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15

Stress Physiology

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It is difficult to define precisely plant stress because the term *stress* is used in reference to perturbations from normal conditions at various levels including the environment, the whole plant, and even the cellular and subcellular level. For example, drought as an environmental stress causes water stress, or water deficit, to develop in plants. In turn, a water deficit affects such physiological processes as translocation at the whole plant level; leaf expansion and gas exchange at the organ level; and photosynthesis at the subcellular level. Since the final result is reduction in growth and yield, perhaps stress can be defined simply as any condition that reduces yield below the maximum attainable level.

What constitutes a stress varies with the genotype and development stage of a plant. For example, a temperature low enough to injure the soybean [*Glycine max* (L.) Merr.] cv. Ransom at flowering might not injure a more chilling-tolerant cultivar such as Fiskeby V, and a night temperature injurious during flowering of either cultivar might be harmless or even beneficial during seed filling. Some environmental stresses, such as temperature and soil water potential, can be measured more accurately than others, such as soil aeration, mineral deficiencies, or biotic stresses. Likewise, the effects of a stress such as drought can be measured more accurately than the effects of certain other stresses such as chilling or deficiencies and toxicities of mineral elements.

Stresses operate at all levels from whole plants to the cellular and subcellular level, and in time scales ranging from weeks to hours, or even seconds in the case of sun flecks. For example, while upper leaves of a crop canopy are exposed to full sun, lower leaves are shaded and photosynthesis is reduced. At the same time, the water stress that often develops in the exposed upper part of the canopy reduces photosynthesis on a relatively immediate time scale by causing closure of stomata and

by affecting electron transport and carboxylating enzymes. While turgor loss causes closure of stomata in minutes, on a longer time scale of days it also decreases the leaf area available for photosynthesis by reducing leaf expansion. The major objective of this chapter is to identify some of the important stresses and describe how they alter physiological processes to affect growth and yield.

The stresses to which plants are subjected can be grouped into three categories of soil, atmospheric, and biotic stresses. Among the soil conditions that affect plant growth are available water content of the soil, soil aeration, soil structure, soil temperature, soil pH, mineral deficiencies and toxicities, and salinity. The major atmospheric factors include light, air temperature, humidity, wind, carbon dioxide (CO₂) concentration, and air pollutants. Biotic stress includes competition with weeds and other plants of the same crop, insects, nematodes, and various pathogenic organisms. All of these environmental factors reduce yield by creating physiological stresses within the plants. Lack of space limits discussion in this chapter to only a few among these important stresses. We have considered effects of stresses caused by temperature, water, light, CO₂ concentration, and metal toxicity. Effects of others, including biotic stresses, soil pH and mineral deficiencies, and soil structure are topics of other chapters.

It is difficult to estimate the relative importance of individual stresses because each is more or less random in occurrence and is influenced by interactions with the others. Droughts, unseasonably late or early frosts, and outbreaks of insects or diseases of epidemic proportions are largely unpredictable and the damage they cause depends on their duration and the stage of plant development at which they occur. In modern agricultural systems that incorporate the best cultivars and pest management practices on good soil, atmospheric conditions (or weather) continues to be the principal factor limiting the yield of soybean and other crops. As Watson (1963) wrote, climate determines what crops farmers can grow, but weather determines the yield that they obtain. The importance of weather with respect to crop yields is emphasized by Hudson (1977) and others in Landsberg and Cutting (1977). According to Boyer (1982), the average farm yield of soybean in the USA is only 27% of the record yield, and most of the difference between record and average yields is caused by water and temperature stresses.

15-1 TEMPERATURE STRESS

The well-defined, seasonal cycle of temperature in the Corn (*Zea mays* L.) and Soybean Belts determines the times of planting and harvesting of soybean. Cold soil; low air temperatures; and the danger of late spring frosts limits early planting, while late summer droughts and early autumn frosts are threats to late plantings. In addition, the large temperature perturbations above and below normal during the growing

season (Fig. 15-1) constitute relatively unevaluated hazards to the growing crop. The potential for damage from these temperature variations depends on the stage of crop development at which they occur (Table 15-1). Both air and soil temperatures need to be considered. Low soil temperature early in the season is a limiting factor for germination and seedling development and early frosts truncate pod development, while high air temperatures in July and August affect physiological processes adversely. Important interactions occur among temperature, solar radiation, and water stress (Dale, 1983; Mederski, 1983; Shaw, 1983). High temperature often is associated with drought and with high vapor pressure deficit and rapid transpiration.

The length of the growing season for photoperiodically sensitive crops such as soybean is defined by a complex interaction between temperature and photoperiod (Jones and Laing, 1978; Thomas and Raper, 1978, 1983a, 1983b). Nevertheless, the range in genotypic diversity for photoperiodic sensitivity is sufficient for soybean in North America to be cultivated from the long growing season of the southern Cotton Belt to the short frost-free season of southern Canada and worldwide from the tropics of

Table 15-1. Temperature requirements during various stages of soybean development. From Holmberg (1973).

Stage of development	Temperature range		
	Minimum	Adequate	Optimum
	°C		
Germination	6-7	12-14	20-22
Emergence	8-10	15-18	20-22
Formation of reproductive organs	16-17	18-19	21-23
Flowering	17-18	19-20	22-25
Seed formation	13-14	18-19	21-23
Ripening	8-9	14-18	19-20

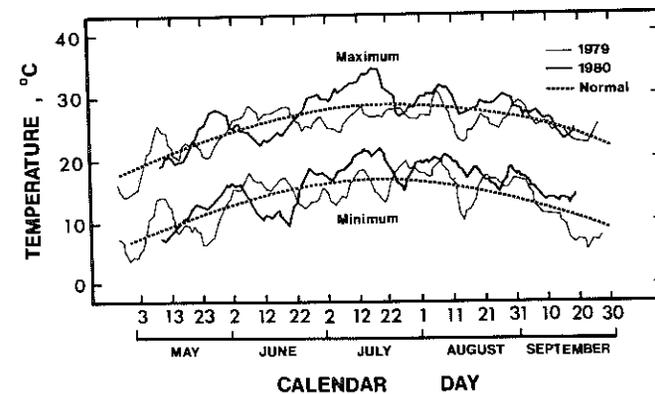


Fig. 15-1. Seven-day moving averages of daily maximum and minimum air temperatures for middle day of period for May through September 1979 and 1980, and normal maximum and minimum temperatures for 1953 to 1979, for West Lafayette, IN. From Dale (1983).

Brazil to subarctic Sweden and Siberia. Given the range of photoperiodic diversity within soybean for time of flowering and maturation, length of the frost-free growing season may be less of a determinant for acceptable production areas than other temperature characteristics of climate. For example, in Oregon the frost-free season is long enough but low night temperatures limit bean yields (Seddigh and Jolliff, 1984).

15-1.1 Seed Germination

Soybean seed generally will germinate between 10 and 40°C (Mederski, 1983) and seed of the more chill-tolerant cultivars such as Fiskeby V and 'Amurakaja 310' will germinate at temperatures of 6 to 8°C (Holmberg, 1973). There is at least one report of germination at 2 to 4°C (Inouye, 1953). Although there are interactions between temperature and both cultivar and depth of planting on rate of emergence (Grabe and Metzger, 1969), the most rapid emergence generally occurs at 25 to 30°C (Mederski, 1983). Final emergence is not greatly affected at temperatures between 16 and 32°C (Stuckey, 1976). The slower emergence at low temperatures, however, increases the probability of injury to seedlings from fungi and insects. Especially when seed are planted deeply, low temperatures decrease the ability of seedlings to overcome the mechanical resistance of soil (Tanner and Hume, 1978).

Little has been published on the physiological basis for slow germination of soybean seed at low temperatures. Perhaps it can be explained by the slow rate of enzyme-mediated processes involved in respiration and hydrolysis of food reserves and the slow rates of translocation of metabolites at low temperatures. However, Arrhenius plots for enzyme systems extracted from germinating seed are quite different from those for seed germination and seem to refute all the usual explanations for poor germination at low temperature except the possibility of protein denaturation (Simon, 1979). Seed germination involves activity of a wide range of enzymes, and it is not surprising that the composite result fails to fit the curve for simple enzyme systems. The extensive injury to membranes that often occurs when seeds imbibe water at low temperatures (Chabot and Leopold, 1982; Leopold, 1980) also may be a factor in poor germination and subsequent poor growth of soybean in cold soil (Hobbs and Obendorf, 1972).

15-1.2 Vegetative Growth

Late frosts can cause freezing injury to soybean seedlings. While seedlings were not killed at -4°C, seedlings of several soybean cultivars were killed with brief exposure to -6°C (Abel, 1970). Chilling injury, however, can be caused by less extreme temperatures. In reviews by McWilliam (1983) and Wilson (1983), many examples are cited of injury to plants of tropical and subtropical origin, including soybean, by exposure to temperatures between 10 and 15°C. The degree of injury de-

pends on the severity and duration of exposure to low temperature and on the level of irradiation during exposure. Plants can withstand lower temperatures without injury to chloroplast ultrastructure during darkness at a high humidity than during exposure to light (Wise et al., 1983). Since the extent of chilling injury was aggravated in darkness as well as in light by a lowered humidity (Wise et al., 1983), the involvement of light in susceptibility to chilling injury may be at least partly associated with promotion of leaf water deficits.

There is scant doubt that water stress is involved in chilling injury. There is uncertainty, however, about the importance of the reduction in water absorption caused by chilling. Taylor and Rowley (1971) concluded that the direct effects of chilling on photosynthesis and the indirect effects from inhibited water absorption are about equally important. While low root temperatures certainly inhibit water absorption (Fig. 15-2), shoot chilling has more serious effects than root chilling on growth (Musser et al., 1983a). When root-zone temperature was maintained at 25°C, chilling shoots of 2-week-old soybean at 10°C for 1 week resulted in temporary reduction in leaf water potential, leaf elongation, rate of leaf emergence, stomatal conductance, and CO₂ uptake (Table 15-2). All of these characteristics returned to control levels after rewarming. Root chilling had smaller effects on the vegetative characteristics than shoot chilling, and simultaneous root and shoot chilling resulted in no more injury than

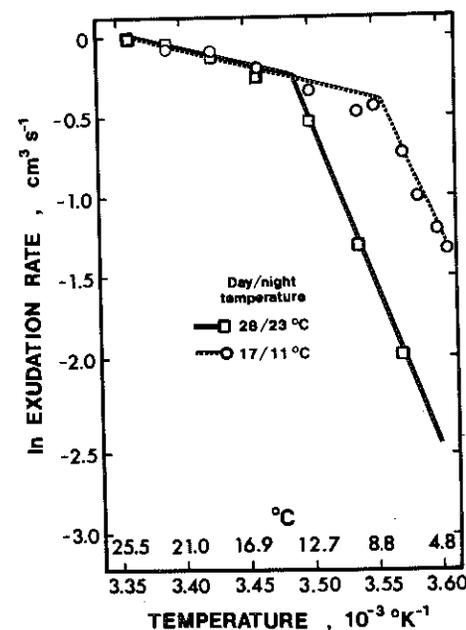


Fig. 15-2. An Arrhenius plot of water flow through excised soybean roots under pressure for root systems grown at day/night temperatures of 28/23 and 17/11°C. From Markhart et al. (1979).

Table 15-2. Physiological responses of Ransom soybeans to 7 days of root or shoot chilling during vegetative growth. From Musser et al. (1983a).

Physiological processes	Chilling treatment		
	Control, 25°C	Root chilled to 10°C	Shoot chilled to 10°C
Time between emergence of leaves, days	1.7	2.0	3.7
Rate of leaflet elongation, mm day ⁻¹	18.7	10.1	3.7
Leaf water potential, MPa	-0.8	-0.9	-0.3
Leaf osmotic potential, MPa	-1.1	-1.0	-1.8
Leaf turgor potential, MPa	0.2	0.1	1.6
Abaxial stomatal conductance, cm s ⁻¹	1.5	0.2	0.3
Carbon dioxide uptake rate, % of control	—	70	40-45

shoot chilling alone. It appears that vegetative growth can recover from short periods of chilling with a minimum of injury.

The opinion that a night temperature lower than the day temperature is favorable for growth of most plants (Went, 1953) is questionable as a generality. Vegetative growth of soybean at a mean daily temperature of 23°C was altered little whether the mean temperature was achieved by day/night temperatures of 26/20 or 29/17°C or kept constant at 23/23°C (Warrington et al., 1977). Apparently, if a constant day and night temperature is near the optimum for the plant, warm days and cool nights provide no additional benefits for vegetative growth. If, however, net photosynthesis during the day is limited by above optimum temperature or low radiation levels, a cooler night temperature can partially compensate for the reduced carbon fixation rate by the lowered respirational loss of carbon (Wann and Raper, 1979, 1984). But while these simple relationships with temperature may apply during vegetative growth, the interactions between temperature and photoperiod on reproductive morphology and physiology of soybean plants have a more complex relationship with growth (Thomas and Raper, 1978, 1983b; Thomas et al., 1981).

