FOOD LEGUME IMPROVEMENT
FOR ASIAN FARMING
SYSTEMS

No. 18

1664

Food Legume Improvement for Asian Farming Systems

Proceedings of an international workshop held in Khon Kaen, Thailand, 1–5 September 1986

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Limits Imposed by Climatological Factors

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CLIMATE is the major component of the environment conditioning the regional and seasonal adaptation and yield of crop plants. While climate is not homogeneous in either space or time, generally similar patterns prevail over quite wide geographic areas, and the cyclic changes in these patterns provide the seasons. It is within the context of these broader effects that the other components of the environment (i.e. the edaphic and biotic) affect plant performance — both directly and in interaction with climate and each other — to condition adaptation to specific environments. Improving climate adaptation is therefore fundamental to the process of crop improvement, which in this paper is considered in its broadest sense, viz. the manipulation of both genotype and environment to respectively maximise genetic potential and minimise environmental constraints to expression of that potential.

Leaving aside questions of desertification, nuclear winters and glasshouse effects, there is little man can do to influence climate on a geographic scale, and nothing he can do to manipulate it in a directed sense. Thus attempts to minimise climatic limits are constrained to the localised scale of the individual field and the crop microenvironment, or to trying to avoid the problem altogether by restricting the climate that the crop experiences. The opportunities for improving crop performance through breeding are somewhat less constrained, plants having been exposed to a reservoir of genetic variation in plant response exists for most climatic factors. The problem thus becomes one of first defining appropriate climatic adaptation and then combining it with other desirable (e.g. agronomic) traits.

In this paper, the limits imposed by climatic factors to the yield of the tropical food legumes are discussed in relation to improving their productivity in Asian farming systems. It is not a comprehensive review of the influence of various climatic factors on plant performance per se. The key climatic factors influencing the tropical food legumes — radiation, temperature, daylength and water — are each examined in turn, and discussed in the context of adaptation and the opportunities for crop improvement.

Radiation

.Photosynthesis provides the basis of dry matter (DM) accumulation and plant growth, and thus the amount of solar radiation entering the plant's environment establishes, in the absence of other climatic constraints, the upper limit of productivity. Over the past several decades, substantial progress has been made in developing a conceptual and analytical framework for describing the conversion of radiant energy to crop yield and the impact of other factors such as temperature and water (e.g. Charles-Edwards 1982; Warren-Wilson 1971; Monteith 1972, 1981). In the simplest approach, economic yield can be expressed as the product:

$$Y_e = \left\{Q\right\} \times \left\{i\right\} \times \left\{E_c\right\} \times \left\{p\right\} \qquad (1)$$

where:

Y_e = economic yield
Q = cumulative radiation incident on the crop
i = proportion intercepted by the crop
. E_c = conversion efficiency to TDM
p = partitioning efficiency to economic yield

An examination of the four components of the above relationship helps to illustrate the potential role of various physiological and environmental factors in contributing to variations in crop performance, and thus to identify where opportunities exist for improvement. It also serves as a framework for subsequent discussion of the

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other climatic factors, since the constraints imposed by them operate through one or more of these four processes.

Cumulative Incident Radiation

One of the main determinants of the cumulative energy falling on the crop is simply the duration of crop growth. In this context, the effect of those climatic factors which determine crop phenology is to establish the time limit for energy input for that crop i.e. to establish its 'phenological potential'. The second main determinant of cumulative incident radiation is level of insolation. Near the equator, year-round variation in average daily irradiance is small (ca10%) because seasonal variation in both daylength and maximum sun elevation is relatively small (Nieuwolt 1972). Moving progressively to higher latitudes however, seasonal variation in both daylength and maximum sun elevation increases, and so does year-round variation in total daily irradiance. For example, at latitudes 20–30°, in what may be loosely termed the subtropics, the combination of high sun elevation and longer days around the summer solstice can provide daily irradiance 15% higher than at the equator. Conversely, the combination of low sun elevation and shorter days around the winter solstice in the subtropics provide daily irradiances of only a third to half the average at the equator.

In practice, these generalised patterns are substantially confounded by variations in cloudiness. Most pronounced are the differences in irradiance induced by cloudiness between rainy and dry seasons, which it is suggested could result in up to 50% higher yield potential for the latter (Versteeg and van Keulen 1986). Levels of irradiance can present a severe constraint to growth of the legume component in various mixed cropping systems e.g. inter-, alley, relay and companion cropping. Research on inter- and mixed cropping systems has identified the need for the legume to complement the other component(s) in terms of phenology and leaf area development to maximise interception and minimise intercomponent competition (Willey et al. 1981). There are no known systematic attempts to improve adaptation of food legume species to low light environments, such as under young rubber and oilpalm where crops can be grown for several seasons until irradiance levels become too low (Laosuwan et al. 1985).

There is evidence that such an approach may be profitable. Recent studies with leguminous ground covers under sorghum and sunflower have shown that *Vigna trilobata* compensates for low irradiance levels with higher specific leaf areas and increased partitioning of DM into leaf area development (Leach et al. 1986). In the Philippines, evaluation of food legumes under full sun and 50% shade indicated shading reduced yields of soybeans only 30% (Catedral and Lantican 1986) compared with 68% for mungbean (Lantican and Catedral 1986), although in part, the mungbean response related to increased incidence of leaf disease. There was differential genotypic response to shade in both species.

Radiation Interception

Numerous empirical studies have shown that within a closed crop canopy, irradiance is attenuated downwards with cumulative leaf area index (LAI) in approximate accordance with Beer's Law, with an extinction coefficient (k) characteristic of the canopy. The main influences on k are the orientation, angle, size and dispersion of leaves, and prior to canopy closure, spatial arrangement of plants. However, k can be influenced by the proportion of diffuse to direct radiation. Thus the LAI necessary to effect ⩾95% interception of incident radiation ('critical' LAI) depends partly on the level and nature of irradiance, and the extinction coefficient for that crop. Critical LAI values for the large-leaved food legumes fall in the range of 3–3.5 depending on genotype and spatial arrangement (e.g. Muchow and Charles-Edwards 1982; Shibles and Weber 1966), but can exceed 5 for small-leaved pigeonpeas (Rowden et al. 1981).

