Soybean Yield Formation: What Controls It and How It Can Be Improved

James E. Board and Charanjit S. Kahlon
School of Plant, Environmental, and Soil Sciences
Louisiana State University Agricultural Center
US

1. Introduction

Soybean [*Glycine max* (L.) Merr.; family leguminosae, sub family Papilionoideae; tribe Phaseoleae] is the most important oilseed crop grown in the world (56% of world oil seed production) (US Soybean Export Council, 2008). Major producers are the US (33% of world production), followed closely by Brazil (28%) and Argentina (21%). Remaining producers are China, India, and a few other countries. Currently, soybean is grown on about 90.5 million hectares throughout the world with total production of nearly 220 million metric tons (US Soybean Export Council, 2008). At current prices, total value of the world's soybean crop is about $100 billion. Soybean is used as human food in East Asia, but is predominately crushed into meal and oil in the US, Argentina, and Brazil; and then used for human food (as cooking oil, margarine, etc.) or livestock feed (Wilcox, 2004). These uses are derived from the crop's high oil (18%) and protein (38%) content. Soybean meal is a preferred livestock feed because of its high protein content (50%) and low fiber content. Soybean oil is mainly used by food processors in baked and fried food products or bottled into cooking oil. Other uses are biodiesel products and industrial uses. Global demand for soybean has been increasing over the last several years because of rapid economic growth in the developing world and depreciation of the US dollar (US Soybean Export Council, 2008).

In response to this demand, world production has been increasing through a combination of increased production area and greater yield. Among major producers, most of this increase in Argentina and Brazil has come from increased production area, whereas in the US it has come from increased yield (US Soybean Export Council, 2008). However, over the last 10 years US soybean yields have been increasing by only 66 kg ha^{-1} yr^{-1} compared to 396 kg ha^{-1} yr^{-1} for corn (USDA, 2007). An even greater problem is the disparity in yield between the three main producing countries [US, Argentina, and Brazil (2,800 kg ha^{-1})] and that in the remainder of the world (1,510 kg ha^{-1}) (US Soybean Export Council, 2008). Because of the limited potential for increasing production area, it is very important that yield be accelerated in order to meet increasing global demand. Our objective is to describe the basic processes affecting yield formation in soybean and to apply this information to development of management and genetic strategies for increasing soybean yield. First, we will outline potential yield gains possible with management modifications in soybean. Secondly, the main abiotic and biotic stresses will be detailed describing their modes of action on yield.

This will be followed by development of a paradigm integrating how these stresses act on crop growth dynamics and yield component formation to affect final yield. This paradigm will be applied to examples of everyday problems faced by soybean farmers in coping with environmental stresses such as determination of stress-prone developmental periods, identification of stress problems affecting yield, determining the efficacy for modified management practices, and predicting yield potential of a field. Once environmental parameters have been discussed, a similar analysis will be applied to genetic strategies for yield improvement. Our objective here is to identify which plant factors explain yield improvement during cultivar development. Such factors may serve as indirect selection criteria for increasing the efficiency of cultivar development breeding programs.

2. Enviromental stress and soybean yield

Recent yield increases for soybean production in the US (66 kg ha^{-1} yr^{-1}) can be attributed to both a genetic and environmental component (USDA, 2007). Comparison of old and new US soybean cultivars have shown a range of genetic gain from cultivar development of 10 to 30 kg ha^{-1} yr^{-1} (Boerma, 1979; Specht and William, 1984; Specht et al., 1999; Wilcox, 2001). More recent research has indicated gains towards the higher end of this range (Kahlon et al., 2011). Thus, it can be approximated that recent yield gains within the US are about 50% due to cultivar genetic improvement and 50% to improved cultural practices. Potential gains from improved cultural practices for any given locale are usually determined by comparing farmer yields with those done using recommended practices (Foulkes et al., 2009). In the US, many states conduct these studies within farmer fields in which one area of a field receives typical practices and an adjacent area receives recommended practices (Louisiana Agric. Ext. Serv., 2009). In Louisiana, the typical soybean farmer produces an average yield 70% of that expected if recommended production practices were followed. Similar yield potential studies in other parts of the world show yields ranging from 60 to 80% of the optimal level (Foulkes et al., 2009). This yield gap is attributed to a suboptimal physical environment (i.e. inadequate solar radiation, temperature, photoperiod, water, soil factors) coupled with inadequate application of fertilizer and pest control. Thus, improvement of cultural practices can be expected to increase yield anywhere from 25 to 66%. Yield increases for countries outside the US, Brazil, and Argentina would be even greater, since their yield levels are substantially below those of the major producers (1510 vs. 2800 kg ha^{-1} , US Soybean Export Council, 2008).