Growth of a plant involves numerous processes with different optimum temperatures, and the optimum temperature for growth of the whole plant can be quite different from that for individual processes. For example, photosynthesis of individual soybean leaves increases with increasing temperature to between 35 and 40°C and then begins to decline (Hofstra and Hesketh, 1969), while respiration usually continues to increase with temperature above the optimum for photosynthesis (Ormrod, 1964). Yet, dry matter accumulation in the whole plant begins to decline as air temperature increases above about 28 to 30°C (Raper et al., 1977; Wann and Raper, 1979). The lower temperature optimum for growth of the whole plant probably is a result of the complex behavior at different levels of plant organization and of imbalances among different physiological processes (Gold and Raper, 1983). For example, increasing temperature affects dry matter accumulation on the morphological level

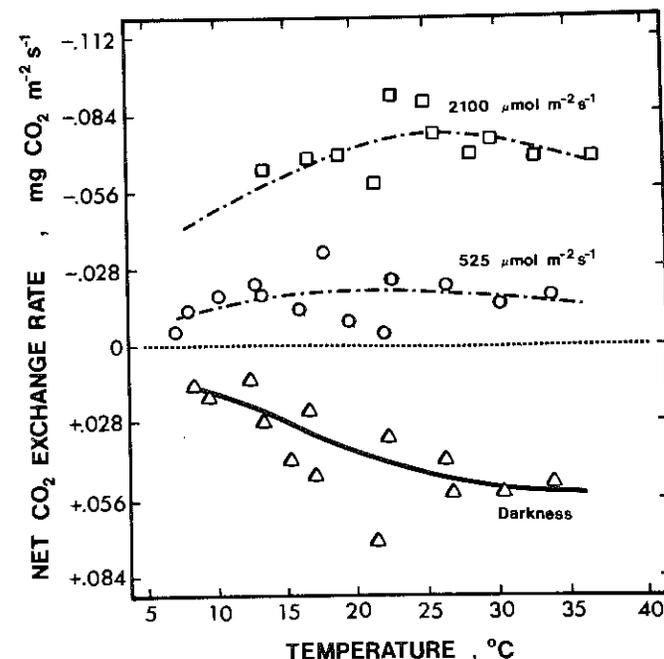


Fig. 15-3. Effects of temperature on CER of 30-day-old bean plants at 31.4 and 125 klux (about 525 and 2100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and in darkness. From Ormrod (1964).

through both direct effects on leaf initiation (Thomas and Raper, 1976) and indirect effects of increased leaf water deficits on leaf expansion (Hsiao, 1973) as well as on the metabolic level of photosynthesis and respiration. The effects of temperature at the morphological level of leaf initiation and expansion are irreversible and occur on a time scale of hours or days while on the level of physiological processes such as photosynthesis and respiration, responses often are reversible on a time scale of seconds or minutes. Moreover, within the same level of organization, physiological processes such as photosynthesis and respiration have different Q_{10} values (Wann and Raper, 1979). For example, dark respiration rate continues to increase with temperature beyond the temperature for maximum rate of photosynthesis (Fig. 15-3). It seems unlikely that the explanation of differences in high temperature responses of plant growth will be found by research only at the subcellular or molecular level.

Changes in temperature affect growth through altered partitioning of photosynthate between organs (Wann and Raper, 1984). Translocation rates of organic compounds in the phloem, however, are relatively insensitive to temperatures above 10°C (Wardlaw, 1974; Wardlaw and Bagnell, 1981). Localized chilling of stems of *Phaseolus vulgaris* (L.) at about 10°C does not directly inhibit the driving force of translocation, but results in damage to the cytoplasm lining the sieve tubes to cause blockage of sieve plates (Giaquinta and Geiger, 1973) or damage to the cytoplasm

of companion cells (Geiger, 1976; Gunning and Robards, 1976). Translocation rates thus are not directly dependent on temperature within the growing range, but rather can be considered to be responsive to temperature indirectly through the effects of temperature on photosynthetic and respiration rates that affect concentration of soluble carbohydrates in the source pool and the size and metabolic activity of the receiving (sink) organ (Wann and Raper, 1984). For example, low temperature reduces translocation of photosynthate into soybean seed both by decreasing unloading into the seed coat and by reducing embryo growth (Thorne, 1982).

Most studies of the relationship between temperature and growth, at least after seedling emergence, are based on aerial temperatures. Since seasonal changes in soil temperature at depths of 10 cm or more usually lag somewhat behind air temperature, surface soil is usually cooler than the air in the spring and warmer in the autumn. Mederski (1983) reported several experiments indicating that a root temperature of about 25°C resulted in maximum nodule development and plant growth. Since average soil temperature at a 10 cm depth usually is below 25°C in northern Ohio until mid-July (Mederski, 1983), soil temperatures may be below the optimum during much of the growing season in a considerable part of the production areas for soybean. In most experiments in controlled environments, soil and air temperatures are varied simultaneously; however, the effects of root and shoot chilling on growth may be quite different (Table 15-2). Shoot dry weight of 'Bragg' soybean grown for 37 days at a soil temperature of 15°C was less than that at 30°C (Trang and Giddens, 1980), and the vegetative dry weight of 'Wells' soybean dependent on N₂ fixation was 10 times greater after 63 days at a root temperature of 20°C than at 13°C for a 28/21°C aerial temperature (Duke et al., 1979). This temperature effect probably involved both a delay in establishment of functional nodules and a reduction in nodule activity (Jones et al., 1981; Raper and Patterson, 1980). However, for hydroponically grown Ransom soybean supplied with adequate nitrate, vegetative dry weight after 26 days was reduced 20% for plants grown at a root temperature of 18°C relative to 24°C (Rufty et al., 1981). The plants demonstrated a capability for acclimation to the cool root temperature since relative growth rates during the latter part of the experimental period were similar at both 18 and 24°C.

Low root temperatures cause immediate reduction in water absorption, development of water stress (Musser et al., 1983a), and reduction in rate of leaf expansion (Table 15-2). At temperatures of 20 and 14.5°C, water flow through excised root systems under pressure was only 60 and 30%, respectively, of that measured at 25°C (Markhart et al., 1979). Thus, even moderate cooling of the soil early in the growing season might cause enough water stress to reduce leaf expansion. That there is some acclimation of root functioning at low temperatures is evident from the occurrence of a distinct break in Arrhenius plots (Fig. 15-2) of water flow under pressure at about 14°C for soybean grown at 28/23°C and at 8.7°C for soybean grown at 17/11°C (Markhart et al., 1979). The acclimation

root systems kept at low temperatures for several days apparently is associated with an increased proportion of unsaturated fatty acids of new roots developed during exposure (Markhart et al., 1980; Osmond et al., 1982). Since acclimation may require several days, sudden cooling of the soil can produce severe water stress in shoots. The effects of root chilling are temporary, however, and no permanent damage results (Musser et al., 1983a).

The decreased flow of water through chilled root systems will decrease that fraction of ion uptake that depends on mass flow to reach the root surface. Both Clarkson (1976) and Markhart et al. (1979), however, found that activity of the ion pump responsible for transport of ions into the xylem increased with low temperatures in slowly transpiring plants. Acclimation of uptake rates of nutrients occurs with the production of new roots during exposure to cool root temperatures (Osmond and Raper, 1982; Osmond et al., 1982; Rufty et al., 1981). The reduction in rate of shoot growth that accompanies cool root temperatures, at least partly in response to water deficits, temporarily reduces the requirement for mineral nutrients before roots acclimate. A similar case may be made for N₂ fixation. While low root temperatures reduce nodule formation and activity (Lindeman and Ham, 1979), as well as shoot growth, nodules are developed and shoot growth recovers as roots are warmed (Duke et al., 1979). A greater potential problem is posed when stimulation of shoot growth by high aerial temperature results in a N requirement of seedlings that exceeds cotyledonary reserves or soil supply before active nodules are formed (Jones et al., 1981). The resulting N stress, with reduced leaf production and plant growth, may be exaggerated if soil temperatures remain cool and further delay nodule activity.

15-1.3 Reproductive Growth

The effects of temperature on flowering and pod and seed development have received less attention than the effects of photoperiod. Several studies, however, have shown important interactions between temperature and photoperiod with respect to both flowering and pod set. More flowers and pods occurred on Ransom soybean grown at day/night temperatures of 26/22 and 22/18°C than on those grown at 30/26 and 18/14°C (Thomas and Raper, 1977). In fact at 18/14 and 30/26°C very few pods were set although the plants flowered profusely, suggesting that both low and high temperatures resulted in pod abortion. Plants at the intermediate temperatures produced both more nodes and axillary branches and more flowers and pods per node. Similarly, a delay in photoinduction of flowering permits greater production of nodes and branches, leading to increased numbers of pods and seed yield (Patterson et al., 1977; Thomas and Raper, 1977).

Temperatures below 15°C prevent pod formation on many soybean cultivars, although some can set pods at temperatures as low as 10°C (Hume and Jackson, 1981). Based on 10 yrs of observations, Holmberg

(1973) reported that a mean temperature of about 17°C during and after flowering is required for good flowering and pod set of cultivars grown in Sweden. However, varieties from the east coast of Hokkaido and the islands of the Okhotsk Sea, as well as some of their descendents such as Fiskeby V, have a somewhat lower minimum temperature.

Temperature has separate effects on floral induction and pod development. 'Chippewa' soybean grown in cool locations flower profusely, but set few pods (Soldati and Keller, 1977). When day or night temperatures were 10 to 14°C following application of an inductive photoperiod, floral initiation and anthesis occurred for Ransom, but no pods were set (Thomas and Raper, 1977, 1978, 1981). A chilling temperature of 10°C applied during the 1st week of inductive photoperiod reduced the number of floral primordia 22% and delayed anthesis by a week (Musser et al., 1983b). Chilling during either the 2nd or 3rd week of induction also delayed anthesis by a week, but had no effect on the number of floral primordia produced. Regardless of which week chilling stress was applied, number of pods was less than for control plants. Reduced production of pods for plants chilled during the 1st week of reproductive development was associated with reduction in number of floral primordia, while the reduction in pods of plants chilled during the 3rd week was associated with increasing flower abortion. Chilling at anthesis during the 4th week of inductive photoperiod also caused flower abortion and reduced pod set. In rice (*Oryza sativa* L.), chilling injury at temperatures below 15°C results from male sterility caused by damage to developing pollen grains (Lin and Peterson, 1975; Nishiyama and Sataka, 1979). Chilling also causes male sterility in sorghum (*Sorghum bicolor* L. Moench) (Brooking, 1976). In soybean, however, pollen is formed between 2 and 3 weeks after initiation of the floral primordium (Kato et al., 1954). Since chilling during the 3rd and 4th week of induction resulted in flower abortion (Musser et al., 1983b), male sterility cannot be the only cause of flower abortion. Other potential causes of chilling injury need to be investigated.

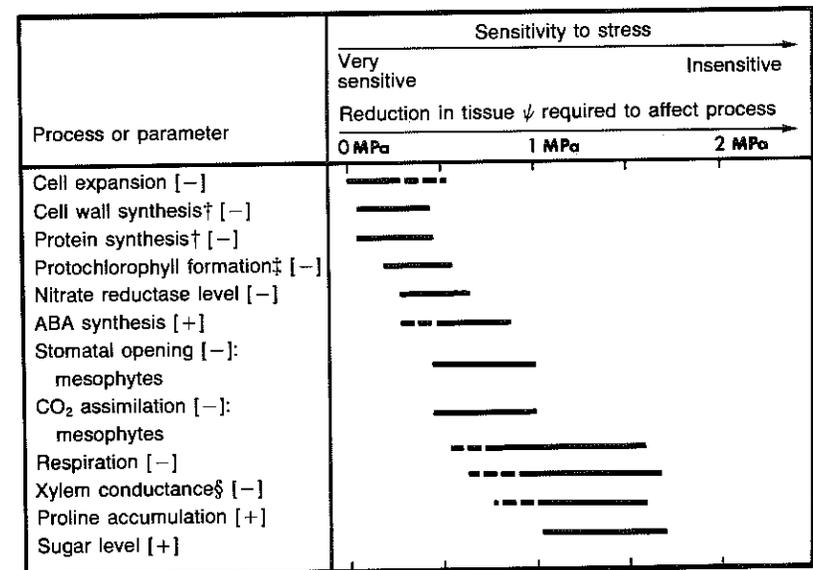
Soybean yields in the field might be affected by both low and abnormally high temperatures. Temperature data (Fig. 15-1) from West Lafayette, IN, indicate several occasions when temperatures below 15°C might have injured reproductive development. Severe abscission of pods occurs in the absence of water stress at 40°C (Mann and Jaworski, 1970). While chilling injury may be more probable in the field than direct injury from such extremely high temperatures, especially in the cooler regions of major production areas (Fig. 15-1), even the relatively mild temperatures of 30/26°C can reduce pod set in Ransom (Thomas and Raper, 1977, 1981).

The effects of temperature during seed maturation can be carried over to the next growing season through altered seed quality. Optimum temperatures for seed ripening are reported (Holmberg, 1973; Sato and Ikeda, 1979) to be within a range of 25°C during the day and 15°C during the night. The higher temperatures that occur during seed ripening of early maturing soybean in midwestern (see Fig. 15-1) and southeastern

regions of the USA can reduce subsequent germination (Green et al., 1965) and may be responsible for wide variations in germinability and seedling vigor from year to year. This view is supported by observations that tobacco (*Nicotiana tabacum* L.) seed matured at temperatures of 22/18 or 26/22°C produce more vigorous seedlings than seed matured at 30/26°C (Thomas and Raper, 1975). But perhaps a more serious problem is frost injury to ripening seed. Danger of injury from frost decreases rapidly as the water content decreases (Judd et al., 1982). Seed in green pods, which contain about 650 g kg⁻¹ of water, are injured at -2°C while seed in brown pods, which contain 350 g kg⁻¹ of water, are not injured at -12°C. Injury by both high temperatures and frost may involve interference with synthesis of specific proteins formed during slow drying in the late stages of seed development (Adams et al., 1982, 1983).

