Improving Breeding Efficiency for Early Maturity in Peanut

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I. INTRODUCTION

A. General

Peanut, also referred to as groundnut (*Arachis hypogaea* L., Fabaceae), an annual legume, is an important source of edible oil and vegetable protein. Its seeds contain about 48 to 50% oil and about 26 to 28% protein. They also are a rich source of minerals, vitamins, and dietary fiber. Peanut seeds can be eaten raw, roasted, or boiled, or made into a paste, popularly known as peanut butter and chutneys, or can be used in the preparation of different confections. The haulms are used as fodder, and the cake, after extraction of oil, is used in the livestock feed industry. Peanut shells are used as fuel, as filler in the feed industry, and in cardboard making. Being a leguminous crop, peanut enriches the soil with nitrogen and is therefore valuable in cropping systems. It is simultaneously a food crop and a cash crop, providing smallholder families with dietary protein, high-grade fat, and cash income from sale on local markets.

Peanut is cultivated in over a 100 countries in tropical, subtropical, and warm temperate regions of the world. The approximate limits of the present commercial production are between latitudes 40° N and 40° S. It is grown on 26.4 million ha with a total annual production of 36.1 million t and an average productivity of 1.4 t ha^{-1} (FAOSTAT 2004). Asia, with about 25 countries and 54.2 % of the area, produces 67.2% of the world's production. It is followed by Africa (about 46 countries) with 41.5% area and 24.7% production. North America in 2.3% of the area and South America in 1.4% of the area produce 5.4% and 2.0% of the world's production, respectively. The production of peanut in Europe is negligible. Important peanut-producing countries are China, India, and Indonesia in Asia; Nigeria, Senegal, and Sudan in Africa; the United States in North America; and Argentina and Brazil in South America.

B. Cropping Practices and Crop Duration

Peanut is grown in high-input commercial, semicommercial, and subsistence farming systems. In the high-input system, cultivation is completely mechanized; in the subsistence system, it is mainly manual with minimum on-farm inputs. In the commercial system, the peanut is grown as the sole crop, whereas in semicommercial and subsistence farming, it may be grown as a sole crop, intercropped, or as a mixed crop. The semiarid tropical region, characterized by unpredictable

rainfall, contributes more than 90% of the world's peanut production. Generally, only one major crop of peanut is grown each year in the rainy season. However, in many Asian countries with climatic conditions (mainly temperature) favorable to peanut, two or three crops are harvested per a year, either with irrigation or on residual soil moisture.

In a monocropping situation, duration of the crop depends on the number of days of favorable temperatures for crop growth and plant extractable soil moisture availability either through irrigation or rains. In some agroecologies in the United States and China, the crop duration may reach 160 to 180 days. In many agroecological situations—where there are short growing seasons, end-of-season droughts, early frosts, cultivation in residual soil moisture, or multiple cropping—however, short-duration cultivars are needed to escape adverse climatic conditions and late-season diseases and insect pests. In specific intercropping systems, early-maturing cultivars offer less competition to the later-maturing crops. Multiple cropping is more frequent in the rice-based cropping systems in East and Southeast Asia and intercropping in South Asia.

Short duration of a genotype is a relative term. In terms of calendar days, it may be different for different situations. For example, a 140-day cultivar in the United States or a 120-day cultivar in China may be classified as a short-duration cultivar in these countries. However, in South and Southeast Asia, a short-duration cultivar should not exceed 100 days to maturity. Similarly, along the northern fringes of the Sudan-Sahelian region in West Africa, which may have a very short rainy season, the duration of the cultivar should not exceed 90 days (Virmani and Singh 1986).

II. BOTANY

Cultivated peanut is a member of Fabaceae, tribe Aeschynomeneae, subtribe stylosanthineae. The genus *Arachis* is divided into nine sections. Section *Arachis* contains *Arachis hypogaea*, which is divided into two subspecies, *fastigiata* Waldron and *hypogaea* Krap et Rig. Subspecies *hypogaea* contains two botanical varieties, *hypogaea* (Gregory et al.) and *hirsuta* Kohler, while subspecies *fastigiata* consists of four botanical varieties: *fastigiata, peruviana* Krapov. & W.C. Gregory, *aequatoriana* Krapov. & W.C. Gregory, and *vulgaris* C. Harz (Krapovikas and Gregory 1994).

In subspecies *hypogaea*, the central axis is without flowers and reproductive and vegetative nodes alternate regularly (alternate ramification)

on lateral branches. Genotypes belonging to subspecies *hypogaea* are generally late in maturity and have postharvest seed dormancy. In subspecies *fastigiata*, the central axis is with flowers, and reproductive and vegetative nodes show no order (sequential ramification) on lateral branches. Genotypes belonging to subspecies *fastigiata* generally mature early and lack fresh seed or postharvest seed dormancy. The other differences between the two subspecies are summarized in Holbrook and Stalker (2003).

A. Reproductive Biology

Inflorescences are borne in the axil of leaves of a peanut plant. They are either simple or compound monopodia, and each has up to five flowers. Generally, only one flower per inflorescence is open at any given time. Onset of flowering is independent of day length. However, short-day conditions or increasing mean temperatures up to 30°C enhance number of flowers (Bagnall and King 1991a). Flowering in peanut can appear as early as 17 to 18 days after emergence and can last 85 to 100 days depending on the cultivar, climatic conditions and the cultural practices followed. Both bimodal and continuous flowering patterns are reported in the literature. Flowering with abrupt alternation of high and low frequencies during the major portion of the flower production period is observed in all botanical types. This cyclic behavior of flowering is not closely related with climatic conditions (Smith 1954). The number of flowers produced per plant may range from 40 to 250 in subspecies *hypogaea* (Seshadri 1962) and from 95 to 148 in subspecies *fastigiata* (Krishna Sastry et al. 1985). However, only 8 to 20% flowers develop into mature pods (Cahaner and Ashri 1974; Krishna Sastry et al. 1985). A large number of early-formed flowers develop into pods (Gregory et al. 1951; Cahaner and Ashri 1974). Pods initiated earlier have faster growth rate and greater number of seeds than pods initiated later in the season (Williams 1979). Flowers that appear 70 days after sowing do not form mature pods. Suppression of the late-formed flowers leads to better development of early-set pods (Har-Tzook 1970; Ono and Ozaki 1971).