Clearly, radiation falling on bare ground is wasted energy, and the sooner a closed canopy is formed, the greater will be the total energy intercepted. Thus spatial arrangements e.g. isometric sowings and higher densities, which enhance early LAI development will, in the absence of stress, also enhance total DM production. However, vegetative growth in excess of that necessary to form a closed canopy represents DM that might more efficiently be used for seed DM. This need to optimise LAI provides the basis of genotype × sowing date × density interactions in phenologically unstable crops such as the tropical food legumes (see later).

Radiation falling on non-photosynthetic tissue such as woody stems, senescent leaf, flowers or ripe pods is also wasted energy. Thus the photosynthetic efficiency of pods relative to leaf in top-podding crops such as some cowpea, pigeonpea and mungbean genotypes remains to be clarified, since a significant proportion of the total incident energy during podfilling can be intercepted by the flowers and pods (e.g. Rowden et al. 1981). Actively growing soybean (Spaeth and Sinclair 1983) and cowpea (Littleton et al. 1981) pods can recycle much of the CO_2 evolved by respiring seed, but are not capable of net CO_2 uptake even in full sunlight.

A detailed analysis of the growth of two (top-podding) mungbean lines showed that for closed canopies, photosynthetic conversion efficiencies

declined following the start of pod growth (Muchow and Charles-Edwards 1982a). Further, above-ground growth rates during the reproductive phase (Muchow and Charles-Edwards 1982b) were only around 80% that of a black gram line, in which pods were located within the canopy. It is tempting to speculate these differences may have been due to the significant interception of radiation by the mungbean pods, but with a lower E_c, perhaps because of the proportion of interception by already ripe pods.

Efficiency of Conversion

Growth rate in the absence of stress is a linear function of the amount of radiation intercepted (e.g. Muchow and Charles-Edwards 1982a; Shibles and Weber 1966), with the slope of the relationship providing an estimate of E_c. Physiological factors which might conceivably contribute to differences in E_c include the inherent photosynthetic capacity of leaves, the balance between photosynthesis and respiration, and canopy extinction coefficients.

In the tropical food legumes, genotypic variation within species in photosynthetic efficiencies has been found (e.g. Dornhoff and Shibles 1970) although its contribution to differences in DM accumulation is small relative to variation in leaf area and light interception (e.g. Duncan et al. 1978). Thus the productivity in terms of DM accumulation of differing genotypes is remarkably similar once a closed canopy has been formed. Likewise, much of the large variation in initial crop growth rate among food legume species can be ascribed to differences in leaf area expansion rate. In pigeonpea for example, relative higher partitioning of DM into roots appears to slow initial crop growth rate through slower leaf area development (Sheldrake and Narayanan 1979).

Enhanced leaf photosynthetic capacities are often related to compensatory mechanisms, such as thicker leaves but with slower leaf expansion rates (Charles-Edwards 1982). Thus the potential contribution of selection for improved photosynthetic capacity appears small. Various attempts have been made to manipulate canopy architecture to reduce k and increase E_c by distributing the incident radiation over as much leaf area as possible. The experience with leaf size and shape (Mandl and Buss 1981; Wien 1982) has not so far been encouraging.

Partitioning

Harvest index (HI) depends on the relative durations of the vegetative and reproductive phases, the proportion of DM (or more appropriately, energy) assimilated during the reproductive phase and partitioned into reproductive growth, and the

amount of assimilate remobilised from vegetative to reproductive organs. Much of the advance in cereal yields has been from improvement in HI, rather than in total crop DM (Donald and Hamblin 1976), and as is discussed later, the trend is similar with the tropical food legumes. In effect, the direction is toward a shorter vegetative period combined with more determinate or synchronised growth, so that following the onset of flowering a higher proportion of assimilate is partitioned into reproductive growth. At the same time, the relative contribution to yield of stored assimilate is declining.

For example, in some of the more recent improved groundnut genotypes (ICRISAT 1983), partitioning of DM into the pods after the onset of flowering exceeds 90%, establishing potential growth rates of 100-125 kg/ha/d and a yield potential in the absence of stress of 7 t/ha of nuts-in-shell. Similar advances are being made with short duration pigeonpea (Byth et al. 1981).

Temperature

Effects on Growth and Development

Temperature affects the rates of the metabolic processes involved in growth and development. Usually, temperature responses take the form of a skewed, optimum-response curve characterised by three cardinal temperatures, the optimum, minimum and maximum. In general, developmental processes (such as germination, ontogenetic change, leaf initiation, meiotic division) are more sensitive to temperature than growth or photosynthesis per se, and have more sharply-defined optima, although there is substantial differential sensitivity among processes. At extremes of temperature, cellular ultrastructure, most particularly membrane structure and function, can be irreversibly damaged.

Temperature effects in the suboptimal range can often be approximated by a simple linear function (Monteith 1981), and where the diurnal range of temperatures does not encompass high or low extremes, a linear function of daily mean temperature can be used to approximate temperature responses in the field (Angus et al. 1981). This implies in effect that the 'cumulative' temperature (accumulated daily above a 'base' temperature at which the process rate approaches zero, and expressed as day-degrees) needed to complete the process is constant. This thermal constant has been termed the 'thermal time' for that process (Monteith 1981).

Experimental estimates for base temperatures and thermal time for germination of a range of tropical food legumes (Angus et al. 1981), and estimates of the time needed for germination at 16 and 25°C are shown in Table 1, along with those of several

effect on each varies greatly. In most situations, the main effects are likely to be on Q_i through crop duration (a phenological factor) and rate of leaf area development. Temperature can influence leaf area development through effects on rates of both photosynthesis and respiration. While photosynthesis has a very broad optimal range and is therefore only marginally responsive to temperature, short-term responses of reproductive rate increase with temperature (Wardlaw 1979). Thus, at higher temperature Ec might be expected to decline, although Monteith (1981) argues that over time temperature represents a fixed proportion of respiration. There is relatively little information available for tropical food legumes about the effect of temperature on HI, although there is evidence in soybeans (Seddigh and Jolliff 1984) and Vigna spp. (Lawn 1979b) that cool night temperatures can depress HI. Clearly, extremes of temperature which reduce the reproductive sink through effects on gametogenesis will substantially reduce HI.