15-2 WATER STRESS

Water stress can be caused either by an excess of water that injures root systems by deficient aeration or by a deficit in available soil moisture that results in dehydration of the shoots. Water stress, whether caused by flooding or drought, affects every aspect of plant growth, including the anatomy, morphology, physiology, and biochemistry (Fig. 15-4). Severity of water stress varies from transient midday reductions in cell and leaf expansion and temporary reduction in stomatal conductance, to



† Fast-growing tissue. ‡ Etiolated leaves. § Should depend on xylem dimension.

Fig. 15-4. Approximate sensitivity to water stress of a number of plant processes. From Hsiao (1973).

physical disruption of chloroplast structure accompanied by reduced photosynthesis and growth, and finally to death from tissue dehydration. Water stress at every stage of plant development can reduce yield directly or indirectly, but the extent of yield reduction from water stress varies with stage of development. This is particularly true of the brief and randomly occurring periods of drought or flooding that characterize the major production areas of midwestern and southeastern USA.

15-2.1 Seed Germination

The process of germination requires imbibition of water and is accompanied by a high rate of respiration. Excessive soil moisture limits the oxygen available for the respiratory processes of germination. A combination of cold soil and excess water may be especially damaging to germination and emergence. Cell membranes of seeds allowed to imbibe water at low temperature can be injured (Bramlage et al., 1978; Chabot and Leopold, 1982; Willing and Leopold, 1983), and immersion of soybean seed in cold water for periods as short as an hour results in reduced germination and seedling growth (Hobbs and Obendorf, 1972; Simon, 1979).

Germination and emergence are reduced more often by dry soil than by flooding. The water content of soybean seeds must reach about 500 g kg⁻¹ of dry weight to insure germination, in contrast to corn seeds which require only about 300 g kg⁻¹ (Hunter and Erickson, 1952). Seeds planted in soil that is too dry for germination often absorb enough water to be invaded and damaged by soil fungi. The data on the soil water potential limiting seed germination are unsatisfactory because of differences in terminology and methods. For example, Hanks and Thorp (1957) reported that when the soil water content was one-half of field capacity in a fine sandy loam emergence of soybean, wheat, and grain sorghum seedlings was reduced below emergence when the soil was at field capacity; however, they provided no data on soil water potential. Hunter and Erickson (1952) reported that soybean germinated at a soil moisture tension of -0.6 MPa, while corn germinated at -1.25 MPa. In contrast, Heatherly and Russell (1979) reported that an acceptable rate of emergence was not obtained below -0.06 MPa in a silt loam nor below -0.07 MPa in a fine clay soil. Seed germination is influenced both by the soil water potential and by the area of contact between seed and soil, which increases with decreasing particle size (Collis-George and Hector, 1966). This may contribute to the inconsistency among reports. Also, emergence of germinated seedlings in drying soil is hindered by formation of a surface crust (Hanks and Thorp, 1957).

15-2.2 Vegetative Growth

Plant growth depends on the photosynthetic rate per unit leaf area, the total leaf area available for photosynthesis, and leaf area duration.

These and other processes are affected by water stress (Fig. 15-4). Thus total photosynthesis of water-stressed plants is decreased by reductions in rate of carbon fixation per unit leaf area resulting from premature stomatal closure and nonstomatal inhibition of the photosynthetic machinery, and by reductions in photosynthetic surface area caused by decreased leaf enlargement and hastened leaf senescence. Stomatal conductance and rates of photosynthesis and transpiration decrease simultaneously in water-stressed soybean (Fig. 15-5). There is, however, discussion about the extent to which stomatal closure reduces photosynthesis vs. the possibility that nonstomatal reduction in photosynthesis causes closure of stomata in water-stressed plants (Farquhar and Sharkey, 1982). The large decrease in stomatal conductance reported (Bunce, 1978a) for soybeans at 40% relative humidity without any reduction in net photosynthetic rate indicates that stomatal closure can occur independently of photosynthetic rate.

Leaf water potentials lower than -0.5 MPa seem to affect chlorophyll formation (Alberte et al., 1975, 1977) and at about -1.0 MPa cause disorganization of chloroplast structure (Mohanty and Boyer, 1976; Vieira da Silva et al., 1974). This reduces electron transport and both cyclic and noncyclic photophosphorylation and decreases activity of ribulose biphosphate carboxylase and other important enzymes involved in carbon assimilation. The effects of water stress on photosynthetic rates of soybean leaves are readily detectable at leaf water potentials of about -1.0 to -1.2 MPa (Boyer, 1970a; Boyer et al., 1980, Cure et al., 1983). Photosynthetic rate declines rapidly with further reductions in leaf water potential to about -1.8 MPa, and then continues to decline gradually with decreasing potential (Fig. 15-5 and 15-6). The effects of water stress on photosynthetic rate are reversible down to leaf water potentials of about -1.6 MPa or less in growth chamber conditions when other environmental stresses are absent (Cure et al., 1983; Mohanty and Boyer, 1976).

Respiration also decreases with leaf water potential, but in a different pattern than photosynthesis (Fig. 15-7). Dark respiration rate declines from about -0.6 to -1.6 MPa, then remains unchanged to the most severe stress imposed of -4.0 MPa. From these data it appears that photosynthesis is decreased more by water stress than is respiration, and

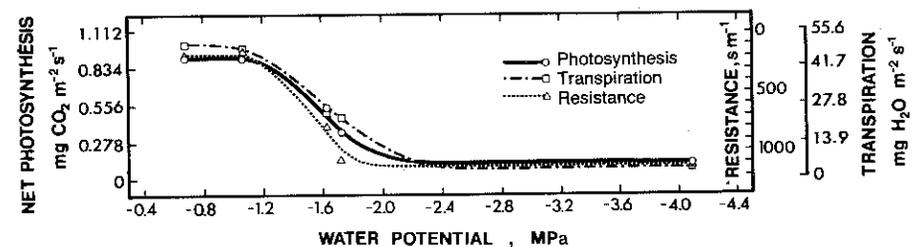


Fig. 15-5. The relationships among leaf water potential, photosynthesis, transpiration, and stomatal resistance in soybean. From Boyer (1970a).

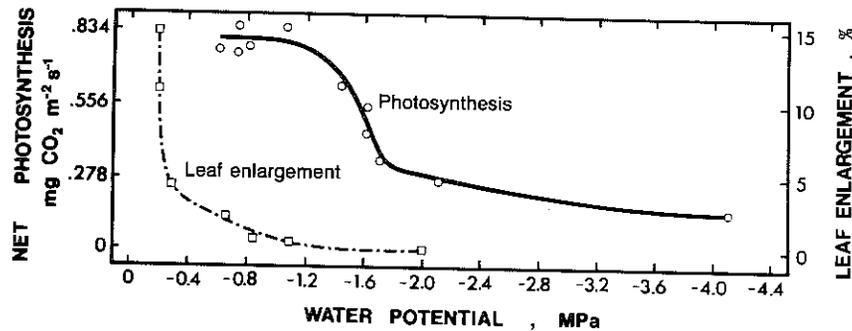


Fig. 15-6. The relationships among leaf water potential, leaf elongation, and photosynthesis of soybean. From Boyer (1970b).

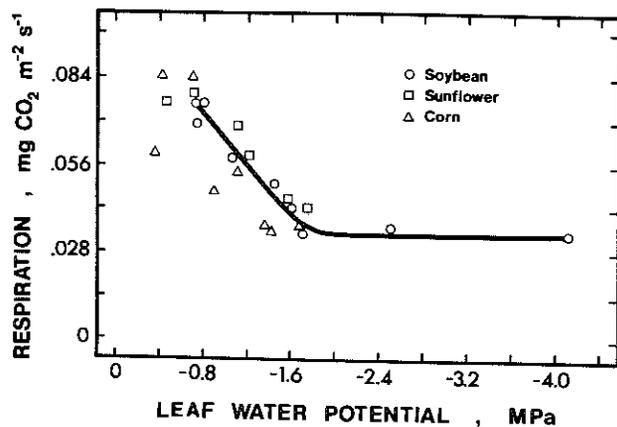


Fig. 15-7. Effect of decreasing leaf water potential on the rate of dark respiration of soybean, sunflower, and corn. From Boyer (1970b).

high temperatures have a greater impact than water stress on respiration (Fig. 15-3).

Translocation continues at water stresses lower than those inhibiting photosynthesis. Wardlaw (1974) concluded that the velocity of translocation is not greatly reduced until water potential drops as low as -2.0 to -3.0 MPa. This conclusion has been contested (see Ashley, 1983); however, the direct effects of water stress on translocation are difficult to determine. While velocity may be unaltered by leaf water potentials in the range of -1.0 to -2.0 MPa, the inhibition of photosynthesis in this range (Fig. 15-5 and 15-6) greatly reduces the amount of assimilate available for translocation (Silvius et al., 1977). Also, water stress directly shifts partitioning of assimilates between shoot and root by altering the relative size and activity of these sinks. Sharp and Davies (1979) observed with corn seedlings grown in pots that the proportion of total dry matter translocated to roots was increased during a single drying cycle, and also during the middle of the drying cycle the dry weight and length of roots

were greater for stressed than for well-watered plants. Although decreases in stomatal conductance and leaf and root water potentials of the seedlings coincided with the decline in substrate water potential during the interval of enhanced root growth, root osmotic and total water potentials fell in unison; thus, root turgor remained nearly constant so that root expansion continued in the drying substrate. Other data (Eavis and Taylor, 1979; Hsiao and Acevedo, 1974; Osmond and Raper, 1982) also can be interpreted to indicate an absolute increase in translocation of assimilates to roots during a slight moisture stress in the shoot.

The importance of water stress in altering size of cells and tissues often is underestimated relative to the direct effects on metabolic activity. Cell and leaf expansion are more sensitive to water stress than is photosynthetic rate (Fig. 15-4 and 15-6), and in fact a decrease in rate of leaf enlargement usually is the first visible evidence of developing water deficit. Thus, a slight stress of -0.2 to -0.8 MPa that does not affect the current photosynthetic rate can have a long-term impact on plant growth, especially if the stress occurs early in development, by irreversibly reducing total leaf area available for photosynthesis. The interrelationships among leaf water potential, leaf expansion, and photosynthesis are discussed by Bunce (1977, 1978a).

Cell expansion generally is assumed to be closely correlated with turgor pressure, and it is true that some minimum turgor pressure is necessary for cell expansion (Cleland, 1971). Above the threshold value, however, cell expansion is not necessarily closely related with turgor, and the relationship between plant water status and cell expansion often seems complex. Cell expansion depends on biochemical factors affecting extensibility or modulus of elasticity of cell walls and on physical factors controlling diffusion of water into cells. The influx of water into cells is dependent on a gradient of decreasing water potential toward the growing region, which in turn depends on a supply of solutes to the expanding cells. It is possible for the turgor pressure to be similar in growing and nongrowing tissues if the osmotic and water potentials are lower in the growing tissue (Cavaliere and Boyer, 1982). Since water potential becomes zero in fully turgid cells, preventing further influx of water, cell enlargement should be increased by slight loss of turgor. In fact, Bunce (1977) observed larger soybean leaves with larger epidermal cells under conditions where mild water stress developed than under conditions which did not produce measurable water stress. More severe stress reduced the size of epidermal cells and leaves.

Soybean shoots grow more at night than during the day, but roots grow more during the day (Bunce, 1978b). This probably is because they are less subject to daytime water stress than the shoots (Sharp and Davies, 1979). Roots maintain a higher turgor than leaves during the day. Thus, during the day when leaf expansion is limited by the lowered leaf-water potential, photosynthates are more readily available for translocation to roots. At night stomatal closure relieves leaf water stress, resulting in increased turgor and more cell expansion, and the shoots become stronger

sinks for carbohydrate than the roots, resulting in reduced root growth. In contrast to the low leaf expansion during the day for soybean grown in controlled environments (Bunce, 1978b), leaves of rice enlarged more during the day when turgor was low than at night when it was high (Cutler et al., 1980). The reduction in enlargement at night was related to lower temperatures at night, and when night temperatures were raised to approach day temperature, leaf enlargement at night was increased. Chilling temperatures can decrease leaf expansion of soybean even though the turgor of chilled leaves remains high (Table 15-2).

Water stress reduces N_2 fixation. Since a very close association exists between leaf-water potential, photosynthetic rate, and acetylene (C_2H_2) reduction activity of intact soybean plants subjected to a single cycle of water stress and recovery (Huang et al., 1975a, 1975b; Patterson et al., 1979), part of the reduction can be attributed to reduced availability of photosynthate for translocation to the nodules. Part of the reduction in N_2 fixation by water stress is a direct effect on water potential within the nodules. Dinitrogen fixation activity of nodules is reduced as water potential decreases (Huang et al., 1975a, 1975b) and ceases irreversibly in detached nodules when fresh weight drops below about 80% of the fully turgid weight (Sprent, 1971). Perhaps the physical alterations of nodules caused by water stress (Parkhurst and Sprent, 1975) are responsible for the delayed recovery of nodule activity upon rewatering relative to recovery of either photosynthetic activity of leaves (Huang et al., 1975b) or energy charge of the adenylate pool of the nodules (Patterson et al., 1979).

