to protect the plants for up to 6–7 weeks after planting. Some applications are comparatively inexpensive and, when combined with 2 or 3 postflowering foliar applications (Gardona or Gardona + Thiodan), should provide a high level of economical plant protection throughout the growing period of the crop. Finally, the harvested, threshed, and properly dried seeds can be safely stored in tightly closed plastic bags of 0.3 mm thickness, holding 40–50 kg of grain, and to which 18 g of carbon tetrachloride have been added (Caswell, 1968).

3. *Cultural and Biological Controls*

The possibilities for cultural and biological controls and host plant resistance must not be overlooked and should be investigated intensively in the future. There already appears to be a genetically controlled mechanism for low level tolerance or resistance to thrips (IITA, 1973); but the possibility of resistance to pod borers has not yet been established. Lorz (1970) suggested that ZIPPER CREAM with thick pod walls might have resistance to pod-puncturing insects. Todd and Canerday (1969) observed Fla 453-01 to be least damaged by the cowpea curculio, and Ala 963-8 and Va 59-119 impaired larval development of the pest. Chandola *et al.* (1969) found T.2 to be resistant to *Bruchus* sp. Generally then, the pests of cowpeas in the tropics are indeed formidable, and problem solving must proceed on all fronts—both in the direction of rapidly developing chemical protectants as well as the longer-term cultural, biological, and host plant-resistant aspects.

D. Diseases and Nematodes

There are several major disease problems of cowpeas in the lowland tropics, although overall reduction in yield may be less than insect predations, at least in West Africa (IITA, 1973). The major problems in southern Nigeria include the following:

I. Fungal and bacterial diseases
  1. Seedling blights and wilts
    a. *Rhizoctonia solani*
    b. *Pythium aphanidermatum*
    c. Secondary—*Colletotrichum* sp., *Fusarium* sp., and *Botryodiplodia theobromae*

2. Stem blight—*Colletotrichum lindemuthianum*
3. Leaf spots
   a. *Cercospora cruenta*
   b. *Cercospora canescens*
   c. Bacterial pustule (*Xanthomonas vignicola*)

II. Virus diseases
1. Cowpea green mottle virus (green blister)
2. Cowpea yellow mosaic virus (or yellow flecks)

III. Nematodes
1. Root nematode (*Meloidogyne incognita*)
2. Root lesion nematode (*Pratylenchus* sp.)
3. Spiral nematode (*Helicotylenchus pseudorobructus*)
4. String nematode (*Belonlaimus gracilis*)

IV. Phanerogram parasites
Striga gesnerioides—a parasitic weed on the roots of cowpeas in tropical Africa

Delassus (1970) also mentions several species occurring in the drier francophone regions of Africa:

1. Rust or blight—*Uromyces appendiculatus*
2. General wilting or withering—*Neoscosmopora vasinfecta*
3. Affecting stems, foliage and pods: *Cercospora* sp., *Helminthosporium* sp., *Leptosphearula* sp., *Choenephora* sp., and *Rhizoctonia bataticola*

1. Losses in Production

Separately and collectively, diseases can result in reduced grain yields and loss of foliage. In southern Nigeria losses in stand and grain productivity have been estimated as high as those tabulated below.

Disease	Reduction
1. Seedling blights (fungus)	75% Stand
2. Anthracnose	50% Yield
3. Leaf spots (*Cercospora*)	30% Yield
4. Bacterial pustule	12% Yield
5. Viruses—yellow mosaic	50% Yield
6. Nematodes—root knot	25% Yield

Seedling blights do not reduce yields directly, and if the loss in stand occurs early, adjacent plants tend to compensate for the dy.. g plant in terms of increased and extended branching and fruiting (IITA, 1973). In studies on *Cercospora* leaf spots at Ibadan, direct yield losses from *C. canescens* and *C. cruenta* were observed to be 18 and 42%, respectively (IITA, 1973). A single benomyl (Benlate) spray applied 5 weeks after planting controlled these diseases in a determinate variety, but reduced yields by 20% in an indeterminate variety.

2. *Fungicides*

The most practical and promising approach to disease problems generally is through host plant resistance and by chemical seed dressings. A new systemic fungicide, chloroneb (Demosan 65 W) alone or in combination with thiram at the rate of 2 g per kilogram of seeds has given excellent results in experiments carried out at Ibadan (IITA, 1973). Potassium azide at 2000 ppm used for soaking seeds for 5–10 minutes protected seedlings for up to 21 days from *Rhizoctonia* sp., *Sclerotium rolfsii* and *Pythium* sp. in experiments carried out by Gay (1970) in Georgia, USA. Other fungicides like Dithane M-45, benomyl (Benlate), carboxin (Vitavax) or the copper-based compounds like Perenox and Kocide can be used as foliage sprays to control several diseases but are seldom economic on a commercial scale.

Host Plant Resistance. Preliminary evaluation of comprehensive germplasm collections indicates that several sources of tolerance or resistance to all major diseases and viruses in southern Nigeria are available (IITA, 1973). Earlier investigations have identified many sources for resistance to various diseases, but more recent reports describe the following specific host plant resistance:

1. Rust (*Uromyces phaseoli* var. *vignae*)—QUEEN ANNE is immune to all races; previously PINKEYE PURPLE HULL, TEXAS CREAM, and CREAM 40 were resistant (Heath, 1971; Gay, 1971).
2. Viruses (bean yellow mosaic, cucumber mosaic, mottle viruses)—ALABAMA 3-6-5, ALABAMA 91-7, and PRINCESS ANNE were resistant (Harrison and Gudauskas, 1968); cowpea mosaic virus in India—MS 9081, EC 2085, EC 4216, and EC 4203 were resistant (Govindaswamy *et al.*, 1970; Khatri and Chenulu, 1971).

The nature of rust immunity in QUEEN ANNE results from cell necrosis and formation of calloselike sheaths enclosing the haustorium; in other varieties, resistance was due to hypersensitivity and death of the invaded host cells in observations made by Heath (1971).

E. PHYSIOLOGY

Information on physiological processes in the broader sense includes both developmental aspects and the influence of external factors interacting with those processes. Among these external factors are daylength, light quality, temperature, elevation, humidity, water relationships, pests and diseases, mineral nutrition, soil physical and chemical characteristics, harvesting procedures, and other factors.

1. Reproductive Ontogeny

Flowers are borne in racemose inflorescences at the distal ends of peduncles arising from leaf axils. They are arranged alternately in acropetal succession with up to 8–12 pairs per inflorescence, although usually only the first two pairs develop. The flower is large, has a straight keel, and is normally white or blue. There are ten diadelphous stamens, the vexillar one being free; the ovary is sessile and multiloculate, and the style is bearded along the inner side, ending in an oblique stigma. A high rate of abortion occurs in the cowpea plant which normally produces 100–500 flower buds of which 70–88% are shed before anthesis. Of the remaining 12–30% up to half abort prematurely, so that only 6–16% of the total flower buds produce mature fruits (Ojehomon, 1968a,b). Flower loss is compensated for by setting more buds on secondary and tertiary branches, but this mechanism is limited. Ojehomon (1970) demonstrated a 43% reduction in seed yield per plant by removing all flowers for 12 days after anthesis. However, individual flowers represent very little loss in dry weight (0.01 g) and therefore do not constitute a very large sink (Summerfield *et al.*, 1973).

2. Light and Photoperiod

Short-day cultivars are commonly grown in the higher tropical latitudes to assure maturation toward the end of the rainy season with more efficient utilization of moisture and production of better seed quality through regulation of flowering toward the end of the rainy season. Photoinsensitive varieties are often grown in low tropical latitudes and in long-day temperate regions. However, short-day plant types will often produce excessive vegetation to the detriment of grain yield when planted earlier than optimal for that cultigen (Summerfield *et al.* 1973).

The optimal photoperiod for induction of flowering in cowpeas is 8–14 hours from studies carried out by Wienk (1963) on 14 cultivars and 15 photoperiods varying from 6 to 24 hours. Moreover, many cultivars respond to light quality by becoming etiolated with twining leaders under reduced light. This effect results in the climbing habit when grown in association with other crops and weeds. Under artificial lighting, the use of "daylight" fluorescent tubes with a 5% tungsten supplement was found to normalize growth in cabinet experiments in England (Summerfield and Huxley, 1972).

Photosynthesis. Studies on absorption of radiation at the 2-leaf and 4-leaf stages in Guadeloupe (French West Indies) showed that the greatest proportion of radiation is adsorbed in the morning when conditions are favorable for photosynthesis, but at midday adsorption was less, thereby

preventing a buildup of high temperatures in the leaves (Varlet-Grancher and Bonhomme, 1972).

3. *Temperatures*

Radiant energy directly affects both air and soil temperatures, which in turn can limit the growth process in various ways. In some recent experiments carried out at the University of Reading, Summerfield *et al.* (1973) have amply demonstrated the profound effects of night temperatures (19° and 24°C) on both vegetative and reproductive development in terms of growth, days to first flower, and seed yields in 30 cultivars studied. Moreover, air temperatures also influence rhizobium activity and nodulation as shown in experiments conducted by Dart and Mercer (1965). Maximum dry matter production occurred at 27°C day and 22°C night temperature in the cowpea rhizobial system in the range of 21° to 36°C day and 16° to 31°C night temperatures studied. They concluded that air temperature is of considerably greater importance than either light intensity or nitrogenous fertilizers in the symbiotic system.

The conclusions reached by these investigators are that initiation of the reproductive process occurs as a balance between vegetative growth and concentration of the flowering stimulus, and that temperatures could act to either increase vegetative growth or reduce the floral stimulus.

4. *Water Requirements*

The cowpea can be highly drought resistant, being grown in subhumid to semiarid conditions. However, it may also be reasonably tolerant of high soil moisture from preliminary studies on hydromorphic soils at Ibadan (IITA, 1973). Most of the cowpea crop is grown under rainfed conditions, but it may also be grown with surface or sprinkler irrigation in different parts of the world; or on residual moisture on soils with high water-holding capacity (e.g., after rice).

Moisture stress resulting in temporary wilting can reduce productivity considerably during the period from emergence to first flower, but may not significantly affect yields thereafter in determinate varieties (Huxley and Summerfield, 1973). However, Doku (1970) found nodulation to be reduced when moisture was limiting particularly when combined with long days (16 hours vs 11 hours, 48 minutes).

5. *Mineral Nutrition*

The requirements of cowpeas for nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur have been partially established under certain conditions and for specific genotypes. However, there is very litle information on minor nutrient requirements, except for assumptions based on re-

sults with other grain legumes. Thus, molybdenum, manganese, copper, zinc, and boron may be required for effective nodulation and increased productivity. It has been estimated that each ton of cowpea seeds exports the following minerals: N = 40 kg, P_2O_5 = 17 kg, K_2O = 48 kg, CaO — 16 kg, MgO = 15 kg, and S = 4 kg.

Information available on major nutrients other than nitrogen is summarized as follows:

1. *Phosphorus*—field applications of 100–200 kg/ha of superphosphate are commonly recommended (Sellschop, 1962). Absorption of phosphorus occurs primarily at the end of the growing period and is mainly transported to the seed (Jacquinot, 1967). Foliar application may be more efficient than soil application (Mohta and De, 1971).

2. *Potassium*—this element is transported mainly to the stem in early growth and later to the seeds (Jacquinot, 1967). Field response to potassium by cowpeas has been low in Africa although K_2O applications of 40 kg/ha have increased nodulation in eastern Nigeria (Tewari, 1965). In the southeastern United States, Worlev *et al.* (1971) recommended that the level of elemental potassium not exceed 42 kg/ha.

3. *Calcium*—this element stimulates nodulation and may affect the release of molybdenum in acid soils. Most calcium is taken up during the first 40 days of growth, but may accumulate in the leaves in replacement of potash during later growth (Jacquinot, 1967). On acid soils cowpeas may benefit from application of 1.6–2.8 tons of lime per hectare (Sellschop, 1962).

4. *Magnesium*—uptake is maximal during the last third of the growth stage and foliar concentrations are slightly higher than in other plant organs (Jacquinot, 1967). Growth responses to magnesium have not been studied.

6. *Nitrogen Fixation*

Among the major elements, very little response to nitrogenous fertilizers is realized when seeds are properly inoculated or the appropriate rhizobial cultures occur in the soil. Therefore, it is usually more efficient to improve conditions tending to maximize the rhizobial process:

1. Inoculation with efficient strains of rhizobium if nodulated cowpeas or related species have not recently been grown on the land. Efficient strains may double yields in comparison with some indigenous rhizobium (IARI, 1971).

2. Improving soil moisture and mulching increased nodule production, but excessive cultivation decreased nodulation in Malaya (Masefield, 1957).

3. Temperatures of 24°C were optimum for primary root nodulation; but 33°C was found optimum for secondary root nodulation by Dart and

Mercer (1965). Number of plants nodulating and nodulation per se were decreased in a linear manner as temperatures increased from 31°C to 42°C (Philpotts, 1967).

4. Photoperiod affects nodulation and the latter is reduced by photoperiods longer than 16 hours although moisture may not be limiting (Doku, 1970).

5. Applications of phosphorus increases nodulation (Tewari, 1965), but nodulation is reduced by high soil nitrogen during early growth (Ezedinma, 1964).

6. Selfing tended to increase nodulation when two lines were crossed together, suggesting the accumulation of "+ factors" and the possibility of increasing nitrogen-fixing efficiency through breeding (Doku, 1970).

Fixation of nitrogen by cowpeas was estimated by Nutman (1971) at 73–240 kg/ha per annum. Nitrogenous substances are usually concentrated in the leaves during vegetative growth and then transported to the seeds during the grain filling period. It is further estimated that about 40 kg of nitrogen are exported from each ton of cowpea seeds harvested from a hectare of land (Jacquinot, 1967). Generally then, it can be assumed that the symbiotic nitrogen fixing process is adequate for cowpea production at current productivity levels if conditions for nodulation are favorable.

F. Management

Productivity in cowpeas grown in Africa is very low being only 100–300 kg/ha of dry seeds. This is attributable to its being cultivated in subsistence agriculture as a secondary crop in association with cereals like sorghum, millet, or maize. In this situation cowpeas are frequently planted broadcast at 22–33 kg/ha after the cereal is about 50 cm tall. After germination the seedlings are often thinned out (and used as a pot herb) depending on the cultivator's judgment on availability of moisture which may be in excess of the cereal's needs that season, and to maximize dry seed yields of the "beans." In this system, cereals constitute the major energy source for the cultivator and his dependants and are given first priority in the season's activities. If additional lands are cultivated beyond the yearly subsistence needs they are usually planted to a cash crop like cotton or groundnuts.

1. Associated Cropping

Mixed cropping has been demonstrated to be more highly productive than sole cropping of millet and cowpeas in Niger. The mix grown on 1 hectare plots produced yields of 682 kg and 1525 kg of peas and millet, respectively, compared with 1072 kg of peas and 905 kg of millet from pure stands of one half hectare each. However, profits from sole cropping

were greater as a consequence of the higher market value of cowpeas (Nabos, 1970). Of course, cowpeas can also be quite successful and profitable grown as a sole crop when pests and diseases are controlled. Yields ranging from one to three tons per hectare are obtained in small plots, and at these levels would more than compensate for both the costs of protection and the returns from the associated crop at current market valuations. Nevertheless, adoption of monoculture systems may depend on developing both high-yielding cereals and legumes together with "packages" of reliable production practices to enable nonmechanized agricultural units to attain higher levels of productivity on limited cultivated areas.

2. *Date of Planting*

Day neutral cowpeas can be planted any time of the year in lower tropical latitudes when moisture and fertility are adequate and satisfactory pest control is achieved. At Ibadan, good growth of photoperiod-insensitive cultigens occurs at any time of the year, including the dry season, late November to March, if irrigation is available (IITA, 1973). However, it is highly desirable for maturation to occur during bright, sunny weather to reduce pod and seed damage from both insects and diseases (McDonald, 1970b). Since most cultivars commence flowering optimally from 35 to 70 days after germination, date of planting should be so timed that protracted rainy periods are over by the time the crop begins flowering. Thus, at Ibadan, late May and late August are better for day neutral types, whereas at higher latitudes in monomodal or monsoon type climates, a late June or early July planting may be preferable. Daylength-sensitive strains should not be planted in the first season in bimodal rainfall regions.

3. *Populations and Spacings*

In mechanized agriculture, cowpeas are usually planted in rows 75–100 cm apart, 7–10 cm within the row, and at a seed rate of 17–28 kg/ha. For forage, cowpeas may be broadcast at seed rates of up to 100 kg/ha and mixed with sudangrass, sorghum, or maize (Sellschop, 1962). In African mixed cropping systems cowpea seeds are frequently broadcast at a seed rate of 22–33 kg/ha. In francophone Africa, hill plantings (2–3 seeds per drop) are recommended at spacings of 50 × 50 cm or 50 × 60 cm for early cultivars, and wider for late or spreading varieties (Silvestre, 1970b).

4. *Fertilization*

Fertilizer experiments in West Africa have shown low but significant responses to the three major nutrients nitrogen, phosphorus, and potassium (Nabos, 1970). The most common recommendation is for phosphorus at 20–60 kg of P_2O_5 per hectare, but potash may be included at the rate

of 30–60 kg of K_2O per hectare if known to be deficient; and perhaps a light application of nitrogen—15–30 kg of nitrogen per hectare—can be profitable.