Implications for Adaptation and Improvement

The tropics are characterized by generally warmer temperatures, with thermal uniformity both diurnally and over seasons. Temperature per se is unlikely to be a significant factor limiting yield of the tropical food legumes in the coastal lowlands. However, in continental areas, at higher elevations, and in the main, cooler temperatures, particularly at night, cause the most serious constraints for later summer sowings in the subtropics (e.g. Affonila and Whiteman 1975; Lawn 1979b), winter sowings in continental areas (e.g. Lawn et al. 1984) or at higher altitudes (Williams et al. 1975). Problems with high temperature stress are most likely in continental areas (e.g. Warring and Hall 1983).

Thus, temperature can influence economic yield through each of the components of the model in Equation 1, although the relative magnitudes of the response to temperature stress.

In particular, both in high (Warring and Hill 1983) and low (Laws and Hume 1983) meiotic division during gametogenesis are very sensitive to temperature change. Pollen formation fails in the range of < 8 – $> 32°C$ (McPherson et al. 1985). Symbiotic N fixation (Layzell et al. 1983) and the rates for leaf emergence are faster in the range $20-34°C$, but once the optimum temperature for rates of development prior to floral initiation in a range of photoperiod genotypes is around $20-34°C$, the rates of leaf emergence are fastest in the range $8 - > 32°C$ (McPherson et al. 1985).

Thus for example, optimum temperatures for various processes may differ substantially. Thus for example, optimum temperature for leaf development prior to floral initiation in a range of photoperiod genotypes is around $20-34°C$, but once the optimum is passed, increasing temperature, the optimum during metabolic activity. However, the optimum for increasing temperature progressively reduces rates of growth and development, often very sharply, during the reproductive base temperatures for several species is for warmer complex, although generally the effect is for warmer temperatures to hasten development. One of the main effects of temperature in several species is for temperatures to modulate the critical photoperiod of a genotype (Hadley et al. 1983). More recent analyses suggest that in an analogous manner daylength may influence base temperatures in relation to photoperiodic response. One of the main effects of temperature in several species is to hasten development. The effect of increase in temperature above the base temperature reduces rates of growth and development, often very sharply, during growth and development. Increasing temperature progressively increases the rate of development (Roberts and Summerfield 1987).

In photoperiod-sensitive genotypes, the effect of temperature on various phases of development in the absence of photoperiodic control may be a major determinant of the duration of developmental phases.

In temperate crops for comparison, the main difference between the two groups is in base temperature, because the two (as taken by the tropical legumes) of the cooler temperature.

Similar relationships have also been shown between emergence at the cooler temperature.

Opportunities to limit temperature constraints to yield of the tropical food legumes through agronomic approaches are in practical terms few, and limited mainly to decisions on where and when to sow. Not surprisingly, the generalised patterns described above have substantially determined traditional patterns of seasonal production and, because species differ in temperature response, the geographic patterns of distribution of their production. For example, temperatures in the northern areas around Chiang Mai in Thailand are too cool for mungbean during the dry season but not for soybean (Na Lampang 1985). There have been some limited attempts (e.g. with soybean — Bharati et al. 1983) to extend the range of production through seed acclimatisation treatments, but with little success.

There are large opportunities for genetic improvement however, both in terms of expanding the seasonal and regional range over which individual crops might be grown, and in improving yield within existing production areas. In those crops for which information is available, there are numerous examples of differential genotypic sensitivity to suboptimal temperatures, and to high and low temperature extremes. In many cases, these differences relate directly to the latitude of origin of the genotypes, implying differentiation has occurred as a direct consequence of past selection pressures. In addition to this intra-cultigen variation, there exist for most food legumes related wild subspecies (Smartt and Hymowitz 1985), which are likely to be a rich source of adaptive traits such as differential temperature response (cf. Lawn et al., these proceedings).

To date, most effort has been directed at improving adaptation to cooler temperatures, with some success (Voldeng et al. 1982; Holmberg 1973). However, opportunities for genetic improvement in relation to temperature responses remain largely unexploited. In most cases, little is known about the complexity of genetic control of differential responses, and the consequent difficulties in making progress. Genetic advance may be further hindered by lack of correlation between sensitivities at different stages (Hume and Jackson 1981) and between different processes (McPherson et al. 1985).

Research is needed at this stage to identify effective selection criteria and efficient screening techniques, to allow identification of temperature response types within segregating populations. In this context, physiological criteria may assist. For example, a heat tolerance test for soybean and other crops has been developed, based on leakage of electrolytes from heat damaged leaf tissue (Bouslama and Schapaugh 1984). Chlorophyll fluorescence has been used to identify tolerance to

temperature extremes in potato (Smillie et al. 1983), and the potential exists for assays based on metabolic processes in seedlings or perhaps even in tissue culture where problems with plantlet regeneration can be overcome.

Daylength

Photoperiodism

Daylength is the other major climatic factor influencing the rate of ontogenetic development in plants. It is the most predictable of the climatic variables, which is presumably why photoperiodism has assumed major adaptive significance. Photoperiodism provides a mechanism whereby the plant's life cycle can be matched to seasonal change and thus to variation in other, growth-limiting climatic factors such as temperature and water. Its most dramatic effect is on the progress of plants from a vegetative to reproductive state, and it has been most extensively studied in this context.

All of the tropical food legumes exhibit photoperiodism, and all are short-day plants (Roberts and Summerfield 1987). In those species which have been extensively studied, most lines show quantitative short-day flowering response, although qualitative response types occur (Aggarwal and Poehlman 1977; Hadley et al. 1983; Lush and Evans 1980; McPherson et al. 1985; Turnbull et al. 1981). In most species, there also exist either day neutral or relatively daylength insensitive genotypes, at least in the context of rate of development to flowering (Aggarwal and Poehlman 1977; Ariyanayagam and Spence 1978; ICRISAT 1983; Inouye and Shanmugasundaram 1984; Turnbull et al. 1981). Usually, but not always, insensitivity is associated with earliness of flowering.