15-2.3 Reproductive Growth

The reproductive stage of plant growth is particularly sensitive to water stress (Begg and Turner, 1976), and soybean is no exception (Doss et al., 1974; Martin et al., 1979). A major portion of the variation in soybean yield can be attributed statistically to seasonal variations in rainfall during flowering and fruiting (Runge and Odell, 1960; Thompson, 1970). The extent of yield reduction from a single incident of water stress increases as the reproductive stage advances toward maturity (Table 15-3). The component of yield associated with the reduction also changes from number of seeds and pods for a stress during flowering and early pod-fill stages to size of seed for a stress during seed fill (Constable and Hearn, 1978; Martin et al., 1979; Sionit and Kramer, 1977).

Abscission of flowers, pods, and seeds of water-stressed plants, as well as the later reduction in seed size, may be at least partially a response to water stress through the effects of leaf water deficits on photosynthetic rates that decrease the concentration of assimilates in vegetative pools. Phloem transport to abortive flowers of European blue lupine (*Lupinus angustifolius* L.) is reduced several days before abscission occurs and these flowers accumulate less ^{14}C -labeled assimilate from leaves than flowers that progressed to pods (Pate and Farrington, 1981). Certainly translo-

Table 15-3. Effects on vegetative and seed weight at maturity of withholding water at various growth stages until plants were stressed to a leaf water potential of -2.3 MPa before rewatering. From Sionit and Kramer (1977).

Stage when stressed	Time after emergence days	Vegetative	Seed
		dry weight	air-dried weight
		g plant ⁻¹	
At flower induction	30	65.6	46.9
During flowering	44	76.1	49.8
Start of pod formation	57	80.4	36.5
During seed filling	65	84.6	32.5
Unstressed control	—	89.9	58.5

cation to reproductive sinks should be responsive to the decrease in assimilate concentration of vegetative pools that occurs during water stress (Cure et al., 1985). If the stress is relieved prior to seed filling, photosynthesis can recover, growth can resume, and the remaining seeds can continue to develop to normal size (Patterson et al., 1979; Sionit and Kramer, 1977). If, however, photosynthesis is reduced by short periods of water stress in the range of -1.0 and -1.6 MPa after pod and seed set, size of the reproductive sink demand is not adjusted during the stress period (Cure et al., 1985). The associated reduction in rate of N_2 fixation, that even in the absence of stress is exceeded by the rate of N accumulation in seed, results in an increased rate of N remobilization from leaf pools (Cure et al., 1985). As a consequence, during a late-season water stress N in leaves can be reduced below the concentration necessary for maintenance of photosynthetic capacity, the period of seed filling abbreviated, and weight per seed reduced (Boote et al., 1978; Cure et al., 1985).

15-3 LIGHT

Light affects plant growth chiefly through photosynthesis and photomorphogenesis. While the flux of radiation within the photosynthetically active range of the spectrum is of primary importance in growth and yield of plants, the effect of light on plant form, and hence on distribution of photosynthetically fixed carbon, cannot be ignored. Included among pigment systems known to be involved in photomorphogenic responses are phytochrome, β -carotene, and riboflavins. The involvement of the phytochrome system in photoperiodic regulation of reproductive development, however, is the most studied of these photomorphogenic systems and is a major influence altering growth and soybean yield.

15-3.1 Photosynthetically Active Radiation

Total energy entering the plant system is dependent in part on the maximum photosynthetic rate per unit leaf area and in part on interception of photosynthetically active radiation (PAR) by the total leaf area

of the plant. While the maximum photosynthetic rate depends on age and N level of the leaves, water status, temperature, and CO_2 concentration, interception of PAR is affected both by flux density of radiation above the canopy and distribution within the canopy. For field-grown soybean, most radiation is intercepted by leaves near the surface of the canopy (Sakamoto and Shaw, 1967a). While increased vertical orientation of leaves (Duncan, 1971) can enhance interception of radiation at leaf area indices (LAIs) (leaf area per unit ground area) greater than about 3.0, dry matter production by field-grown soybean reaches a maximum as LAI approaches 4.0 (Shibles and Weber, 1965). A LAI of 4.0 normally occurs late in vegetative growth. During much of the vegetative growth phase, photosynthesis can be limited by periods of reduced radiation as well as by factors such as temperature and water stress that both reduce the rate of leaf expansion and limit maximum photosynthetic rate. Although photosynthetic efficiency declines as leaves age even in an open canopy, photosynthetic efficiency of each successive newly expanded trifoliolate remains high (Fig. 15-8). Increases in leaf number after a LAI of 4.0 is attained thus may contribute to continued high levels of canopy photosynthesis until vegetative growth ceases.

Once the canopy of soybean is closed, photosynthetic rates measured for individual leaves (Sinclair, 1980) or the whole canopy (Sakamoto and Shaw, 1967b) of field-grown soybean do not respond to increases in diurnal radiation above about 50 to 60% of the maximum noon-time solar radiation during the summer months. This plateau probably is influenced by the midday deficits in leaf water potential that are associated with

excessive transpiration and are common even when soil moisture is readily available (Boyer et al., 1980; Jung and Scott, 1980). Whether or not the plateau in photosynthetic response represents light saturation, photosynthetic photon flux density does not appear to be the limiting factor for photosynthetic performance of field-grown soybean for much of the day. In controlled environments, however, net CO_2 exchange rates (CER) of fully expanded upper leaves of soybean were reduced from 0.74 to 0.52 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ when photosynthetic photon flux density was reduced from 700 to 325 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (Ruffy et al., 1981). Over a 4-week period of vegetative growth beginning at the V2 developmental stage, partitioning of the reduced photosynthate under the low radiation level had a synergistic effect on reducing total plant growth and photosynthetic rates. The 30% reduction in net CER when radiation was lowered from 700 to 325 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ resulted in a 55% reduction in leaf area and a 60% reduction in total plant dry matter accumulation. Clearly, periods of reduced radiation during early vegetative development can reduce growth through combined effects of lowered photosynthetic rates per unit leaf area and consequentially reduced rates of leaf area expansion. While photosynthetic rate per unit leaf area following a period of low radiation may be increased as radiation returns to normal levels, delayed canopy closure may still reduce total light interception and vegetative growth.

Intense solar radiation also can be a stress. Increases in leaf temperature of field-grown soybean follow the diurnal pattern of solar radiation, with the differential between leaf and air temperatures increasing during the morning to a maximum at midday and then decreasing in the afternoon (Jung and Scott, 1980). Transpiration rates during the day follow the same diurnal pattern, and during the period of maximum midday solar radiation they often exceed flow rates of water through roots even when availability of soil water is not limiting (Boyer, 1971; Boyer et al., 1980; Ghorashy et al., 1971). The high midday radiation during summer months thus often reduces photosynthetic activity and seed yields by increasing thermal load and transpiration rate of leaves (Boyer et al., 1980).

15-3.2 Photomorphogenic Radiation

Regulation of development by photomorphogenic radiation, particularly by wavelengths in the 660 to 730 nm range that activate the phytochrome system, have a major impact on growth and yield of soybean. During vegetative growth, a low ratio of 660 to 730 nm wavelengths stimulates leaf enlargement and stem and petiole elongation of many species (Downs, 1955; Kasperbauer, 1971; Parker et al., 1949), including soybean (J.F. Thomas and C.D. Raper, unpublished data). Since leaves transmit more 730 than 660 nm radiation, Kasperbauer (1971) has demonstrated with tobacco that as the canopy closes the partially shaded plants within the canopy develop longer internodes and elongated leaves. While such photomorphogenic reactions of plants may enhance inter-

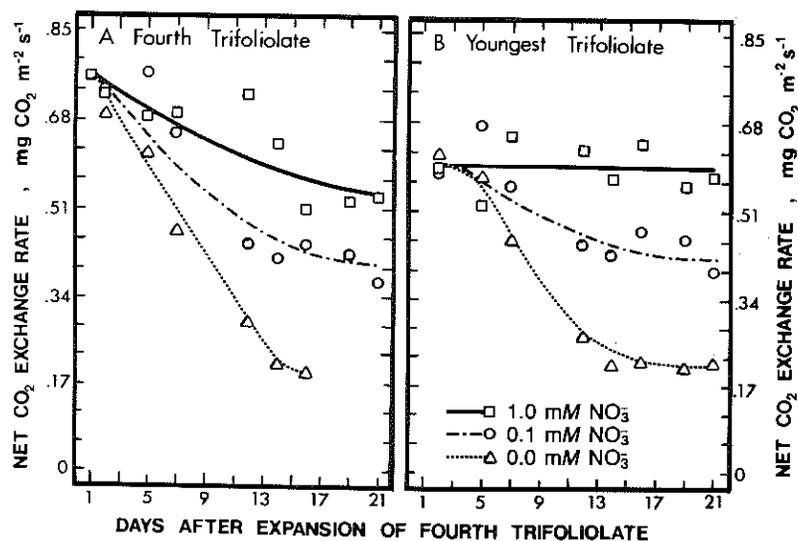
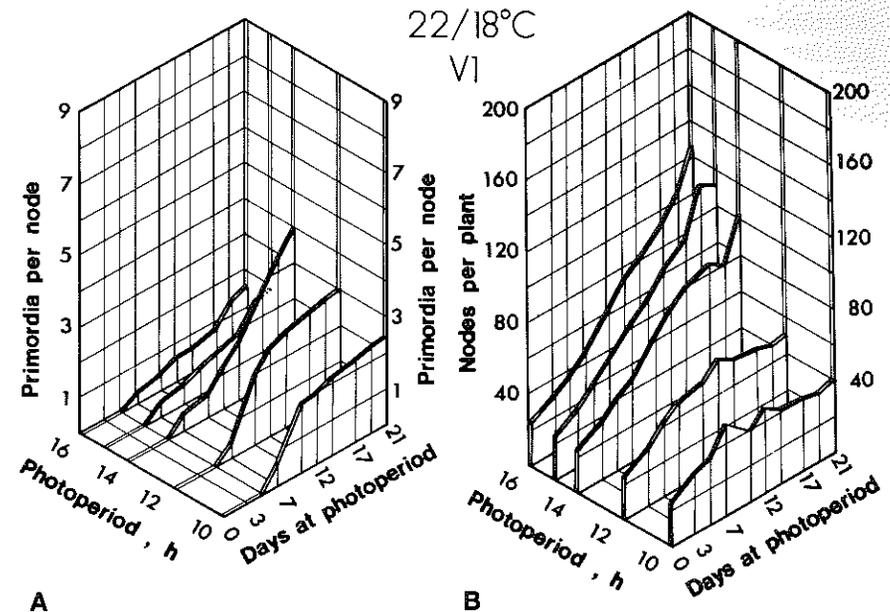


Fig. 15-8. Net CER for soybean at three levels of NO_3^- in hydroponic culture: (A) the fourth trifoliolate leaf measured over a 21-day period after expansion, and (B) the most recently expanded mainstem trifoliolate during the 21-day period. Unpublished data from the study of Ruffy et al. (1984).

ception of PAR as the canopy closes, the photoperiodic reactions of soybean during reproductive development have a greater influence on yield.

Soybean generally is a short-day species, and when all aspects of reproductive development are considered, few cultivars are insensitive to photoperiod (Murfet, 1977). The course of reproductive development after evocation of the flowering response includes as discrete physiological events the initiation of floral primordia, development of floral structures leading to anthesis, embryo and seed development, and seed maturation (Kato et al., 1954). Sensitivity to photoperiod is subject to change throughout reproductive development, and variations in photoperiod have been observed to alter rates of reproductive development both before (Thomas and Raper, 1983a, 1984) and after (Cure et al., 1982; Johnson et al., 1960; Raper and Thomas, 1978; Thomas and Raper, 1976) anthesis.

Of all the reproductive events, floral initiation is perhaps the least sensitive to photoperiod length. The first flower primordia appears almost as soon under a long, 16-h photoperiod as under a short, 10-h photoperiod (Thomas and Raper, 1983a). Subsequent flower development, however, is much slower under long photoperiods, and the time to anthesis is more than doubled (Thomas and Raper, 1983a). Floral initiation always occurs first in a meristem in an axil of a leaf along the mainstem (Borthwick and Parker, 1938b; Nielsen, 1942; Thomas and Raper, 1983a) and then proceeds acropetally and basipetally on the mainstem and out along branches. Given an insufficient number of inductive short days, soybean initiates floral primordia at only a few mainstem nodes while other nodes and the shoot apex continue to initiate only vegetative structures (Borthwick and Parker, 1938b; Nielsen, 1942). In contrast, under continuous 10- and 12-h photoperiods floral initiation in the determinate cv. Ransom occurs quickly, leading within 7 to 10 days to transformation of the terminal shoot apex to its reproductive phase of development (Thomas and Raper, 1983a) and cessation of node production by all meristems (Fig. 15-9). The first discrete floral primordia occurs under long 14- to 16-h photoperiods almost as soon as under 10- to 12-h photoperiods, but floral initiation proceeds much more slowly under long photoperiods and plants retain the capacity for vegetative node production concomitantly with reproductive growth for an extended time (Fig. 15-9). Eventually, plants under the longer photoperiods switch from the dual mode of vegetative and reproductive growth to only reproductive growth, but with a greatly increased number of mainstem (Fig. 15-10) and total (Fig. 15-9) nodes. Along with the slow completion of the floral initiation process under the long photoperiods, time to anthesis of the first flower at a mainstem node of Ransom increased from 28 days at 10- and 12-h photoperiods to 68 days at the 16-h photoperiod, and time to anthesis at the terminal shoot apex increased from 35 to 78 days (Thomas and Raper, 1983a). These results confirm that, while reproductive development leading to anthesis is accelerated with decreasing daylength, the response is quantitative rather than absolute. It also appears from the data for Ransom that the concept of an absolute critical photoperiod, which generally



A **B**
Fig. 15-9. Mean number of (A) floral primordia per node and (B) total nodes per plant produced by Ransom soybeans transferred to 10-, 12-, 14-, 15-, and 16-h photoperiods at the V1 developmental stage and grown for 21 days at 22/18°C day/night temperatures. From Thomas and Raper (1983a, 1984).