Most flowers are self-pollinated before or as they open, and cross-pollination is rare. The pollen tube takes 10 to 18 hours (hr) after pollination to reach the ovary and effect fertilization (Smith 1956). After fertilization, the flowers wither rapidly and the intercalary meristematic cells that comprise the basal tissue of the ovary produce a geotropic stalklike structure called a peg (or a gynophore). Initially associated with embryo development, the peg grows at first slowly and then rapidly. The tip of the peg usually contains two (sometimes three to five, depending on the

botanical variety) fertilized ovules. At the time of peg growth, the embryo is at the 8- to 12-cell stage and becomes quiescent (Pattee and Mohapatra 1987). Peg growth continues until penetration into the soil (after 8–14 days of fertilization), and when it receives mechanical stimulus the peg transforms into a pod (Zamski and Ziv 1976). Ovules and embryos then start growing, mature to form seeds within the pod, which later become dry and brittle to form the shell. In Spanish genotypes (var. *vulgaris*), pods are ready for harvesting after about 7 weeks; Virginia genotypes (large-seeded types of var. *hypogaea*) mature after about 11 weeks of underground development (Schenk 1961).

B. Physiology

Ong (1986) concluded that temperature is the dominant environmental factor that influences peanut development. The life cycle of a peanut plant has been divided into different vegetative (VE, V0, and V1 to VN) and reproductive stages (R1 to R9) based on discrete, objective, and visually identifiable events (Boote 1982). VE refers to emergence, V0 to flat and open cotyledons at or below the soil surface, and V1 to VN to development of corresponding nodes on the main axis. R1 refers to the beginning of the bloom, R2 to beginning peg, R3 to beginning pod, R4 to full pod, R5 to beginning seed, R6 to full seed, R7 to beginning maturity, R8 to harvest maturity, and R9 to overmature pod. An R stage remains unchanged until the date when 50% of the plants in the sample demonstrate the desired trait of the next R stage. The V and R stages in peanut overlap. Rate of node development is dependent on air and soil temperature, availability of soil water, and plant maturity. Stress, whether water, heat, or nutrient, can decrease the rate of plant development (Craufurd et al. 1993) including the rate of pod formation in peanut (Williams and Boote 1995). In addition, reproductive development is influenced by photoperiod. These effects have important consequences for the duration of developmental and growth stages.

1. Reproductive Yield. Duncan et al. (1978) described the reproductive yield (Yr) in this way:

$$Yr = C \times Dr \times p$$

where
        C is the mean crop growth rate
        Dr is the duration of reproductive growth
        p is the mean fraction of crop growth rate partitioned toward the reproductive organs (assessed by harvest index, HI)

Variations in mean growth rate (C) are dominated by environment (E) and genotype (G) × E interactions because the photosynthetic variation in a species is small, while the scope for radiation interception is very large. Once light interception by a peanut crop is complete, the major sources of yield variation between cultivars lie in their partitioning and duration (Duncan et al. 1978). Various environmental challenges also influence C, p, and Dr. For example, drought will influence C and p, calcium deficiency will influence p, and foliar diseases will mainly influence C (Williams 1992). Temperature and photoperiod also have profound influences on vegetative and reproductive growth and development in peanut. Photoperiod has a marginal influence on time to flower initiation. Its main effects are observed on reproductive efficiency. Long days stimulate vegetative growth and reduce pod yield by affecting p (Wynne et al. 1973; Wynne and Emery 1974; Emery et al. 1981; Nigam et al. 1994). Flowers, pegs, pod number, and pod and seed weight are enhanced under short-day conditions by greater p and/or increased duration of effective pod-filling phase (Witzenberger et al. 1988; Bagnall and King 1991b; Nigam et al. 1994). However, the effect of photoperiod occurs only above a certain critical temperature lying between 22/18°C and 26/22°C regimes (Nigam et al. 1994). High soil temperature reduces dry matter accumulation, flower production, the proportion of pegs forming pods, and individual seed mass (Golombek and Johansen 1997; Prasad et al. 2000). Genotypic variation exists for photoperiod × temperature interaction (Nigam et al. 1998). Temperature and irradiance play a major role in determining crop duration and p. Photo-thermal quotient (PTQ MJ m^{-2} degree-day^{-1}, derived from total short-wave solar radiation incidence during the growing season and CTT) could largely explain the variation in HI across locations, provided the data were not confounded by the effects of photoperiod (Bell and Wright 1998).

2. Thermal Time and Phenological Development. In both photoperiod-insensitive and sensitive genotypes of annual crops, maintained in a given constant photoperiod, the rate of progress toward flowering is a positive linear function of temperature from a base temperature, T_b, at which the rate is zero, up to an optimum temperature, T_0, at which it is maximal. Between these limits, the relation may be described as

$$1/f = a + bT$$

where

f is the time from sowing to first open flower

T is the mean temperature

The values of a and b are specific to the genotype but, in photoperiod-sensitive genotypes held in any constant photoperiod, the value of a is, in addition, a function of photoperiod.

Above T_0, the values of constants will differ from those for the sub-optimal range and the relation (and so the sign of the parameter b) will be negative (Summerfield et al. 1991). There is variation in Tb for different phenological stages and among genotypes. In their study, Bell et al. (1991) did not find differences in Tb values for seedling emergence, but for days to first flower, the Tb values for Spanish genotypes were higher than those for the Virginia and Valencia genotypes. However, thermal times for flowering were lower for the Spanish than for the Virginia and Valencia types. Variation in Tb values for seedling emergence has been observed among genotypes (ICRISAT, unpublished data). For peanut, Tb ranges between 9°C and 13°C and T_0 between 27°C and 32°C (Williams and Boote 1995).