The inability of a soybean farmer to achieve optimal yield, when adapted cultivars are grown, is caused by environmental stress. We define environmental stress as a deficiency or excess of some factor large enough to significantly reduce yield and/or impair crop quality. Environmental stresses are divided into two kinds, abiotic and biotic. Abiotic stresses are non-living stresses which can be divided into atmospheric factors (e.g. solar radiation, air temperature, humidity, and rainfall) and soil factors (eg. fertility, pH, compaction, waterlogging, soil structure, saline intrusion). Biotic stresses are living factors which are generally referred to as pests (weeds, insects, diseases, and nematodes). Although environmental stresses can initially affect crops by several physiological mechanisms, in most cases the final effect on yield occurs by reducing the canopy photosynthetic rate [uptake of CO_2 m^{-2} (land area) d^{-1}] (Fageria et al., 2006). Canopy photosynthesis combines the plant's basic genetic photosynthetic capacity per unit leaf

area (leaf photosynthesis) with leaf area index (LAI, leaf area/ground area ratio) and canopy architecture to give a comprehensive picture of the crop's ability to obtain CO_2 from the atmosphere. The importance of the photosynthetic reactions in crop growth and yield formation cannot be overestimated. It is estimated that 75 to 95% of crop dry weight is derived from CO_2 fixed through photosynthesis (Imsande, 1989; Fageria et al., 2006). Photosynthesis produces the basic carbohydrates used for producing more complex carbohydrates, proteins, and lipids, all of which contribute to dry matter (Loomis and Connor, 1992a). It also supplies the chemical energy for metabolism. Because of this close linkage between canopy photosynthesis and dry matter accumulation, seasonal crop patterns of canopy photosynthetic activity and crop growth rate [CGR, dry matter accumulation per day per m^2 [g m^{-2} (land area) d^{-1}] parallel one another (Imsande, 1989). For the remainder of the chapter, CGR will be used synonymously with canopy photosynthetic rate.

Both parameters increase slowly after emergence and then increase exponentially until early reproductive development (Fig. 1) [R1-R3, stages according to Fehr and Caviness (1977) (see Table 1 for definitions and descriptions)] (Imsande, 1989). Plateau rates are maintained until R5 and then fall as the seed filling period progresses. Seasonal total dry matter (TDM) curves reflect these patterns for CGR and canopy photosynthetic rate (Fig. 2, Carpenter and Board, 1997). The first period of seasonal dry matter accumulation is called the exponential phase. Growth is initially slow, but increases exponentially with plant size until maximal light interception is achieved. At this point, maximal CGR is achieved and the crop enters the linear growth phase where CGR is relatively constant (subject to stress-induced decreases). As senescence nears and leaf fall commences, the CGR slows until reaching zero. This last period is called the senescent phase. Crop growth rate is an example of a growth dynamic parameter. Growth dynamic parameters are rates and levels of total dry matter (TDM), dry matter partitioning (e.g. harvest index), leaf area index (LAI), light interception (LI), and radiation use efficiency that characterize soybean's seasonal growing pattern (Loomis and Connor, 1992a). Canopy photosynthetic rate and CGR are important to study because they directly control TDM production. Final yield is a function of TDM produced and the percentage of dry matter transferred into the seed (i.e. harvest index) (Loomis and Connor, 1992a). Crop growth rate, in turn, is regulated by the level of ambient light and the percentage of this light intercepted by the crop [the two terms combined will be called light interception (LI)]. The importance of LI in controlling CGR is derived from its use as an energy source to produce ATP and NADPH for fixation of CO_2 into carbohydrates. The effect of LI on CGR and TDM is measured by radiation use efficiency (dry matter/intercepted light; g MJ^{-1}). Optimal radiation use efficiency depends on the absence of any stress reducing the effect of LI on TDM. Light interception and radiation use efficiency are controlled by LAI and net assimilation rate [dry matter produced per unit leaf area; g m^{-2}(leaf area) d^{-1}]. Crop growth rate is maximized when LAI is large enough to intercept 95% of the sun's light [3-4 for narrow rows; 5-6 for wide rows (Board et al., 1990a)], sunlight is not blocked by clouds, and no stress factors are present to interfere with the ability of intercepted light to stimulate net assimilation rate and CGR (as measured by radiation use efficiency). For example, a crop can be maximizing LI, but if drought stress is present and the stomata are closed so CO_2 cannot enter the leaf, net assimilation would fall, reducing CGR and TDM. This effect would be reflected in reduced radiation use efficiency.