Rate of development after induction in the tropical food legumes is also commonly sensitive to daylength, although the relative sensitivity during later phases of growth remains to be clarified. However, it seems likely that their evolution as summer-growing plants would have favoured the development of a post-inductive requirement for daylengths at least as short, if not shorter, than those required for rapid induction. The limited available evidence tends to support this supposition. In soybean, for example, exposure to non-inductive long days following initiation can cause reversion to the vegetative state (Lawn and Byth 1973) and in some genotypes at least, continued exposure to short days beyond induction is necessary to ensure the formation of viable pollen (Fisher 1963). In cowpea (Lush and Evans 1980), the asiatic *Vigna* species (Lawn 1979a), pigeonpea (Wallis et al. 1985) and soybean (Lawn and Byth 1973; Board and Hall 1984), exposure to long days after floral induction/

initiation can variously extend the duration of the flowering period, reduce the synchrony of flowering, podset and pod maturation, and extend the post-flowering period by delaying pod ripening and/or inhibiting leaf senescence and abscission.

Groundnut is somewhat unusual in that it is relatively insensitive to photoperiod prior to flowering, but some genotypes are quite sensitive in post-flowering development (J.H. Williams unpubl.).

In soybean, growth of plants in relatively long days following induction has been shown to enhance vegetative growth (Guiamet and Nakayama 1984) and reduce the partitioning of DM and N (Cure et al. 1982) to pods and seeds. Long days also delayed the transition of stem apical buds to a reproductive state, altering apical dominance and consequently branching habit and stem growth (Thomas and Raper 1983). Conversely, exposure to relatively shorter days during reproductive growth can enhance HI and, except for short duration lines where vegetative growth is already limiting, result in at least similar yields in shorter time (Schweitzer and Harper 1985). In essence, the effect of daylength post-induction is one of altering the balance between reproductive and vegetative growth, with longer days enhancing the tendency to continued vegetative growth and expression of indeterminateness, and reproductive growth enhanced by shorter days.

Thus, the main effect of daylength is to determine, in concert with temperature, crop phenology (i.e. the timing of particular ontogenetic events in the crop cycle, and the durations of the phases between those events). As such, daylength directly influences the potential productivity through its influence on crop duration (i.e. the 'phenological potential'). It also influences productivity indirectly, through the matching of various phases of growth with changes in other growth-limiting environmental factors, which in turn influence the efficiencies of interception and use of energy. The other important effect in the tropical food legumes is on the synchrony of flowering, podset and maturity, and the relative partitioning of DM between vegetative and reproductive growth, which contributes to differences in HI.

Photoperiodism and Adaptation

Daylength varies systematically across latitude and season, with the longest day in midsummer and the shortest in midwinter. With annual crops such as the tropical food legumes, therefore, the daylength experienced by the crop depends on both the latitude and date of sowing.

Several aspects of the role of daylength in conditioning adaptation with respect to latitude and sowing date warrant elaboration. Firstly, in most of the tropical food legumes, there exists a wide range of differential genotypic response, and most usually, differential response can be directly related to latitude of origin (e.g. Byth 1968; Lawn 1979a). Generally, lines which are later flowering in relatively short days originate in the tropics, and those which require longer days to delay flowering originate at progressively higher latitudes. Because they are short day plants, sensitive genotypes will be earlier flowering the closer they are grown to the equator (Hartwig 1970; Lawn et al. 1984). Likewise, they will flower earlier when sown after the summer solstice than before it, and, in the absence of confounding temperature effects, when grown as dry season crops (Pookpakdi 1984).

Secondly, for summer crops, the seasonal variation in daylength is greater and therefore occurs more rapidly in the subtropics than the tropics, so that relatively small changes from any particular sowing date will ensure crops experience progressively larger changes in daylength as they are moved further into the subtropics. Consequently, the potential magnitude of effects of sowing date within the season becomes more pronounced moving away from the low latitude tropics.

Thirdly, in the tropics per se, although seasonal variation is smaller, the range of potential sowing dates is extended because temperatures are generally sufficiently warm for year-round cropping, and the differences in daylengths experienced between wet and dry season crops become comparable with those due to varying sowing dates for summer grown crops in the subtropics. At very low latitudes (<10°), the maximum range in daylength is 1 hr, and the differences in average daylengths experienced by wet and dry season crops are small.

Where the tropical food legumes are grown as summer season crops, the effects of long days on development after floral induction are not usually of practical concern. These crops are sown either prior to, or around, the summer solstice, and in most daylength sensitive genotypes, induction occurs some time after the solstice. Thus flowering and subsequent phases occur during progressively shortening days, and any requirement for short days post-induction is automatically satisfied. However, for very early sowings, induction may occur during the shorter days preceding the summer solstice (Board and Hall 1984; Lawn 1979a). Likewise, very early flowering genotypes may also flower prior to the solstice, so that subsequent development phases are exposed to comparatively long days, leading to problems in synchrony of development.

Undoubtedly post-induction effects emerge as the potentially most significant problem with dry season or 'winter' crops in the tropics, which experience reverse profiles of daylength (and often

temperature) to those for wet season crops. Sown sometime after the autumnal equinox, these crops flower during the shortest days around or after the winter solstice. Thus, they complete their growth in lengthening days, sometimes maturing after the spring equinox, where irrigation is available. The latter crops experience longer days during late reproductive growth than do summer grown crops at any latitude maturing after the autumnal equinox. The consequence can be disastrous, with prolonged and asynchronous flowering and podset, and delayed leaf senescence and/or pod ripening (Lawn et al. 1984).

Photoperiodism and Crop Improvement

Photoperiodism has undoubtedly been the climatic response most successfully accommodated, and indeed exploited, in improving the tropical food legumes, and photoperiodic effects can and have been used to improve breeding methodologies, e.g. by facilitating hybridisation, synchronising flowering among diverse parents (Hadley et al. 1983) and enabling rapid generation turnover (McPherson et al. 1985).