The cumulative thermal time (CTT) is measured in day-degrees (°Cd) above the base temperature and is calculated on successive days by subtracting the base temperature from the mean daily temperature and adding each value to the subtotal accumulated since the seed was sown. In photoperiod-insensitive genotypes, the CTT for maturity does not differ across environments barring the influence of environmental factors other than photoperiod. For photoperiod-sensitive genotypes, the CTT will vary with photoperiod over the photoperiod-sensitive range. All associations, which are described earlier, function within the range of Tb and T_0. At higher temperatures, the start of pod and seed filling can be delayed substantially in some genotypes (Craufurd et al. 2002), which will affect the crop duration.

Genotypic differences for heat tolerance have been reported in peanut (Craufurd et al. 2003). Mills (1964), Emery et al. (1969), Williams et al. (1975), Ono (1979), Leong and Ong (1983), Mohamed (1984), Ong (1986), and Ketring and Wheless (1989) determined the CTT requirement of different phenological phases in peanut. Solar radiation, particularly during the first 75 days of growth, also affects the peanut maturity (Holaday et al. 1979).

C. Methods of Maturity Estimation

Determination of optimum maturity in peanut is critical as it affects marketable yield, quality, and flavor of the produce. The indeterminate and subterranean fruiting in peanut confounds the estimation of optimum maturity. Indeterminate fruiting characteristic of peanut results in seed of varying maturities on the plant as harvesttime approaches.

Sanders et al. (1982) reviewed several methods to determine crop maturity in peanut. These methods are variations of four approaches: indirect methods (days after planting, heat units), relative color evaluations (internal pericarp color, oil color, methanol extract, pod maturity profile), weight and weight relationships (kernel density, seed to hull ratio maturity index), and quantification of a specific component (arginine maturity index and protein markers). Some methods are more complex than others to evaluate, and each method has deficiencies. General use of some of the methods, such as days after planting and oil color, is precluded as they are highly influenced by environmental conditions. Pod maturity profile and seed to hull ratio maturity index are some of the better methods for estimation of maturity. However, the most commonly used method by small farmholders in developing countries is internal pericarp color because of its simplicity. When 75 to 80% pods in cultivars belonging to subspecies *fastigaita* and 70 to 75% pods in cultivars belonging to subspecies *hypogaea* show internal pericarp darkening, the crop is ready for harvest.

III. GENETICS AND BREEDING

A. Inheritance, Heritability, and Combining Ability of Early Maturity and Its Components

The genetics of maturity in peanut is not well defined, largely because of the difficulty of defining maturity for an indeterminate, nonsenescent plant (Kvien and Ozias-Akins 1991). Although several authors have reported genetics of plant maturity, pod/seed maturity, and components of maturity, their inferences are inconclusive.

Badami (1923 and 1928) reported earliness recessive to late maturity, whereas Patel et al. (1936) and Hassan (1964) found late maturity incompletely dominant over earliness. In both cases, a single gene was involved. On the other hand, Samooro (1975) reported four or fewer genes for seed maturity. When Holbrook et al. (1989) used the hull-scrape method to estimate pod maturity, they reported four or five genes with complete dominance of lateness over earliness and absence of reciprocal differences. Tai and Young (1977) studied inheritance of free arginine level in peanut seed and reported partial dominance of low arginine level (an indicator of seed maturity) with two major genes, several minor genes, and their interactions. Upadhyaya and Nigam (1994) reported a single gene with an additive effect for the control of days to first flower, three genes with two types of epistatis (dominant-recessive, 13 late: 3 early

and duplicate-dominant, 1 late: 15 early) for days to accumulation of the first 25 flowers, and the absence of reciprocal differences for these traits. They also reported that the genes for early accumulation of flowers in 'Chico' and 'Gangapuri', the two early-maturing cultivars, were located at different loci. For days from seedling emergence to first flower, Vindhiyavarman and Raveendran (1996) reported two recessive genes acting in an additive manner.

The inheritance of maturity and its components has also been studied using diallel, line × tester, and generation mean analyses. Parents with good general combining ability for early maturity have been reported (Basu et al. 1986). Parker et al. (1970) found significantly higher variance for general combining ability (gca) than specific combining ability (sca) for time of emergence (measured in hours), time first leaf opening cotyledonary branch (in hr), time first leaf opening main stem (in hr), days to first flower, and number of flowers per plant (at 32 days) under a controlled environment. Similarly, Wynne et al. (1970) and Nigam et al. (1988) reported a higher magnitude of gca than sca variance for days to first flower under field conditions. Gibori et al. (1978) reported significant additive genetic variance with bidirectional dominance for days to first flower. Mohammed et al. (1978) observed highly significant additive genetic variance for pod and seed maturity indices. However, Ali et al. (1999) reported both additive and dominance genetic effects for maturity index (ratio of number of mature to total number of pods). They did not detect epistatis. Khalfaoui (1990b) studied heredity of extreme precocity (ability of a genotype to form highest proportion of ripe pods rapidly) in a cross between two Spanish cultivars, '73–30' and 'Chico', using days from sowing to emergence (S-E) and from emergence to first flowering (E-F), number of flowers produced during the first four days of flowering (4F), and percentage of ripe pods 80 days after sowing (% RP, using internal pericarp color as pod maturity indicator) as parameters. He reported extremely limited variation for S-E between the two parents, making it difficult to study genetic effects. For E-F, highly significant additive and significant dominance, additive × additive and dominance × dominance effects, with duplicate digenic interaction were observed. For 4F, allelic interactions involving more than two genes or linkage effects between the genes were reported. For %RP, highly significant additive and significant dominance effects were observed. The additive effect for %RP was markedly greater than the dominance effect and two to three genetic factors were responsible for the difference between the two parents. Transgressive segregation was observed in favor of flowering precocity, intense flowering, and pod ripeness precocity. The genetic correlation between S-E and E-F

(0.50** ± 0.12) and S-E and 4F (0.41** ± 0.13) was moderate, but there was no genetic correlation between S-E and %RP and the correlation between 4F and % RP (0.29* ± 0.14) was slight. Thus, S-E, E-F, and 4F, being genetically independent or only loosely linked with %RP, cannot be used effectively to select for precocity of % RP. However, in eight cultivars previously studied (Khalfaoui 1990b), a close linkage between % ripe pods at 90 days and the flowering rapidity and intensity indicated that flowering characters favored genotype precocity.