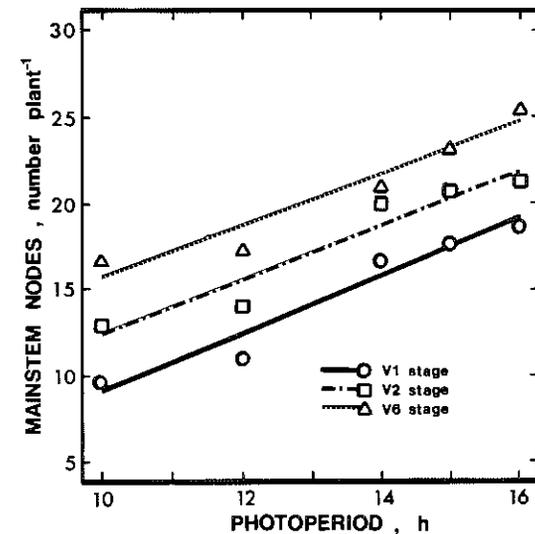


Fig. 15-10. Mean number of mainstem nodes per plant produced during a 21-day period after being transferred to 10, 12, 14, 15, and 16-h photoperiods at V1, V2, and V6 developmental stages. From Thomas and Raper (1984).

is considered as the daylength beyond which floral initiation fails to occur and less than which floral initiation abruptly terminates vegetative development, is misleading for soybean.

Changing daylengths should be considered as gradients of a stress. Although floral initiation may occur at the most undifferentiated axillary meristems (Borthwick and Parker, 1983a) as daylength after planting increases toward the summer solstice, the increasing photoperiods result in deceleration of the floral initiation process and promote continued vegetative development concomitantly with reproductive development. After the summer solstice, however, decreasing photoperiods accelerate completion of floral initiation and cessation of vegetative meristem development. The decreasing photoperiods also are associated with suppressed apical dominance as evidenced by increased internode elongation of branches relative to mainstem of Ransom when photoperiod was reduced from 16 to 10 h (Thomas and Raper, 1983b).

Photoperiod duration during vegetative growth and the transition from vegetative to reproductive growth phase has little direct effect on partitioning of dry matter among leaves, stems, and roots of Ransom soybean (Thomas and Raper, 1983b). Indirectly, however, the increased production of vegetative meristems under longer photoperiods (Fig. 15-9) establishes the potential for differences in dry matter accumulation and partitioning which occur as soybean that were moved from long to short photoperiods at varying ages approach maturity (Raper and Thomas, 1978; Thomas and Raper, 1977). This is emphasized when the effect of photoperiod on rate of continued reproductive development is considered. The successively shorter days that occur during reproductive development after the summer solstice accelerate the rate of seed growth and maturity (Cure et al., 1982; Johnson et al., 1960; Raper and Thomas, 1978; Shibles, 1980). In fact, for several indeterminate cultivars grown under natural photoperiods in field culture, the earlier developing seeds from pods at lower nodes had slower growth rates than seeds from pods set later at upper nodes as photoperiod became shorter (Gbikpi and Crookston, 1981).

Photoperiod has a relatively greater effect on accumulation rate of N than total carbon in seeds. The N concentration in seeds decreases as photoperiod increases (Cure et al., 1982, 1985; Gbikpi and Crookston, 1981). The lower rate of N accumulation by seeds under longer photoperiods is associated with retention of higher concentrations of N in leaves (Cure et al., 1982, 1985) and greatly reduced senescence and abscission of leaves at seed maturity (Cure et al., 1982, 1985; Raper and Thomas, 1978). Conversely, concentration of total nonstructural carbohydrates in leaves during reproductive growth is greater under the shorter photoperiod (Cure et al., 1985). This apparent effect of photoperiod on partitioning of carbohydrate possibly is regulated by activity of sucrose-phosphate synthase that alters the partitioning of photosynthate between nontranslocatable starch and readily translocatable sucrose (Chatterton and Silviu, 1979; Huber et al., 1984; Rufty et al., 1983).

The rapidly declining photoperiods during seed growth in field culture may be involved in the late-season declines in N_2 -fixation activity frequently noted in field experiments (Hardy et al., 1968; Harper, 1974; Klucas, 1974; Lawn and Brun, 1974), but not necessarily in glasshouse (Israel, 1981) or growth chamber (Cure et al., 1985) studies. For nodulated Ransom soybean grown in controlled environments and entirely dependent on symbiotic fixation as the source of N, accumulation of N in the plant continued at near constant rates throughout and after completion of reproductive growth in well-watered plants under both long- and short-day photoperiods (Fig. 15-11). Nitrogen accumulation rates under long- and short-day photoperiods declined rapidly in response to a water stress during early seed filling. However, while the N_2 -fixation rates remained low throughout the remainder of reproductive growth under short-day photoperiods, under long-day photoperiods N_2 -fixation rates recovered after rewatering (Fig. 15-11). The lower rate of N accumulation by seeds under long-day photoperiods apparently averted the depletion of N reserves in vegetative tissues during the stress that occurred under short-day photoperiods (Cure et al., 1985). Conservation of N reserves in leaves

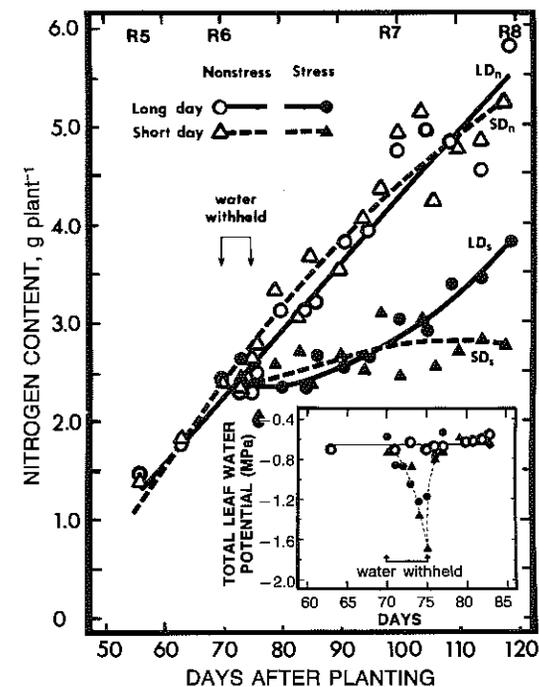


Fig. 15-11. Nitrogen accumulation in the combined vegetative and reproductive organs of the shoots of Ransom soybeans grown under long-day (LD) and short-day (SD) photoperiods after pod set. Half of the plants at each photoperiod were subjected to a single episode of water stress (SD_s and LD_s) at the R6 developmental stage and half were nonstressed controls (SD_n and LD_n). Leaf water potentials are shown in inset. From Cure et al. (1982, 1985).

under long-day photoperiods may explain the ability of plants to more fully recover photosynthetic and N_2 -fixation capacity following a stress. When one considers the transient midday water stresses that occur even in well-watered plants in field culture (Boyer et al., 1980), but not necessarily in glasshouses or growth chambers, the interaction between stress-reduced photosynthetic capacity and the enhanced N partitioning to seeds by decreasing daylengths may explain late season declines in N_2 fixation in field culture.

It has not been established whether the photoperiodic signal alters partitioning during seed growth by affecting the export from the source leaves or import by reproductive tissues. The embryo itself is responsive to photoperiod under *in vitro* culture; however, in contrast to the response observed for seeds in attached pods, growth rates of *in vitro* cultured embryos increased as photoperiod increased (Raper et al., 1984). Several explanations are possible for this contrast. One could be that photoperiod directly alters source activities or growth regulator production in leaves (Cure et al., 1982). Another could be that regulation of substrate transport from pod to embryo through the seed coat is subject to photoperiodic regulation. From experiments in which attached flowers and young pods were shaded or given supplemental light, it appears that light perceived by these structures themselves had a role in regulating their abscission and accumulation of ^{14}C -photoassimilates (Heindl and Brun, 1983). Also, the *in vitro* growth of both excised seeds and seeds in excised pods requires light, but the growth rate of seeds in pod culture is slower than that of excised seeds (Hsu and Obendorf, 1982). Certainly, the import of sucrose by attached embryos from the vascular supply of the pod involves energy-dependent transport through the seed coat (Thorne, 1981, 1982). Since seed coats of excised seeds rupture and are shed within a few days of *in vitro* culture, more work is needed to elucidate the possible role of seed coat and pod wall tissues in photoperiodic regulation of seed growth rate. Finally, photoperiodic control of *in vivo* seed growth could involve regulation at both source and sink sites. Regardless of the tissues that perceive the light response, it appears that, as duration of photoperiod decreases during seed development, the ability of the embryo to utilize substrates decreases. Thus, the enhanced growth rate of seed that was observed *in vivo* as photoperiod decreased perhaps was regulated by the rate at which substrates from the source organs were made available to the embryos.

15-4 CARBON DIOXIDE

The CO_2 concentration in the global atmosphere has been increasing since 1958 (Keeling et al., 1976) and is expected to reach about $600 \mu L L^{-1}$ by 2025 (Gribbin, 1981), or double the concentration existing early in this century. The first reaction to the projected increase in CO_2 concentration often has been to assume that crop yields will be increased by

as much as 30% because of increased rates of photosynthesis (Kimball, 1983). However, inspection of data from research on effects of enriched- CO_2 concentrations on various species of plants indicates that the effects are far from simple (Kramer, 1981; Raper and Peedin, 1978; Thomas et al., 1975). Firstly, photosynthesis under field conditions is limited by environmental factors in addition to CO_2 , including water, light and nutrients. Secondly, growth and yield depend on morphological and physiological factors in addition to the rate of photosynthesis (Evans, 1975, 1980; Gold and Raper, 1983). The absolute limit on enhancement of growth by CO_2 enrichment must reflect the finite limitations imposed by rates of leaf and flower initiation. The maximum rates for cell division and elongation establish the minimum intervals between initiation of successive leaves or floral primordia from a meristem and the development of axillary meristems. In the absence of environmental stresses, growth rate cannot be increased by increased CO_2 levels once the morphological limit is reached. The morphological limit at which CO_2 enrichment no longer accelerates growth can be readily approached under controlled-environment conditions (Rufty et al., 1981). Carbon dioxide enrichment under field conditions, however, may increase growth and yield by enhancing physiological processes that often are limited by environmental stresses.

15-4.1 Photosynthesis and Growth

Short-term experiments involving exposure of plants to enriched levels of CO_2 for a few hours or days have contributed to a frequent, but erroneous, impression that net CER per unit leaf area is always increased. Experiments lasting several weeks or months, however, indicate that while the net CER usually is increased, especially in the seedling or vegetative stages, it often declines after a few days or weeks (Clough et al., 1981; Kramer, 1981; Mauney et al., 1978). An important reaction of the plant to this initial enhancement of photosynthetic rate in response to CO_2 enrichment is a rapid increase in leaf area. The increased leaf area frequently persists through later growth so that even when net CER and net assimilation rates decline during later growth, dry matter accumulation per plant continues to increase. Such is the case for apically dominant sunflower (Mauney et al., 1978) and tobacco (Raper and Peedin, 1978). Net CER for sunflower after several weeks of CO_2 enrichment was similar to that at ambient concentration, and for tobacco was slightly less than that at ambient concentration. However, dry weights of plants of both species were increased because of the increase in leaf area. Conversely, soybean lacks strong apical dominance, and can maintain enhanced photosynthetic rates over prolonged periods of CO_2 enrichment (Hardman and Brun, 1971; Mauney et al., 1978; Rogers et al., 1983; Sionit, 1983; Sionit et al., 1984). Additionally, leaf area of soybean is increased under CO_2 enrichment (Jones et al., 1984; Rogers et al., 1984).