Developmental Stages	Descriptions of Developmental Stages
Vegetative Stages	
VE	Emergence - cotyledons have been pulled through the soil surface.
V1	Completely unrolled leaf at the unifoliate node.
V2	Completely unrolled leaf at the first node above the unifoliate leaf.
V5	Completely unrolled leaf at the fifth node on the main stem beginning with the unifoliate node.
Reproductive stages	
R1	First flower: One flower at any node on the plant.
R3	Pod initiation: Pod 0.5 cm (1/4″) long at one of the four uppermost nodes on the main stem with a fully developed leaf.
R4	Pod elongation: Pod 2 cm (3/4″) long at one of the four uppermost main stem nodes with a fully developed leaf.
R5	Seed Initiation: Seed within one of the pods at the four uppermost main stem nodes having a fully developed leaf that is 0.3 cm long (1/8″).
R6	Full seed stage: Pod at one of the four uppermost main stem nodes having a fully developed leaf that has at least one seed that has extended to the length and width of the pod locule.
R7	Physiological maturity: Presence of one pod anywhere on the plant having the mature brown color. 50% or more of leaves are yellow.

Table 1. Descriptions of the vegetative and reproductive developmental stages of soybean during the typical growing season.

Dry matter accumulation is important in yield formation because yield components recognized as important in controlling yield on the environmental level [node m^{-2}, reproductive node m^{-2} (node bearing a viable pod), pod m^{-2}, and seed m^{-2}] are responsive to TDM accumulation (Egli and Yu, 1991; Board and Modali, 2005). Yield components are morphological characteristics whose formation is critical to yield. For soybean, yield

components which have potential to influence yield are seed number per area (seed m^{-2}), seed size (g per seed), seed per pod (no.), pod number per area (pod m^{-2}), pod per reproductive node (no.), reproductive node number per area (reproductive node m^{-2}), percent reproductive nodes (%; percentage of nodes becoming reproductive), and node number per area (node m^{-2}). Yield components in soybean can be organized into a sequential series of causative relationships where: yield is controlled by primary yield components seed size and seed m^{-2}; seed m^{-2} is controlled by secondary yield components seed per pod and pod m^{-2}; pod m^{-2} is controlled by tertiary yield components pod per reproductive node and reproductive node m^{-2}; and reproductive node m^{-2} is controlled by quaternary yield components node m^{-2} and percent reproductive nodes. Thus, yield components are the vehicle through which canopy photosynthetic rate and CGR affect yield.
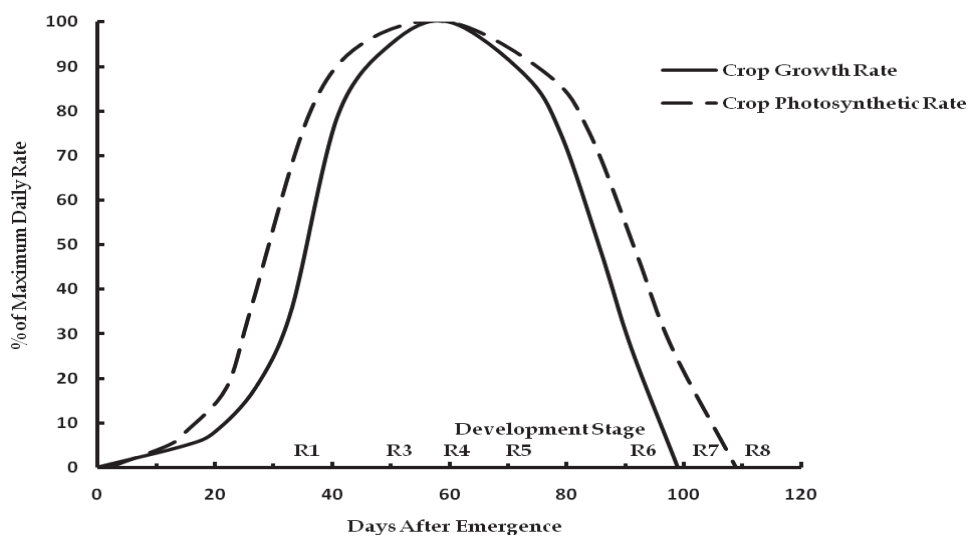

Fig. 1. Temporal profiles of the relative daily rates of plant growth and canopy CO_2 exchange. Profiles for dry matter accumulation and canopy CO_2 exchange were derived by curve fitting. For each of these two parameters several sets of published data, obtained with field grown plants, were plotted and the best-fit curves were generated. Curve presented in Imsande (1989).

Development and growth of soybean during the growing season are summarized in Fig. 3. Soybean development is separated into the vegetative development period (emergence to R1) and reproductive development period (R1 to R7). However, vegetative growth (leaves, stems, and nodes) extends from emergence to R5 (Egli and Leggett, 1973). The reproductive development period is separated into the flowering/pod formation period (R1 to R6) and the seed filling period (R5 to R7). The seed filling period, in turn, is divided into the initial lag period of slow seed filling (R5-R6) and the rapid seed filling period (R6-R7) when seed growth rate is maximal (Egli and Crafts-Brandner, 1996). Pod and seed numbers are determined by R6 (Board and Tan, 1995), before rapid seed filling starts. The linkage of