Several workers reported estimates of broad sense and narrow sense heritability of maturity and its components in peanut (Table 6.1).

The studies just described indicate that maturity is not simply inherited. However, components affecting early maturity are highly heritable, suggesting that selection for earliness can be successful in early segregating populations.

Table 6.1. Heritability estimates of maturity and its components in peanut.

Trait	Broad-Sense Heritability Estimates	Reference
Days from sowing to seedling emergence	48–83% (51%)*	Khalfaoui 1990b
Days from seedling emergence to first flowering	49–81% (23–39%) 11–55% 96.9%	Khalfaoui 1990b N'Doye and Smith 1993 Mazumdar et al. 1969
Days to 50% flowering	96.3% 66.5–72.5%	Islam and Rasul 1998 Singh and Singh 1999
Days from emergence to accumulation of 10 flowers	22–65%	N'Doye and Smith 1993
Days from emergence to accumulation of 25 flowers	17–61%	N'Doye and Smith 1993
Number of flowers produced during the first four days of flowering	16–44% (9–38%)	Khalfaoui 1990b
Days to maturity	98.6% 91.7% 80.5%–96.7%	Mazumdar et al. 1969 Islam and Rasul 1998 Singh and Singh 1999
Fruit maturity based on oil pigmentation	69–95%	Gupton and Emery 1970
Low arginine level in seed (maturity)	69–93%	Tai and Young 1977
Maturity based on hull-scrape method	71%	Holbrook et al. 1989
Percentage of ripe pods 80 days after sowing	13–41% (24%)	Khalfaoui 1990b
Maturity index	Fairly high	Ali and Wynne 1994

*Values in parentheses are estimates of narrow-sense heritability.

B. General Breeding Procedures for Early Maturity

In most breeding programs, a predetermined crop duration (in calendar days) is defined depending on the local/regional/cropping system requirements. Generally, days to flowering, profuse early flowering, and days to maturity are taken into account while selecting parents as sources of early maturity. In segregating populations, a cutoff date based on predetermined crop duration is set and the populations are uprooted for visual observation of pod maturity based on internal pericarp color. Plants with a higher percentage of mature pods and high pod yield are selected for further laboratory evaluations for seed appearance, uniformity, and maturity. The selected material is advanced to the next generation. Advanced breeding lines are evaluated for two to three years in on-station replicated trials with staggered harvesting starting from a predetermined date. In addition to pod yield and pod and seed maturity, extent of further gains in pod yield, seed weight, and shelling turnover in the following staggered harvesting are taken into account while selecting advanced breeding lines. Those with high pod yield and pod and seed maturity and minimum gains in pod yield, seed weight, and shelling turnover over the preceding harvest are selected for further multilocation evaluation and selection.

As temperature is the predominant environmental factor that influences the growth and development of peanut plant (Bell et al. 1994), estimation of crop duration in calendar days at a given season/location seldom relates with that of at other seasons/locations. Significant genotype × environment/location × year (Fincher et al. 1980; Roy et al. 1980; Pattee et al. 1980; Court et al. 1984; Knauft et al. 1986), harvest date × sowing date and harvest × cultivation (Mozingo et al. 1991) interactions on optimum harvest date are reported.

CTT has been used in many crops to overcome the problems associated with the use of calendar days to describe the duration or optimum harvest time of a cultivar. However, doubts have been expressed on the ability of simple cumulative thermal time models to accurately predict phenological development in peanut (Mills 1964; Ketring and Wheless 1989; Hammer et al. 1992). The delays in phenological development after the first flowering could occur because of flower or embryo abortion (Bell et al. 1994), water deficit, or extreme heat (Ketring and Wheless 1989). Solar radiation, particularly during the first 75 days of growth, also affects the peanut maturity (Holaday et al. 1979). Since 1991, CTT (°Cd) is now used at ICRISAT Center (Patancheru, 18°N, 78°E) to determine the date of harvesting when breeding for early-maturing cultivars (Rao et al. 1991; Upadhyaya et al. 1992). Based on 23 years (1974–1996)

meteorological observations, assuming 15 June as the sowing date, a peanut crop accumulates (on average) about 1239 °Cd in 75 days, 1474 °Cd in 90 days, 1717 °Cd in 105 days, and 1954 °Cd in 120 days in the rainy season (June–October). In the postrainy season (November–April), the number of calendar days required to accumulate these CTTs is about 30 days more than during the rainy season due to lower temperatures. For early-maturing cultivars, 1470°Cd representing 90 days in the rainy season was selected, as it is the preferred duration in South and Southeast Asia. A computer program is used to calculate accumulated °Cds each day from the date of sowing using 10°C as base temperature (Tb) to estimate the date of harvesting. Early-maturing cultivars developed at ICRISAT have been released for cultivation in many countries (ICGV 86015 in Nepal, Pakistan, Sri Lanka, and Vietnam; ICGV 86143 in India, Vietnam, and Zambia; ICGV 86061 in Congo and Philippines; ICGV 86105 and ICGV 88023 in Guinea Conakry; ICGV 86065 in Mali; ICGV 86072 in Bangladesh; ICGV 86082 in Burkina Faso; ICGV 92195 in India; and ICGV 93382 in Myanmar). Use of CTT in breeding for early-maturing cultivars is able to account for about 70 to 80% variation in crop duration across locations/seasons (ICRISAT unpublished data). In addition to temperature, other climatic factors, particularly solar radiation, need to be integrated in the model to improve prediction of maturity and stability of crop duration across years and locations.

C. Breeding Strategies for Increased Efficiency

In breeding for early maturity, it is helpful to partition crop duration into different segments/stages and examine the possibility of shortening their duration individually and collectively with an overall aim to reduce crop duration. These segments/stages include days to germination and emergence, days to first flower after emergence, days from opening of first flower to opening of a given number of flowers per plant, and days from opening a flower to maturation of seeds that develops from that flower. It is also important to take into account the time from seed maturation to major deterioration of the strength of the peg (Bailey and Bear 1973) to avoid seed losses during harvest.