The widest use of photoperiodic response has been made in the context of matching crop growth cycle to the environment, usually to maximise exploitation of the period when other climatic factors such as water or temperature are favourable, but occasionally to avoid the occurrence of critical growth phases during periods of high likelihood of particular stresses. For example, Putland and Imrie (these proceedings) describe the use of photoperiodic response to delay maturity of mungbean beyond the end of the rainy season and thus minimise the risk of weather damage to ripening seed.

In several species, the generally high correlation between time to flowering and crop duration has been exploited to develop an index whereby different daylength responses among cultivars can be classified and their likely region of adaptation indicated. This has resulted in various 'maturity group' classifications to discriminate between genotypes (Aggarwal and Poehlman 1977; Sharma et al. 1981; Shibles 1980). The differentiation among genotypes is largely due to differences in critical daylength, although clearly, variation in other parameters (e.g. relative sensitivity, length of juvenile phase, differential sensitivity post-induction), as well as differential temperature effects on all these, will contribute to maturity differences.

The most sophisticated example of a maturity group system is that employed for soybeans in North America (see Shibles 1980), whereby cultivars are classified into at least twelve groups, so that each

group is 'adapted' over a latitudinal range of only about 4°. 'Appropriate' adaptation or crop ideotype in this system is effectively defined so as to match crop duration to the duration of favourable temperatures. Movement of a cultivar to a zone of higher group number than its adaptation would result in it becoming too early, and in a zone of lower group number it would not mature before the onset of frost.

The North American maturity group system for soybeans has been of limited value in the subtropics and tropics (Shanmugasundaram 1976), one reason being that water rather than temperature is the main climatic constraint to growth. This introduces the need for greater flexibility in the crop ideotype which need to be considered (cf. Byth et al. 1981), in part because the year-round favourable temperatures of the tropics increase the range of cropping opportunities and in part because of the inherently greater variability of rainfall as a climatic factor. The former is exemplified in Thailand where soybean and other food legumes are grown in the early or late rainy season as well as the dry season (Na Lampang 1985). The crops thus sample a wide range of photothermal regimes, and necessitate greater flexibility in agronomic approach (Pookpakdi 1984).

The latter is exemplified in subtropical and tropical Australia, where the advent of adequate sowing rains is the main determinant of sowing date for raingrown summer crops (Lawn et al. 1984). In that situation, the existence of cultivar x sowing date x density interactions is turned to advantage to increase flexibility of the crop ideotype (Lawn et al. 1977; Lawn 1983a), by extending both the range of potential sowing dates and geographic range over which given varieties can be effectively grown. This greater flexibility also assists scheduling of crop rotations in double-cropping areas.

One of the most interesting developments has been to directly exploit the photoperiodic effects on both phenology and morphology which contribute to genotype x latitude/sowing date x density interactions and thus manipulate crop ideotype (e.g. Byth et al. 1981; Schweitzer and Harper 1985; Sheldrake and Narayanan 1979; Spence and Williams 1972; Wallis et al. 1985). The approach relies on the fact that when short-day plants are grown in daylengths which are short relative to their range of quantitative sensitivity, crop duration is shortened and the less vegetative, shorter plants are therefore less prone to lodging and leaf diseases. Moreover, flowering, podset and pod maturity became more synchronous, particularly in the physiologically indeterminate species such as cowpea, mungbean, black gram and pigeonpea. Reduced biomass per plant is compensated for in part by increased plant density and by increases in

HI, a trend which effectively mimics that experienced a decade earlier in the cereals.

A related trend is the development of early-flowering, day-neutral or relatively photoperiod insensitive lines (e.g. Ariyanayagam and Spence 1978; Byth et al. 1981; Sumarno 1984) as an attempt to: (1) broaden the adaptation of lines by reducing the magnitude of potential daylength effects; (2) improve adaptation to water limiting situations e.g. as rainfed crops (Hadi and Orantz 1981) or post-rice crops (Sumarno 1985); or (3) improve suitability for use as short season relay crops in intensive cropping systems (Benjasil and Na Lampang 1984).

The use of photoperiod insensitivity has not been universally successful, however, partly because of its frequent association with extreme earliness. In soybean for example, complete insensitivity has usually been accompanied by a preflowering period of < 28 days and, except where associated with determinateness or an extended flowering period (Thouye and Shanmugasundaram 1984), by short stature, lowset pods and limited yield potential. The discovery of a source of reduced sensitivity which may be related to an extended juvenile phase (Hartwig and Kiihl 1979) offers the hope of breaking this apparent nexus, so that yield potential need not be sacrificed. Thus far, insensitivity as an approach has been most effective in pigeonpea (Byth et al. 1981; Wallis et al. 1985) which has an extended juvenile phase, and, in the context of mechanised agriculture, those pulses such as cowpea and mungbean which bear their pods high in the canopy.

Water

Tropical monsoon Asia can be broadly divided into three basic climatic zones (cf. Nieuwolt 1972) viz. the equatorial monsoon climates, where both 'summer' and 'winter' monsoons bring rainfall, the wet/dry monsoon climates, where rainfall comes during the summer monsoon while the winter monsoon is dry, and the dry tropics where neither monsoon brings much rainfall. Within the wet/dry monsoon pattern, the trend is for the duration of the rainy season to shorten with increasing latitude and distance from the sea. These broad patterns are, however, very much disturbed, by local orography and geography, and rainfall is very unpredictable, varying in intensity and duration with time and place.

In terms of water supply to the plant, the picture is further complicated by local topographic and edaphic factors which influence runoff, infiltration, storage, and subsequent availability. Thus, depending on time of year, a given field might be arid or flooded, and in the rainy season, plants within a crop might alternately experience water supply deficits and excesses. It is even possible for different plants within a crop to be simultaneously droughted or waterlogged depending on topography. Both conditions substantially limit yield of mesophytic plants such as the food legumes.

Water Deficit and Productivity

A number of comprehensive reviews on the effects of stress induced by water deficit are available (Mussell and Staples 1979; Paleg and Aspinall 1981; Turner and Kramer 1980). In terms of the model outlined earlier in Equation 1, the main effects of water deficits can be summarised as follows:

1. A decrease in cumulative radiation interception through reduced rates of leaf initiation and/or expansion, reduced leaf area duration through faster senescence rates and/or phenological adjustment and paraheliotropic leaf movements and leaf rolling (Hughes and Keatinge 1983; Lawn 1982a; Muchow 1985). Soil water deficits during establishment can also reduce plant stand.