Worley *et al.* (1971) made definite recommendations on plant nutrients for southern Georgia, USA: nitrogen, 27–55 kg/ha; phosphorus, 12–24 kg/ha; and potassium, not more than 46 kg/ha. They further observed contents of copper, zinc, aluminum, and titanium in the foliage to be negatively correlated ($r = -0.36$) with seed yields. In India, foliar sprays of 60 kg P_2O_5 per hectare were even more effective than the same application banded beside the row (Mohta and De, 1971).

5. *Weed Control*

Weed competition becomes the major constraint when other factors are not limiting. Mechanical cultivation or hoeing may be the most practical means of control under most tropical conditions, but several weedicides have been tried with varying success in different regions. Trifluralin at 0.56–1.12 kg/ha applied presowing and immediately harrowed or rotovated in has given good control in the United States (Ogle, 1967). Chloramben (Amiben) at 3 kg/ha has generally given good results; but hand weeding, for the first month after planting of short duration, determinate cultivars, has given as good yields as clean weed control plots in southern Nigeria (IITA, 1973).

6. *Cover Cropping*

The effectiveness of cowpeas in rapidly covering the soil surface and preventing loss of topsoil has been amply demonstrated in runoff experiments in southern Nigeria. Cowpeas proved superior to maize and other cereals for this purpose (IITA, 1973).

7. *Harvesting the Leaves*

The young shoots, leaves, and even roots of cowpeas are used as pot herbs in most parts of Africa. If the tender green leaves are plucked before the reproduction phase begins, the plant continues to produce new leaves. Mehta (1971) demonstrated that it was possible to remove all tender leaves up to a maximum of three times at weekly intervals during the vegetative stage of growth without reducing the final seed yield.

G. Utilization

The primary use of cowpeas is for the dry pulse, but the green pods, green seeds, seedlings, and tender young leaves are often used as pot herbs. Canning and freezing shelled green peas has become an important industry in parts of the United States in recent years, having exceeded 40 million pounds by 1971. The vegetation also makes excellent hay, and the surplus culled and broken seeds can be used as a protein concentrate for domestic

animals. Cowpeas cook more easily and quickly than *Phaseolus* beans and are therefore favored when fuel is scarce. Cowpea hay is high in nutrients, and its fiber is more easily digested than lucerne fiber. Moreover, it is excellent for grazing by milk-producing animals.

Cowpeas are the preferred pulse crop in many regions, particularly in tropical Africa. This is fortunate since they do provide an important source of proteins, caloric energy, and other nutrients with a minimum amount of cooking or preparation. Moreover, the levels of toxic substances and antimetabolites like the trypsin inhibitor, hemagglutinins and flatus factors are minimal in the cowpea (Liener, 1969).

1. Food Preparations

In Africa cowpeas are consumed in three basic forms of which there may be many variations. Most frequently they are cooked together with vegetables, spices, and other ingredients to make a thick soup or gruel which is eaten in association with the basic staple such as preparations of cassava, yams, plantain, or cereals. The second preparation would be as deep-fried cakes (akara balls) prepared from a dough of decorticated cowpea flour to which onions and seasonings are added. The third preparation is steamed bean cakes (moin-moin in Nigeria) prepared from decorticated cowpea flour to which chopped onions and seasonings have been added. In preparing the flour, the testas are removed first by soaking in water and rubbing. Rough or wrinkled testas are preferred, as they soak quickly and are easily removed.

2. Nutritive Qualities

Although low in toxic substances, cowpeas have been shown to contain trypsin and chymotrypsin inhibitors (Ventura and Filho, 1967) and may have a cyanogen as high as 2 mg per 100 ml of extract (Montgomery, 1964). Therefore, cooking is needed to inactivate these undesirable principles. In terms of proximate principles, the dry pulse contains the following constituents.

Constituent	Percent
Water	11.0
Protein	23.4
Carbohydrate	56.8
Fat	1.3
Fiber	3.9
Ash	3.6

Contents of calcium (90 mg/100 g), iron (6–7 mg/100 g), nicotine acid (2.0 mg/100 g) and thiamine (0.9 mg/100 g) are high and contribute substantially to these requirements in tropical diets (Platt, 1962).

VI. Mung Beans

Green, golden, and black gram are now considered to belong to the same species, *Vigna radiata* (L.) Wilczek formerly placed in *Phaseolus* as *P. aureus* Roxb. (mung bean, green and golden gram) and *P. mungo* (L.) Hepper, (black gram, urad, mash, woolly pyrol). Verdcourt (1970) has recommended retaining the subspecies designation to maintain the separate identities of the two races as *V. radiata* var. *aureus* for mung bean/green gram and *V. radiata* var. *mungo* for black gram. The putative wild ancestors are believed to be *Vigna* (*Phaseolus*) *radiata* var. *sublobata* (*Roxb.*) Verdc. and/or *Vigna* (*Phaseolus*) *trinervius* (Wight and Arn.) Verdc., which occur wild in India.

The two subspecies can usually be distinguished from each other by the pod characteristics. The variety *aureus* has spreading or reflexed pods with short hairs, globose seeds, and flat seed hilums, whereas in the variety *mungo* the pods are erect or suberect with long hairs, the seeds are larger, oblong, and smooth, and the hilum is concave. For purposes of this paper both subspecies will be referred to under the term "mung beans" unless otherwise specified as green or black gram.

A. Importance and Utilization

Mung beans are important crops in southeastern Asia, and particularly in India, where about 0.30 million tons of green gram and 0.44 million tons of black gram are grown annually on 1.4 and 1.5 million hectares, respectively. They are particularly esteemed for their excellent quality, high digestibility and freedom from the flatulence effect associated with other pulses. They are frequently fed to children, convalescents, and geriatrics or used when "breaking" a long fasting period, owing to their ease of digestibility. Black gram is particularly highly prized in the vegetarian diets of high caste Hindus. The haulms are used for fodder, and the bean husks and small broken pieces are useful as a feed concentrate. The crop is also grown for hay, green manure, and cover crop. Green gram makes better hay than black gram, as the stems and leaves are less hairy.

1. Food Preparations

The dried pulse can be split or eaten whole after cooking and made into a soup of dhal (porridge) to be eaten with a cereal. The beans can also be used in various deep-fried and spiced dishes like noodles, balls, or snacks, or baked in bread and biscuits after parching removing the testa and grinding into flour. They are also widely relished as bean sprouts, which are prepared by soaking the dry beans overnight, draining, placing

them in containers in a dark place and sprinkling with water every few hours. In about a week the sprouts are ready to eat. One kilogram of dry beans makes 6–8 kg of sprouts. The green pods and seeds can be cooked as vegetables (Purseglove, 1968).

2. *Ecology*

Mung beans are grown in the southeastern Asia at low to intermediate elevations, on rainfed lands, and frequently following rice. They perform best on good loamy soils with a well distributed rainfall of 750–900 mm per year, but are reasonably resistant to drought and somewhat susceptible to waterlogging. However, black gram is well adapted to clayey soils and is frequently grown on black cotton soils in India. Mung beans are also grown to a limited extent in Eastern Africa, primarily to cater to the Asian demand, and show considerable agronomic potential in West Africa as well (IITA, 1973).

a. Alkalinity and Salinity. Both black and green gram grow well under both alkaline and saline conditions. One cultigen of black gram (T.9) was quite tolerant of both salinity (up to 4.3×10^{-13} EC) and alkalinity (90% exchangeable calcium) in Uttar Pradesh, India (Mehrotra and Gangwar, 1964). In other experiments Sharma *et al.* (1971) obtained good germination of cultivars Nos. 19, 21, and 3 in solutions of $NaHCO_3$ and Na_2CO_3 from 1–6 mmhos/cm at 25°C. Other cultivars, Nos. 36 and 92, RS 4, and RS 5, were considered suitable for saline soils when $CaCl_2$ was not the predominant salt.

b. In Cropping Systems. Mung beans are frequently grown as short-term crops following the main crop, such as rice, utilizing end-of-season precipitation and residual moisture, or are intercropped with other species like cereals, sugarcane, or cotton. In Taiwan, mung beans have been highly profitable intersown with spring-planted sugarcane (Tse and Hsueh, 1965). They can also be undersown with a cereal, like maize, in north India, and when planted within 2 weeks of maize produced above 200 kg of dry seed per hectare (Pathak *et al.*, 1968). Mung beans having small seeds and quick early growth make excellent cover and green manure crops in Australia, producing up to 9 tons of green material for plowing down (Chapman and Garioch, 1966; Gonzales, 1962).

B. Description and Varieties

Morphology

The mung bean is an erect or suberect, deep-rooted, much branched, rather hairy, annual herb, 0.3–1.5 m tall. In some respects it resembles

cowpeas, but tends to be more erect and is less twining. The leaves are alternate, trifoliate, and dark or medium green; the leaflets are ovate and are sized about 1.5–12 × 2–10 cm; and the petioles are long. The inflorescence is an axillary raceme, and the peduncle is 2–13 cm long. The standard is yellowish and 1.1–1.7 cm in diameter. The keel is spirally coiled with a hornlike appendage. Germination is epigeal. Other distinctive characters useful in distinguishing these two subspecies from other *Vigna* and from each other are listed in the accompanying tabulation.

Character	Subspecies	
	aureus	*mungo*
Plant height	Up to 1.5 m	Up to 0.80 m
Stipule shape	Ovate	Falcate
Inflorescence type	Axillary raceme	Raceme may be branched
Florets per peduncle	10–20	5–6
Calyx bracts	Same length as calyx	Longer than calyx
Pod attitude	Spreading, reflexed	Erect or suberect[a]
Mature pod size	0.4–0.6 × 4–10 cm	0.6 × 4–7 cm
Mature pod color	Gray or brownish	Buff to dark brown
Pod hairiness	Moderate, short hairs	Profuse longer hairs
Seeds per pod	10–15 Seeds	6–10 Seeds
Seed shape	Globular	Oblong, square
Weight of 100 seeds	3–5 g; up to 8 g	About 49 g
Seed color	Green, yellow, blackish	Black, occasionally green
Hilum	Round, white, flat	White, concave
Testa	Has fine, wavy ridges	Smooth, without ridges

[a] Pods of var. *mungo* are shorter, thicker, hairier and have a characteristic short, hooked beak.

a. Embryology. Embryology and seed structure follow that of other *Vigna* species and were described by Misra and Sahu (1970). They observed the ovule to be campylotropous, bitegmic, and crassinucleate and that the embryo with cotyledons occupies the entire seeds. The nuclear endosperm disappears upon maturation, and the testa is formed from an outer palisadelike epidermal layer and some cells from the outer integument.

b. Varietal Types. There are two major types in var. *aureus* depending on seed color: (1) yellow or golden gram has yellow seeds, is generally low in seed production, has a tendency to shatter and is used mainly for forage or as a cover crop; (2) green gram has dark or bright green seeds, is more prolific, ripens more uniformly, has less ten-

dency to shatter and is more commonly planted as a pulse. The bright green types are preferred for sprouting.

C. Plant Improvement

The major volume of information and improvement work on mung beans has been done in India in recent years. There have also been limited reports from southeastern Asia and tropical Americas. The following sections will treat recent progress in plant improvement in green and black gram during the later 1960's and early 1970's. A bibliography of 344 references comprising the world literature on mungbean has been compiled by Poehlman and Yu-Jean (1972) of the University of Missouri.

1. Pollination

Mung beans including black gram are highly self-pollinated and have about 42% cleistogamy. Flowering usually commences 6–8 weeks after planting. Pollen is shed on the evening before the flowers open. By the afternoon of opening, the petals fade and drop off. Rain is detrimental to good pod setting. Therefore emasculation must be done on the morning of the day before flower opening. Sometimes pods form but have no seeds. Hand emasculation is somewhat complicated by twisting of the keel, which usually does not exceed 360°. The chromosome complement is $2n = 22$.

2. Germplasm Evaluation

More than 2000 mung bean accessions had been assembled by mid-1973 at the Asian Vegetable Research and Development Center (AVRDC) located in Taiwan. The AVRDC will become a global center for assembling, maintaining, and evaluating germplasm for this species (McKenzie, 1973). However, smaller collections have been studied at other locations, chiefly in India, where 878 accessions were assembled and evaluated by the Regional Pulse Improvement Project (RPIP, 1967, 1968, 1969); in Azerbaijan, USSR (Rimikhanov, 1968); and at the University of Missouri, where 249 strains were assessed for several botanical characters in both replicated and unreplicated trials (Yohe *et al.*, 1972; Yohe and Poehlman, 1972; Watt *et al.*, 1973). Variation in botanical characters and components of yield have been evaluated in studies on 16 green grams and 12 black gram cultivars representing a broad range of genetic diversity in the two subspecies at Hissar, India (Chowdhury *et al.*, 1968; Chowdhury *et al.*, 1969).

In the Missouri studies the range of variability in 12 plant characters was evaluated over a three-year period from 1970 to 1972 at Colombia,

Missouri. Variability in all characters was considerable, as demonstrated in the accompanying tabulation.

Character	1971 (203 cvs)		1972 (70 cvs)	
	Range	Mean	Range	Mean
Seed yield (kg/ha)	12–2548	924	10.7–1966	1273
Plant type[a]	1–6	3.2	1–5	2.7
Leaf size[b]	2.8–7.5	5.7	5.0–7.9	7.2
Days to flower	40–119	59	43–84	58
Days to ripe[c]	56–120	880	59–112	79
Plant height (cm)	24–82	58	42–94	67
Branch length (cm)	13–76	51	34–85	61
Pods per plant	4–235	115	20–192	106
Seeds per pod	5–14	10.7	7–14	11.5
1000 seed weight (g)	24–75	45	22–66	58
Virus score[d]	1–100	34.1	1–80	18
Mildew score[e]	1–5	3.6	1.7–5.0	3.2
Protein[f]	22.1–31.2	26.5	—	—
Lysine[g]	5.90–8.45	7.27	—	—

[a] 1 = prostrate; 5 = erect.
[b] 1 = 6.1 cm²; 4 = 26.0 cm²; 8 = 145.4 cm².
[c] Days to first ripe pod.
[d] Proportion of plot showing virus symptoms.
[e] 1 = resistant; 5 = susceptible.
[f] Kjeldahl analysis of seeds.
[g] Expressed as percent of protein.

3. *Breeding Methodology*

Conventional methods have been used almost exclusively in breeding mung beans. These include pedigree selection, mass selection, backcrossing, multiple line crossing, mutation breeding, and interspecific crossing. Radiation with X-rays was reported by Van Emden (1960, 1962) and resulted in developing an early maturing, highly branched, profusely fruiting line named Jumbo Mung 1000 R/252. Ultraviolet and infrared radiation was applied to root tips of both green and black grams by Prasad (1967). He found that infrared radiation had a greater inhibition on germination than ultraviolet treatment. However, 48% of the UV-radiated plants developed chimeral branches with quadri- and quinquefoliate compound leaves. Utilization of the male gametocide 2,2-dichloropropionic acid produced male sterility in cultivar T.51 and was attributable to the excessive stickiness of chromosomes resulting in bridges, laggards, and consequently to formation of micronuclei and polysporads (Kaul, 1970).

Crosses between green and black grams have been highly successful (ICAR, 1952). However, other "interspecific" or wider crosses have not been widely recorded as feasible since Strand (1943) reported crosses between *P. vulgaris* and *P. mungo*.

4. *Genetic Investigations*

There is only limited information on genetic aspects like inheritance, heritabilities, genetic variation, heterosis, and gene action in the mung bean. Most of the genetic studies on this species have been carried out in India and have focused on some aspects important in breeding this crop.

a. Simply Inherited Characters. Some simply inherited characters have been studied including growth habit, daylength sensitivity, shattering, leaf shape, and plant coloration. The more recent findings are tabulated below.

Character	Inheritance	Reference
1. Pod veining (ventral suture)	Purple-red dominant to absence of veins	Pathak and Singh (1963)
2. Ripe pod color	Black dominant to light green	Pathak and Singh (1963)
3. Stem color	Purple dominant to green	Pathak and Singh (1963)
4. Growth habit	Semispreading dominant to erect	Pathak and Singh (1963)
5. Twining habit	Nontwining dominant to twining	Pathak and Singh (1963)
6. Photosensitivity	Insensitivity dominant to photosensitivity (one gene pair)	Verma (1971)
7. Shattering	Pod shattering dominant to nonshattering	Verma (1969)
8. Leaf shape (var. *mungo*)	Hastate leaves dominant to ovate (two gene pairs)	Singh and Singh (1971)
9. Black-spotted testa (Bsp)	Spottedness dominant to no spots	Singh and Singh (1970)
10. Shiny testa	Nonshiny testa dominant to shiny; shiny expressed only in presence of Bsp	Singh and Singh (1970)

b. Variability. Considerable genetic and environmental variability was observed by Joshi (1969) and Singh and Malhotra (1970a). In the latter study, a collection of 75 indigenous and exotic strains were evaluated for eight quantitative characters contributing to seed yield. Wide genotypic and phenotypic variability was observed for all characters, but genotypic correlation coefficients were greater than phenotypic or environmental coeffi-

cients. Singh and Malhotra (1970a) concluded that selection for 100-seed weight, which had the highest variability and very high genetic advance, would be the most effective character. However, they also observed genetic advance to be high for pod number, bunch (cluster) number, and seed yield, but these characters had low heritability estimates.

In other investigations, Empig *et al.* (1970) found heritability estimates low for most yield components, except for number of days to flowering and maturity. Tomar *et al.* (1972) obtained higher heritability estimates for pod length or seed number per pod in the rainy season than in the dry season, but heritability estimates for branch number were higher in the dry season.

c. Associations of Characters. Several simple and multiple character correlations have been reported recently by Singh and Malhotra (1970b) and Tomar *et al.* (1972). These can be summarized briefly as follows:

1. Seed yield—positively correlated with pods per plant, pod clusters per plant, pod length, seeds per pod, and seed size.
2. Seed size—negatively associated with number of seeds per pod and pods per plant.
3. Branch numbers—positively correlated with plant height and pod number.