Cultivar differences exist in days to emergence and tolerance to cold temperatures during germination. Cultivars with large seeds generally take longer to emerge, and those with tolerance to cold temperature are able to emerge early under low temperature conditions. Early emergence hastens early flowering, which in turn hastens maturity. Due to the indeterminate growth habit, peanut produces more flowers on a plant than it can support to produce pods and seeds. In cultivars of

differing maturity periods from very early to late, Bear and Bailey (1973) observed a high proportion of the first 25 flowers developing into mature pods. Days to flower (Yadava et al. 1981; Yadava et al. 1984; Khalfaoui 1990b; Islam and Rasul 1998) and days to production of first 50 flowers from planting (Khalfaoui 1990b) are related with maturity. A wide variation was observed among Spanish (var. *vulgaris*) genotypes in number of days required to produce 40 flowers; those that accumulated these flowers early produced higher plant yield (Krishna Sastry et al. 1985). In addition to temperature, the rate of peg growth and distance of its axil from the soil surface may have influence on this period. In case of erect growth habit (subspecies *fastigiata*), short plant stature and smaller internodal length may help to reduce this period by a few days. The latter will also help in case of runner and semirunner growth habit (subspecies *hypogaea*) types and will result in more uniform maturity.

When the duration requirement is 120 to 125 days or above, it is not difficult to breed new cultivars with desired crop duration and high yield potential. However, it may entail some penalty in seed size in large-seeded types. Breeding for short duration becomes a challenging task when the duration requirement is less than 100 days with high yield potential. It generally limits the choice of botanical types to subspecies *fastigiata* var. *vulgaris* in a breeding program. Due to the alternate flowering habit in subspecies *hypogaea*, it is difficult to reduce crop duration below 115 days in this botanical group. Based on the botanical characteristics and physiological behavior of the crop, the following characteristics could be visualized for attaining short duration of the crop: short plant stature (plant height in case of subspecies *fastigiata* and plant spread in case of subspecies *hypogaea*) with smaller internodal length, faster germination and emergence, fewer days to first flowering, and accumulation of a maximum number of early flowers, more flowers per node, absence of late flowers, fewer days after fertilization for a peg to enter soil, faster pod and seed growth, high seed partitioning, and high shelling turnover. To capitalize on the full potential of the genotypes with the aforementioned traits, it would be essential to modify crop husbandry to accommodate larger numbers of plants per unit area to provide quick ground cover and to provide plants with required nutrients and other inputs. The following considerations in breeding strategy will help to achieve the objective of early maturity.

1. Selection for Low Tb and CTT for Various Phenological Stages. Although some genetic variation in Tb and CTT for different phenological stages among genotypes has been reported (Bell et al. 1991; Williams and Boote 1995), more studies are needed to discern these traits and identify

genotypes with low Tb and CTT. Within the available genetic variation, selecting the genotypes with low Tb and CTT for different phenological stages will help reduce crop duration considerably. It may not be possible to select for these traits in segregating populations. But these criteria can be applied in selecting parents for hybridization and in evaluation of advanced breeding lines under controlled environmental conditions.

2. Selection for Tolerance to High Temperature. In situations/places where temperatures can go high during the cropping of peanut, tolerance to high temperatures will be essential to ensure high yields and required crop duration. Drought often results in high air and soil temperatures. High temperatures delay the start of seed filling; reduces total plant biomass, root/total biomass ratio, and seed yield (Wheeler et al. 1997; Craufurd et al. 2002); and delays crop maturity (Bell and Wright 1998). While Wheeler et al. (1997) did not observe adverse effects of high temperature on seed harvest index, Craufurd et al. (2002) found 0 to 65% reduction in this trait under high temperature. Prasad et al. (2000) observed significant reductions in total dry matter production, partitioning of dry matter to pods, and pod yield under high air and/or soil temperature. High air temperature did not affect flower production but significantly reduced the proportion of flowers setting pods, and pod numbers. However, high soil temperature significantly reduced flower production, pod set, and seed weight. The effects of high air and soil temperatures were mostly additive and without interaction. Various researchers have reported genotypic differences in tolerance to high temperature (Wheeler et al. 1997; Prasad et al. 2000; Craufurd et al. 2002). The genotypic differences in the response of peanut yield to episodes of high temperature stress are due to differences in the timing of seed filling (Wheeler et al. 1997; Craufurd et al. 2002).

3. Selection for Photoperiod-Insensitive Genotypes. For location-specific genotypes, photoperiod insensitivity may not matter much, but for wide adaptation, it would be essential to ensure stability in yield potential and crop duration. Nigam et al. (1997) reported additive gene action in some crosses and partial dominance to dominance in other crosses for response to photoperiod in peanut. They further suggested that the selection for this trait be delayed to later generations because of practical difficulties in evaluating it in segregating populations. Genotypic variation exists for photoperiod × temperature interaction (Nigam et al. 1998).

4. Selection for High Crop Growth Rate and Partitioning. As yield is a function of C, Dr, and p (Duncan et al. 1978), reducing the total crop

duration while maintaining Dr will have little effect on pod yield of a genotype provided the required plant density is maintained in the field. However, the reduction in crop duration will have to come through reduction in duration of vegetative phase (i.e., early onset of flowering). For substantial reduction in crop duration, some sacrifice in Dr may also be required. The adverse effect of reduction in Dr can be neutralized if it is accompanied with increased C and p. Genotypic variation in HI and total dry matter is reported in peanut (Velu and Gopalkrishna 1985; Sharma and Varshney 1995; Dwivedi et al. 1998). Sharma and Varshney (1995) observed high broad sense heritability for HI and its component traits. Ntare and Williams (1998) reported low heritabilities for C, p, Dr, and yield, but higher heritability for p than yield, C was largely responsible for low heritability of yield, and indirect selection for yield via p was 22% more effective over direct selection. Their results also indicated that selection for yield and physiological components in segregating populations may be difficult. While biomass is controlled by both general (gca) and specific combining ability (sca) effects, HI is predominantly controlled by gca effects (Dwivedi et al. 1998). Both combining ability effects interact with environments. The sca effects for biomass and HI are insensitive to photoperiod, while the gca effects for HI are sensitive. Lal et al. (2006) observed highly significant gca variance for HI. Nigam et al. (2001) also reported significant additive, dominance, and additive × additive genetic effects for HI. However, additive genetic effects were more important than the dominance effects. Tolerance to high temperatures will also help in maintaining C and p in high-temperature environments. While selecting parents for hybridization, it is desirable to select those that have high C and p across photoperiod regimes besides other traits associated with early maturity. Selection for biomass and HI can be practiced in early-segregating generations.