The response to CO₂ enrichment generally appears to be largest in seedling and juvenile stages of development and decreases as plants age (Thomas et al., 1975). Even for soybean, although net CER may be greater in both vegetative and reproductive stages when atmospheric CO₂ is enriched, the rates are higher during vegetative growth than during reproductive growth (Hardman and Brun, 1971; Mauney et al., 1978). Part of the decline with age in responsiveness to elevated CO₂ level may be attributed to the declines that normally occur in photosynthetic rates as leaves growing at ambient levels age (Fig. 15-8). Part, however, may be related to the existence of strong sinks for photosynthate. If the ratio of leaves to pods is varied, high rates of photosynthesis are prolonged when the reproductive sink is emphasized (Peet, 1984). There also is a strong sink in rapidly growing seedlings. Soybean leaves do not attain their maximum photosynthetic activity until after full expansion (Ojima et al., 1965; Woodward and Rawson, 1976), and young expanding leaves for a time are net importers of photosynthate rather than exporters (Thaine et al., 1959; Thrower, 1962). With its general lack of strong apical dominance and potential for profuse branching (Thomas and Raper, 1977, 1978, 1983b), the proportion of juvenile to mature leaf tissue can remain quite high in soybean, and combined with the associated expansion of stem and root tissues (Rufty et al., 1981), vegetative soybean plants have constantly expanding sink capacity for utilization of photosynthetically produced carbohydrates. The high sink capacity continues with the utilization of photosynthate to meet the high energy requirement of developing seed with their high protein and oil composition (Sinclair and de Wit, 1975).

When grown in CO₂-enriched atmosphere, the decline in photosynthetic rate of soybean was most rapid in plants with low sink demand (Clough et al., 1981; Peet, 1984). This decline has been related to the extent of build-up of nonstructural carbohydrates in leaves (Mauney et al., 1979). Part of the increase of nonstructural carbohydrates, especially starch, in leaves perhaps can be attributed to limits in the sucrose-phosphate synthase system because the normally low activity of sucrose-phosphate synthase is reduced further at high CO₂ levels (Huber et al., 1984). However, part may be attributable to a limited sink demand even during seed development (Peet, 1984). Under ambient CO₂ levels in controlled-environment studies when stresses were nearly absent, nonstructural carbohydrates in leaves and stems increased during seed filling (Cure et al., 1985), even though fruit loads for these plants represented more than 70% of shoot dry weight at physiological maturity (Cure et al., 1985). It thus seems that reproductive sink demand does not necessarily exceed photosynthetic capacity for soybean under ambient CO₂. Moreover, leaf mass increases under elevated CO₂ and, unless pod set is increased proportionately, CO₂ enrichment may actually increase the ratio of photosynthetic source to reproductive sink for soybean. Another sink for photosynthate in soybean, however, is the nodulated root system. In many plants, relative root mass increases under elevated CO₂ levels (Thomas

et al., 1975), even though most experiments with elevated CO₂ have been conducted using plants grown in pots where restricted root growth may underestimate the importance of roots as sinks. For nodulated root systems, not only is the increased growth a sink for photosynthate (Finn and Brun, 1982), but also the high respiratory requirement for maintenance (Minchin and Pate, 1973) and functioning (Ryle et al., 1979a, 1979b, 1983; Williams et al., 1982) of nodules increases the sink activity of root systems and can alter the source-to-sink ratio of soybean during both reproductive and vegetative growth. Studies of long-term effects of CO₂ level on physiology and productivity of soybean must include determinations of relative changes in source and sink activities before cause-and-effect relationships can be established.

15-4.2 Interaction of Carbon Dioxide Concentration with Other Stresses

Many studies of effects of elevated concentrations of CO₂ are made under favorable growing conditions, but under field conditions effects are complicated by availability of water, nutrients, and light, and by competition with weeds. In general, drought tolerance appears to be increased by an increased atmospheric concentration of CO₂. For example, water-stressed wheat (*Triticum aestivum* L.) under high CO₂ in growth-chamber conditions yielded about 50% more than nonstressed wheat under normal CO₂ levels (Sionit et al., 1980, 1981). The growth of soybean also was reduced less by water stress under elevated than under normal concentration of atmospheric CO₂ (Huber et al., 1984; Rogers et al., 1984). Part of the increase in drought tolerance at increased atmospheric CO₂ levels is associated with decreased stomatal conductance (Fig. 15-12). Transpiration rate per unit leaf area is reduced by the decreased stomatal conductance caused by elevated levels of CO₂ (Egli et al., 1970; Rogers et al., 1984), but elevated CO₂ promotes increased photosynthetic rates (Sionit et al., 1984) despite the decreased stomatal conductance (Fig. 15-12). This increases water-use efficiency (Jones et al., 1984; Rogers et al., 1984). Although the decreased transpiration rate can enhance drought tolerance by decreasing water utilization from the drying soil, the increased leaf area resulting from elevated CO₂ levels can result in an increased rate of water utilization per plant. Part of the increased drought tolerance at elevated CO₂ levels, particularly at low plant populations, also must be attributed to increased root growth and proliferation that exploits a greater volume of soil for available water.

The requirements for N and other mineral nutrients to support long-term increases in growth are increased with increased levels of atmospheric CO₂. Additional assimilation of nutrients, particularly N, are required to support initiation of new tissues and continued activity of physiological processes, although to some extent concentration of N and other nutrients in expanded leaf tissues can be diluted by increased levels of nonstructural carbohydrates (Thomas et al., 1975; Williams et al., 1981;

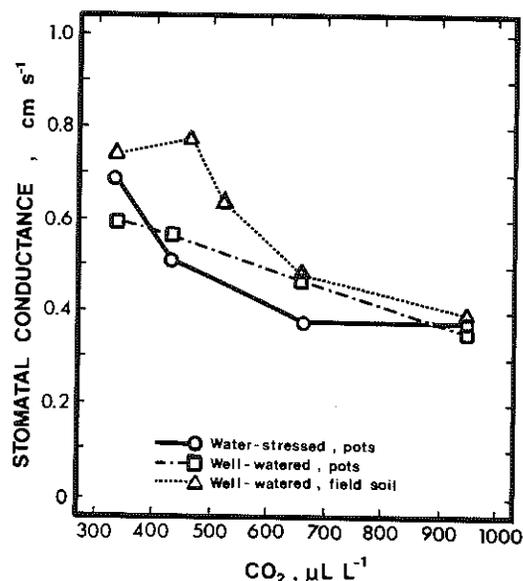


Fig. 15-12. Effect of CO₂ on stomatal conductance of water-stressed and well-watered soybean grown in pots and of well-watered soybean grown in field soil. From Sionit et al. (1984).

Wong, 1979). Obviously, growth and yield even under elevated CO₂ levels are subject to the availability of nutrients. An increased production of photosynthate, however, can somewhat increase accumulation of nutrients through increased partitioning of carbohydrates to roots (Sionit, 1983) and the resultant increase in N₂-fixation activity (Phillips et al., 1976) and volume of soil exploited by increased root length. While CO₂-enhanced photosynthesis might increase nutrient uptake from soils with low nutrient concentrations by increasing root mass and extension, this does not lessen the nutrient requirements for maximum growth and yield nor the necessity for adequate fertilization of nutrient-deficient soils to obtain a response to CO₂ enrichment.

The greatest benefits of an increase in global CO₂ probably will occur in sunny climates where irradiance is high rather than in regions with cloudy weather during the growing season. The response of plants to increased CO₂ concentration generally is greater at high irradiance levels, but there are differences among species. The dry weights of both soybean, a C₃ species, and corn, a C₄ species, were greater at 675 μL L⁻¹ than at 350 μL L⁻¹ CO₂ with both 600 and 1200 μmol m⁻²s⁻¹ of PAR (Sionit et al., 1982). However, the response of soybean was greater than that of corn. The increases in dry weight for soybean between 350 and 675 μL L⁻¹ CO₂ were 72.7 and 76.4% at the low and high radiation levels, while the increases for corn were only 18.9 and 18.6%.

A depletion of CO₂ may occur within soybean canopies on sunny, windless days (Allen, 1975; Baldocchi et al., 1983). There have been only

limited studies on the long-term effects of CO₂ depletion on crop plants. These studies indicate differences in response among species to CO₂ stress. For tobacco (Raper and Downs, 1973; Raper et al., 1973), leaf area and specific weight were not greatly altered when plants were allowed to reduce CO₂ to about 200 μL L⁻¹ in a growth chamber without supplementation to maintain the concentration, but stem elongation and dry weight, as well as carbohydrate content of leaves, were significantly reduced relative to plants grown at CO₂ levels maintained at 350 to 400 μL L⁻¹. For soybean (data of H.D. Gross as reported by Downs, 1983) and snap bean (*Phaseolus vulgaris* L.), leaf size and number were reduced when CO₂ in growth chambers was depleted to 200 μL L⁻¹ (Downs, 1980). While the 150 to 200 μL L⁻¹ differentials of these studies were far greater than the 10 to 30 μL L⁻¹ differentials that occur within soybean canopies in the field (Allen, 1975; Baldocchi et al., 1983), the results do establish the possibility that part of the response of plants to elevated CO₂ levels may be a result of reduced stress within the canopy.

Increases in the atmospheric CO₂ concentration likely will change the relative competitive capacities among crop plants and weeds (Patterson and Flint, 1980). As CO₂ concentration increases, C₃ weeds probably will become more competitive with C₄ crops, but C₄ weeds will become less competitive with C₃ crops such as soybean. Because the effects of CO₂ on growth usually are greatest during the seedling stage when crop and weed competition is most important, the probable reduction in competitive capacity of C₄ weeds relative to soybean with increased CO₂ is particularly important when considering the effects of biotic stress on yields. Also, the increased concentration of carbohydrates and decreased concentration of nitrogenous compounds in soybean leaves as atmospheric CO₂ concentration is increased may result in more extensive damage to leaves by insects (Lincoln et al., 1984).

15-5 METAL TOXICITY

Most of the metals can cause toxicities in plants growing in nutrient culture or in limited sites where soils have been contaminated by mine spoils or certain fungicides (Foy et al., 1978). Few metals, however, frequently cause phytotoxicity in soybeans under field conditions. The exceptions are Al and Mn which often can be important causes of stress in soybean on acid soils (Brown and Jones, 1977a).

15-5.1 Aluminum Toxicity

Aluminum toxicity is associated with increased susceptibility to drought stress and reduced accumulation of P, Ca, Mg, K, Fe, and N (Foy et al., 1969; Johnson and Jackson, 1964; Plant, 1956; Rorison, 1965; Sartain and Kamprath, 1975, 1978; Wright and Donahue, 1953). The primary processes affected by Al toxicity in crop plants are cell elongation

in roots (Matsumoto et al., 1977; Wallace and Anderson, 1984) and cell division in the root apices, probably caused by formation of strong complexes with nucleic acids (Trim, 1959) during mitosis (Clarkson, 1965; Horst et al., 1983; Matsumoto and Morimura, 1980). This results in production of stubby lateral roots lacking the fine branching necessary for efficient absorption of nutrients and water from soil (Foy et al., 1978; Sartain and Kamprath, 1975). Nodule numbers also are reduced by high Al concentration (Sartain and Kamprath, 1975).

Aluminum toxicity occurs in acid soils with a high exchangeable Al saturation (Adams and Lund, 1966; Lund, 1970; Sartain and Kamprath, 1975). Such soils are prevalent in the southeastern USA (Cassel, 1983), as well as in extensive areas of Africa, South America, and Southeast Asia (Van Wambeke, 1976). While liming is effective in reducing the exchangeable Al in the plow layer (Armiger et al., 1968; Kamprath, 1970; Sartain and Kamprath, 1975), liming subsoils is difficult. Thus, penetration of roots into subsoil layers and efficient exploitation for water and nutrient reserves may be restricted by Al toxicity. As is evident from studies in which chisel plowing was used to disrupt a tillage-induced pan at the base of the Ap horizon of a Wagram loamy sand (loamy, siliceous, thermic *Arenic Paleudult*), there is a potential for enhanced yields of soybean with more extensive development of roots in subsoil horizons. Root growth and water extraction from the subsurface horizons and grain yield of soybean were increased when the mechanical impedance of the pan was reduced by tillage (Cassel, 1983; Kamprath et al., 1979; Martin et al., 1979). These studies, which were conducted at a site with a long history of cultivation and management, have the additional implication that continued applications of chemical fertilizers and lime to the Ap horizon of sandy soils in humid regions can result in sufficient leaching to increase the base saturation of subsurface horizons (Chaiwanakupt and Robertson, 1976; Juo and Ballaux, 1977; Terry and McCants, 1968, 1970; Volk and Bell, 1945).

A management-induced change in soil chemistry is only one possible explanation for increased proliferation and activity of roots in a subsoil with high exchangeable Al in its native state. Another possibility is the differential tolerance to Al that exists among soybean cultivars (Brown and Jones, 1977a; Hanson and Kamprath, 1979; Sartain and Kamprath, 1978). The difficulty and time involved in increasing base saturation and reducing exchangeable Al in subsoils makes selection for Al tolerance a more feasible goal for enhancing rooting activity in acid soils than changing the chemistry of the subsoil. There are several mechanisms for Al tolerance. One is cell membranes, possibly the plasmalemma, that are differentially permeable to Al and prevent entrance of Al into the root cells (Ali, 1973). There also is evidence that the gelatinous mucilage secreted by roots, particularly at the root tips, protects root meristems by adsorption of Al (Hecht-Buchholz and Foy, 1981; Horst et al., 1982) or chemically similar metal ions (Clarkson and Sanderson, 1969). Another mechanism is internal chelation of Al within the cytoplasm, possibly by

organic acids (Grime and Hodgson, 1969; Jones, 1961; Lunt and Kofranek, 1970). Other studies show that plants vary in ability to increase the pH of the rhizosphere (Marschner and Römheld, 1983). Cultivars that increase the pH absorb less Al because of its lower solubility at high pH (Foy et al., 1967). In nodulated root systems of soybean, however, N₂ fixation decreases pH of the rhizosphere by uptake of cations in excess of anions (Israel and Jackson, 1982). None of these mechanisms have been identified as involved in the differential tolerance to Al among soybean cultivars. Nevertheless, tolerance among cultivars, as established by rates of root growth of 5-day-old seedlings in nutrient solution containing Al, is heritable (Hanson and Kamprath, 1979). However, the relationship between responses of seedlings, which sometimes are more susceptible to Al toxicity (Thawornwong and Van Diest, 1974), and of plants grown in soil is not established (Hanson and Kamprath, 1979; Sartain and Kamprath, 1978). Increased tolerance of older roots may be a more pertinent criterion of ability of roots to penetrate into the unlimed subsurface horizons.