Path coefficient analysis showed that pods per plant, seeds per pod, and seed size had greatest direct influence on seed yield, assuming constancy of other yield components.

d. Heterosis. Considerable heterotic effects that sometimes persisted into the F_2's were observed by Singh and Jain (1970) in the F_1's of various mung bean combinations in a 7-line diallel series. Heterosis was observed in seed yield, pod length, and branch number, and the best combinations were Hyb. 45 × 305 and T.51 × D. 45-6.

e. Autotetraploidy. Colchicine-induced autotetraploids were studied by Kumar (1945). He observed that the tetraploids exceeded their diploid progenitors in length and width of the flower petal and in the pod and seed diameters, but other components of yield were reduced, resulting in lowered yields. He concluded that colchicine-induced tetraploidy would have limited value in improving the mung beans.

D. Plant Protection

The mung bean is susceptible to many of the same diseases and pests that attack other legumes in southeastern Asia. However, in the United States and in Africa it is somewhat less susceptible to the problems confronting *Phaseolus* beans, soybeans, or cowpeas. Heavy incidence of virus has occurred in certain genotypes and seasons in West Africa, but the hairy

pods and smaller seeds may confer somewhat lowered attractiveness to cowpea pod-boring pests in Africa.

1. Insect Pests

Some of the same insect pests of beans and cowpeas also attack the mung bean in the tropics—although perhaps to a lesser extent. In India and southern Asia the hairy caterpillar (*Diacrisia obliqua*), bean fly (*Melangromyza phaseoli* COQ), pulse beetle (*Callosobruchus chinensis Linn.*) and other species attack these crops (Jakhmola and Singh, 1971; Sepswadi and Meksongsee, 1971). In West Africa cowpea pests attack these crops but at a much lower incidence than for *V. unguiculata* (IITA, 1973). Use of contact and systemic foliage and seed dressing chemicals as specified for other pulses is highly effective.

2. Diseases

Mung beans are susceptible to nematodes; a root rot caused by *Sclerotium rolfsii* Sacc; downy mildew (*Erisiphe polygoni* DC.); rust [*Uronmyces appendiculatus* (Pers.) Unger]; leaf spots caused by *Cercospora spp.* and *Macrophomina phaseoli;* halo bright (*Pseudomonas phaseolicola*); and several viruses (yellows, mosaic, crinkle, stunt, and flower abortion).

Control. Host plant resistance is the most practical control measure for diseases attacking the well developed plant. Sources of resistance to some of these diseases can be summarized as follows:

1. *Macrophomina* leaf spot: BR-68 and T-29 (Kumar *et al.*, 1969).
2. Viruses (various): in the United States M101, M238, M330, M118, M221, M174, M235 were resistant (Yohe *et al.*, 1972; Watt *et al.*, 1973); in India T.65 and T.67 appeared to be resistant (Srivastava *et al.*, 1969).
3. Downy mildew: In the United States M221, M243, M210, M319, M330, M358, M366, M81, M183, M90, M238, M4, M195, and M409 were resistant (Yohe *et al.*, 1972; Watt *et al.*, 1973).
4. *Sclerotium* leaf spot: four strains resistant, 11 strains moderately susceptible out of 21 tested (Mishra *et al.*, 1971).
5. Halo blight: Peruvian sources showed resistance in Ohio (Schmitthenner *et al.*, 1971).
6. Cyst nematode: resistance to *Heterodera glycines* observed in Jumbo, but OKLAHOMA 12 and KILOGA were susceptible in studies carried out by Epps and Chambers (1959).

It is particularly encouraging that reasonably good resistance to the major disease problems has been found with relative ease and in comparatively limited collections of germplasm. It is also interesting that germplasm evaluation in Missouri identified strains like M238 and M330 with good resistance to both downy mildew and viruses (Watt *et al.*, 1973).

E. Physiology

There have been reasonably intensive investigations into the metabolic processes and enzymatic systems in the mung bean, but relatively limited information is available on effects of daylength, quality of light, temperatures, mineral nutrition, and water on plant growth and development. Recent findings on physiological processes are discussed briefly in the sections to follow, with major emphasis on information of greatest use to plant improvers.

1. Light and Photoperiod

The existence of both day-neutral and short day types in mung beans have been recorded. Rimikhanov (1967) grew both mung beans and cowpeas under 9-hour and natural (14.5–15.0 hour) daylengths in Azerbaijan, USSR. He observed a shortening of the growth by 11–22 days, decrease in size of plant and reduced number of seeds per plant under short-day conditions. In other experiments on dates of sowing in India, Sen and Chedda (1960) proposed a black gram breeding system utilizing shortening daylengths for purposes of synchronizing flowering and hybridization, and utilizing long days to screen for day neutrality.

2. Metabolic Processes in Seedlings

Metabolic processes and enzymatic systems during germination and in etiolated mung bean seedlings have been studied intensively in reference to their utilization for bean sprouts. Quantitative determinations of cell wall constituents of growing seedlings showed marked changes during early growth in experiments conducted by Franz (1972).

a. Promoting Germination and Rooting. Optimum germinating temperatures for mung beans were 24–32°C, but black gram germinated almost as well at 16°C, although more slowly, in experiments carried out by Knapp (1966). Several investigators have studied the effects of growth-promoting substances in stimulating rooting in mung bean cuttings. Hormones like 2-thiouracil, 5-bromodeoxyuridine, indoleacetic acid (IAA), abscissic acid, and ethephon applied to hypocotyl cuttings markedly increased root formation, whereas uracil, thymidine, IAA, GA_3, and kinetin reduced the number of length of roots formed (Chin *et al.*, 1969; Jackson and Harvey, 1970; Krishnamoorthy, 1970; Anzai *et al.*, 1971). Soaking seeds in *O*-fluorophenoxy-α-methylacetic acid or *N*-benzyl-*O*-fluorophenoxyacetamide at 50 ppm for 6 hours drastically reduced radicle growth and development during the first 72 hours of growth and also decreased the activities of β-glycerophosphatase and phytophosphatases (Tewari,

1968; Tewari and Kathju, 1969). Paul *et al.* (1970) observed that exogenous GA_3 promoted α-amylase and ribonuclease, whereas chloramphenical, actinomycin D, and 5-fluorouracil were inhibitory to net enzyme synthesis during germination.

b. Cell Wall Constituents. Cell walls of seedlings 2–4 days old were composed of 30% α-cellulose, 50% hemicellulose, and 20% pectin. After 4 weeks the constituents had changed to 60% α-cellulose, 30% hemicellulose, and 10% pectin.

c. Oxygen Uptake. Oxygen uptake during germination of 30°C was investigated by Morohashi and Shimokoriyama (1972b). They observed that O_2 uptake increased rapidly for 4–5 hours, remained constant for 1–2 hours, and then increased again. Citric and malic acid were the major organic acid constituents, aspartic acid being converted into malic acid during the first 9 hours. Ethanol fermentation occurred early, but CO_2 fixation was low in the early stages.

d. Light Effects in Germinating Seedlings. Etiolated mung bean seedlings contain several carotenes and xanthophylls, but illuminated seedlings increased more rapidly in xanthophylls than in carotenes. Among the latter, lutein increased more rapidly than β-carotene in studies carried out by Valadon and Mummery (1969). Dodge *et al.* (1971) demonstrated rapid formation of chloroplasts in 7-day-old etiolated seedlings when supplied with diuron and sucrose together with light at 500–2000 lux.

Jaffe (1970) and Yunghans and Jaffe (1972) found acetylcholine to be present in all organs of light- and dark-grown seedlings of mung bean, the highest concentrations occurring in buds and secondary roots. Exposure of roots to red light in presence of acetylcholine caused a rapid utilization of ATP pools, whereas far red light appeared to inhibit this utilization. Tanada (1972) in other red light experiments concluded that phytochrome in bean seedling tissues acts in conjunction with growth regulators like IAA and ABA to produce rapid changes in root tip surface changes—ABA inducing positive and IAA negative potentials. Racusen and Miller (1972) confirmed these observations and further noted effects of light qualities. They observed no effects of green light below 880 mV nor of red light below 220 mV on electrical potentials of root tips.

In other radiation experiments, Murray and Newcombe (1970) noted the inhibitory effects of low level X-ray (100 R and 1000 R) treatments on seedling growth and development. Ting and Ho (1971) subjected germinating seedlings to magnetic fields of 5000 gauss at 30°C and observed an accelerated breakdown and translocation of phosphorus-containing materials and secretion of nitrogen-containing compounds by the embryo.

e. Enzymatic Processes in Seedlings. The literature on this subject is voluminous and secondary in the improvement and production of mung

beans. The reader is therefore referred to the following recent papers pertaining to various subject fields in this area:

1. DNA and RNA synthesis: Ong and Jackson (1970); Parekh *et al.* (1969); Kobayashi and Yamaki (1972).
2. Starches and sugars: sucrose and fructose—Grimes (1969), Delmer and Albersheim (1970), Heuser and Hess (1972); glucose metabolism—Franz (1972), Clark and Villemez (1972), Ikeda (1968); mannose—Vessal and Hassid (1972), Heller and Villemez (1972), and Brar and Elbein (1971, 1972).
3. Phospholipid synthesis: Katayama and Funahashi (1969).
4. Phosphorus metabolism: Ong and Jackson (1972a), Mandal and Biswas (1970), Mandal *et al.* (1972), Delmer and Albersheim (1970), Majumdar *et al.* (1972).
5. Organic acids: malic, citric, and aspartic acids—Morohashi and Shimokoriyama (1972a); alicylic acid—Minamikawa *et al.* (1968).
6. Amino acids: alanine—Kasai *et al.* (1971); methionine—Sakai and Imaseki (1972), Truelsen (1972); aspartate transcarbamoylase—Ong and Jackson (1972b); aromatic amino acids—Gilchrist *et al.* (1972).
7. Other compounds: chalcones—flavanones isomerases—Hahlbrock *et al.* (1970); carotenoids—Valadon and Mummery (1969); isozymes in hypocotyl cuttings—Chandra *et al.* (1971).

3. *Soil Moisture and Temperature*

Effects of soil moisture on formation of hard seeds in mung bean (cultivar BLACK MAPTE No. 1) were studied by Ishii (1968, 1969). He found that when soil moisture was reduced from 50 to 20% during the flowering-ripening process that more than 90% hard seeds were formed, particularly at the lower nodes.

4. *Mineral Nutrition*

Limited studies on mineral nutrition in plant tissues of mung beans have been reported. Most of these investigations were carried out in field trials, but some experiments have included tissue analysis and tracing of physiological processes. Recent information on specific elements is summarized under the respective sections to follow.

a. Phosphorus. The most economic level of phosphorus application in commercial production of mung beans and black gram is 15–40 kg P_2O per hectare with overall yield increments of about 25% (Singh and Virk, 1965; Sekhon *et al.*, 1966; Behl *et al.*, 1969; Sreenivas *et al.*, 1968; Rajagopalan *et al.*, 1970; Chowdhury and Bhatia, 1971b; Mandloi and Tiwari, 1971; Prasad *et al.*, 1968). However, on some lateritic soils with high phosphate fixation capacity, good response is obtained up to 100 kg of P_2O_5 per hectare. Simple superphosphate has generally been more effective than more concentrated forms, probably as a response to sulfur contained in superphosphate (Deshpande and Bathkal, 1965). Banding the fertilizer has been superior to broadcast application (Chowdhury and

Bhatia, 1971b); and foliar applications of 11 kg of P_2O_5 per hectare have been more effective in increasing yields than 22 kg of P_2O_5 per hectare applied to the soil (Deshpande and Bathkal, 1965). Compost and farmyard manure at up to 5.6 tons/ha further increased yields when added to P_2O_5 applications (Sreenivas *et al.* 1968; Rajagopalan *et al.*, 1970).

The response to phosphorus in mung bean, as in other legumes, is quite complex. It is sometimes considered the pivotal element without which other nutrients are ineffective or even detrimental. Phosphorus deficiency in the presence of adequate amounts of other nutrients produces stunted plants with small, dark green leaves with high contents of total and soluble nitrogen but low in protein associated with an accumulation of arginine in experiments carried out by Pandey (1968).

Phosphorus also had a beneficial effect on both rhizobial activity and plant growth in studies carried out by Iswaran *et al.* (1969). They observed better growth and greater uptake of phosphorus in well nodulated pot grown plants supplied with P_2O_5 at the rate of 80 kg/ha. Shanker and Kushwaha (1971) obtained increased uptake of nitrogen, potassium, calcium and magnesium in addition to phosphorus from applications of 44.8 kg P_2O_5/per hectare to black grams in experiments in north India. Contents of nitrogen and phosphorus were highest 30–50 days after sowing, whereas potassium and calcium were highest at 30 days and magnesium increased up to 70 days of age.

b. Sulfur. Addition of sulfur to mung bean in sand culture was investigated by Arora and Luthra (1971a,b). They observed increasing sulfur in the nutrient solution up to 90 ppm, with or without additional nitrogen, increased the contents of total, soluble, and proteinaceous nitrogen; but decreased the amide, amino, ammonium, and nitrate *N* in plant tissues. Moreover, the sulfur contents of leaves increased with increasing sulfur application, reaching a maximum at 50 days after planting. The sulfur contents of leaves were significantly correlated with contents of methionine, cystine, and cysteine in the mature seeds up to a maximum of 90 ppm in the nutrient solution.

c. Other Nutrients. There are comparatively few recent reports on nutrients other than phosphorus and sulfur in mung beans. However, application of micronutrients investigated by Abutalybov and Samedova (1966) showed that cobalt, molybdenum, or manganese increased the total amounts of amino acids in mung bean leaves at the 7-leaf stage; whereas, zinc and copper applications decreased the amino acid contents. Sodium humate up to 0.1% of soil with or without nitrogen markedly increased the length and growth of shoots and roots, resulting in increased dry matter production in uninoculated pot-grown mung beans. The effects were most pronounced when nitrogen and humate were applied together (Khandelwal

and Gaur, 1970). In other experiments in India, Iswaran *et al.* (1972) observed foliage sprays of 1% sucrose solutions applied at weekly intervals significantly increased seed yields of inoculated, pot-grown mung beans.

4. *Nitrogen Fixation*

Inoculation with appropriate rhizobium has been found beneficial where plants of the same host range have not been grown recently. Structure and development of *P. mungo* root nodules including the enveloping membrane of the bacterium were studied and described by Narayana and Gothwal (1964) and Prasad and De (1971). In experiments carried out in USSR by Dorosinskii and Lazareva (1967) on several species to determine host range, the following results were obtained:

Rhizobium source	Species with effective activity	Survival only
Peanuts	Cowpeas-black gram	Lupines
Cowpeas	Black gram	Peanuts-lupines
Lupines	—	Peanut-cowpeas
Blackgram	Cowpeas-lupines	Peanuts
Soybeans	Lupines	Peanut-gram-cowpeas

In central India, Singh and Choubey (1971) demonstrated a wide range of rhizobial acceptability in mung bean using local strains A, B, or C, and inoculation was roughly equivalent in seed yields (1.23–1.36 tons/ha) to between 20 and 40 kg of nitrogen per hectare applications in inoculated plots.

a. Nutrients on Rhizobial Development. In Australia, Brockwell (1971) found mung beans inoculated with rhizobial strain CB 756 had significantly lower nodulation when fertilized with 75 kg of nitrogen per hectare. However, addition of nitrogen did increase seed yields by 27% or 641 kg at the first harvest in the absence of inoculation. Iswaran *et al.* (1969) demonstrated the beneficial effect of 80 kg of P_2O_5 per hectare on inoculated mung beans in terms of increased dry matter content and phosphorus uptake by the plant. The nitrogen content of *P. mungo* nodules was increased significantly from 3.97 to 5.01% by removing flower buds as they developed and fertilizing with phosphorus and potassium in experiments carried out by Kulimbetov (1968).

b. Soil Conditions. Rhizobial sensitivity to extremes of soil pH was studied by Yadav and Vyas (1971). They observed that *P. mungo* and *P. acontifolius* rhizobia were sensitive to chlorides and sulfates of sodium and potassium, but *P. aureus* rhizobia were unaffected by up to 3% saline solutions. Magnesium salts in less than 1% solution were stimulatory, but

$NaHCO_3$ at concentrations of 0.4–0.6% was critical for all rhizobia tested. Rhizobia survived at pH 10, but were inhibited at pH 3.5 or lower.

c. Insecticides Residues. DDT in the soil at levels up to 40 ppm in pot trials had no adverse effects on *Rhizobium* in mung bean roots, nor on the amounts of leghemoglobin in root nodules. However, at 100 ppm DDT nodulation was prevented and seed/plant yields were reduced to about a tenth of the control except where 1 ppm of farmyard manure was added to the soil (Gaur and Pareek, 1969; Pareek and Gaur, 1970).

5. *Growth Regulators*

Growth regulators sprayed on black gram (*P. mungo*) at early and full flowering stages were investigated in India by Mehrotra *et al.* (1968). They obtained increases in seed yields of 35% from NOA (β-naphthoxyacetic acid) applied at 50 ppm + *p*-CPA (para-chlorophenoxyacetic acid) at 5 ppm; 36% increase from NAA (naphthaleneacetic acid) sprayed at 25 ppm; 39% increase from *p*-CPA applied at 5 ppm; and 56% increase from NOA sprayed at 50 ppm. Yield increases were ascribed to an increase in number of pods and seeds per plant, but had very little effect on seed size.