5. Selection for High Water-Use Efficiency. CTT works satisfactorily when other factors affecting growth are not limiting. Under rainfed conditions where long and frequent dry spells occur, CTT and other parameters may lose their significance and the soil moisture availability becomes the main determinant of crop duration. Although mild water stress promotes flower, peg, and pod production, the crop growth slows down under severe moisture stress and increases again as the soil moisture becomes available. Field experiences have shown that the crop duration may get prolonged depending on the severity, frequency, and duration of dry spells in rainfed cultivation. Under moisture limiting conditions, high water-use efficiency, ability to recover quickly from drought, and high partitioning will be paramount considerations along

with CTT that will influence the crop duration. The two traits that are associated with high water-use efficiency, low specific leaf area (SLA) and high soil plant analytical development (SPAD) chlorophyll meter readings (SCMR), show high (66.0%) and moderate (40.7%) heritability, respectively (Vasanthi et al. 2004). SCMR is also strongly correlated with pod yield and other economic traits, such as 100-seed weight (Upadhyaya 2005). SLA is reported under the control of additive, dominance, and additive × additive genetic effects. However, additive genetic effects are more important (Nigam et al. 2001). Lal et al. (2006) observed highly significant variance of general combining ability (gca) for SLA and SCMR. The specific combining ability (sca) variance was also highly significant for SCMR, but its magnitude was very low. They also found significant reciprocal effect for SLA. Thus, selection for these traits can be effective in the early generations. For SLA, the choice of female parent in the improvement of the trait would be crucial.

6. Diversification of Sources of Earliness in Maturity. 'Chico' has been used extensively as a source of early maturity in peanut breeding programs around the world. It belongs to subspecies *fastigiata* var. *vulgaris* and was released in 1975 in the United States (Bailey and Hammons 1975). 'Chico' is a selection from PI 268661 introduced into the United States in 1960 from Rhodesia (present Zimbabwe), where it was originally introduced from Krasnodar, Russia. It takes 80 to 85 days to mature in the rainy season at ICRISAT Center. The plants are small with very small two-seeded pods and low yield. Other sources of early maturity selected from introduced materials include 'Shepharadi No. 9', 'Congo', 'Avir' (Gibori et al. 1978) and 'JL 24' (Patil et al. 1980). These genotypes are reported to mature in 90 to 100 days. Mutation has also been induced to create sources of early maturity/early maturing cultivars. Examples for varieties include T × AG 1, a gamma ray mutant of 'Spantex', in the United States (Simpson and Smith 1986) and 'Luhua 6', a gamma ray mutant of 'Baisha 1016', in China (Qui et al. 1990). Mutants have also been used in hybridization to develop sources of earliness such as T×AG 2 (R 25 (a mutant) × TPL 206-6-1) in the USA (Simpson and Smith 1986) and TG 1E (Tall Mutant x TG 9) and TG 2E (Dwarf Mutant × TG 3) in India (AICORPO 1983 and 1984). Simpson (1990) reported an extremely early-maturing wild species *Arachis praecox* Krapov., W.C. Gregory and Valls (Collection No. Valls Simpson Gripp-6416, A genome), which matures in 45 days. This has been crossed with B genome species, *A. batizocoi* Karp. & W.C. Gregory (GKP 9484), the chromosome number doubled, and then crossed to *A. hypogaea* at the Texas Agricultural Experiment Station, Texas, to introgress genes for early maturity into cultivated background. However, the A

genome species took much longer to mature when grown at ICRISAT Center (ICRISAT, unpublished data).

The sources of early maturity used in breeding program at ICRISAT include 'Chico', 91176, and 91776 (sister breeding lines from TG 3 × 8068 cross from Tindivanam, Tamil Nadu, India), TG 1E, TG 2E, and TG 3E ('TG 17' × 'Chico') (all breeding lines from Bhabha Atomic Research Centre, Trombay, India), 'Gangapuri' (a landrace from Khargone, Madhya Pradesh, India), and 'JL 24' (a selection from EC 94943, released as Phule Pragati in India). These take 90 to 100 days to mature at ICRISAT Center. 'JL 24', a released cultivar in India, is popular among the farmers because of its early maturity, medium seed size, and high shelling turnover. Because of these desirable traits, it was also released in Myanmar, Congo, Philippines, Zambia, Mali, and Malawi. Among the several short-duration breeding lines developed at ICRISAT, ICGV # 92196, 92206, 92234, 92243, and 92267 have been registered as improved germplasm (Upadhyaya et al. 1998, 2002). Their maturity period at ICRISAT Center is similar to that of 'Chico', but they have higher pod yield and larger seed size than 'Chico'.