2. A reduction in the efficiency of utilisation of intercepted radiation, largely through a reduction in carbon exchange rates (Cortes and Sinclair 1986) associated with reduced stomatal conductance; and

3. A reduction in partitioning efficiency, either because of a shortening of the duration of reproductive growth or because of the abscission of pod and seed sinks (Korte et al. 1983b).

The relative effect of water deficit on each of the above depends in large part on timing relative to crop ontogeny, and duration and intensity. For example, Muchow (1985) reported that where water deficits developed gradually from sowing, the reduction in light interception due to reduced leaf area development was initially greater than that in conversion efficiency for a range of food legumes. Only after a prolonged drought, when the intensity of the deficit was strongest, were the effects on conversion efficiency comparable with those on interception. However, when an intense deficit developed rapidly following the establishment of a closed canopy, the reductions in E_u were relatively large. Likewise, water deficits during reproductive growth reduced leaf carbon exchange rates for soybean by 25% (Cortes and Sinclair 1986), although deficits occurring late in reproductive growth also promoted leaf senescence.

The effect of water deficit on sink development also depends largely on timing relative to crop ontogeny. Usually, water deficits during reproductive development prior to rapid seed growth reduce pod numbers through abscission of, variously, flower buds, flowers and small pods (e.g. Korte et al. 1983b). Water deficit progressively later in ontogeny results mainly in abortion of seeds within pods and, ultimately, in smaller seed. Seed size is most likely to be reduced when water deficits

late in crop growth promote leaf senescence and advance crop maturity.

In addition to constraints to the carbon economy of food legumes, N fixation is extremely sensitive to water deficits (Pankhurst and Sprent 1975; Weisz et al. 1985). In large part, the effects appear to be due to rapid and direct effects of stress on the permeability of the nodule cortex to oxygen although it is likely there are also longer-term, indirect effects of carbon supply on nodule development and activity. The consequence is a substantial reduction in N accumulation under drought conditions (e.g. Chapman and Muchow 1985).

The extent to which effects of water deficit during growth translate into reductions in seed yield in turn depend on their severity and timing, and subsequent pattern of water supply (e.g. Korte et al. 1983a; Nageswara Rao and Williams, in press). In general, the earlier in crop growth the deficit occurs, the greater the opportunities for subsequent compensation, provided subsequent water supplies are adequate. The effects of a water deficit during vegetative growth can be fully compensated for in situations where water supply during subsequent growth is adequate. This is achieved by either subsequent vegetative growth, as with indeterminate varieties (e.g. Villalobos-Rodriguez and Shibles 1985), or by increased HI, as with 'full-season' varieties where vegetative growth tends to be in excess of that required to ensure full light interception during reproductive growth (e.g. Nageswara Rao et al. 1985; Ashley and Ethridge 1978). In this sense, short duration, determinate lines are more susceptible to water deficits during vegetative growth.

Food legumes are generally most sensitive to water deficit during reproductive growth, particularly during the time when pod numbers are being determined (e.g. Korte et al. 1983a; Nageswara Rao and Williams, in press). Beyond that time the opportunities for compensation are much reduced, although in most food legumes some yield homeostatic potential exists through compensatory change in seeds per pod and/or seed size (cf. Korte et al. 1983b). In many species, e.g. groundnut (Williams et al. 1986), cowpea, mungbean and black gram (Lawn 1982a), less determinate genotypes produce new flushes of flowers and pods when water deficit during reproductive growth is relieved. In groundnut, some genotypes respond to the relief of water deficit with a rapid increase in pod initiation without the development of new flowers, implying an ability to sustain a number of viable but non-developing embryos during the period of deficit (Williams et al. 1986).

Increasing the 'determinateness', or degree of synchrony of flowering and podset, may increase the vulnerability of food legumes to intermittent water deficit during reproductive growth by shortening the period over which pods are set. For example, Villalobos-Rodriguez and Shibles (1985) reported that the relative effects of water deficit during reproductive growth were greater in determinate compared with indeterminate tropical soybeans. Likewise, the groundnut cultivar JL 24, which has a highly synchronous podding habit, has proven very susceptible to intermittent water deficit in studies at ICRISAT (Nageswara Rao and Williams pers. comm.). However, synchronous podding may be of benefit in the case of terminal water deficit (see below).

Strategies for Improvement

Numerous studies show that like most crops, the food legumes respond positively to irrigation. In practice, however, opportunities for irrigation are very limited, with farmers usually preferring to use scarce water resources for the production of more profitable crops. At best, sufficient water may only be available for supplementary irrigation, and in this case the most efficient use will be made of water applied during the pod-formation/seed-filling phases (cf. Nageswara Rao et al. 1985).

In the absence of irrigation, attempts to overcome limits imposed by water deficit must focus heavily on: (1) agronomic approaches to improving the conservation and storage of soil water; and (2) agronomic and genetic approaches to improving the effectiveness of water use and water use efficiency (WUE) by minimising the impact of water deficits. The latter approaches are of main interest here. Most important is the effectiveness of water use, since biomass is a linear function of water use (e.g. Lawn 1982b), and water left in the soil is unexploited potential.

A comparison of the performance of four groundnut genotypes to intermittent water deficit at ICRISAT (Table 2) suggests improvements in WUE are possible. Although all four lines used the same amount of water, there was large variation in both WUE and HI, presumably because of differential tolerance to/recovery in the pattern of water deficit imposed in that study (Williams et al. 1986).

Likewise, isotopic discrimination has identified genotypic variation in WUE (Farquhar and Hubick 1985). Genotypic differences have also been observed in groundnut in terms of the ability to continue to initiate pods after the onset of drought.