6. *Seed Storage*

Investigations on storability of grain legumes in sealed and open containers for up to 18 years were carried out in the USSR by Gvozdeva and Zhukova (1971). They found that *P. aureus* survived storage better than *P. vulgaris* var. Triumf, which retained its viability intact for the full period in hermetically sealed containers at 10% moisture. Open containers were much less satisfactory for preserving viability than hermetically sealed ones.

F. Management

Mung beans require good soil tilth. In India, black grams are frequently grown after rice or mixed with rice and other crops both in summer or winter (in the south). They may be broadcast or planted in rows at the rate of 11–17 kg/ha. In rows 25–90 cm apart the seed rate can be 5–9 kg/ha for green gram and 11–13 kg/ha for black gram. The crop normally matures in 80–120 days but has a tendency to shatter; therefore, the first harvest should be picked after about 2 months in early strains. Yields of 300–500 kg/ha are common, with occasional exceptional yields of up to 1100 kg/ha obtained under favorable growing conditions. However, experimental plot yields up to 2700 kg dry seed per hectare have been obtained (Watt *et al.*, 1973). Yields of dry hay in golden gram may range from 2.2 to 6.0 tons/ha, but is usually less for green gram.

1. *Populations and Spacings*

Field trials of mung beans planted in hills 25 cm apart with 75 cm between rows and varying numbers of plants per hill were investigated by Natribhop *et al.* (1972). They observed increased seed yields of approximately 55 kg/ha for each additional plant per hill up to 5 plants per hill (53,500 plants per hectare) with maximun seed yields of 617 kg/ha. In northern India, Sharma (1969) found 60-cm rows superior to 30-cm or 45-cm rows in June plantings, but 30-cm rows were superior for July 15 plantings of black gram. However, seeding rates of 15–25 kg/ha produced similar yields (470–510 kg/ha).

2. *Chemical Weedicides*

The effects of MCPE on mung beans and other species were investigated by Gupta and Mani (1964). They found berseem, chick-peas, and cowpeas highly susceptible to "normal" applications. However, at the same dosages green gram, black gram, and hyacinth beans (*Lablab niger*), although temporarily stunted, recovered later without loss in final yields. Pre- and post-emergence herbicides trials on several legume species carried out by Gentner and Danielson (1965) showed the best preemergence herbicides overall to be trifluralin, diphenamid, pebulate, siduron, CDAA, CPD, CP 31393, RP-2929, chlorpropham, and dinoseb.

G. Chemical Composition

Dried seeds of mung beans contain about 9.7% water, 23.5% protein, 1.1% fat, 57–58% carbohydrates, 3.3–3.8% fiber, and 4.0–4.8% ash (Purseglove, 1968). Both carbohydrate and protein fractions are highly digestible and used in feeding infants, geriatrics, and convalescents and in "breaking" religious fasts in India (Pant and Tulsiani, 1968).

Protein Quality. Seed proteins have been analyzed by several investigators. Many experiments were carried out without specifying genotype, environment, and management practices. Generally, the mung bean is similar to other grain legumes—especially other Vignas in protein quality. Gonzalez *et al.* (1964), studied 12 amino acids in mung bean and found the highest to be isoleucine and the lowest cystine. Sayanova (1970) identified ten salt-soluble protein fractions, and Kasai *et al.* (1971) found high concentrations of gamma peptides but not in the seedlings. They found no significant relationship between the amino acid composition of the protein and the free acid composition of the protein and the free amino acid composition of seeds or seedlings.

It appears that protein quality in terms of sulfur amino acids can be influenced to a degree by sulfur fertilization (Arora and Luthra, 1971a,b). However, Totawat and Saxena (1971) observed that saline irrigation water

could reduce contents of lysine, arginine/histidine, aspartic acid/glutamine, threonine, alanine, proline, and cystine in mung bean.

H. Potential

The mung bean—both green and black gram—has definitely not received the attention deserved in proportion to its potential in the lowland tropics. Present yield levels are among the lowest of the major grain legumes. To a degree, this results from poor response to improvements in cultural practices. Therefore, plant improvement efforts should be directed primarily toward increasing the yield potential and physiological efficiency in growth processes. Other important objectives would be insensitivity to daylength and other environmental factors, and stabilization of productivity over a wide range of growing conditions. Associated with these basic characters must be resistance to the major diseases and pests of the region while retaining consumer acceptability and improving the inherent nutritional qualities of the plant.

The mung bean has many desirable attributes, chief among which are a high consumer preference for pulse and vegetable forms in Asia, and a worldwide demand for bean sprouts used in Chinese dishes. The United States alone consumes about 25 million pounds of mung beans annually—primarily for sprouting. It therefore has export potential as a cash crop and improved productivity levels would markedly increase the production and use of this highly promising crop.

VII. Secondary Species

There are at least 20 grain legume species and subspecies representing 14 genera of largely undetermined importance in the lowland tropics in addition to peanuts, pigeon peas, cowpeas, and mungbeans. Of these, about eight species, including bambara groundnuts, moth bean, cluster beans (guar), hyacinth bean, dry beans, soybeans, lima beans, and African yam beans, are known to be the predominating species in certain areas. Many of the secondary species, however, have exceptional productivity potential, unique characteristics of adaptation, known resistance to pests and diseases, and significant nutritive qualities. Production statistics for these legumes, if available at all, are usually extrapolations from rough estimates in limited areas and are often included under the general heading "Other and Unspecified Species" in official reports.

Secondary grain legumes are described and categorized according to ecological zones in which they are presumed to be best adapted and most extensively utilized. The lowland tropics are defined as areas lower than about 600–800 m elevation lying between the Tropics of Cancer and Capricorn. They include these moisture zones: (1) semiarid tropics: less than

600 mm annual precipitation; (2) subhumid: 600–1000 mm; (3) humid: 1000–1500 mm; (4) very humid:above 1500 mm annual precipitation. It should be emphasized that these are only approximations and that there is considerable overlapping of conditions and species adaptation within and between moisture zones and elevations depending on soil conditions, proximity to coastal areas or deserts, moisture distribution, relative humidities, ambient temperatures, cloud cover, indigenous vegetation, prevalence of pests and diseases, genotypes available, and local demands.

A. Semiarid Lowland Tropics

Sustained cultivation of all rainfed crops is hazardous in the semiarid tropics, especially below the 500 mm rainfall belt; it is almost nonexistent in areas with less than 300 mm precipitation, except for low areas, or under irrigation. Nevertheless, distribution and reliability of rainfall and other conditions are very important considerations in this as in other tropical cropping zones. Generally the higher the latitude, the more concentrated is the rainfall pattern and therefore the more favorable the conditions for cultivated crops.

The more important secondary hot-weather grain legumes grown in the semiarid lowland tropics include moth and cluster (guar) beans in southern Asia; bambara groundnuts, Kersting's groundnut, and locust beans in Africa; and tepary beans in both the Old and New Worlds. These species (described in the following sections) are usually secondary to short-season groundnuts, cowpeas, and even pigeon peas.

1. Moth Bean

Mat or moth bean, *Vigna acontifolia* Marechal (formerly *Phaseolus acontifolius* Jacq.) is an important pulse of the semiarid regions adjoining tropical deserts. It has $2n = 22$ chromosomes, is highly self-fertilized, has epigeal germination, and is native to India, Pakistan, and Burma, where it occurs both wild and cultivated. It is a short, compact plant and grows best under uniform high temperatures and well distributed rainfall of up to 750 mm per annum, but resists dry periods by remaining dormant. It is a slender, trailing, and hairy herb with deeply divided leaflets which easily distinguish it from other grams. It is usually grown mixed with cereals like pearl millet or sorghum and is used as a pulse and for hay. Seed yields average around 300–400 kg/ha, but up to 1500 kg of seeds per hectare, and dry hay yields of 6–8 tons per hectare have been recorded.

2. Cluster Beans (Guar)

Guar, *Cyamopsis tetragonolobus* (L.) Taub (syn. *C. psoralides DO*), is frequently grown in southern Asia for its tender green pods cooked as

vegetables, as well as for its dry seeds, fodder, and as a cover crop in the drier tropics. The flour from dry seeds is mucilaginous (mannogalacton) and has exceptional viscosities, possessing 5–8 times the thickening power of corn starch. The dry seeds contain 33.3% protein and 40% carbohydrates.

Description. The genus *Cyamposis* includes three species with $2n = 14$ chromosomes and is indigenous to Africa and Asia. Guar probably originated in India. It is very hardy, drought resistant, and grows very well on alluvial and sandy loams in hot weather. It is a robust, bushy annual, 1–3 m tall, has stiff branches with white hairs, and bears small flowers in dense axillary racemes or clusters. Pods are linear in stiff, erect clusters. It is frequently broadcast at 10–20 kg of seed per hectare and commences bearing after 12–14 weeks. Yields of 10,000 kg green fodder and 600–800 kg of dry seed are obtained per hectare under dryland, and double this quantity under irrigation in India.

3. *Tepary Bean*

This species (*Phaseolus acutifolius* Gray var. *latifolius* Freem.) originated in the New World, probably in the southwestern United States and northwestern Mexico, where it occurs wild. It is particularly suited to hot, arid, and low humidity conditions, and will usually produce a crop when other beans fail, maturing out as quickly as two months. Under dryland conditions yields of 500–700 kg of dry seeds per hectare can be obtained, whereas with irrigation 800–1500 kg/ha may be realized. It has $2n = 22$ chromosomes, germinates epigeally, and the seeds absorb water very easily. In most soils the testa wrinkles within 5 minutes; in warm water it wrinkles in 3 minutes. It is believed to have been introduced into the Old World fairly recently. It is grown to a limited extent in the drier regions of southern Asia and in both West and Eastern Africa as far south as Lesotho and Botswana.

4. *Bambara Groundnut*

This crop [*Voandzeia subterranea* (L.) Thou.] is also known as the Congo goober, earth pea, kaffir pea, jugo bean, Madagascar or stone groundnut, guerte/gertere (Arabic), and voandzu. *Voandzeia* is most extensively cultivated in Africa, where as much as a third of a million tons may be grown on an estimated 400 thousand or more hectares. Major producers are Nigeria (estimated 100,000 tons), Niger (30,000 tons), and Ghana (20,000 tons); but it is grown widely in Eastern Africa as well. This crop is most extensively grown on very poor sandy soils which are marginal for other pulses and groundnuts. It is grown primarily for its seeds, which can be eaten semiripe or as a pulse after soaking and cooking, or parched and ground into flour. The ripe seeds contain about 20% pro-

tein, 4–7% fat, and 50–60% carbohydrate. It may be grown intermixed with cereals like pearl millet or sorghum or in pure stands and matures in about 4 months. It has few diseases and pests and normal yields are 500 kg of dry seeds per hectare, although occasional production levels exceeding 2500–3000 kg of shelled nuts per hectare have been reported from Malawi and Rhodesia (Stanton, 1966).

a. Adaptation and Description. Bambara groundnuts are indigenous to Africa with a broad range of variation occurring in West Africa or East Africa and Madagascar. It reached Brazil and Surinam in the 17th century and was later taken to the Philippines and Indonesia. It is an annual herb with short, creeping, highly branched stems, rooting at the nodes, and with very short internodes giving the plant a bunchy appearance. The chromosome complement is $2n = 22$. It is outwardly similar to ordinary peanuts, except that it is trifoliate, bearing elongated leaflets on long, hairless petioles carried at a wide angle to the stem. The style is short, bent, hairy along the surface, and the stigma is small and laterally positioned. Flowers are cleistogamous and after fertilization the peduncle, with a swollen tip bearing a brush of hairs behind, bends into the soil pulling the developing pods along. The plants are usually earthed up to facilitate this process. Fruits are rounded, wrinkled when mature, about 2 cm in diameter, and usually 1- or 2-seeded. Seeds are often patterned, sometimes with an eye, range in color from white to red or brown, are round, smooth, hard, and may be up to 1.5 cm broad and weigh 50–75 gm/100 seeds.

b. Recent Investigations. Several recent studies on culture and growth habits of *Voandzeia* have been carried out in Ghana by Doku (1968, 1969) and Doku and Karikari (1970a,b) and in Rhodesia by Johnson (1968).

5. *Kersting's Groundnut*

This species (*Kerstingiella geocarpa* Harms) is superficially similar to Voandzeia and is important in Dahomey, Upper Volta, and Sudan. It is also a herb with prostrate rooting branches that fruits below ground. It can be distinguished from *Voandzeia subterranea* by its deeply divided calyx with narrow lobes and glabrous style. The axillary flowers are subsessile, have two-seeded fruits about 2 m long which are buried by carpophores similar to *Arachis hypogaea,* and it is therefore different from *Voandzeia.* Nutritionally it has good amounts of the essential amino acids, but like other legumes it is somewhat deficient in S-bearing amino acids.

B. Subhumid Tropics

The largest group of tropical grain legumes—seven species including the four major crops—occurs in this agro-climatic zone (600–1000 mm annual precipitation). In addition to peanuts, pigeon peas, cowpeas, and mungbeans, this group also includes horse gram, hyacinth bean, and locust

bean. However, genotypic representations from all seven species occur in the semiarid zone and some extend into the humid zone as well. Moreover, *Phaseolus* beans, soybeans, rice beans, and jack beans are also cultivated in the subhumid zone, particularly in areas with a better distribution of rainfall.

Since most tropical regions have distinct wet and dry seasons, late plantings—perhaps following a main crop such as rice or maize—make it possible to successfully grow even semiarid crops in humid or very humid regions. However, most, if not all, grain legumes produce higher seed yields of better quality when final maturation coincides with bright, sunny weather.

The three secondary species to be discussed briefly in the following sections include two herbs, and a noncultivated tree whose fruits and seeds are gathered. The locust bean is not used directly as a pulse, but rather as a flavoring in sweet preparations and native stews. However, it does make an important contribution to nutritional requirements of millions of inhabitants of tropical savannahs, particularly in West Africa. It also represents the stabilizing potential for perennial and tree crops in providing proteinaceous and other essential nutrients in human diets.

1. *Horse Gram*

The horse or Madras gram, *Dolichos uniflorus* Lam. or *D. biflorus* Auct., is indigenous to the Old World—about 100 species have been reported. It is considered the poor man's pulse crop in southern India, a country producing 390,000 tons on 1.8 million hectares. It is consumed like other pulses, but in Burma it may also be fermented to make "soy sauce." It is grown as a hardy, drought-resistant dryland crop in areas of moderate rainfall (less than 900 mm) or planted after the rains have ceased, since the developing buds and pods are susceptible to rotting in humid weather. It matures in 4–6 months, producing only 150–300 kg/ha of dried seeds plus animal forage.

Description. The horse gram is a low-growing, slender, suberect annual herb with slightly twining, downy stems and branches 30–50 cm high. Flowers are borne in axillary racemes clustered at nodelike thickenings of the peduncle. The flowers are about the same size as cowpeas, and the keel is uncoiled, but bent inward at right angles, rather than curved as in *Vigna*. The pod is large, somewhat hairy, flat, usually curved and beaked, and the seeds are smaller than those of the hyacinth bean. The chromosome complement is $2n = 24$.

2. *Hyacinth Bean*

The species *Lablab niger* Medik. is also known as the bonavist, dolichos, lablab, seim lubia, India butter, and Egyptian kidney bean (syn. *Dolichos*

lablab L.; *Lablab vulgaris* Savi). The young pods and tender green beans are used as a vegetable, and the dry seeds as a pulse. It is also grown for forage and as a cover crop in rotation with sorghum and cotton in the Sudan Gezira. It is a hardy, drought-resistant, dryland crop for low rainfall areas (600–1000 mm) in the tropics—Egypt, Sudan, India, and southern Asia. It is an herbaceous perennial herb usually grown as an annual and is often twining, but bush forms do occur. The pod is similar to that of a lima bean, but normally contains 3–5 seeds. The seeds are similar in size to those of a medium lima bean, but plumper and have a characteristic arid or projection from the hilum extending one-third the circumference of the seed making it easy to identify. Two botanical varieties are recognized: (1) var. *lablab* (var. *typicus* Prain.)—short lived, twining, perennial herb; pods are longer, more tapering with seeds parallel to the suture; grown mainly for green pods; (2) var. *lignosus* (L.) Prain—longer lived, semierect, bushy perennial also called Aust. dian pea. Pods are shorter, more truncated and the long axis of the seeds is at right angles to the suture. The plants have a strong unpleasant smell and are used mainly as a dry pulse and fodder.

These variety identifications are confused, however, and frequent hybridization occurs giving rise to numerous intermediate types.The chromosome complement is $2n = 22$ and 24. Germination is epigeal requiring 5 days, self-pollination is predominant, but some outcrossing may occur. *Lablab niger* is apparently closely related to *Dolichos uniflorus*, as hybrids between the two species have been obtained.

Adaptation. The hyacinth bean can tolerate poor soils if well drained and is usually photoperiod sensitive—some cultivars require 6–7 weeks to flower, depending on planting date. The garden type hyacinth bean is often planted in heavily manured and irrigated pits at the rate of 6–10 seeds per hole in midsummer and harvested for green pods from December to March, after which they may be kept for a second year. Field crops are often intersown with cereals like ragi (*Eleusine coracana*) and receive little attention. Yields of dry seeds average 400 kg/ha in mixtures, and up to 1300 kg/ha in pure stands.