Some of the early-maturing cultivars (< 100 days) released/registered include 'Pronto' (Kirby and Banks 1980) and 'Spanco' (Kirby et al. 1989) from 'Chico' × 'Comet' cross in the United States; 'Dh 40' (Dh 3–20 × TG 2E), 'TNAU 97' [G 961 × ('CO 1' × PPG 3)] (Sridharan et al. 1991), 'ALG (E) 57' ('CO 2' × ICGV 86687) (Vindhiyavarman and Raveendran 1991), and 'GG 3' ('GAUG 1' × 'JL 24'), 'GG 5' (27-5-1 × 'JL 24'), 'GG 12' ('Shulamit' × 'GAUG 10'), 'TG 26' (BARCG 1 × TG 23), 'R 9251' ('JL 24' × TG 23), 'JL 220' (JL 80 × VG 77), 'M 522' (PG 1 × F 334-AB-14), 'RS 138' (a selection from introduction from Brazil), 'VRI 3' (J 11 × Robut 33-1) (extra early), and 'Co 4' ('TMV 10' × ICGS 82) (Basu et al. 2002) in India; and '55-437' (a selection from a population of South American origin, drought resistant), '73-30' (61-24 × 59-127), '47-10' (a selection from a Madagascar population), 'Te'3' (a selection from a local population from southern Burkina Faso), 'TS 32-1' ('Spantex' × 'Te 3', moderately drought resistant), 'KH 149 A' (GH 119-7.I.II-III × 91 Saria, rosette resistant), 'KH 241 D' (GH 1185.2 II × 91 Saria), and 'A-124 B' (a selection from local 'Loudima Red' population) in West Africa (Bockelee-Morvan 1983). Except for 'A-124 B', which is a Valencia type, all other short-duration varieties in West Africa are of Spanish types. Recently the Groundnut Germplasm Project for West and Central Africa (Mayeux et al. 2003) recommended the following cultivars, which mature in 90 days or less: 'ICG (FDRS) 4' ('Argentine' × PI 259747, rust resistant), 'GC 8-35' ('55-437' × 'Chico', drought resistant), '55-21' ('55-437' × 'Chico', drought resistant), '55-33' ('55-437' × 'Chico', drought

resistant), 'SRV 1-3' (a selection from recurrent selection program, drought resistant), 'SR 1-96' (a selection from recurrent selection program, cultivar known as 11908-13, drought resistant), 'Fleur 11' (an introduction from China, drought resistant), and '78-936' (an introduction from China, drought resistant). 'GC 8-35', '55-21', and '55-33' are reported to mature in 80 days and '78-936' in 75 to 90 days in West and Central Africa.

The genetic base for sources of early maturity remains narrow. Further, sources have not been studied in detail for various traits associated with early maturity. Khalfaoui (1990b) suggested the use of days from planting to first flower, from planting to production of more than three flowers per day, and days from planting to accumulation of 50 flowers per plant as potential selection criteria for early maturity among the germplasm lines. Among more than 15,000 germplasm accessions maintained in the RS Paroda Gene Bank at ICRISAT, 21 landraces (16 Spanish and five Valencia types) have been identified as sources of early maturity (ICRISAT 2003). Many of these with better agronomic traits (ICG # 3540, 3631, 4729, 9427, and 9930) are comparable to 'Chico' in maturity. Some of these outyield JL 24 in harvests at 1240 °Cd (ICG # 11914, 13585, 14728, and 14814) and at 1470 °Cd (ICG # 3631, 4558, 4890, 5560, 13585, and 14788). Limited information is available on genetic diversity for early maturity and its components. Phenology and physiology of the stable and agronomical superior sources of early maturity need to be studied in detail to identify genotypes differing in various components of earliness in maturity. Similarly, their genetic constitution and allelism should be determined. Those differing in genetic constitution for early maturity and its components should be crossed with each other to pyramid diverse genes in a single background.

A review of the pedigrees of the released cultivars indicates that the genes for early maturity may also be available outside the known sources of early maturity. As segregation for lateness was observed in 'Chico' × 'Gangapuri' (both sources of early maturity) and its reciprocal cross (Upadhyaya and Nigam 1994), there is a possibility of finding early-maturity segregants in crosses between two normal-maturing varieties. These genes for early maturity are likely to be different from those accessed from regular sources of early maturity.

7. Evaluation in Target Environments/Cropping Systems. In most breeding programs, varieties are evaluated for crop duration and yield under a sole crop situation. However, their evaluation in the target environment/cropping system would be desirable to identify the most suitable genotypes for maximum returns.

Under rainfed conditions, incorporation of fresh seed dormancy in short-duration cultivars will be required to inhibit sprouting of mature seeds if rains occur at the time of harvest. Both monogenic with dominance or partial dominance (Stokes and Hull 1930; Ramachandran et al. 1967; Lin and Lin 1971; Bhapkar et al. 1986; Upadhyaya and Nigam 1999) and polygenic (Hull 1937; John et al. 1948) control for fresh seed or postharvest seed dormancy are reported. Khalfaoui (1991) observed additive, dominance, and digenic epistatic effects involved in the control of fresh seed dormancy. Several sources of fresh seed/postharvest seed dormancy in a Spanish background are now available (Bockelee-Morvan 1983; Upadhyaya et al. 1997) and can be used in breeding programs.

8. Opportunities for Biotechnological Interventions. Compared to many other crops, the progress in genomics research in peanut has been slow. The search for polymorphic markers and those linked with different traits needs to be intensified to saturate the linkage maps and extend the use of marker-assisted selection in peanut. The identification of quantitative trait loci (QTLs) associated with difficult-to-measure physiological traits associated with early maturity and their consequent use in marker-assisted breeding will help to increase efficiency in breeding efforts. Comparative mapping studies of QTLs for such traits already identified in other legume crops should be useful.

D. Other Issues in Breeding for Early Maturity

Some other desirable traits may have a bearing on crop duration. These need to be given due consideration while breeding for short duration varieties.

1. Yield Potential. Compared to the medium- and long-duration cultivars, the yield potential of short-duration cultivars is lower (Khalfaoui 1990b). To improve yield potential, high growth rates and partitioning, early podding, modification of pod weight, and modification in planting pattern will be essential (Duncan 1975; Duncan et al. 1978). A modification in planting pattern to rapidly establish a full canopy to intercept incident photosynthetically active radiation (PAR) will be required for achieving good yield potential (Bell et al. 1994). A yield potential of 3.0 to 3.5 t ha^{-1} should be an achievable target in 90- to 100-day cultivars.