environmental stress with canopy photosynthetic activity, CGR, yield component formation, and yield can be illustrated by examining the effects of the three most common abiotic stresses for soybean production: temperature extremes, drought, and canopy light interception (Hollinger and Angel, 2009).
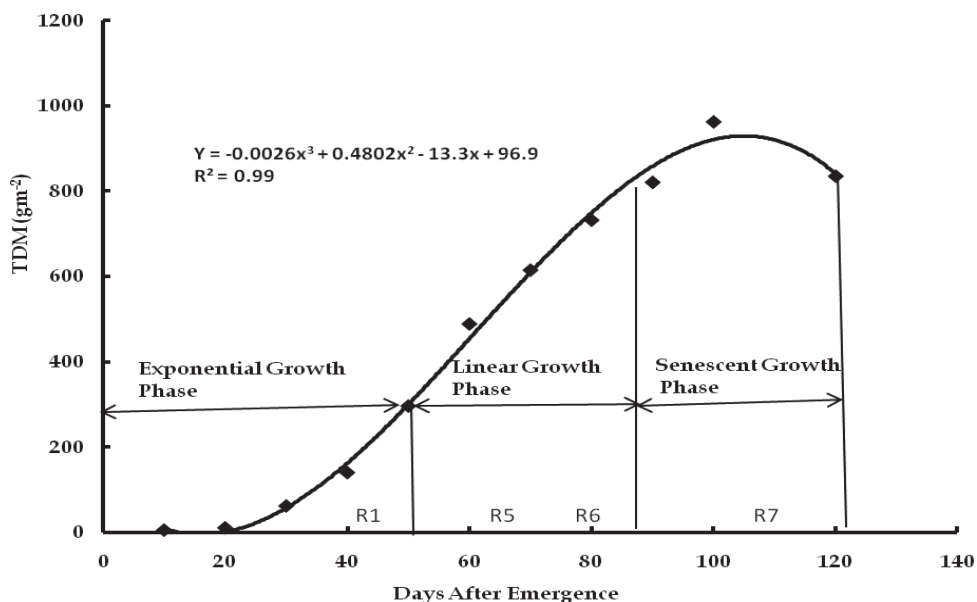

Fig. 2. Seasonal growth curve for a typical soybean crop showing the progression of total dry matter (TDM) accumulation across the exponential, linear, and senescent growth phases. Data adapted from Carpenter and Board (1997).

2.1 Temperature extremes and soybean yield

Temperature stress in soybean is manifested through effects on photosynthesis and CGR (Paulsen, 1994), reproductive abnormalities (Salem et al., 2007), and phenological events (Huxley and Summerfield, 1974). Among these factors, the effect on canopy photosynthesis and CGR has the greatest effect on yield. Temperatures above 35^0 C can inhibit pollen germination and pollen tube growth (Salem et al., 2007; Koti et al., 2004). However, since anther dehiscence occurs at 8 to 10 A.M., temperatures in most soybean growing areas would not be above the critical level during these events. The effect of warmer temperature interacting with shorter photoperiod to hasten phenological development (Hadley et al., 1984) can result in small plants having insufficient light interception for optimal canopy photosynthesis and crop growth rate (Board et al., 1996a). Thus, temperature effects on phenology indirectly affect yield through the same processes as direct temperature effects on canopy photosynthesis and CGR. Determination of heat units for soybean developmental timing uses a base temperature of 7^0 C, minimum optimum temperature of 30^0 C, maximum optimum temperature of 35^0 C, and an upper limit of 45^0 C (Boote et al., 1998).
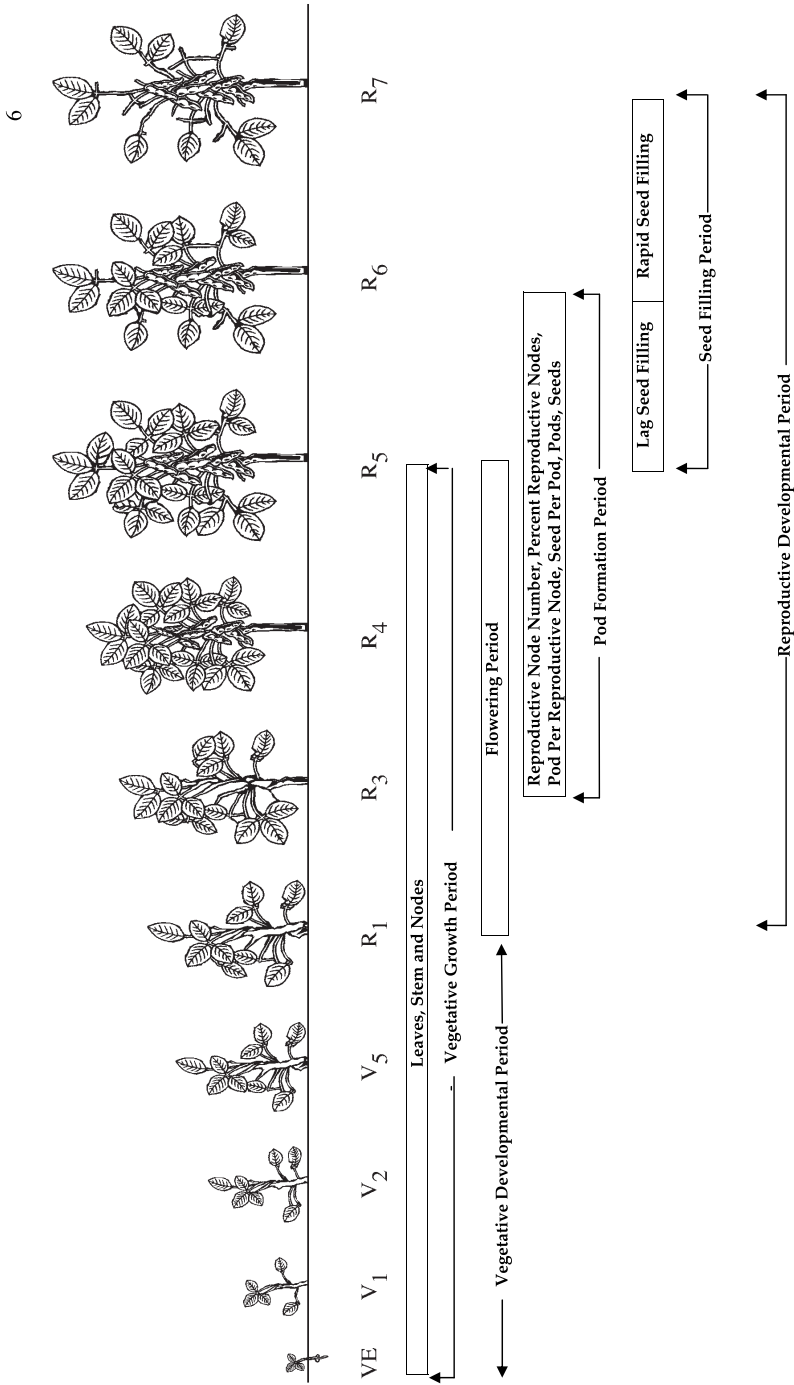
Fig. 3. Progression of vegetative organs and yield components across the developmental and growth periods of Soybean. Definitions and description of stages are in Table 1. Stages according to Fehr & Caviness (1977).