3. *Locust Bean*

Fernleaf, nitta tree, nere, or nele are some of the common names for *Parkia* spp., particularly *P. filicoides* Welw. (syn. *P. clappertonia*) and *P. biglobosa* Benth. (also *P. oliveri*), which become large trees but are seldom planted. They occur throughout the African savannah zones. The seeds are not used as a dietary staple, but are cooked and fermented to make a condiment widely used as a food flavoring. The fruit pulp from immature pods is sweet; it is a popular flavoring in desserts and drinks and is particu-

larly nourishing by virtue of its high content of sulfur amino acids—up to 2.9 g of methionine and 3.8 g of cystine per 16 g of nitrogen, dry weight (Busson *et al.*, 1958). The locust bean also contributes to soil fertility through its ability to extract plant nutrients from the deeper soil layers and by leaf shedding. "Pure" strands of this species are estimated to contribute yields of 350–500 kg of dry seeds per hectare planted like an orchard (Stanton, 1966).

C. Humid Tropics

The humid tropics classification of 1000–1500 mm annual rainfall is arbitrary, and many leguminous species, including the four major ones, span the range from less than 600 to more than 1000 mm precipitaton. Perhaps the most widely adapted species is the pigeon pea, which occurs in all four zones. However, species and genotypes adapted to high rainfall areas tend to be sensitive to environment, so that flowering and maturation occur at the end of the rains or well into the dry season.

Five species and four genera, including soybeans, *Phaseolus* (dry) rice, jack and sword beans are considered to occur in this group. Most of these species do not require 1000 mm of rainfall to produce satisfactorily but perform better when moisture is well distributed. They are therefore classified for the humid zone, where better distribution of moisture occurs. Jack beans are not only drought resistant, but also tolerate waterlogging and salinity better than many other grain legumes, and hence are classified for this zone.

1. Common Bean

The common, dry, dwarf, kidney, french, navy, snap, runner, salad or string bean (*Phaseolus vulgaris* L.) is the most widely grown and best known of all *Phaseolus* species. Although extensively cultivated at intermediate and higher elevations, it is grown to a very limited extent in the lowland tropics (usually in the vegetable form) being highly susceptible to pests, diseases, high temperatures and even short periods of water stress. Although certain black-seeded cultigens are better adapted to the lowlands, their acceptability is less than that of the lighter colored seed types. Nevertheless, considerable plantings are made both for vegetables and as a pulse, with variable results. Commercial yields of 500 to 1200 kg of dry seeds per hectare are reasonable for short-term production of 56–90 days.

2. Soybeans

The soybean, *Glycine max* Merr., is predominantly a crop of temperate regions and intermediate elevations in the tropics and is probably the most

advanced and best developed of all legumes. It has been extensively grown for a long time as a basic food crop of the low elevations in southeastern Asia (Indonesia, Philippines, Malaysia). More recently, investigations in India, the West Indies, and both East and West Africa have demonstrated that soybeans can be very successfully grown in the lowland tropics under favorable conditions. At present there is no other species that can so consistently produce on a hectare per day basis both high yields of good quality protein and oil. The major deterrent to increasing production of this species in many tropical regions is lack of markets and understanding of its cultivation and utilization. However, there is a rising demand for both industrial proteins and vegetable oils, together with an increasing consumption of processed foods in the rapidly growing urban areas of the tropics. In fact, it is usually easier to transplant industrial processing into new areas and developing regions than to change traditional agricultural practices or social habits.

a. Adaptation and Problems. Soybeans grow best at maximum temperatures between 27°C and 32°C, have a wide range of adaptation of soil types, but thrive best on sandy or clayey loams in areas with hot, damp weather. They are somewhat less drought resistant than cowpeas, but tolerate waterlogging better. They are mostly short-day plants requiring 14–16 hours of darkness to flower, but a wide range of maturities and determinancies exist. Maturities may range from 75 to 200+ days depending on the genotype and environment. They respond well to fertilization and require a special strain of *Rhizobium japonicum* for proper inoculation—particularly when grown in new areas.

In tropical Africa diseases and insect pests that affect the soybean are fewer than for cowpeas, but in southeastern Asia (Indonesia) the reverse may apply. Bacterial pustule (*Xanthomonas phaseoli* Bows. var. *sojensis* Hedges), viruses (soybean mosaic and yellow bean mosaic), root knot nematode (*Meloidogyne incognita*), and cyst nematode (*Heterodera* sp.) may be the most serious problems. In southern Nigeria there has been considerable difficulty in obtaining good stands during hot, dry weather as a result of high soil temperatures (above 35°C) causing the seed to rot. Resistance to shattering and lodging in commercial varieties are also essential attributes in the tropics.

b. Utilization. The rapid increase in soybean production appears highly likely in view of its export potential and currently exceptionally high world market prices. This situation will tend to familiarize the crop in tropical areas outside of the regions of traditional use. It is suggested, however, that rather substantial inputs in terms of education and extension will be required to induce people unfamiliar with the crop to use the soybean directly for food owing to the rather sophisticated methods of preparation

required to make it palatable. First, whole beans require heating or boiling intact for 15–20 minutes to inactivate the enzyme lipoxidase in the testa (which produces an off-flavor, beany, or painty taste), hemagglutinins, trypsin inhibitor, and other toxic substances. In southeastern Asia they are frequently eaten as green beans (vegetable), split, sprouted, processed into soy milk (cooking and pressing), fermented into sauce utilizing *Aspergillus oryzae,* or made into curds and cheese. In Indonesia the boiled beans are fermented with *Aspergillus* sp. to make a cheeselike preparation called *tempe.*

c. Recent Investigations. Perhaps the most successful campaign to introduce soybeans and find solutions to production and utilization problems has been in India with assistance from a USAID-sponsored contract with the University of Illinois. In Africa, French-sponsored research organizations have centered their activities mainly in Madagascar with testing and management experiments in the Cameroons and Centralafrique (Silvestre, 1970a; Marquette, 1970). In anglophone Africa genetic recombination has been employed in breeding programs at Nachingwea, Tanzania (Aukland, 1966, 1967), Makerere University (Radley, 1971), and in Nigeria (Van Rheenen, 1972; Ebong, 1970a; IITA, 1973).

Major objectives in soybean improvement for the lowland tropics have been the following: (1) wide adaptation and stability of yields—particularly insensitivity to daylength and temperature fluctuation; (2) earlier maturation to better accommodate short bimodal rainfall patterns and permit multiple cropping; (3) improvement of quality for direct food use; (4) resistance to shattering and lodging; (5) germinability under high soil temperatures; (6) resistance to insect pests like thrips, foliage feeders, and pod bores; (7) resistance to diseases, particularly nematodes, viruses, and bacterial pustule.

Broadly based and multifaceted improvement programs are required to realize these objectives. However, considerable progress has already been made, particularly in India for the higher tropical latitudes. In Africa, yield testing and other experiments have identified several widely adapted, high-yielding cultivars, including: BOSSIER, HARDEE, CLARK 63, CHUNG HSING 1, IMPROVED PELICAN, and CES 486 in West Africa; DAVIS, DARE, CLARK, KENT, NATHO, and MORISSONNEAU in Madagascar; some of these, BUKALASA 4 and recombinations from crosses between HERNON 237 and LIGHT SPECKLED from Tanzania (Silvestre, 1970b; Marquette, 1970; Leakey, 1970; IITA, 1973). Among varieties and strains showing photoperiod and temperature insensitivities very useful in breeding programs are: GRANT, CLARK 63 and SRF 300 from the USA; FISKEBY V from Sweden; TOCKACHINAGAHA from Japan; and HSHI HSHI from Taiwan (Summerfield and Huxley, 1973; Radley, 1971).

3. *Rice Bean*

This species, *Vigna umbellata* (Thumb.) Ohwi and Okashi, was formerly classified as *Phaseolus calcaretus* Roxb. It occurs wild from the Himalayas and central China to Asia and is cultivated as a dried pulse in India, Burma, Malaysia, the Philippines, and other parts of southeastern Asia, but it is grown to a very limited extent in Africa. The beans are frequently cooked with or instead of rice. The green pods and tender leaves are used as vegetables and the whole plant may be used for fodder or as a cover crop. It is a vigorously climbing or suberect annual which produces long, slender, glabrous, shattering pods, with various colored, medium-small (8 mm-long) seeds. It is frequently grown in rotation with rice, producing a crop in as little as 60 days. Yields are usually low at 200–300 kg per hectare, but it performs well under humid conditions with fewer pests and diseases than most other legumes. It also tolerates high temperatures and is moderately drought resistant.

4. *Jack and Sword Bean*

Jack beans (*Canavalia ensiformis* L. and *C. plagiosperma*) and sword beans (*C. gladiata* Jacq.) are used as a green vegetable (immature pods), dry pulse, and the vegetative portion may be grown for forage, green manure, or cover crop. However, dry *C. gladiata* seeds may contain toxic substances. All three species are very hardy, deep-rooted, and exceptionally drought resistant, and tolerate waterlogging, shade, and saline soils better than many other grain legumes. The extremely large tough pods and hard seeds (2–3 cm long) germinate epigeally and very quickly (48–72 hr); and the developing plant is exceptionally free of insects and diseases under some tropical conditions.

The large dry seeds are hard to cook and can be somewhat toxic requiring boiling in salt water for several hours with a change of water. The jack bean is also an important source of urease and of the lectin (cell-agglutinating agents) concavalin A, which occurs at levels of 2.5–3.0% by weight in dry seeds and is being used in medical research (Sharon and Lis, 1972). This particular lectin has a special affinity for agglutinating cells transformed by DNA tumor viruses or carcinogens.

Dry seed yields of jack beans can be considerable even on poor soils where up to 2000 to 2500 kg/ha are reported. Production is scattered generally throughout West Africa and in Zaire and Angola.

D. Very Humid Tropics

There are comparatively few well-adapted grain legumes for the very humid tropics, that is for the humid Guinean and Rain Forest Zones where

annual rainfall exceeds about 1500 mm and humidities are constantly in the high 90°'s F as a result of heavy surrounding vegetation or location effect. However, some of the species allocated to the humid tropics are or could possibly be extended into the more humid regions. These might include in approximate descending order of adaptation (1) jack beans, (2) rice beans, (3) pigeon peas, and (4) soybean. Of these, jack beans and soybeans tolerate waterlogged and partially saline conditions better than most grain legumes, whereas rice beans and pigeon peas require good drainage but withstand high humidities during growth. However, all species produce better yields and seed quality when rainfall is light during flowering and they mature out in dry weather.

There are about five species confined mainly to the humid tropics. Three of these—African yam bean, Mexican yam bean, and winged bean—all produce edible tubers similar to the sweet potato, which may be eaten fresh or cooked. Sometimes the inflorescences are nipped off to increase tuber size and productivity. The five humid, lowland tropical species are further described separately.

1. Lima Beans

The species *Phaseolus lunatus* L. is also known as butter bean, sieva bean, Madagascar bean, and Burma bean. There are several forms which are grown for both dried and green shelled beans and are considered to originate in Central America—probably in Guatemala, where wild endemic forms occur and from whence the large white types were spread southward to Peru by the Incas, the small-seeded forms northward through Mexico to the southern United States and eastward to the West Indies, and from there to Brazil (tropical, perennial types) according to Mackie (1943). The latter are short-day plants with high contents of hydrocyanic acid. The large-seeded types (*P. lunatus* f. *macrocarpus*) have been found in Peruvian excavations dating to 6000 to 5000 BC. Early Spanish explorers carried the Caribbean type limas with them across the Pacific to the Philippines and southern Asia, but African limas trace their origin back to Brazil, although large types grown in Madagascar came originally from Peru. It is one of the major pulse crops of the humid rain forests of Africa, being most extensively grown in Madagascar where as much as 30,000 hectares are planted annually. Burma is a major producer in Asia.

a. Adaptation and Problems. There are two basic plant types—bush types 30–90 cm tall and twining, climbing herbs 2–4 cm tall—both weakly perennial in growth habit. They tolerate wetter weather during active growth than *P. vulgaris* but require moderately dry weather to produce good quality dry seeds. High temperatures tend to inhibit fruit setting, but the small or sieva group are more resistant to hot, arid conditions. Early bush types mature within 100 days but large-seeded Peruvian types may require

7–9 months to reach maturity. Under humid tropical conditions (in West Africa), lima beans are much less affected by diseases and insect pests than most other grain legumes, although in some areas pod borers and leafhoppers attack them. Major diseases reported are downy mildew (*Phytophthora phaseoli* Thaxt.), pod blight (*Diaporthe phaseolorum* Sacc.), anthracnose (*Colletotrichum lindemuthianum* Bri. and Cav.), fusarium root rot, rust (*Uromyces phaseoli* Arth.) and viruses.

b. Improved Strains. Varieties adapted to the tropics include the bush types, FORDHOOK 242 with large thick seeds, and BURPEE BUSH. Recommended pole limas for green beans include KING OF THE GARDEN and FLORIDA SPECKLED BUTTER. For production of dry seeds in California, VENTURA having large flat beans, and WILBAR and WESTERN with small thin seeds, are the most important types, and both are semiclimbers. Dry seed yields exceeding 2000–2500 kg/ha have been observed in southern Nigeria (IITA, 1973).

c. Botanical. The chromosome complement of *P. lunatus* is $2n = 22$; germination is epigeal, and up to 20% outcrossing occurs. Hand crossing is sometimes difficult owing to diminutive flowers and a high degree of abortion. However, genetic male sterility has been utilized to facilitate the genetic recombination procedure. The seeds vary in size from 45 to 200 g per 100 seeds; range from flat to rounded "potato" types; and may be white, ivory, red, purple, brown, or black in solid colors or mottled.

2. *Winged Bean*

This plant (*Psophocarpus tetragonolobus* L.) is also known as goa bean, four-angled bean, Manila bean, princess pea, and asparagus pea (not to be confused with *Lotus tetragonolobus* L. also called asparagus or winged pea). The winged bean probably originated in tropical Asia and is fairly extensively cultivated by the Melanesians in New Guinea. It is grown primarily for its immature pods cooked like French beans, but the partially and fully ripe seeds are eaten after parching in Java and New Guinea. The tubers are smaller than *Pachyrrhizus* spp. and are eaten raw or cooked, particularly in Burma; and the young leaves, shoots, and flowers may also be eaten as a vegetable. It may also be grown for fodder, as a cover crop or for green manure because of its exceptionally good nodulation.

a. Adaptation. Winged beans perform best in hot humid climates and are remarkably free of pests and diseases in southern Nigeria (IITA, 1973). Loamy soils are best and the crop does not tolerate waterlogging. However, it does require ample, well-distributed moisture—perhaps in excess of 1500 mm annual rainfall or irrigation to perform well. It has exceptional ability to nodulate—one plant studied by Masefield (1961) produced 585 g of fresh nodules, compared with only 1.5 g of fresh nodules

for *P. vulgaris* plants. However, experiments with winged beans in southern Nigeria have sometimes produced comparatively slow growth accompanied by markedly chlorotic, light-green foliage, suggesting poor nodulation or unavailability of the most effective rhizobial strains.

b. Description and Nutritive Values. The winged bean is a twining, glabrous perennial herb usually grown as an annual. The pods are large varying from 16 to 36 cm, have four jagged-edged wings and enclose 8–17 medium to large, globular seeds (up to 300 g/100 seeds). The ripe seeds are rich in both protein (up to 37.3%) and oil (15.0–18.1%) from investigations carried out by Pospisil *et al.* (1971). The tubers may also contain up to 24% crude protein on a dry weight basis (Burkhill, 1967). The oil is high in unsaturated fats with only 28.8% saturated fatty acids, and 126 mg per 100 mg of tocopherol (dimethyltocopherol—both alpha and beta forms). The protein is also high in essential amino acids: cystic acid = 2.6% of protein; lysine = 8% of protein; histidine = 2.7% of protein; threonine = 4.5% of protein; and methionine = 1.2% of protein (Pospisil *et al.*, 1971).

Investigations in Southern Nigeria (IITA, 1974) demonstrated a wide range in productivity of seeds and tubers in the winged bean cultigens. Dry seed yields from small plots planted in mid-May at Ibadan ranged from 948 to 2010 kg/ha. One of these cultigens, TPI 6 produced dry seed yields of 1653 kg/ha and fresh tuber yields of 1288 kg/ha. Tubers from the four cultigens observed were analyzed biochemically and contained: 41.4% dry matter, 18.7% crude protein, 50.4% starch, 1.1% ether extract, 2.0% ash, and 19.0% crude fiber. Although not all the crude protein is assimilable, the tuber constitutes another form of nutrient which is producible in areas or seasons unfavorable to seed development, such as high incidence of pests and diseases and where humidities remain high throughout the ripening period. Moreover tubers are partially storable in the ground until required for consumption.

3. African Yam Beans

This pulse (*Sphenostylis stenocarpa* Harms.) is a slow growing, herbaceous climber frequently grown in association with the common yam (*Dioscorea* spp.) and beans, in humid and forested regions of the African lowland tropics. It is grown both for its seeds and tubers which resemble the sweet potato tuber in size and shape (7–13 cm long), but tastes more like an Irish potato.

a. Description. The plant may be procumbent, twining, or erect, and the leaflets are lanceolate or ovate. The flowers are multiple and borne on axillary peduncles. The calyx is broadly cupular, and shortly, undulately lobed. The stigma is flat and broad like a spatula. The fruits are linear,

up to 30 cm long, glabrous and become tough and hard when ripe. The seeds are ellipsoidal, smooth, shiny, and hard when ripe (Hutchinson and Dalziel, 1958).

b. Utilization. The tough pods and hard seeds appear less susceptible to pest attacks either in the field or storage than beans or cowpeas, but the seeds require several hours of soaking before cooking. However, the seeds may have an excellent protein with exceptionally high levels of methionine (up to 1.92 g per 16 g of nitrogen) and cystine (1.44 g per 16 g of nitrogen). They are also high in glutamic acid and highly palatable.