2. Seed Size. Breeding for large seed size while keeping the crop duration short is unlikely to succeed. Not only do large seeds take more time

to develop and mature, they also take more time to germinate and emerge when sown. Other contributing factors being equal, the small and medium-size seeds will require less time to develop and mature and will have no prolonging effect on crop duration.

3. Resistance to Foliar Fungal Diseases. Early leaf spot (*Cercospora arachidicola* Hori), late leaf spot (*Phaeoisariopsis personata* [Berk. & M.A.Curtis] van Arx), and peanut rust (*Puccinia arachidis* Spegazzini) occur wherever peanut is grown. Genetic resistance to these diseases has usually been associated with low yields and late maturity. Aiming at higher levels of resistance in early-maturing background will be difficult to achieve. A moderate level of resistance will have only limited influence on crop duration and would also stabilize productivity in a cropping system.

IV. CULTURAL MANIPULATIONS TO SHORTEN CROP DURATION

Cultural practices can hasten crop maturity by advancing phenological development through temperature in microenvironment. In North Vietnam, peanut seeds are soaked in lukewarm water for 24 h to sprout them. The sprouted seeds with protruding radicles are sown directly in fields with fine tilth. The sowing is followed by light manual irrigation on the ridges. This enables early emergence of the crop in spite of low temperatures prevailing during February in the country. Recently seed priming is receiving attention in India and Vietnam, where seeds are soaked for 8 h in water and then dried back to their original water content. A primed seed will germinate only if it takes up additional moisture from the soil after sowing. Apart from swelling slightly and weighing more, primed seed can be treated in the same way as non-primed seed. Peanut cultivation under polyethylene mulch, commonly practiced in Central China and North Vietnam, among other advantages, also helps to reduce the crop duration by raising the soil temperature, which leads to early emergence of the crop, early flowering, and early maturity of the pods. Elevated soil temperature helps to compensate for low air temperature and results in higher radiation use efficiency (Awal and Ikeda 2003). Sowing depth is another factor that influences the days to seedling emergence. Deeper sowing delays emergence and weakens the seedlings, which in turn influences crop yield and duration. The normal recommended sowing depth is 5 centimeters (cm). The seeds can be sown at a shallower depth to hasten seedling emergence,

provided the field is irrigated frequently until the seedlings are well established. In China, growth hormones such as Fosamine and 2,3,6-trichlorobenzoic acid (TCBA) are used to stop late flowers, thereby enhancing the filling of earlier-set pods and uniform maturity. For arresting excessive vegetative growth, Paclobutrazol (P 333) in China and Vietnam and Kylar in the United States are used.

V. SUMMARY

Following conventional approach based on calendar days to flower and maturity, location-specific early-maturing cultivars have been released. But it has been difficult to reduce the crop duration to less than 100 days without sacrificing yield potential. Further, these cultivars did not always maintain their early-maturity trait across locations/seasons. The approach was improved by making use of cumulative thermal time (CTT) instead of calendar days while selecting for early maturity in segregating populations and staggered harvesting based on CTTs in trials of advanced breeding lines. This modification helped in creating stability in the early-maturity trait of breeding lines across locations/seasons. To develop cultivars with less than 100 days duration, which are required in South and Southeast Asia, further improvements in the approach will be necessary. Based on the botanical characteristics and physiological behavior of the crop, these characteristics could be utilized for attaining short duration: short plant stature (plant height in case of subspecies *fastigiata* and plant spread in case of subspecies *hypogaea*) with smaller internodal length, faster germination and emergence, fewer days to first flowering, accumulation of maximum numbers of early flowers, more flowers per node, absence of late flowers, fewer days after fertilization for a peg to enter soil, faster pod and seed growth, high seed partitioning, and high shelling turnover.

Selection for low base temperature (Tb) and CTT for different phenological stages (germination and emergence, first flower after emergence, opening of first flower to opening of a given number of flowers per plant, and opening a flower to maturation of seeds that develops from that flower) can individually and collectively lead to a considerable reduction in crop duration. However, it should be ensured that the reproductive duration is not adversely affected. To compensate for any reduction in reproductive duration and to enhance yield potential of short-duration cultivars, it would be essential to select for high crop growth rate and partitioning, tolerance to high soil and air temperatures, high water-use efficiency, and photoperiod insensitivity. Some of these physiolo-

gical traits are not easy to measure in segregating populations. Until marker-assisted selection becomes possible for these traits in peanut, the emphasis should be on evaluating the parents chosen for hybridization and breeding lines in advanced generations. Early maturity and its components (pod/seed maturity, days to flower, days to 50% flowering, and days to accumulate first 10 or 25 flowers) are highly heritable traits, and selection in early generations should be successful. Similarly, physiological traits such as biomass, harvest index, and water-use efficiency (as measured by specific leaf area and SPAD chlorophyll meter readings) show enough additive and additive × additive genetic variance for exploitation either in early or late generations. However, some of these traits may not be easy to measure in segregating generations; thus they could be evaluated in later generations. Selection for photoperiod insensitivity should also be done in later generations.

There is a need to diversify sources of early maturity in peanut. Germplasm lines should be studied in detail for component traits of early maturity and other physiological traits so that parents with differing traits could be crossed to accumulate diverse desirable genes. As large seed size and resistance to foliar diseases will prolong the crop duration, only medium seed size and moderate levels of resistance should be incorporated in early-maturing varieties. To capitalize on the full potential of the genotypes with aforementioned traits, it is essential to modify crop husbandry to accommodate larger number of plants per unit area to provide quick ground cover and to provide required nutrients and other inputs. Some cultural practices can also hasten germination, emergence, flowering, and maturity by modifying microclimate.

Along with cumulative thermal time and other desirable morphological traits, SCMR has been integrated in the breeding scheme for early maturity at ICRISAT. As a noninvasive surrogate of water-use efficiency, SCMR is easy to operate, reliable, fairly stable, and low cost. It is also strongly correlated with pod yield and 100-seed weight. It can be used to screen large numbers of breeding populations in the field. Meanwhile search for markers linked to specific traits, such as water-use efficiency, harvest index, and foliar disease resistance, is in progress.

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