Both agronomic and genetic strategies for improving yield in drought environments can be broadly grouped into those of drought 'escape' or 'resistance'. In turn, the latter can be further

Genotype	Total water use (%)	Water use efficiency (%)	Harvest Index (%)
TMV 2	98	111	181
Robut 33-1	101	125	156
NC Ac17090	101	118	125
EC 76446(292)	100	100	100

subdivided into strategies to reduce the rate of water use, sustain the rate of water uptake, or to tolerate tissue water deficits. Resistance can also potentially contribute to plant survival and potential for recovery if and when the water deficit is relieved.

Targeting the Environment

The most appropriate strategies for crop improvement in drought environments depend on the likely pattern of water availability and of the likelihood of variations about that pattern (Lawn 1982b; Williams et al. 1986). In Southeast Asian cropping systems, the two situations most commonly confronted are: (1) terminal droughts, where the quantity/duration of water supply is relatively fixed by soil storage so that the plant is exposed to water deficit only toward the end of growth; (2) intermittent droughts, where the crop may be exposed to droughts of variable intensity and duration at any stage of growth. Examples where terminal droughts can be expected include post-rainy season crops following rice and areas of seasonally-defined, but reasonably reliable rainfall. Intermittent drought confronts most upland crops, except in the most reliable rainfall areas.

In the case of terminal drought, the aim is to ensure full use of available water with the maximum possible being used over the reproductive phase. The most appropriate improvement strategy is drought escape, although a level of tolerance of tissue water deficits late in growth may facilitate maximum water extraction. Choice of sowing date and sowing arrangement/density can be respectively used to match crop phenology to environment and influence rate and effectiveness of water use. For example, equidistant spatial arrangements can enhance early LAI development and water use but favour more effective exploitation of soil water at depth in interplant spaces (Lawn 1983b).

The importance of matching crop to environment is illustrated by the situation with groundnut at ICRISAT, where in the absence of drought the yield potential of genotypes maturing in 110 and 140 days is respectively 4.5 and 6.0 t/ha, whereas if a terminal drought commences after 100 days, the respective yields are 3.0 and 0.7 t/ha for these same lines (Nageswara Rao and Williams, pers. comm.).

Where the duration or amount of water supply is very reliable, the most efficient mechanism to achieve escape is likely to be rapid phenological development such that the crop matures before water supply ceases. A synchronised reproductive growth habit would enable maximum partitioning into seed and also facilitate matching crop duration to water supply. However, where the year to year *duration of water supply* is variable, *the most* productive mechanism is likely to be rapid phenological development combined with plasticity in the duration of the reproductive phase. Thus, in those years where water is available for longer, reproductive growth can be extended to take advantage of it.

With intermittent droughts, the most successful strategies *will be* those based on resistance — particularly those which favour recovery following stress — combined with a limited array of management options. Such options include choices of sowing date/phenology to minimise the coincidence of critical growth stages with periods of high likelihood of drought.

Breeding for Tolerance/Escape in Food Legumes

Various physiological mechanisms that contribute to resistance or escape of drought have been identified in food legumes (Table 3). The most important escape mechanism is rapid development, which is being widely exploited in soybean, mungbean and cowpea with the development of short duration lines for post-rice crops. A related escape mechanism, often associated with indeterminate growth, is phenological plasticity, whereby the duration of reproductive growth depends on the continued availability of water. This mechanism has been observed in some mungbean and black gram (Lawn 1982a) and chickpea lines (Sheldrake and Saxena 1979).

Mechanisms contributing to resistance through reduced water loss include differences in stomatal sensitivity, cuticular conductance, paraheliotropic leaf movement, and in the rates of change in leaf area either through reduced leaf expansion or advanced abscission (Lawn 1982a; Sinclair and Ludlow 1986; Muchow 1985). Each of these

TABLE 3. Physiological mechanisms contributing to drought escape or tolerance identified in various of the tropical food legumes.

Strategy & mechanism	Example of occurrence
A. Escape	
* Rapid progress to flowering	Short duration genotypes e.g. of cowpea, soybean & mungbean (cf Hall & Grantz 1981; Summarno 1985)
* Plasticity in reproductive phase	In several *Vigna* spp. (Lawn 1982a) and chickpea (Sheldrake and Saxena 1979)
B. Resistance	
I. Reduced water use	
* Stomatal closure	Variation among spp. (Lawn 1982a; Muchow 1985)
* Reduced cuticular conductance	Variation among spp. (Sinclair & Ludlow 1986) & within soybean (Paje et al. pers. comm.)
* Slower leaf area development	Variation among spp. (Lawn 1982a; Muchow 1985)
* Shorter leaf area duration	Variation among spp. (Lawn 1982a; Muchow 1985)
* Paraheliotropic leaf movements	Variation among spp. (Lawn 1982a; Muchow 1985)
II. Improved water uptake	
* Improved root function e.g. density & depth	Variation in groundnut (Williams et al. 1986) & among spp. (Angus et al. 1983; Lawn 1982a)
III. Desiccation tolerance	
* Osmotic adjustment	Variation among spp. (Ludlow pers. comm.) & some within pigeonpea (Flower & Ludlow 1987)
* Lower critical relative water contents	Variation among spp. (Sinclair & Ludlow 1986)

mechanisms results to some degree in reduced productivity although mechanisms such as stomatal sensitivity, cuticular conductance and leaf movements appear more conducive to rapid recovery following the relief of drought. Increased rooting density and rooting depth contribute to sustaining water uptake and species differences have been observed (Angus et al. 1983; Lawn 1982b). Mechanisms which contribute to enhanced tolerance of tissue water deficits include osmotic adjustment and desiccation tolerance (Flower and Ludlow 1986; Sinclair and Ludlow 1986).

Comparative studies suggest that there is strong interrelationship between various mechanisms, and that several may operate in concert, perhaps causally, to give rise to overall strategies of response. Thus, it appears to be the various combinations of these which make some species better adapted to certain patterns of drought stress than others (Angus et al. 1983; Lawn 1982b; Sinclair and Ludlow 1986; Muchow 1985). Substantial research remains to clarify these interrelationships and their consequences for crop water use and yield. It also remains to be seen to what extent the various mechanisms can be exploited within any particular species.