Ten tuber-bearing yam beans averaging fresh tuber yields above 2 tons/ha were grown and analyzed biochemically at Ibadan, Nigeria in 1973 (IITA, 1974). These ten lines averaged 25.7% dry matter, 15.7% crude protein, 58.1% starch (of which 27.1% was amylose), 0.56 ether extract, 4.8% crude fiber and 3.6% ash.

Nicol (1959a,b) studied the utilization of yam bean in Nigeria and found the crop grown in such disparate regions as Okuta (West of Ilorin near the Dahomey border); at Bida and Mbanegi near Obuda in the Eastern Region primarily for the tubers; whereas at Esike near Enugu (East Central State) it was grown mainly for the seeds. It is also cultivated in Central African Republic, Cameroons, Zaire, Ethiopia, and various other parts of East and Central Africa.

c. Potential. The African yam bean is nearly always grown interplanted with other crops, usually with staked yams. Attempts at sole cropping have not been very successful owing to spread of diseases (wilt) in pure stands. There are no records of seed yields nor productivity levels in this crop; although preliminary observation trials at Ibadan, Nigeria in 1973 suggest that tuber-producing ability is at least partially dependent on genotype. Significant tuber production was realized in 28 out of 64 yam bean collections; the six highest yielders averaged fresh tuber yields of 2717 kg/ha, the highest, TSs 20, producing 4211 kg/ha in small plots, although nearly all plots were heavily infected by virus (IITA, 1974).

4. *Mexican Yam Bean*

Two of the six species of *Pachyrrhizus* are cultivated for their edible tubers—*P. erosus* spring. and *P. tuberosus*. *P. erosus* was spread from its origin in Mexico to the Philippines in the 17the century, and *P. tuberosus* appears to have originated in the Amazon headwaters region.

Adaptation and Use. Yam beans (jicama) are indigenous to Central America and occur wild in Mexico. They are best adapted for growing in the hot, humid tropics on well-tilled, loose sandy soils. The high moisture tubers may be cooked or eaten raw with salt and spice, and the young pods of *P. erosus* may be eaten like French beans; but the roots, mature seeds and leaves contain a toxic substance—rotenone. The young pods

of *P. tuberosus* are not eaten, as they are covered with irritating hairs, but this species produces larger tubers. *P. erosus* is widely grown in home and market gardens in southeastern Asia, particularly in Singapore, southern China, Thailand, and even in Hawaii (Purseglove, 1968). Exceptionally high yields of fresh tubers—22 tons/ha in addition to 2.65 tons/ha yields of dry seeds (nonedible)—were obtained from replicated experiments conducted in southern Nigeria in 1973 (IITA, 1974). When analyzed these tubers were found to contain 12.1% dry matter and 9.9% crude protein on a dry weight basis.

5. *Velvet Beans*

There are two species of *Mucuna* grown as pulse in various parts of tropical Africa. Both are vigorous, herbaceous climbers with long duration, often requiring 8–12 months to fruit. The fruits of velvet beans (*M. pruriens* var. *utilis*) are medium in size, whereas the fruits of horse eye bean (*M. sloanei* Adars., syn. *M. urens*) are large. However, the pods of both species are distinctive in appearance and frequently covered with profuse, stiff, golden, urticating hairs giving them a velvety appearance.This feature together with extreme hardness of testa in horse eye bean render them unpleasant to harvest and thresh, but may impart a measure of protection against insects and animal pests. The seeds are cooked or roasted, husked, ground into flour and used in soups and stews. In Indonesia, the seeds may be fermented and used like *tempe* from soybeans. Apparently the flour has good thickening properties as less than 10–12 large seeds of horse eye beans are reported to make a "gallon of thick soup." They are a secondary species in such diverse regions as southeastern Asia—primarily Indonesia—and in tropical regions of Africa, such as southern Nigeria, Dahomey, Senegal, Upper Volta, Sudan, and Mozambique.

A very similar woody climber, *Dioclea reflexa* Hook., also has extremely hard seed testas like those of *M. sloanei*. It has been reported to occur from Sierra Leone and Guinea eastward to the Cameroons. However, there is comparatively little evidence of its extensive use for food, and it may be only an occasional "gathered" crop used sporadically or in times of scarcity.

VIII. Conclusions

Twenty-four grain legume species contribute significant amounts of food, animal feeds, and industrial products in the lowland tropics. However, only four species—peanuts, pigeon peas, cowpeas and mung beans (both green and black grams)—made up 87% of both the cultivated area and total production on a worldwide basis. Peanuts alone comprise 52% of this production, although an estimated 80–90% of peanut production in the tropics went into industry or was exported.

Among the lowland tropical legumes the improvement of peanuts in the tropics has received major emphasis owing to their industrial and export potential, and it now appears feasible to draw on extensive knowledge and genetic materials from temperate soybean improvement programs—at least in the beginning. Comparatively little in-depth plant improvement has been done on cowpeas, pigeon peas, and mung beans; and virtually nothing has been done on secondary species like bambara groundnuts and yam beans which are so important in the African tropics; on winged beans, velvet beans and jack beans in the more humid areas; nor on moth or tepary beans for the semiarid regions. Fortunately, there is a modest background on lima beans improvement in temperate regions, and hyacinth bean and horse gram have received a little interest in India.

1. Comparative Features of Tropical Species

Some botanical and adaptive characters of tropical lowland grain legumes can be summarized in tabular form to facilitate direct comparisons of their potential for specific situations (Appendix Table III). Although species are grouped according to their presumed ecological use patterns, considerable overlap occurs in adaptation and in microclimates of particular locales within regions.

a. Plant Types. Most grain legumes are twining, semiprostrate or climbing in their unimproved state. However, several species do have erect, self-supporting structures, including: locust bean—a tree; pigeon peas—semiwoody shrubs; and jack beans. There are three small bunchy herbs with underground fruiting: peanuts, bambara, and Kersting's groundnuts. Several others have erect or semierect bushy forms with implications of photosynthetic efficiency, high yielding potential, convenience of growing, and adaptability for mechanization. These include: soybeans, mung beans, cowpeas, horse gram, *Phaseolus* beans, jack beans, lima beans, moth beans and tepary beans. Twelve species are classified as annuals and thirteen are more or less perennial, although both forms frequently occur in the same species.

Lodging occurs frequently in the erect and semierect *Vigna* and *Phaseolus* species and in soybeans, but is much less of a problem in pigeon peas and jack beans. Shattering is also a major problem in grain legumes, particularly in the more primitive and wild species, and where frequent wetting and drying out occurs. Shattering is most serious in soybeans and also in the tepary bean, rice bean, and wild/weedy *Vigna* species. Less susceptible are pigeon peas (except the long-podded PHILIPPINE cultivars), cultivated cowpeas and mung beans.

b. Soil and Climate Preferences. Most species require well-drained sandy to sandy loam soils. However, a few, like jack beans, soybeans, black grams, and rice beans, tolerate heavy soils well and even waterlogging to

some extent. Black gram, mung beans, and rice beans are frequently grown after rice. Jack/sword beans also have some tolerance of salinity, and certain species of *Canavalia* are used in coastal regions, where they are exposed to salt sprays and possibly brackish water for binding sand and sand dunes. The semiarid species are usually more sensitive to waterlogging, but also perform better under low humidities and bright sunshine. If grown under more humid conditions they are often subject to heavy disease and insect attack. Some of the long duration climbers like yam, velvet, horse-eye, and *Dioclea* beans may be tolerant of shade and very "moist" soils, as they are usually grown in the humid forested zones with high amounts of cloud cover.

c. Susceptibility to Pests and Diseases. A subjective and somewhat arbitrary assessment of susceptibility to pest and diseases suggests that several species, including *Voandzeia, Kerstingiella, Cyamopsis, Parkia, Canavalia, Vigna umbellata, Phaseolus lunatus, Psophocarpus, Sphenostylis, Pachyrrhizus, Mucuna,* and *Dioclea* have comparatively fewer pest and disease problems when grown in their regions of adaptation. However, peanuts, cowpeas, and *Phaseolus* beans are frequently highly susceptible to various diseases and pests even in their optimal ecologies. In these situations plant protection is often the major management input. For example, in the subhumid regions of Nigeria, an effective insect control program can increase yields of cowpeas on the order of 5–10 times or more.

d. Yielding Ability. It is interesting to consider authentic yield records as one indication of the potential of different species, since "average" yields may indicate that the crop was grown outside of its adaptive ecology, was intermixed with other species, used for other purposes (leaves, green pods, or tubers), or grown as a catch crop. However, there is good evidence to confirm that soybeans on both an average and maximum record basis have the highest yielding potential at present, both in terms of quantity and quality (high protein and oil content). However, it is very interesting that some hitherto relatively unimproved species like pigeon peas (3000–5000 kg/ha of dried beans) and jack beans (4600 kg/ha dry seeds) can produce high yields under certain circumstances. Even short-term crops like bambara groundnuts (2600–3000 kg/ha), cowpeas (2800 kg/ha), mung beans (2600 kg/ha), *Phaseolus* beans (2500 kg/ha) have high yielding potentials for the periods they occupy lands. At Ibadan, where it is comparatively "easy" to obtain 2800 kg/ha of soybeans or about 32 kg of dry seed per ha/day, short duration cowpeas (65–70 days) will normally produce 1500 kg or up to 25 kg dry seeds per ha/day (IITA, 1973).

2. *Utilization Aspects*

The total benefits from growing grain legumes are frequently ignored both in commercial cropping systems and in the decision-making process

when allocating resources for crop research. In order to emphasize the positive aspects of growing tropical legumes, the broad array of uses for these crops as well as their beneficial effects both on the soil and crops to follow are briefly summarized in the sections below.

a. Utilization for Food. The many uses of grain legumes and the broad array of dishes that can be prepared from dried pulses or tender green pods and seeds are reasonably familiar. However, it is not so widely recognized that extensive use is made of young seedlings and tender green leaves as pot herbs and as such contribute excellent quality protein (up to 35% crude protein) to the diet. Moreover, the use of tubers from winged and yam beans is hardly known, nor are there any definite reports on productivity levels and nutritive values of leguminous tubers, although results at Ibadan (IITA, 1974) suggest that winged bean and African yam bean tubers can range from 17–20% and 13–18% crude protein, respectively, on a dry weight basis.

Many grain legumes have special features of utilization and of nutritional value. Some also contain toxic properties, metabolic inhibitors, off-flavor enzymes, or flatulence factors. Fortunately, the most important of these factors are dissipated in the cooking process, except the flatulent sugars—stachyose and raffinose.

b. Forage and Cover Cropping. The important role of grain legumes on succeeding crops or their use for forage is frequently ignored. Some of the best forage and grazing comes from several tropical species like the procumbent or semierect cultivars of cowpeas, tepary beans, horse gram, mung beans, rice beans, velvet beans, guar, soybeans, and others. It is not unusual to obtain more than 20–40 tons of high protein green matter or 5–10 tons of dry hay within a comparatively short time (60–80 days) from thickly-planted grain legumes. Similarly, these and other species are valuable for their fertility-restorative abilities, and as cover crops to protect erodable soils. Spreading types of cowpeas have shown excellent cover in erosive situations, and the winged bean has such excellent nodulating and nitrogen-fixing abilities that sugarcane is reported to give up to 50% higher yields following *Psophocarpus* than in ordinary rotations in Burma. In southern Georgia (USA) seed cotton yields were increased from 918 lb/acre following cotton to 1578 lb/acre following velvet beans plowed down as green manure (Martin and Leonard, 1967).

3. *Opportunities for Improvement*

It is both surprising and encouraging that some "neglected" pulses like pigeon peas, lima beans, bambara groundnuts, mung beans, and jack beans occasionally demonstrate remarkable productivity potential and often without serious problems or substantial management inputs. This sug-

gests that comparatively modest investments on improvement could pay off handsomely and quickly. Nevertheless, it would probably be unrealistic to activate major improvement efforts on more than four or five of these secondary species at the present time at least at the international level. However, it may become expedient over the longer term as demand increases, more marginal lands are brought under cultivation and resources become available to mount programs on some of the more promising of these "secondary" species. Furthermore, localized interests may well decide that emphasis on some presently obscure species lies within the realm of their national goals.

a. Collecting Germplasm. Since secondary species are quickly lost with the expansion of more sophisticated farming systems, there is an urgent, immediate need to thoroughly and systematically collect and maintain indigenous germplasm. It should also be noted that the large-seeded legumes may be more closely related than heretofore suspected (the majority have $2n = 22$ chromosomes). Therefore, even obscure species could have important breeding potential when techniques are developed to readily combine diverse genetic stocks.

b. Selection of Species. The choice of species worthy of in-depth improvement must be made on a rational basis considering their present importance, preference for food, intrinsic problems (pests and diseases), inherent productivity potential, nutritional qualities, genetic diversity available and ease of genetic manipulation. Using these guidelines the first order of priority should be focused on the four species discussed in detail in this section: (1) peanuts, (2) pigeon peas, (3) cowpeas, and (4) mung beans. These four crops must receive broadly based support at both international and national levels.

The second order of priority for species with regional potential at the outset is considered to be (1) lima bean for its exceptional range of adaptation, freedom from diseases and pests, high yield potential and excellent nutritional quality; (2) soybean for its industrial and market demands, exceptional yielding potential, broad range of adaptability, and reasonable freedom from pests and diseases; (3) hyacinth bean for adaptation to subhumid and semiarid conditions, broad range of uses, and productivity on poor soils; and (4) bambara groundnut for its widespread importance in tropical Africa, excellent adaptation to areas with low and unstable moisture conditions, freedom from pests and diseases and excellent grain quality.

A third order of priority is assigned to species with more localized adaptation and use but with considerable potential for expanded production. It is assumed that these species would be of greater immediate concern to national interests. These include: (1) African yam beans—for adaptation to the humid tropics, exceptionally good quality protein (high in essen-

tial amino acids) and excellent taste qualities; (2) winged bean—exceptionally broad array of uses, high quality of product (leaves, green pods, dry seeds, and tubers), and freedom from pests and diseases; (3) velvet bean—broad range of uses, vigorous growth and freedom from pests and diseases; (4) jack beans—exceptional adaptive qualities, high yield potential, and medicinal purposes; (5) horse gram—productivity under very poor soil conditions and high yields of both seed and forage; (6) moth bean—exceptional tolerance of extreme conditions of drought and high temperatures; (7) cluster bean—adaptation to high temperatures and low moisture, exceptional production of seeds, pods, and forage and possible commercial production of mucilage.

4. *Strategy for Diversification*

The range of environmental conditions and crop hazards in the lowland tropics is nearly infinite. It is reasonable to assume that many of the major agronomic problems of specific crops can be solved through combinations of broadly based research in the areas of plant improvement, plant protection, growth processes and management. However, some constraints on individual species may not be amenable to solution at prevailing levels of technology. It may be much more expedient to offer other species for those situations. Moreover, complex multiple and mixed cropping systems require several productive and trouble-free crops. Since optional secondary crops inevitably have deficiencies of their own requiring attention, there is a question of allocating research efforts. Diverting resources from established major objectives could result in net loss in overall productivity, since human needs and tropical environments with attendant hazards are dynamic, requiring constant vigilance.

While it is unrealistic to expect all 24 species to receive full research support, there are certain mitigating factors favoring an increased interest in secondary legumes. The rapidly rising food prices and current world shortage of energy and fertilizers provides incentives to explore more efficient sources of nutrition. Moreover, the fact that the global network of international agricultural research institutes is committed to including the four major lowland species and *Phaseolus* beans in their improvement activities should relieve some of the pressure on national programs. It is hoped that individual countries and regional organizations could divert a portion of their research resources to some of those secondary tropical legumes with localized interest. Since these developments will take some time, it is essential to assemble, collect, and maintain the germplasm of these species before they are irretrievably lost in the accelerated ecological changes occurring with rapidly increasing population pressures.

Appendix: Tables

TABLE I
Trends in the Estimated Production of Grain Legumes for Intermediate-High and Lowland Tropical Regions for the Periods 1948-1952, 1961-1965, and 1971

Crops and species	1948-1952		1961-1965		1971	
	Area (M ha)	Prod. (M tons)	Area (M ha)	Prod. (M tons)	Area (M ha)	Prod. (M tons)
Intermediate-high elevations						
1. Dry beans (*Phaseolus vulgaris*)	4.24	2.31	6.55	3.74	8.38	5.53
2. Dry peas (*Pisum* spp.)	1.53	1.05	1.76	1.32	1.50	1.18
3. Broad beans (*Vicia faba*)	0.30	0.23	0.40	0.29	0.47	0.32
4. Chick-peas (*Cicer arietinum*)	8.25	4.27	9.79	5.88	8.50	5.69
5. Lentils (*Lens esculenta*)	0.70	0.31	0.96	0.45	0.95	0.48
6. Soybeans (*Glycine max*)[b]	0.08	0.07	0.44	0.49	1.96	2.60
7. Other (20%)	1.14	0.40	1.01	0.44	0.80	0.38
Subtotal	16.24	8.65	20.91	12.62	22.56	16.03
Increase over 1948-1952 (%)	—	—	28.70	45.9	37.2	101.2
Lowland tropics						
1. Peanuts (*Arachis hypogaea*)[c]	8.98	6.40	14.48	11.52	14.87	13.01
2. Asian grams (dry beans)[d]	4.26	1.08	7.43	2.12	7.80	2.52
3. Pigeon peas (*Cajanus cajan*)	2.41	1.40	2.69	1.76	2.91	2.61
4. Cowpeas (*Vigna unguiculata*)	1.31	0.44	2.42	0.96	2.99	1.08
5. Soybeans[e]	0.42	0.29	0.66	0.45	0.70	0.51
6. Other (80%)	4.05	1.60	4.03	1.78	4.01	1.91
Subtotal	21.42	11.21	31.60	18.58	33.28	21.64
Increase over 1948-1952 (%)	—	—	47.00	65.8	55.4	93.0
Total (both elevations)	37.66	19.86	52.51	31.20	45.56	37.67
Increase over 1948-1952 (%)	—	—	39.40	57.10	47.5	89.7

[a] M ha = million hectares; M tons = million tons; Prod. = Production.
[b] African and American tropics.
[c] Production expressed in shell.
[d] "Dry bean" production in Asia.
[e] Soybeans in tropical Asia.