15-5.2 Manganese Toxicity

The primary symptoms of Mn toxicity, in contrast to those of Al, involve leaf abnormalities. Symptoms in soybean include crinkling, chlorosis, and necrotic lesions of leaves (Heenan and Campbell, 1980; Heenan and Carter, 1976, 1977). Reciprocal grafts between rootstocks and shoots of two soybean cultivars differing in tolerance to Mn have demonstrated that the tolerance is related to shoot factors rather than root activity (Heenan and Carter, 1976). The reduction in growth and yield associated with Mn toxicity apparently is caused by disruption of photosynthetic processes (Jackson, 1967) through biochemical disorders (Foy et al., 1978) or reduction in leaf area by decreased cell division or expansion (Terry et al., 1975).

While Mn toxicity is a problem primarily in acid soils, susceptibility of plants growing on acid soils high in extractable Mn is influenced by weather. Manganese toxicity of tobacco frequently occurs in the cooler mountain regions of North Carolina, but seldom occurs in the warmer piedmont regions despite similarities in soil pH and levels of extractable Mn (Rufty et al., 1979). More direct evidence of an interaction between temperature and susceptibility to Mn toxicity is available from glasshouse experiments. Löhnis (1951) observed that severity of Mn toxicity in bean growing in a glasshouse without temperature control was greater in the cooler areas of the glasshouse than in warmer areas. For both tobacco (Rufty et al., 1979) and soybean (Heenan and Carter, 1977), levels of Mn in nutrient solution that produced toxicity symptoms at temperatures of about 20°C did not produce toxicity symptoms at temperatures of about 28 to 31°C, and the concentration of Mn in leaves at the warmer temperature was similar to, or exceeded, that at the cooler temperatures.

Thus, the effect of temperature on susceptibility to Mn toxicity is not directly related to uptake and accumulation of Mn by the plant.

At high external supply, Mn concentration in leaves generally increases with leaf age, and within a sampling date younger leaves of a plant have lower concentrations of Mn than older leaves (Heenan and Campbell, 1980; Rufty et al., 1979). However, Mn toxicity symptoms in tobacco were most pronounced in younger leaves (Rufty et al., 1979). This suggests that the greatest sensitivity to Mn is during the period of cell division and elongation (Terry et al., 1975). Manganese tolerance related to both cultivar differences (Brown and Jones, 1977b; Heenan and Carter, 1975, 1977) and temperature during growth (Heenan and Carter, 1977; Rufty et al., 1979) likely is related to morphological development of leaves. Rufty et al. (1979) suggested that temperature-dependent tolerance may be associated with rate of vacuolar expansion within leaf cells. Manganese can accumulate in vacuoles (Munns et al., 1963), and increased availability of vacuoles for sequestering Mn (MacRobbie, 1971) away from physiologically active regions of cytoplasm might result in greater tolerance. Similarly, the genotypic tolerance may be associated with time or rate of development of vacuoles in emerging and expanding leaves. Certainly, the relationship between toxic concentrations of Mn and morphological development of leaves needs investigation.

15-6 STRESS TOLERANCE

Generally, identification of stress tolerance has depended on observation of the behavior of plants subjected to the particular stress under investigation (Burton, 1983; Castleberry, 1983). However, it seems probable that more rapid progress could be made in breeding for stress tolerance if plant breeders could identify and concentrate on specific morphological or physiological characteristics conferring tolerance of a specific stress. The chief difficulties with this approach are lack of sufficient information concerning the physiological bases of tolerance and lack of good tests for screening large populations for the desired physiological characters (Blum, 1983; Nelson, 1983).

15-6.1 Chilling Tolerance

Chilling injury provides an example of the difficulties in developing screening procedures to select for specific physiological mechanisms of tolerance. Soil temperatures below about 15°C cause injury to germinating seeds (Hobbs and Obendorf, 1972), and cool soil reduces water absorption (Markhart et al., 1979). Air temperatures below about 13 to 15°C reduce or prevent flowering and pod set (Hume and Jackson, 1981; Musser et al., 1983a; Thomas and Raper, 1978) and affect the photosynthetic apparatus (Musser et al., 1984). But how do low temperatures

produce these effects? Chilling injury is generally attributed to damage to cell membranes (Bramlage et al., 1978; Lyons et al., 1979; McWilliam, 1983), but there is uncertainty concerning the nature of the damage. For several years emphasis was placed on phase changes in the lipids of the cell membranes (Lyons et al., 1979), but this is now questioned (O'Neill and Leopold, 1982; Wolfe, 1978). In any event, it seems likely that chilling injury occurs because cell membranes are unable to maintain their structural organization at low temperatures (Bramlage et al., 1978; Willing and Leopold, 1983). This is particularly plausible for explaining the damage to germinating seeds allowed to imbibe water at low temperatures. It also is important to note that some tissues such as developing pollen grains are more sensitive to chilling than other tissues, resulting in male sterility in chilled sorghum (Brooking, 1976) and rice (Lin and Peterson, 1975; Nishiyama and Sataka, 1979), and possibly soybean (Lawn and Hume, 1985). The reason for this is unknown. However, all of the various chilling injuries associated with reduced floral development probably result from damage to cell membranes (McWilliam, 1983). Until the site and nature of this injury is definitely established, it will be difficult to develop a breeding program based on physiological tolerance.

15-6.2 Drought Tolerance

The causes of injury by water stress are better identified. The behavior of plants with respect to drought can be classified as follows: drought avoidance where plants are not subjected to drought conditions; and drought tolerance either by dehydration postponement or by dehydration tolerance. Plants sometimes can be placed in more than one of these categories.

Complete avoidance of drought generally is impossible in the central and eastern USA where drought occurrence is largely random (Decker, 1983). Where late summer droughts are common, the best cultural approach to drought avoidance is early planting. This requires seed that germinate well and produce vigorous seedlings in cold soil. Apparently, little selection has been done for this character, although cultivars from Hokkaido and eastern Siberia and their progeny seem to possess this characteristic (Holmberg, 1973).

Selection for characteristics that postpone dehydration seems more promising. One of the most common is deep, much branched root systems that absorb water from a large volume of soil. Jordan and Miller (1980) and Taylor (1980) agreed on the desirability of deep rooting. But while Taylor (1980) doubted if cotton (*Gossypium hirsutum* L.) or soybean would benefit from increased root density, Boyer et al., (1980) found that high-yielding soybean cultivars had higher root densities and higher afternoon leaf water potentials than lower-yielding cultivars. Raper and Barber (1970), in an investigation of comparative root systems of 26 genotypes of soybean, found considerable genotypic differences. In single-plant plots, 'Harosoy 63' had nearly twice the root surface and 1.5 times

the root length of 'Aoda', and therefore occupied the soil more thoroughly. Thus, there appears to be some genetic variability available to use in breeding programs to produce whatever type of root system seems most desirable for particular soil conditions and cultural regimes. There also are differences in axial and radial resistance to water flow into and through roots (Newman, 1976), and soybean root systems have a much higher resistance to entrance of water than corn or sunflower (*Helianthus annuus* L.) (Boyer, 1971). It is not known, however, whether there are sufficient differences among soybean cultivars to be of any significance.

The role of the physical properties of soil in determining the amount of available water and the development of roots was discussed by Cassel (1983), Kramer (1983), and Ritchie (1983). Cassel presented considerable data indicating the importance of impermeable soil layers, often caused by farm machinery, on root penetration. The effect on soybean root penetration of deep tillage to disrupt a traffic pan at a depth of about 25 cm is shown in Table 15-4. There is need for root systems that can penetrate soil layers with a high bulk density and that can proliferate in acid subsoils containing high concentrations of exchangeable Al (Cassel, 1983).

The loss of water from leaves depends primarily on stomatal opening and secondarily on leaf orientation and factors affecting transpiration. Stomata that close promptly as leaf water stress increases reduce both transpiration and photosynthesis, but reduce the former more than the latter. The writers are not aware of any systematic survey to determine if there are important differences among soybean cultivars with respect to stomatal response to stress. However, the environmental history of soybean may be more important than varietal differences, because there is evidence that stomata of plants previously stressed close at lower leaf water potentials than stomata of nonstressed plants (Van Volkenburgh and Davies, 1977). There may be sufficient differences in the amount of wax on leaves to affect water loss. Van Volkenburgh and Davies (1977) found wax on the lower surfaces of field-grown soybean leaves but not on leaves of chamber-grown plants unless the latter were grown with cool nights. The cuticular transpiration of detached chamber-grown soybean

Table 15-4. Effect of conventional tillage with a moldboard plow to a depth of 25 cm and in-row subsoiling to a depth of 45 cm on distribution of secondary roots of soybean in a Wagram loamy sand containing a tillage-induced pan between 20 and 30 cm below the surface. From Kamprath et al. (1979).

Depth cm	Dry weight of roots	
	Conventional tillage	Subsoiling
0-10	334	326
10-20	219	198
20-30	64	101
30-45	14	65
45-60	10	74
60-75	6	87

leaves also was higher than that of detached field-grown leaves. Heavy wax deposits decrease transpiration from sorghum leaves (Blum, 1979) more than photosynthesis (Chatterton et al., 1975), thereby increasing water-use efficiency. There also were differences among soybean cultivars in amount of pubescence, but since no important differences occurred in leaf water potential among three isolines of 'Clark' which vary from densely pubescent to glabrous (Ghorashy et al., 1971), it is doubtful that pubescence has much effect on water relations.

Osmotic adjustment refers to a decrease in osmotic potential greater than that caused by loss of water (Turner and Jones, 1980). Such a decrease permits cells to enlarge and stomata to remain open to a lower water potential than would be possible in its absence and postpones injury from dehydration. Osmotic adjustment has been observed in some soybean cultivars, but not in others (Sionit and Kramer, 1977; Turner and Jones, 1980; Wenkert et al., 1978). Apparently there has been no systematic survey for this adaptation in soybean, nor has there been any serious evaluation of its importance in decreasing injury from drought.

15-6.3 Tolerance and Recovery from Stress

No matter how good the plant characteristics that postpone dehydration, plants eventually suffer injury or death from dehydration if the drought is long enough. There is little information available concerning differences among soybean cultivars in ability to recover after severe dehydration. Blum (1979) regards ability to recover after stress as important in sorghum, and it should be important in other crops. The long-flowering period for many soybean cultivars should decrease the possibility of total crop loss from a single episode of drought or chilling during reproductive growth. Musser et al. (1983a) reported some recovery after chilling for Ransom soybean chilled to 10°C for 1 week during floral induction, and Schmid and Keller (1980) reported differences among cultivars in ability to recover after chilling. The chilled plants lost most of the flowers that opened during the chilling period, but after several weeks they resumed flowering and set pods. Water stress during flowering reduced the length of the flowering period of Bragg and Ransom soybean, but stress during early pod formation and seed filling reduced yield more than stress during flower induction and flowering (Table 15-4). It is possible from results of these and other experiments to predict the stage of development at which most injury will result from stress. However, because of inability to predict the time when stress will occur, it is doubtful if farmers can benefit much from this information unless irrigation is available. Perhaps more attention should be paid to selection for longer flowering periods and better recovery after stress.

15-6.4 Performance of Stress Tolerant Cultivars in the Absence of Stress

An important consideration in the breeding of plants for stress tolerance is whether genotypes that yield well when stressed will also yield

well in the absence of stress. This characteristic, known as yield stability, obviously is important where stress occurs more or less randomly and one cannot predict at planting time whether or not a crop will be subjected to stress.

There is some difference of opinion concerning the possibility of the same genotype having a relatively high yield in both the presence and the absence of stress. Orians and Solbrig (1977) stated that "there is an inevitable correlation between ability to photosynthesize rapidly when soil moisture is readily available and inability to extract moisture when soils are drier, and vice versa." They base their argument on the questionable assumption that xeromorphic leaves cannot have a high rate of photosynthesis under favorable conditions, but that under water stress they have a higher rate than crop plants. Some woody plants with xeromorphic leaves, however, have high rates of transpiration (Caughey, 1945), indicating high stomatal conductance, and presumably they also have high rates of photosynthesis. Brigalow (*Acacia harpophylla*) has xeromorphic leaves, but its rate of photosynthesis is as high as that of trees with mesomorphic leaves (van den Driesche et al., 1971).