Effects of temperature on canopy photosynthesis and CGR are characterized by an optimal temperature response range falling between minimal and maximal optimal temperatures, and suboptimal and supraoptimal temperatures falling below and above the optimal range, respectively (Hollinger and Angel, 2009). The most sensitive part of the photosynthetic apparatus to heat stress is photosystem II. Specifically, the splitting of water to provide electrons to the light reactions is inhibited (Paulsen, 1994). Temperatures falling below the minimal optimal level reduce canopy photosynthesis and CGR through reduced reaction rates and/or enzyme inactivation. Studies conducted under constant day time temperatures (12-16 hours per day) across an extended period generally have reported an optimal temperature range for photosynthesis of 25-35^0 C (Jeffers and Shibles, 1969; Campbell et al., 1990; Jones et al., 1985; Gesch et al., 2001; Vu et al., 1997). However, under natural growing conditions, maximal daily temperature usually occurs for only 1-2 hours (Louisiana Agric. Exp. Stn., 2010). When heat stress studies are conducted under more realistic conditions of short-term stress, temperature had to be raised to 42-43^0 C to have a deleterious effect on soybean photosynthesis (Ferris et al., 1998). These results are corroborated by Fitter and Hay (1987) who stated that for plants from most climatic regions, temperatures of 45-55^0 C for 30 minutes were sufficient to cause irreversible damage to the photosynthetic apparatus. In conclusion, under typical growing conditions, the optimal temperature range for soybean canopy photosynthetic rate appears to be 25-40^0 C. A similar optimal temperature range of 26 to slightly above 36^0 C for crop growth rate has also been reported (Sato and Ikeda, 1979; Raper and Kramer, 1987; Sionit et al., 1987; Baker et al., 1989, Hofstra, 1972). Adverse effects on yield were entirely due to high day time temperatures rather than night time temperatures (Hewitt et al., 1985; Raper and Kramer, 1987; Gibson and Mullen, 1996).

At the crop level, heat-stress induced reductions in canopy photosynthesis affect yield components being formed at the time of the stress. Stresses occurring during flowering and pod formation (R1-R5) affect seed number, whereas stress during seed filling (R5-R7) reduces seed size (Gibson and Mullen, 1996). Both reductions were linked with lower photosynthetic rates. Concomitant with these reductions in canopy photosynthesis and yield components are decreased TDM and plant size. Soybean yield was as sensitive to heat stress during flowering/pod formation (R1-R5) as during seed filling (R5-R7). A summary for heat stress effects on yield formation is shown in Table 2.