TABLE II

Regional Production of Lowland Tropical Grain Legumes in 1971 in Millions of Hectares and Metric Tons

Crop		Southern Asia		Tropical Africa		Tropical Americas		World total	
		Actual	Percent[a]	Actual	Percent[a]	Actual	Percent[a]	Actual	Percent[b]
1. Peanuts:[c]	Area[d]	8.19	55.1	5.78	38.9	0.90	6.1	14.87	44.7
	Prod[d]	7.10	54.6	4.84	37.2	1.07	11.1	13.01	60.1
2. Pigeon peas:	Area	2.72	94.0	0.15	5.15	0.04	1.4	2.91	8.7
	Prod	1.87	71.7	0.71	27.2	0.03	1.15	2.61	12.1
3. Cowpeas:	Area	0.03	1.0	2.96	99.0	—	—	2.99	9.0
	Prod	0.02	1.9	1.06	98.15	—	—	1.08	5.0
4. Asian grams:[e]	Area	7.80	100	—	—	—	—	7.80	23.4
	Prod	2.52	100	—	—	—	—	2.52	11.6
5. Unspecified:[f]	Area	3.30	70.1	1.34	28.4	0.07	1.5	4.71	14.2
	Prod	1.70	70.2	0.68	28.1	0.04	1.7	2.42	11.2
All lowland pulses:	Area	22.04	66.2	10.23	30.7	1.01	3.0	33.28	59.9[g]
	Prod	13.21	61.0	7.29	33.7	1.14	5.3	21.64	57.4[g]

[a] Percent of total production of that species grown in the lowland tropics.
[b] Percent of all grain legumes (all species) grown in the lowland tropics.
[c] Since peanuts are one-third shell, net kernel production is estimated at 8.9 million metric tons, or 52.8% of all lowland grain legumes.
[d] Area in millions of hectares and production (Prod) in millions of metric tons given in columns headed "Actual."
[e] "Dry bean" production in Southern Asia is assumed to be predominantly Asian grams (mung beans, black gram, rice bean, and others).
[f] Includes soybeans, presumed to be a lowland crop in tropical Asia.
[g] Proportion of all tropical legumes including intermediate–high elevations.

TABLE III

Some Important Adaptive Features and Botanical Characteristics of Selected Lowland Tropical Grain Legumes[a]

Part A. Semiarid Regions (less than 500–600 mm annual rainfall)

Region and name (presumed origin)	Scientific name	Chromosomes (2n =)	Perenniality[b]	Duration (days)	Plant type/size	Soil and climate preference/tolerance	Pest/diseases susceptibility[c]	Dry seed productivity levels: Average (kg/ha)	Dry seed productivity levels: Maximum (kg/ha)	Purpose and utilization
1. Bambara groundnut (Africa)	*Voandzeia subterranea*	22	A	90 to 150	Small, bunchy herb; prostrate, rooting branches; underground fruiting	Dry, poor soils; high temperatures	VL	750	2600	Unripe seeds eaten fresh; and ripe seeds used as a pulse
2. Kersting's groundnut (Africa)	*Kerstingiella geocarpa*	22	A	90 to 120	Small, bunchy herb; prostrate, rooting branches; underground fruiting	Dry, poor sandy soils; high temperatures and sunshine	VL	500	—	Unripe and mature seeds used as a pulse
3. Moth bean (India/Burma)	*Vigna aconitifolia*	22	A	65 to 90	Slender, trailing hairy herb 10–30 cm tall	Dry, light sandy soils	M	300 to 400	1600	Green pods as vegetable; ripe seeds whole or split as pulse. Forage, hay, and manure
4. Tepary bean (Mexico)	*Phaseolus acutifolius* var. *latifolius*	22	A	60 to 90	Suberect herb, bushy or recumbent, 25 cm high	Dry soils; does not tolerate waterlogging	M	400 to 700	1500	Dry seeds for pulse; forage: 5–10 tons of dry hay
5. Cluster bean (India)	*Cyamopsis tetragonolobus*	14	A	90 to 120	Robust bushy herb	Alluvial/sandy soils; high temperatures	VL	400 to 600	1600	Green beans as vegetable; leaves and stems for forage; dry seeds for mucilage

(*Continued*)

[a] Table III is from Rachie, 1973.
[b] A = annual.
[c] VL = very low; M = medium.

TABLE III (*Continued*)

Table III, Part B. Semiarid to Subhumid Regions (600–1000 mm annual rainfall)

Region and name (presumed origin)	Scientific name	Chromosomes (2n =)	Perenniality[a]	Duration (days)	Plant type/size	Soil and climate preference/tolerance	Pest/diseases susceptibility[b]	Dry seed productivity levels: Average (kg/ha)	Dry seed productivity levels: Maximum (kg/ha)	Purpose and utilization
1. Peanut (Brazil)	*Arachis hypogaea*	40	A	100 to 150	Low bunchy herb; underground fruiting	Friable sandy loams	MH	600 to 800	3000	Industrial: oil, seed cake; dry seeds for cooking, condiments
2. Pigeon peas (E. Africa)	*Cajanus cajan*	22 (44)	P	100 to 300	Semiwoody shrub 1.5 to 5 m tall	Well-drained sandy/clayey loams	L	400 to 500	3000 to 5000	Dry seeds for pulse; unripe seeds as vegetable; forage crop and cover
3. Cowpeas (Nigeria)	*Vigna unguiculata*	22 44	A or SP	65 to 200	Twining, climbing, or procumbent herb; or erect bush: 20–120 cm tall	Well-drained sandy loams; high temperatures	H	300 to 400	2800	Dry seeds as pulse; tender green seedlings, leaves, pods and seeds as vegetables; forage and green manure crop
4. Mung beans/black gram (India/Burma)	*Vigna radiata* and var. *mungo*	22 (24)	A	80 to 120	Erect-suberect, hairy herb; 50–130 cm tall	Well-tilled loams to clays black cotton soils	M	400 to 500	2700	Dry seeds as pulse, split or sprouted; green pods as vegetable; forage
5. Horse gram (So. Asia)	*Dolichos uniflorus*	24	A	120 to 180	Low, slender, semi-erect herb	Tolerates very poor soils	M	200 to 300	800 to 1200	Dry seeds as pulse and animal feed; dry forage and green manure
6. Hyacinth bean (So. Asia)	*Lablab niger*	22 (24)	SP	75 to 300	Herbaceous twining and bush forms	Well-drained; tolerates poor soils and low fertility	M	400 to 500	1500	Young pods and green beans as vegetables; dry seeds for pulse and feed for livestock; forage
7. African locust bean (Africa)	*Parkia* spp.	—	P	—	Tree: 10–30 m	Wide range, alluvial soils	VL	350 to 500	—	Dry seeds fermented as flavoring; fruit pulp also cooked

[a] A = annual; P = perennial; SP = short-term perennial.
[b] VL = very low; L = low M = medium; MH = medium high.

Table III. Part C. Subhumid Regions (1000–1500 mm annual rainfall)

Region and name (presumed origin)	Scientific name	Chromosomes (2n =)	Perenniality[a]	Duration (days)	Plant type/size	Soil and climate preference/ tolerance	Pest/ diseases susceptibility[b]	Dry seed productivity levels: Average (kg/ha)	Dry seed productivity levels: Maximum (kg/ha)	Purpose and utilization
1. Phaseolus beans (C. America)	*Phaseolus vulgaris*	22	A	60 to 100	Dwarf bush to twining/climbing	Light sands and peat, to clayey soils	VH	500 to 700	2500	Dry seeds as a pulse; green pods and beans as vegetable; also for forage
2. Soybeans (S.E. Asia/ China)	*Glycine max*	40	A	80 to 200	Erect bush; also twining 20–180 cm	Tolerates some water-logging	M	600 to 1000	5000 to 6000	Industrial-protein and oil; green seeds as vegetable; dry seeds as a pulse; forage from leaves stems
3. Rice beans (S.E. Asia)	*Vigna umbellate*	22	SP	60 to 90	Erect-suberect/ twining 150–300 cm	Light to heavy soils (after rice)	L	200 to 500	1200	Dry seeds as pulse; green seeds and pods as a vegetable, fodder
4. Jack/sword beans (C. America and Africa)	*Canavalia* spp. *C. ensiformis* *C. gladiata*	22 (44)	P	180 to 300	Bushy, erect 1–2 m; large climber	Tolerates some water-logging	VL	800 to 1000	4600	Green pods as vegetable; ripe seeds as pulse; medicinal—urease and lectin; vegetation for forage and cover

(*Continued*)

[a] A = annual; P = perennial; SP = short-term perennial.
[b] VL = very low; L = low; M = medium; VH = very high.

TABLE III (*Continued*)

Table III, Part D. Humid and Very Humid Regions (above 1500 mm annual rainfall)

Region and name (presumed origin)	Scientific name	Chromosomes ($2n$ =)	Perenniality[a]	Duration (days)	Plant type/size	Soil and climate preference/tolerance	Pest/diseases susceptibility[b]	Dry seed productivity levels: Average (kg/ha)	Dry seed productivity levels: Maximum (kg/ha)	Purpose and utilization
1. Lima beans (C. America)	*Phaseolus lunatus*	22	P	100 to 270	Twining climbers; or bush types	Humid; well drained; aerated soils	VL	500 to 600	2800	Dried beans as pulse; green beans, young pods and leaves as vegetable (seeds may have HCN)
2. Winged bean (tropical Asia)	*Psophocarpus tetragonolobus*	—	P	180 to 270	Twining, glabrous herb, 2–4 m long	Humid climate; loamy soils	VL	400 to 500	2500	Fresh green pods, leaves as vegetable; tubers; dry seeds as pulse; also green manure and forage
3. African yam bean (West Africa)	*Sphenostylis stenocarpa*	—	P	150 to 300	Twining, climbing or procumbent herb, 3–6 m	Humid, well drained loams	L	300 to 500	1200	Dry seeds as a pulse; tubers fresh or cooked
4. American yam bean (Mexico and C. America)	*Pachyrrhizus erosus*	22	P	—	Herbaceous climber, 2–5 m	Humid; well tilled, sandy loams	VL	—	—	Tubers: raw or cooked; green pods: vegetable
5. Velvet bean (Africa)	*Mucuna pruriens* var. *utilis*	—	P	240 to 300	Herbaceous climber, 3–8 m	Humid, poor, sandy loams; high temperatures	VL	700 to 1000	—	Seeds used as pulse; crop also grown for green manure, cover, and forage
6. Horse-eye bean	*Mucuna sloanei*	—	P	240 to 360	Herbaceous climber, 3–10 m	Humid, well drained soils; high temperatures	VL	—	—	Ripe seeds are used as a pulse in thickening soups

[a] P = perennial.
[b] VL = very low; L = low.

TABLE IV
Inheritance of Some Important Genetic Characters in Pigeon Peas
(*Cajanus cajan* Millsp.)

Character	Symbol	Mode of inheritance—pigeon peas	Reference
Plant architecture			
Cotyledon shape		Determined either by pleiotropic action of a leaf shape gene or a gene closely linked to it, pointed leaf apex and lanceolate cotyledon being dominant over rounded apex and ovate cotyledon	Deksmukh and Rekhi (1961)
Foliate condition			
Unifoliate (pointed leaflet) Oval-oblong trifoliate Trifoliate with pointed leaves		In crosses of these types, the trifoliate condition is monogenic and dominant over unifoliate; pointed apex is dominant over the rounded apices and also monogenic. The two gene pairs segregated independently	Deshmukh and Rekhi (1960)
Normal trifoliate leaf	*Tr*	Dominant to unifoliate; monogenetically inherited	
Pointed leaf apex (lanceolate)	*Mc*	Dominant to round apex; monogenetically inherited (obovate)	Rekhi (1966)
Leaf mutants			
Obcordate leaflets	l_1 l_2	A spontaneous mutant having obcordate leaflets with mucronate apices and filiform flower keel depends on pleiotropic duplicate factors l_1 and l_2	Deshpande and Jeswani (1956)
Stature			
Short		Dominant to tall stature of type 80—monofactorial segregation observed in F_2 of both pairs of characters	Shaw (1936)
Growth habit			
Creeping		Segregation data of F_2 showed 13 creeping: 3 erect, suggesting two factors, one of which has inhibiting action	Shinde *et al.* (1971)
Erect		Erect branching, dominant to spreading habit; monogenetically inherited	Rekhi (1966)

(*Continued*)

TABLE IV (*Continued*)

Character	Symbol	Mode of inheritance—pigeon peas	Reference
Spreading		In one cross, erect habit was only partially dominant to spreading habit	Shaw (1936)
Prostrate		True breeding mutant; may be useful as cover crop and soil conservation	Deshpande and Jeswani (1952)
			Chaudhari and Patil (1953)
Dwarf, bushy plant			
Late, brittle stalks		A single recessive gene designated *d* appears to be involved; pollen fertility in the mutant was only 70%	Sen *et al.* (1966)
Fasciation		Mutant had weak, curved stems (purple), with branches fused to the main stem at place of emergence; 11% pollen sterility though many seeds produced; fasciation was recessive to normal	Bhatnagar *et al.* (1967)
Plant color			
Stem color			
Purplish stem		Incomplete dominance over green pigmented stem	Ganguli and Srivastava (1967)
Green stem			
Growth/development			
Time of flowering			
Lateness		Completely dominant in one cross over earliness; incompletely dominant over earliness in another cross	Ganguli and Srivastava (1967)
Steriles			
Steriles			
Sepaloid mutant		Simple leaves replaced normal trifoliate ones and were associated with a sepaloid condition of the flowers	Jeswani and Deshpande (1962)
Weak mutant		Simple leaves on lower part of plant and none on upper part with rudimentary floral organs in addition to dwarf habit and thin, straggling branches	

TABLE IV (*Continued*)

Character	Symbol	Mode of inheritance—pigeon peas	Reference
Cleistogamous mutant		Possessed thick, puckered trifoliate leaves; overall abnormal condition is monogenically recessive to normal, segregates independently of obcordate/lanceolate leaflet gene.	
Inferior stigma		At Niphad (India) a sterile plant found to have stigmas positioned below anthers instead of above them	Patil and Sheikh (1957)
Inflorescence			
Flowering conditions			
Nonflowering		Monogenically recessive to flowering condition; does not appear to be linked to pleiotropic locus controlling trifoliate versus simple leaf and normal versus sepaloid flower	Joshi and Ramanujam (1963)
Flowering			
Inflorescence			
Crowded		Crowded inflorescence of type 5 dominant to open inflorescence of type 80 on a 3:1 ratio	Shaw (1936)
Open			
Pistil			
Multicarpellate condition		Monogenetically recessive to normal unicarpellate condition—the allele appears also to control development of supernumerary petals, the development of stamens into petals or, carpel-like structures and exposed ovules; mutant plants are female sterile, with 80% stainable pollen	Joshi and Ramanujam (1963)
Flower color			
Basic color	*y*	Loci *r* and *p* found to be linked with a recombination frequency of 29.7%; and genotypes *ppV'V'*, *ppV'v* showed incomplete penetration of the *V'* allele, resulting in 13–27% percent of deep-veined individuals recorded under light-veined class	Jain and Joshi (1964)
Absence of venation	*r*		
Interacts with *v* locus	*p*		

(*Continued*)

TABLE IV (*Continued*)

Character	Symbol	Mode of inheritance—pigeon peas	Reference
Flower petal color			
Yellow—entire	*Ap cevs, ap cevs*	Recessive to all other conditions	Menezes (1956)
Yellow with light red veins	*ap ce Vs*	Data showed 3 yellow with deep red veins: 1 yellow with light red veins—independent assortment	Shinde *et al.* (1971)
Yellow with dark red veins	*Ap Ce vs*		Dave (1934)
Purple streaked	*Ap CE Vs*	Dominant to plain yellow: monogenetically inherited	
Blood red (solid	*Ap CE Vs*	Simple dominant to all yellow and yellow with purple	
White flowers (mutent)		Interaction of two duplicate genes W_1 and W_2 and spontaneous mutation of the inhibitory gene I_g conditioning yellow	Patil and D'Cruz (1962)
Wing color			
Orange		Dominant over yellow	Ganguli and Srivastava (1967)
Yellow			
Pods and seeds			
Unripe pod color			
Green with/black diffused	*Lrd*	Data showed 3 green with black diffused: 1 green with black streaks—independent assortment	Shinde et *al.* (1971)
Green with/black streaks	*Ld*		
All green	*ld*	Recessive to all others	
All purple	*LD*	Dominant to all others. "*D*" controls color distribution; incomplete dominance over "*d*"	Menezes (1956) Sen *et al.* (1968)
Dark green		Dominant to light green	Menezes (1953)

TABLE IV (*Continued*)

Character	Symbol	Mode of inheritance—pigeon peas	Reference
Seed coat color			
Purplish black	*PR*	Color is expressed as an interaction of two loci: dominance is simple; black is dominant to chocolate, spotted, and white	Dave (1934) Menezes (1956)
Chocolate	*pR*		
Spotted	*Pr*		
White	*pr*		
Dark purple with blotches		Incomplete dominance over chocolate and light brown	Ganguli and Srivastava (1967)
Brown		Brown is partially or incompletely dominant over white seed coat (monogenic)	Rekhi (1966)
Seeds/pod			
Four-seeded		Four-seeded pods dominant to three-seeded pods; monogenetically inherited	Rekhi (1966)
Three-seeded			
Disease resistance			
Resistance to wilt		Inherited independent of flower color, erect or spreading habit of growth, short or tall stature of plant, crowded or open inflorescence and brown or gray markings of the seeds	Shaw (1936)
		Inheritance of wilt susceptibility suggests its control by 2 or 3 factors not linked with any of the morphological characters studied	

TABLE V

Linkage Groups of Some Important Genetic Characters in Pigeon Peas (*Cajanus cajan* Millsp.)