The data for yield stability of crop plants are conflicting. The thick leaves of soybean plants produced in response to water stress have higher rates of photosynthesis per unit of leaf surface after stress is removed than thin leaves of plants that have not undergone stress (Davies et al., 1977; Van Volkenburgh and Davies, 1977). Plants of soybean, sunflower, and buckwheat (*Fagopyrum esculentum* Moench) genotypes that had been selected for relatively good growth and high rates of photosynthesis when water-stressed produced less dry matter and had relatively lower rates of photosynthesis when grown in moist soil than plants lacking stress tolerance (Bunce, 1981). Similarly, Fischer (1981) observed that increase in yield was positively correlated with increase in susceptibility to drought injury among several wheat (*Triticum aestivum* L.) cultivars. On the other hand, Reitz (1974) stated that hard winter wheats fall into three groups: (i) those yielding relatively well only under stress; (ii) those yielding well only in the absence of stress; and (iii) those yielding well with and without stress, i.e., having a high degree of stability. Although absolute seed yields of eight soybean cultivars were reduced by water stress, the relative ranking for final yields among the cultivars were similar when grown to maturity at deficient soil moisture conditions and when grown at optimum soil moisture conditions (Mederski and Jeffers, 1973).

There also is evidence of yield stability for chilling-tolerant soybean. In one set of experiments, the chilling-tolerant cv. Fiskeby V outyielded four other cultivars when the mean temperature during the 30 days after anthesis were both cooler and warmer than average (Table 15-5). In another comparison, Fiskeby V outyielded four other cultivars in cool and average seasons and in the warmest season was outyielded by only one of the more chilling-sensitive cultivars (Holmberg, 1973). Experiments by Schmid and Keller (1980) also indicated a high degree of yield

Table 15-5. Yield stability for chilling-tolerant cv. Fiskeby V and four less tolerant soybean cultivars in relation to mean temperature during the 30 days immediately following anthesis at Fiskeby, Sweden. From Holmberg (1973).

Cultivar	Seed yield		
	1970	1971	1972
	kg ha ⁻¹		
Toshi-dai 7910	710	1150	1475
Karafuto 1	790	1195	1270
Chishima	825	995	1260
Kamishunbetsu	880	990	1115
Fiskeby V	1390	1500	2150
	°C		
Mean temperature during first 30 days after anthesis†	15.7	17.0	18.8

†Between 1960 and 1972 the average temperature for the first 30 days after anthesis was 16.4°C.

stability over a wide temperature range for certain cultivars of Hungarian origin.

Perhaps the conflict among these reports is related to the mechanisms of stress tolerance involved. None of the specific mechanisms of tolerance were identified. Selection for a physiological mechanism such as osmotic adjustment of chloroplasts during stress, for example, may well provide increased tolerance during stress without reducing photosynthesis in the absence of stress. On the other hand, selection for increased partitioning of photosynthate to roots regardless of stress conditions may enhance yields if drought occurs, but in the uncertain drought conditions of humid regions may represent a wasteful diversion of photosynthates away from seed production in the absence of drought. In selecting for stress tolerance, recognition of the specific mechanism of tolerance and the climatic characteristics of the production area are important.

The performance of stress-tolerant plants in the absence of stress is important in connection with the troublesome problem of screening progeny for tolerance of stress. Blum (1979) suggested that there are three methods available. The one most frequently used is based on the assumption that genotypes which are relatively high yielding in the absence of stress also will be relatively high yielding in the presence of stress. This approach is attractive because differences among genotypes are much greater under favorable conditions and more easily observed. Frey (1964) and Johnson and Frey (1967) found this method satisfactory for oat (*Avena sativa* L.) and Mederski and Jeffers (1973) used it in selecting for drought tolerance of soybean. A second method is to select for high yield under stress and disregard the maximum possible yield. This seems a logical method when the occurrence of stress is certain, but unfortunately differences among genotypes under stress conditions may be small and a large amount of material is required to establish the existence of significant differences (Blum, 1979, 1983). A third, and perhaps better approach (Blum, 1979, 1983), is to assume that yield and stress tolerance

are separate characteristics, just as yield and resistance to various diseases are inherited separately. Once morphological or physiological characteristics that can contribute to stress tolerance are determined, they can be introduced into high-yielding genotypes to combine yield and stress tolerance. For example, soybeans from the east coast of Hokkaido and adjacent islands have considerable chilling tolerance, but are small and low yielding. When crossed with high-yielding cultivars from Europe, however, the result was Fiskeby V and other cultivars with chilling tolerance and relatively stable yield (Holmberg, 1973).

The principal difficulty with a breeding strategy based on physiological characteristics is that we do not yet know enough about the morphological and physiological characteristics that confer stress tolerance, or how they confer it (Eastin et al., 1983). For example, it is not yet fully understood why flower initiation and pod development of soybean are so sensitive to chilling and water stress. Furthermore, good methods are lacking for rapidly screening large populations of plants for stress tolerance.

15-7 RESEARCH NEEDS

The ultimate objective of agricultural research is to find ways to increase the efficiency of crop production. Plant breeders already have provided farmers with soybean cultivars having the physiological and morphological characteristics for potentially high yields, but the full potential for yield seldom is attained because of the various environmental stresses (Boyer, 1982). Thus, the primary need of the farmer is for cultivars that yield well in favorable seasons and suffer the minimum reduction in yield when subjected to the common climatic and soil-related stresses. Research to improve productivity should be based, on one hand, on an understanding of the nature and timing of stresses and, on the other hand, on an understanding of how the stresses disrupt physiological and morphological processes to cause reduction in yield. This requires the cooperative efforts of agronomists, soil scientists, crop climatologists, and plant physiologists to provide the information needed by plant breeders.

15-7.1 Stress Tolerance vs. Avoidance

Once a specific stress is identified as a major factor in preventing attainment of the physiological potential of a cultivar, two approaches are possible for the agronomist and plant breeder. One is to increase tolerance of the stress, and the other is to find ways of avoiding it. In areas with well-defined wet and dry seasons, it sometimes is possible to time plantings so that crops mature before severe drought develops. In the eastern and central USA, however, drought can occur at almost any time during the growing season (Decker, 1983; Shaw, 1983) making avoid-

ance difficult. Emphasis thus must be placed on finding plants with tolerance to drought either through postponement of dehydration or tolerance of dehydration. Tolerance of dehydration is important for survival in natural vegetation, but is less important in crop plants where economic yield rather than survival is of primary concern and severe dehydration usually severely limits crop yields. However, there are good possibilities of postponing dehydration by deeper, more extensively branched root systems and better control of water loss.

Sometimes the possibility of a stress can be eliminated. Water stress can be eliminated by irrigation where water is available, weeds can be eliminated by cultivation or the use of herbicides, and some insects and diseases can be controlled by chemicals and development of resistant cultivars. In many instances, consideration should be given to the ratio of costs to benefits in choosing methods of dealing with stresses. For example, it may be more profitable to sacrifice some yield in order to cut the cost of irrigation or of using pest controls. A low pH of topsoil can be corrected by liming, but it may be more practical to find root systems tolerant of high concentrations of exchangeable Al and Mn in acid subsoils than to attempt to reduce the concentration in the soil (Hanson and Kamprath, 1979; Heenan and Carter, 1976; Sartain and Kamprath, 1978).

15-7.2 Genetic Variability in Response to Stress

Fortunately, soybean has considerable genetic variability for such diverse characteristics as depth and density of rooting, determinate vs. indeterminate growth habit, length of life cycle (maturity group), sensitivity to photoperiod, and tolerance of lower temperature. Other desirable characters would include ability to penetrate soils of high bulk density, tolerance of Al and Mn and ability to tolerate dehydration and resume flowering after a severe drought. There seems to be enough genetic variability for most of these characteristics to justify the expectation that plant breeders will be able to produce cultivars with greater tolerance to most of the stresses that reduce yield. The problem is to determine which among these characters are most important in relation to stress tolerance and yield and to find ways to screen progeny for their presence.

The best approach to take in breeding for plants yielding well under stress depends on the options available. If considerable genetic variability in tolerance of a particular stress exists, then development of stress-tolerant cultivars usually is possible. However, it is no longer satisfactory to ask plant breeders for such broad characteristics as drought or chilling tolerance, because tolerance may depend on any one of several characters or on some combination of the characters. Drought tolerance, for example, might result singularly or in combination from a deep and profusely branched root system, good stomatal control of transpiration, early maturity, osmotic adjustment, tolerance of dehydration, or ability to resume growth after a drought. Agronomists and physiologists must identify

for plant breeders the characters that are most important under various soil and climatic conditions.

In summary, we should not ask plant breeders for stress tolerance, but rather to incorporate the specific characteristics that provide the tolerance into high-yielding cultivars. This requires better information about the characteristics that provide tolerance and better methods of screening plant populations for the characteristics than is presently available. There are problems in this approach to providing stress tolerance (Boyer, 1983; Nelson, 1983; Ritchie, 1983; Vieira da Silva, 1983). Although much research has been done on effects of environmental stresses on primary physiological processes, these seldom have been positively correlated with yield, and research on physiological processes must be better related to critical stages in plant development (Eastin et al., 1983). Thus, it seems that there must be a better understanding of the interaction between environmental stresses, plant processes, and stage of plant development at which stress occurs.

During the late 1960s, genetic engineering has opened up new possibilities for enhancing stress tolerance by transfer of genes from one kind of organism to another (Csonka et al., 1983). Although gene splicing or transfer of genes is difficult in seed plants, it should eventually facilitate improvement in resistance to stresses. Protoplast fusion seems to have considerable potential (Shepherd et al., 1983), and the isolation of useful mutants from cell cultures already is being exploited (Chaleff, 1983). Realization of this developing potential, however, still depends on the ability of agronomists and physiologists to identify specific mechanisms of tolerance and to develop suitable screening techniques.

15-7.3 Screening Techniques

One of the difficult problems in developing stress-tolerant cultivars based on specific characteristics is to find methods of screening large numbers of progeny for the desired characteristics. Screening may require physical measurement of entire root systems under actual or simulated stress conditions, determination of physiological processes such as photosynthesis of plant canopies or of single leaves, measurement of the water status of specific organs such as leaves or stem apices, or the observation of changes in specific cells or organelles for injury to membranes during chilling or osmotic stress. Observation of root systems often requires laborious excavation or expensive measurements of soil water depletion at various distances and depths. Although occasionally gross measurements are made of the water status of plants with infrared thermometers to compare the water status of plots of a large number of genotypes (Blum, 1979, 1983), detailed measurement of stomatal behavior, rates of photosynthesis or transpiration, and leaf water potential in response to water stress are time-consuming and can be done on only a relatively small number of plants.

At one time, it was supposed that plants with high rates of photosynthesis per unit leaf area should be high yielding, but numerous experiments have shown that this is not necessarily correct (Curtis et al., 1969; Evans, 1975; Ford et al., 1983; Sinclair, 1980). The relationship between photosynthesis and biomass production depends on the total leaf area and the length of time during which leaves maintain a high rate of photosynthesis, as well as the rate of photosynthesis per unit leaf area. Biomass production of soybean usually is related to canopy photosynthesis (Egli et al., 1970; Jeffers and Shibles, 1969; Wells et al., 1982), and since this is related to LAI, rapid development of leaves and early closure of the canopy is desirable (Potter and Jones, 1977; Shibles and Weber, 1966). However, increased seed yields cannot result from increased photosynthesis unless the size of the reproductive sink is increased (Clough et al., 1981; Peet and Kramer, 1980). Thus, selection for high rates of photosynthesis measured on single leaves will not necessarily result in increased yields (Ford et al., 1983).

Even if yield were correlated to short-term measurements of photosynthesis, it is difficult to screen large populations from selected crosses for differences in rates. An alternative to the use of whole plants is to devise tests to use on tissue samples such as leaf disks. Sullivan and Ross (1979) tested sorghum cultivars for tolerance of heat and desiccation by subjecting discs of leaf tissue to heat or osmotic stress and then measuring the amount of leakage of electrolytes out of the tissue. Tests for cold and heat tolerance can be made on seeds (Duke et al., 1983). Extensive correlation studies are needed to evaluate the usefulness of these and other rapid-screening techniques. The use of cell and tissue cultures to screen for stress tolerance currently is receiving much attention because it is speedy and requires much less time and space than field tests (Csonka et al., 1983). Cells in culture often exhibit great variability and sometimes develop tolerance to stresses not found in the plants from which they came. They can be subjected to such stresses as heat, cold, salinity, herbicides, and toxins produced by plant pathogens, and then plants can be regenerated from the survivors. Some success has been attained in selection for salt, herbicide, and disease tolerance by this method and more will doubtless be obtained in the future. Use of this method, however, presently is limited by the difficulty in regenerating plants from cell cultures.

Methods involving selection in cell cultures are only effective for tolerance at the cellular level. While tolerance of dehydration operates at the cellular level, postponement of dehydration involves root systems, stomatal behavior, and leaf structure, which can be expressed only at the level of whole plants. Some stresses, such as salinity, operate at both the plant and the cell level. Some kinds of plants succeed in saline environments because they exclude salt, and others succeed because they can tolerate it (Osmond et al., 1980). The salt tolerance of barley (*Hordeum vulgare* L.) callus cultures is similar to that of intact plants, but callus cultures of a halophytic *Salicornia* are as sensitive to salt as those of

nonhalophytes (Chaleff, 1983). Thus, although cell culture has considerable promise as a method of screening, its application is limited to stresses that operate at the cellular level. There will continue to exist a need for screening techniques that can select for stress tolerance at the more complex levels of the whole plant.

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