Similar to heat stress, cold stress also adversely affects canopy photosynthesis when temperatures fall below 25^0 C. This results in less LAI, TDM, seed production, and yield (Baker et al., 1989). However, when research is conducted under cold temperature regimes similar to field conditions (intermittent nightly cold temperature or short-term cold treatments) adverse effects do not occur until temperature drops to 10^0 C (Seddigh and Jolliff, 1984 a,b; Musser et al., 1986). Seddigh and Jolliff (1984 a,b) showed that nightly cold temperature of 10^0 C vs. 16^0 C or 24^0 C slowed CGR during the vegetative and early reproductive periods. However, pod and seed numbers were not reduced, because the cooler temperatures extended the period to R5, thus allowing vegetative TDM accumulation to equilibrate across nightly temperature treatments. The 24% yield loss caused by reducing nightly temperature from 16^0 C to 10^0 C was entirely due to reduced seed size. Musser et al. (1986) reported that 1-wk chilling treatments (10^0 C) during the late vegetative and early reproductive period did not reduce early pod production. Chilling stress is a unique cold effect to plants where temperature at 10-12^0 C or below causes a cell membrane phase transition from liquid-crystalline to solid-gel form (Bramlage et al., 1978). Consequently, cell metabolism is disrupted resulting in potential

adverse effects on yield. In the case of the Bramlage et al. (1978) study, pod numbers equilibrated after return to normal conditions resulting in no effect on yield. Thus, under natural growing conditions, soybean yield is resilient to cold temperatures that fall to as low as 15^0 C. However, temperatures below this level pose a significant risk for reducing yield, especially when they fall to 10^0 C. Yield loss is assured with even short term exposure to freezing temperatures [2 hr a night for 1 wk (Saliba et al., 1982)]. Effects of freezing injury are irreversible. Thus, freezing temperatures during flowering/pod formation (R1-R5) cause much greater yield losses (70% loss) compared with freezing at R6 (25% loss). A summary of cold stress effects on yield formation is shown in Table 3.

Physiological Disruptions	Affected Canopy Level Growth Processes	Affected Yield Components	Temperature Parameters
Impairment of photosystem II	Reduced canopy photosynthesis and CGR	Reduction of seed number or seed size depending on timing of stress.	Short-term exposure to temp.>40^0C
Enzyme denaturation and deactivation	Reduced canopy photosynthesis and CGR	Reduction of seed number or seed size depending on timing of stress.	Short-term exposure to temp >40^0C
Increased development rate	Reduced canopy photosynthesis and CGR by shortening emergence-R5 period	Reduction of seed number.	Under short days development rate increases with degree days [Base temp=7^0C Min. optimum temp=30^0C Max. optimum temp= 35^0C Upper limit=45^0C]. Developmental stage sensitivity to heat stress not clearly defined.

Table 2. Summary of heat stress effects on soybean physiology, growth, and yield components.

2.2 Drought stress and yield

Drought stress (i.e. soil water too low for optimal yield) is recognized as the most damaging abiotic stress for soybean production in the US (Heatherly, 2009). However, only about 8% of the entire hectarage is irrigated. In the main part of the Midwestern US soybean region east of the Mississippi River, little irrigation is done. For example, in Illinois, the nation's largest soybean producing state, most areas receive sufficient rainfall for optimal yield (Cooke, 2009). Soybean water relations are aided by the state's deep soils that allow greater water extraction relative to shallow claypan soils in the Southeastern US. Irrigated areas are concentrated in the drier parts of the soybean growing region (western Midwest or Great Plains states) such as Nebraska where 46% of soybean hectarage is irrigated (Pore, 2009). Irrigation is also common in some Southeastern states where shallow-rooted soils combined with erratic rainfall make drought stress a threat. Currently, about 75% of soybean hectarage in Arkansas is irrigated and the figure for Mississippi is 25-30%. Increased irrigation in the Great Plains and Southeastern states has been stimulated by research showing large yield increases of over 1,000 kg ha^{-1} under irrigated vs. nonirrigated conditions (Specht et al., 1999; Heatherly and Elmore, 1986).

Drought stress is a complicated agronomic problem that is conditioned not only by lack of rain but by evapotranspiration from the soil/plant system, rooting depth and proliferation,

Physiological Disruption	Affected Canopy Level Growth Processes	Affected Yield Components	Temperature Parameters
Reduced metabolic reaction rates	Reduced canopy photosynthesis and CGR	Reduced seed number or seed size depending on timing of stress.	Although 25^0C required for optimal canopy photo. and CGR, cold effects under natural growing conditions usually affect yield only $<15^0$ C.
Chilling stress (Membrane malfunctioning, enzyme inactivation, ion leakage)	Reduced canopy photosynthesis and CGR	Reduced seed number or seed size depending on timing of stress.	$0-10/12\ ^0C$; Yield more affected by chilling stress during seed filling than flowering/pod formation period.
Freezing (cell death) tissue damage	Reduced canopy photosynthesis and CGR	Reduced seed number or seed size depending on timing of stress.	0^0C Yield more affected by freezing during flowering/pod formation than seed filling.