Investigations with pigeonpea have revealed that while osmotic adjustment was high relative to other food legumes, only moderate variation was found among genotypes (Flower and Ludlow 1986). On the other hand, a twofold range in cuticular

conductance has been found in soybean (M. Paje et al., pers. comm.) offering the prospect of improving the survival time of plants during severe water deficits with that species. Wide variation in rooting habit has been found in groundnut, and studies at ICRISAT have shown that this can contribute to differential sensitivity to water deficits (Williams et al. 1986). The genotype NC Ac 17090 is shallow rooted, and much better able to exploit water from light showers, but less so for soil water at depth.

Given the complexity of the interrelationships between the mechanisms in Table 3, it seems unlikely that approaches focusing solely on any one will result in significant advance. Further, the importance of particular mechanisms will most certainly vary among species. Nonetheless, investigations into these mechanisms offer one of the most promising areas for improving drought performance in the food legumes. Certainly, the complexity of the interactions between genotype and timing, intensity and duration of water deficit (e.g. Nageswara Rao and Williams, in press) suggests that alternative approaches based on empirical screening will have to be very specific indeed to the patterns of s‑‑‑‑ being targeted

Limits Imposed by Excess Water

Excessive water can limit yield of the food legumes in several ways. The most common is a reduction in N fixation caused by reduced oxygen

supply to the nodules in temporarily waterlogged soils, an effect often exacerbated by soil denitrification. If the duration of waterlogging is short, the main effect observed is a transient chlorosis and reduction in crop growth rate. However, where waterlogging is prolonged, it can induce the death of roots and nodules, in which case the setback to growth can be serious. In some species, wet soil conditions and the death of roots facilitate the entry of pathogenic organisms (e.g. *Phytophthora* stem rot in cowpea, chickpea and soybean), leading to the death of waterlogged plants from disease.

There is variation among food legume species in tolerance to temporary waterlogging. For example, mungbean, pigeonpea, guar, and moth bean are particularly sensitive while others, most notably soybean, are tolerant. Indeed, studies in Australia have shown that soybean seedlings readily acclimate to growth on saturated soils, providing a shallow zone of aerobic soil is maintained at the soil surface (Troedson et al. 1984). The growth of acclimated soybeans in saturated soil exceeds that of well-watered, conventionally-grown crops, so that provided sufficient time is available following acclimation, yields can ultimately exceed those of well-watered crops.

Apart from agronomic approaches to avoid waterlogging, e.g. through drainage or matching crop to environment, the most promising approach appears to be to select for tolerance among and within species. Tolerance to intermittent waterlogging appears to involve two related components: (1) tolerance of roots and nodules to temporary anaerobiosis; (2) ability of roots and nodules to rapidly recover following soil drainage. Field screening for tolerance to waterlogging has been successful in identifying genotypic differences in several food legumes (ICRISAT 1982, Alvino et al. 1983). In the case of soybeans, it appears it may be possible to select for genotypes which will respond even more positively to saturated soils (Hartley, Lawn and Byth pers. comm.).

Another important constraint imposed by excessive water in some species e.g. mungbean and cowpea, is damage caused to ripening pods by exposure to humid, wet conditions. As discussed elsewhere in these proceedings, opportunities exist either for escape (Putland and Imrie) or tolerance (Imrie et al.). Finally, exposure to humid, wet conditions can favour rank growth, predisposing plants to lodging, or to a host of foliar and pod diseases. If the crops are to be grown in such environments, breeding for disease resistance is the only appropriate solution.

Overview

Earlier in this paper, it was suggested that opportunities to manipulate the crop environment to minimise climatic constraints are limited to the localised scale of the individual field and the crop microenvironment. It is apparent from this brief review that despite this restriction, the opportunities for improving performance of the tropical food legumes through various aspects of management are substantial. The main requirement is a critical analysis of the contribution of the various climatic factors affecting performance in order to identify the major constraints in particular environments. Flexibility in management can often broaden the range of environments over which particular lines can be grown.

It was also suggested that opportunities for genetic improvement were less limited. Nonetheless, it is apparent that the situation is complex, particularly in a relatively underdeveloped group of plants such as the tropical food legumes, where the concept of 'appropriate' climatic adaptation has often been recognised only in its absence i.e. when genotypes have been moved away from the area that most suits them. Only in recent years has breeding for climatic adaptation emerged as a more purposeful, directed concept.

There are several (usually interacting) climatic factors affecting the physiological processes of growth and development, with potentially different levels of complexity of genetic control and different levels of importance to seed yield. In breeding for climatic adaptation the problem is firstly to clarify breeding objectives by identifying the climatic factor(s) of major adaptive significance in the target environment, the process(es) they influence, and the range of different response types. Secondly, effective selection criteria must be defined, and efficient screening techniques designed, to achieve these objectives.

Implicit in this analysis is recognition of a need to try to exploit specific climatic adaptation if yield potentials are to be maximised in the shorter term. The alternative, and longer term approach, is to attempt to breed genotypes which are less sensitive to climatic factors such as daylength, temperature and water. The advantages of the latter approach, if successful, are obvious: the broader adaptation of cultivars would reduce the resources needed for investment in breeding and seed production and distribution, and facilitate the more rapid geographic dissemination of breeding advances made in any one area.

The disadvantage however, is that there is a very real cost in terms of reduced yield potential in particular environments because 'insensitive' cultivars are not completely so. The best broadly

adapted cultivar will have the highest yield over a range of climatic environments but, to the extent that insensitivity is not achieved, will be lower yielding than the best specifically adapted line in each environment. The complexity of the interaction between climatic factors and the growth and development of the food legumes is such that the simultaneous achievement of high yield potential and 'broad climatic adaptation' will be difficult and time-consuming to achieve, particularly in relation to constraints imposed by water and temperature. Thus, the cumulative cost of ignoring specific genotype x climate interactions could be large.

Apart from these biological considerations, the most appropriate balance between emphasis on specific and broad climatic adaptation will depend on the resources available for improvement relative to the diversity of climatic regimes being targeted, and the potential economic significance of each to production of the crop as a whole. Whatever that balance, there is little doubt that directed research, based on an understanding of genotype x climate interaction, will be preferable to a continuation of the empirical research approaches which have characterised much improvement effort to date.

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