Linkage groups in pigeon peas	Reference
1. Erect—Black pod—Lanceolate leaflet shape, I—Bl_p—L_{lt}. The 3 characters have shown recombination values of 40.8% between factors I and L_{lt}; 35.7% between I and B_{lp} and 2.9% between Bl_p and I_{lt}	Patil (1965)
2. There is a complete linkage between orange yellow flowers and purplish black seeds; and between yellow flowers with back of standard having purple veins, the base diffused purple, and purple-green pods. There is a close linkage between yellow flowers with the backs of their standards purple and maroon blotched pods a. Orange yellow flowers—purplish black seeds b. Yellow flowers, back of standard with purple veins, base diffused with purple and purple-green pods c. Yellow flowers, backs of standards purple, close linkage with maroon blotched pods	Dave (1934)
3. Linkage of venation with pigmentation: v = absence of venation, p = interacts with v, y = basic color (flower color and venation) Loci p and v were found to be linked with a recombination frequency of 29.7%, and genotypes $ppVV$, $ppVv$ showed incomplete penetration of the V allele, resulting in a range of 13–27% of the deep veined individuals recorded under the light-veined class	Jain and Joshi (1964)

TABLE VI
Inheritance of Some Important Genetic Characters in Cowpeas
(*Vigna unguiculata* Walp.)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Plant architecture			
Stem			
Swelling	*Sw*	Swelling at base of stem due to an increased amount of parenchyma in the phloem in ssp. *v. sinensis* 'Tanganyika' was monogenically dominant (*Sw*) over normal stems	Roy and Richharia (1948)
Normal			
Leaf shape			
Narrow leaf	*Nlb*	Determined by incompletely dominant gene like ancestral forms	Saunders (1960)
Hastate leaves	LS_1, LS_2	Dominant over rhomboid leaves: LS_1 is essential, while any two of LS_2, LS_3, or LS_4 produce hastate leaves	Jindla and Singh (1970)
Rhomboid leaves	LS_3, LS_4		
Growth habit			
Vining	*V*	Crossed between *Vigna sinensis* and *V. catjang* (close to wild spp.) showed dominance for "wild" characters: vining, earliness, dark-green leaves, dark mottled seeds, resistance to mosaic, and generally vigorous growth	Kovarskii (1930)
Tallness	*T*		
Vininess	V_1, V_2	Governed by duplicate genes	Kolhe (1970)
Plant color			
Foliage color			
Pale green (light)	*Lga*, *Lgb*	Inherited independently as a single recessive gene	Saunders (1960)
Normal	*rr*	Two complementary genes govern foliage color	Kolhe (1970)
Basic plant color	*R*	Plants are green with white flowers and cream seeds; sap-soluble pigment produced only in presence of basic gene for color (*R*, *r*)	Sen and Bhowal (1961), Saunders (1960)

(Continued)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Stem pigmentation			
Base of primary branches	*Pbr*	Purple base of primary branches simple dominant to green	Sen and Bhowal (1961)
Petiole base	*Pb*	Purple petiole base—simple dominant to green	
Growth/development			
Time of flowering			
Earliness Lateness	Ef_1, Ef_2	Early flowering was dominant to late flowering; number of days to flowering appeared to be controlled by the action of duplicate dominant epistasis between two major genes (Ef_1 and Ef_2) in the presence of some minor modifying genes	Ojomo (1971)
		In another experiment, the F_1 was intermediate between the two parents (49 and 94 days) with a tendency toward earliness. The F_2 data suggested that time of flowering may be determined by two complementary factors	Roy and Richharia (1948)
Photoperiod response			
Short day Day neutral		Short-day response simple dominant to day neutrality	Sène (1967)
Steriles and lethals			
Male sterility	*Ms* *ms*	A spontaneous male sterile mutant arose in *Vigna sinesis* ssp *catjang* 'Poona'; pollen meiosis did not proceed beyond early diacinesis. Sterility is controlled by the recessive condition of a single pair of genes (*ms ms*)	Sen and Bhowal (1962)
	Ms_2 ms_2	Sterility discovered at IITA is also controlled by a recessive pair of genes (ms_2 ms_2)	IITA (1974)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Lethal genes	L_1, L_2 L_3, L_4	Seedlings from the cross PORTUGUESE WHITE × LIGHT RED began to show reduced growth and wilting when about 2 weeks old; all succumbed within 6 weeks. Two complementary genes, L_1 and L_2, carried by PORTUGUESE WHITE and LIGHT RED, respectively, were responsible. Two other lethals, occurring at a much earlier stage, were discovered in the F_1 of the cross LIGHT RED × NI and are designated L_3 and L_4	Saunders (1952)
Inflorescence			
Type			
Compound inflorescence	*c*	Compound inflorescence of ssp. *V. catjang* "Poona" was monogenically recessive (*c*) to simple inflorescence	Sen and Bhowal (1961)
Simple inflorescence	*C*		
Flower color			
	W, *H*, *O*	These factors are pleiotropic with those governing seed testa colors and patterns	Jindla and Singh (1970)
Pale	*wHO* *whO*	Dark is dominant to pale or tinged	
Tinged	*WHo* *Who*		
Dark	*WHO* *WhO*	Dark flower color is epistatic to pale and tinged	
Violet	*H* or *D*	Violet flowers with self-colored seeds in presence of the gene *R*	Sen and Bhowal (1961)
Tinged, light blue or violet	*h* or *L*	Tinged flowers with holstein-eyed seeds in presence of the gene *R* Violet flowers dominant over very light violet, *D*, enhances the intensity of color in the presence of *L*	

(*Continued*)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Flower color	*Pf*	Expressed in presence of *R*	Kolhe (1970)
Standard petal	*Ystp*	Expressed in presence of *R*	
Calyx color	*Bcy*	Expressed in presence of *R*	
Pod characters			
Unripe pod color			
Purple	*Pu*	*Pp* produces purple pods only in the presence of *R*; purple pod is epistatic to both cerise and straw-colored pod	El-Murabaa and Mustafa (1970)
	Pp or *Pc*		
Cerise	*pC*		
Straw	*p*, *pc*	Straw-colored phenotype is also produced by *p* in the presence of either *R* or *rr*	
Drab	*rr*	Drab pod color of *Sudani* is controlled by a single gene and is dominant to straw pod color of varieties *Asmirli* and *Fitreiat* (*rr*)	
Red-tipped straw	*Pb*	Red-tipped straw pods formed by *Pb* only in the presence of *R*; in combination with *rr* the pods are straw-colored	
Green pods and purple-tipped pods	*pt*	Allele *pt* may represent 2 alleles, one for a more purple tip and black seeds, and the other for a less purple tip and nonblack seeds.	Sen and Bhowal (1961)
Green pods with a purple ventral suture	*pr*	The dominance relationship between *pg* and *pv* at the unripe stage was reversed at the half-ripe stage	
Purple pods with both sutures green	*ps*		
Green pods with both sutures purple	*Ps*	Respectively, plants homozygous for *ps* and *pu* bore green pods and green pods with faintly purple sutures and tips. Pod color genes appeared pleiotropic with colors of stem, petiole calyx, and standard petal	Saunders (1960)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Brown Speckled	*Y*	Dominant to green and other lighter colors	Saunders (1960)
Yellowish green Green Dark green	*g* *G* *GD*	In order of increasing dominance effects the grade of chlorophyll production in calyx, leaves, and dorsal surface of standard	Sen and Bhowal (1961)
Number of chloroplasts	*g* *G* *Gc*	The number of chloroplasts per cell and their intensity of color and size progressively increased in unripe pods representing the series *gL, GL, Gc* (see unripe pod color)	Sen and Bhowal (1961)
Ripe (dry) pod color			
Brownish-straw Amber-straw		Both monogenically dominant over straw (*rr*) colored ripe pods	Sen and Bhowal (1961)
Pod condition			
Inflated Constricted		Inflated in cv. *Sudani* controlled by a single gene dominant to constricted pods of *Azmirli* and *Fitreiat*	El-Murabaa and Mustafa (1970)
Pod size			
Length (long, short) Size (large, small)		Partial dominance observed for pod length; appeared to be under multiple gene control	Jindla and Singh (1970)
		In other studies the F_1's between short and long pods were intermediate, with a tendency toward short pods	Roy and Richharia (1948)
Pod surface	*Wpa, Wpb*	Two complementary genes responsible for expression	Kolhe (1970)
Seed characters			
Seeds per pod		Heterosis for seeds per pod was exhibited in F_1's of 13 and 16 seeds per pod parent cross. The F_1 produced an average of 18.0 ± 0.52 seeds per pod	Roy and Richharia (1948)

(*Continued*)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Grain deposition	*Dgda* *Dgdb*	Two complementary genes are responsible	Kolhe (1970)
Seed shape			
Cylindrical Kidney-shaped Cordate		Two multiple factors determine the difference between the cylindrical seeds of SUDANI and the kidney/cordate shaped seeds of AZMIRLI and FITREIAT	El-Murabaa and Mustafa (1970)
Seed length	*Lg*	Long seeds (grain) dominant to short seeds	Kolhe (1970)
Testa thickness	*Th*	Two major genes with possible cumulative interaction appear to govern testa thickness in *Vigna unguiculata*	
	Co	The presence of additional minor genes is postulated to account for the variability observed in all phenotypic classes	Ojomo (1972)
Testa color patterns			
	W,H,O	These factors appear to be pleiotropic with those governing flower colors	Saunders (1960)
Self or solid	*WHO*	Dominant *H* is self-colored	
Watson	*WhO*	The symbol *w* is also used for Watson-eyed, being recessive to *H* (self-colored)	
Holstein	*wHO*	Another symbol for holstein-eye (*HH*) is *hh WW*	
Small eye	*whO*	Another symbol for small-eyed (*hh*) is *hh ww*	
Hilum ring	*WHo* *Who* *wHo* *who*	These four genotypes produce a hilum ring	
Large eyed	*Wwhh*	Big-eyed (or Hh)	
Testa color			
Gray White		Black (*Z*) is dominant and epistatic to brown (*B*), which in turn is epistatic to red (*R*). Black is dominant to red	Saunders (1959)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Green Buff Red Brown Black Speckled Mottled Blotched (testa pattern)	 *B* *Z* *S* *U* 	Solid colored testa is brought about by the complementary action of two dominant genes, *H* and *W*; and the patterns "variegated" or "holstein" (*HH*), large eye (*Hh*), small eye (*hh*) find expression in the absence of *W*, which governs a color pattern with an indistinctly limited eye; intensity genes may also play a part	Roy and Richharia (1948) Saunders (1959)
Seed eye color			
Black eye		Epistatic to brown and smoke eyes	Mackie (1934)
Brown eye Smoke eye		The eyed character is a simple recessive so that it can be easily retained in the true-breeding condition	Mackie (1939)
Resistances			
Fusarum wilt (*F. oxysporum, f. trachciphilum*)		Resistance to race 1 is dominant; sources of resistance: IRON, VICTOR, and BRABHAM	Mackie (1934)
		Earliness may permit escape; IRON CLAY also resistant.	Hawthorne (1943)
		Resistance to race 1 but susceptible or tolerant to races 2 and 3: EXTRA EARLY BLACKEYE, PURPLE HULL BUNCH, and MISSISSIPPI CROWDER	Hare (1959)
		Resistance to all three races: IRON, MISSISSIPPI 755, and MISSISSIPPI 57.1	MAES (1959)
Charcoal rot (*Rhizoctonia bataticola*)		Resistant is dominant; sources are: IRON, VICTOR, BRABHAM	Mackie (1934, 1939)
Stem rot		Field resistance: MALABAR, GIANT, and CRISTANDO (when inoculum level is low); immunity: BLACKEYE 5, HAVANA, and SANTIAGO. POONA is susceptible.	Purss (1958)

(*Continued*)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Bacterial pustule (canker) (*Xanthomonas vignicola*)		Resistance is dominant to susceptibility (3:1)	Lefebvre and Sherwin (1950)
		Sources: 451 out of 578 tested at IITA in 1973	IITA (1974)
Powdery mildew		Resistance is recessive to susceptibility and dependent on multiple factors. Sources: *V. sesquipedalis;* also CHINITO and No. 0199	Fennell (1948)
Leafspot diseases (*Cercospora cruenta*)		Resistance is dominant: 454 out of 578 lines tested at IITA were free of disease	IITA (1974)
		Out of 37 lines tested in India, 22 were resistant	Verma and Patel (1969)
Southern bean mosaic virus		Resistance is dominant and single gene. Resistance in 9 varieties; also found in crosses of IRON × GROIT; and in CLAY and CLAY × TORGET	Kuhn and Brantley (1963); Brantley and Kuhn (1970)
Cowpea yellow mosaic		Tolerance attributed to three additive factors: ALABUNCH	Bliss and Robertson (1971)
		Resistance also found in a selection from DIXIELEE and appeared to be dominant (single gene)	
		Resistance was observed to be recessive—single gene pair in PI 297562	Reeder *et al.* (1972)
		Immunity identified in: TVu 39, 45, 99, 103, 106 and 1190	IITA (1974)
Cowpea mottle virus		Tolerance was dominant to susceptibility with either one or two genes involved	Bliss and Robertson (1971)
Cucumber mosaic virus		Resistance due to a single dominant gene in "Black SR"	Sinclair and Walker (1955); DeZeeuw and Crum (1963)
		Other tolerance: GARBANCITO, AZUL GRANDE, CHINITO, and No. 0199	Fennell (1948)

TABLE VI (*Continued*)

Character	Symbol	Mode of inheritance—cowpeas	Reference
Tobacco ringspot virus		Resistance is dominant and linked to CMV susceptibility; an epistatic recessive inhibitor may also be present. Resistant: "Black RS" and mutant of "Black"	DeZeeuw and Crum (1963); DeZeeuw and Ballard (1958, 1959)
Root knot nematodes (*Meloidogyne incognita*)		Resistance is dominant—single gene pair: IRON, VICTOR, BRABHAM	Mackie (1934, 1939)
		Other resistance: PURPLE HULL CROWDER, PINK-EYE; also, M 255, M 455, M 755, and M 855. These were also resistant to *M. javanica* and *M. arenaria*	Ivanoff (1963)
		MISSISSIPPI 755 and 57-1 reported to be resistant	MAES (1959, 1961)
		Early maturity helps plants escape nematodes	Hawthorne (1943)
		Widecrossing with resistant wild species not successful	Saunders and Laubscher (1945)
General resistance			
		Resistance to root diseases and nematodes in IRON, VICTOR, and BRABHAM attributed to high quantity of suberin in root cortex. Dark leaf color was also associated with disease resistance	Mackie (1934, 1939)
		Multiple resistance of MISSISSIPPI 755 and 57-1 obtained from PURPLE HULL CROWDER includes resistance to *Fusarium* wilt, nematodes, and viruses	MAES (1959, 1961, 1963)
Beetle (*Ceratoma trifurcata*)	*Rb*	Resistance is a monogenic dominant	Kolhe (1970)

TABLE VII
Linkage Groups of Some Important Genetic Characters in Cowpeas
(*Vigna unguiculata* Walp.)

Linkage groups in cowpeas	Reference
1. Flower color (*pf*)-standard petal color (*ystp*): crossover value = 20.4%	Kolhe, (1970)
2. Flower color (*pf*)-grain color (*Brg*): crossover value = 20.3%	
3. Grain deposition (*Dgda*)-pod surface (*Wpa*): crossover value = 5.8%	
4. Speckled pod color-speckled seed coat	Saunders (1960)
5. Pale green plant color-seed color pattern (*W*)	
6. Spindly growth habit-purple plant color (*P*)	
7. Speckled seed coat (*S*)-brown pod (*Y*)	
8. Hilum ring pattern-purple pods	
9. Basic color gene (*R*)-mottled seed (*O*)	
10. Black seed coat (*B*)-cerise pod (*pC*)	
11. Gray seed color-late maturity	
12. Pod length-fibrousness	Roy and Richharia (1948)
13. Resistance to root knot nematode-poor seed set (cream and crowder types): weak linkage, but can be broken	Ivanoff (1962)
14. Resistance to tobacco ringspot virus (TRSV) is linked to cucumber mosaic virus (CMV) susceptibility	

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