Table 3. Summary of cold stress effects on soybean physiology, growth, and yield components.

and how much rainfall gets into and stays in the rooting zone (Loomis and Connor, 1992b). Thus, in addition to rainfall, other factors that influence occurrence of drought stress are: tillage systems (conservation vs. conventional tillage), plant genetics (rooting characteristics, stomatal control, leaf reflectance, osmotic adjustments, leaf orientation and size, etc.), climatic factors (relative humidity, temperature, and wind), and soil factors (soil texture and structure, compaction, hardpans, pH, and slope).

Drought stress occurs when loss of water from leaves exceeds that supplied from the roots to such a degree that water potential in those leaves falls to levels resulting in physiological disruptions that eventually reduce CGR and yield (Loomis and Connor, 1992b). Another aspect of drought stress is low water potential in root nodules which reduces nitrogen fixation. Consequently, the crop may become N deficient which can also contribute to reduced CGR and yield (Purcell and Specht, 2004). Although there are many physiological processes potentially affected by drought stress, the main factors which are most important in yield loss are seed germination and seedling establishment, cell expansion, photosynthesis, and nitrogen fixation (Raper and Kramer, 1987). Water entrance and loss from a crop is controlled by water potential, the energy of water measured as a force in bars or pascals (1 bar=0.1 MPa) (Loomis and Connor, 1992b). Water potential differences between components of a system describe the direction of water flow, since water will always flow from a greater to a lesser water potential. Pure water has the highest water potential (0 MPa) and water potential of natural systems will have negative values below that for pure water. In plants, water potential is mainly controlled by solute potential (increased concentration makes water potential lower or more negative) and turgor pressure (positive hydrostatic pressure against the cell wall makes water potential greater or less negative). In soil, solute concentration also affects water potential. However, matric potential (adhesion of water

onto soil particles) is also an important component of soil water potential. Water is lost from the leaves by transpiration to the atmosphere. For this water to be replaced, root water potential must be lower than soil water potential to create water inflow from soil to root.

When a soil is initially at field capacity (maximal water a soil will hold after natural drainage), soil water potential is at about -0.02 MPa (Loomis and Connor, 1992b). This corresponds to volumetric water contents (volume of water per volume of soil) of 0.6 and 0.35 for clay and sand soils, respectively. At night, water potentials for soil, roots, and leaves are in equilibrium. During the day, water loss from the leaves depresses leaf water potential below root water potential resulting in movement of water from root to leaves in the xylem. Consequently, root water potential falls below soil water potential resulting in water flowing into the root. As water is withheld from the crop for successive days, the water potential for soil, roots, and leaves steadily drops. When midday leaf water potential falls to -1.5 MPa, stomata will close to conserve water. Meanwhile, as the soil dries the conductance of water from soil to root drops making it difficult to resupply the plant with water. Continued drought past this point will cause leaf water potential to fall below -1.5 MPa resulting in possible death. Eventually, soil water potential may fall to -1.5 MPa at which point water no longer enters the root from the soil (wilting point). Plant available water is defined as the soil water content between field capacity and the wilting point. Irrigation to avoid drought stress is usually recommended when plant available water falls to 50%, a level indicated by a soil water potential of -0.05 to -0.06 MPa for a silt loam or clay soil and -0.04 to -0.05 for a sandy soil. (Univ. of Arkansas Coop. Ext., 2006). This corresponds to a volumetric water content of 0.4 and 0.23 for clay and sand soils, respectively.

Once injurious soil water potential levels are reached, physiological disruptions occur which adversely affect CGR, yield component formation, and yield. Because of the large amount of water the soybean seed must imbibe for successful germination (50% of fresh weight), adequate moisture at planting is an important agronomic problem. Helms et al. (1996) cautioned that stand establishment could be difficult when soil water is sufficient to cause seed imbibition but not germination. Seed planted into a soil having a gravimetric water content (water wgt./soil wgt.) of 0.07 kg kg^{-1} was great enough for imbibition, but too low for root emergence. Increasing water content to 0.09 kg kg^{-1} allowed successful germination and emergence. Drought stress during the seedling emergence and stand establishment period can result in a suboptimal plant population for optimal yield. Because of low plant population, LAI and LI are inadequate to create a CGR that optimizes yield.

Once successful stand establishment is achieved, one of the most sensitive physiological processes to drought stress is reduced cell expansion resulting from decreased turgor pressure (Raper and Kramer, 1987). As leaf water potential falls, cell and leaf expansion are affected before photosynthesis. Bunce (1977) reported a linear relationship between soybean leaf elongation rate and turgor pressure. Decreasing leaf water potential to -0.80 MPa reduced leaf elongation rate by 40% relative to greater values. Consequently, leaf area and plant dry matter were reduced 60% and 65%, respectively. These results were subsequently confirmed in field experiments (Muchow et al., 1986). Thus, occurrence of drought stress during vegetative growth (emergence to R5) can reduce LAI and LI to levels insufficient for optimal CGR and yield. Decreased photosynthetic rate is not initiated until leaf water potential falls into the range of -1.0 to -1.2 MPa (Raper and Kramer, 1987). The rate starts declining more rapidly as water potential falls below -1.2 MPa. Plants suffering this level of drought would have greater reductions of CGR and yield because not only would LAI

be reduced, but the net assimilation rate (photosynthetic rate per unit LAI) would also be reduced. Drought stress effects on photosynthesis become irreversible once water potential falls below -1.6 MPa.

Another physiological process sensitive to drought stress is nitrogen fixation (Purcell and Specht, 2004). Decreased nitrogen fixation starts when water potential of root nodules starts falling below -0.2 to -0.4 MPa (Pankhurst and Sprent, 1975). Because of the high protein content of its seed, soybean has a greater demand for nitrogen compared with other crops (Sinclair and de Wit, 1976). Soybean obtains nitrogen from fixation and directly from the soil. During seed filling, much of seed nitrogen demand is met by remobilization from the leaves. The contribution of nitrogen fixation to the plant's nitrogen supply varies inversely with soil nitrogen availability (Harper, 1987). In the Midwestern US which has soils of relatively high residual NO_3, about 25-50% of total plant nitrogen comes from fixation. In contrast, in soils having low nitrogen, fixation can contribute up to 80-94% of the plant's nitrogen. Thus, any stress (drought or other) that restricts nitrogen fixation can result in a nitrogen deficiency (leaf nitrogen falling below 4%, Jones, 1998) which can reduce net assimilation rate and CGR. Ample evidence indicates that nitrogen fixation is more sensitive to drought than photosynthesis, TDM accumulation, transpiration, or soil nitrogen uptake (Purcell and Specht, 2004).

Because of its effects on CGR, drought creates changes in certain growth dynamic and yield component parameters. In general, drought stress during the vegetative growth period (emergence to R5) has adverse effects on LAI, TDM, CGR, and plant height (Scott and Batchelor, 1979; Taylor et al., 1982; Muchow, 1985; Meckel et al., 1984; Desclaux et al., 2000; Pandey et al., 1984; Ramseur et al., 1985; Cox and Jolliff, 1986; Constable and Hearn, 1980; Hoogenboom et al., 1987; Cox and Jolliff, 1987). In a dry growing season, nonirrigated vs. irrigated soybean will begin showing diminished TDM accumulation by the late vegetative or early reproductive period (Scott and Batchelor, 1979). By R3, LAI differences between irrigated vs. drought-stressed soybeans will be obvious (Cox and Jolliff, 1987), with concomitant effects on LI and CGR (Muchow, 1985; Taylor et al., 1982; Ramseur et al., 1985; Pandey et al., 1984). Among vegetative growth indicators of drought stress, reduced internode length and plant height are the most sensitive (Desclaux et al., 2000). The effect of drought stress on plant height is reflected in rooting depth (Mayaki et al., 1976b). During the emergence-R5.5 period, rooting depth is twice the plant height. Thus, occurrence of early-season drought impairs the plant's future potential for obtaining water. If a fortuitous rainfall interrupts this impaired growth dynamic process, TDM levels may return to normal without yield being affected (Hoogenboom et al., 1987). However, continuation of drought will accentuate TDM differences between irrigated and nonirrigated soybean. Decreased TDM and yield are closely correlated in such a condition (Cox and Jolliff, 1986; Meckel et al., 1984). In cases where drought stress occurs during the seed filling period, growth characteristics are of course different. Since plant height and vegetative TDM have already been determined, no effect on these parameters is seen. Drought during seed filling accelerates the senescence process by increasing the rate of chlorophyll and protein degradation. This shortens the seed filling period causing reduced seed size and yield (De Souza et al., 1997).

When soybean faces seasonal drought or drought initiated by R1, yield loss results predominately from reduced pod and seed numbers and seed size is relatively unaffected (Sionit and Kramer, 1977; Ramseur et al., 1984; Pandey et al., 1984; Meckel et al., 1984; Cox and Jolliff, 1986; Constable and Hearn, 1980; Lawn, 1982; Ball et al., 2000). Thus, when confronted with drought stress, soybean reduces seed m^{-2} so that normal seed size can be

maintained. Although some have reported mild adverse effects of drought on seed per pod (Ramseur et al., 1984; Pandey et al., 1984), others have shown no effect (Lawn, 1982; Elmore et al., 1988). In contrast, consistent reports have shown pod m^{-2} is reduced by drought during the R1-R6 seed formation period (Sionit and Kramer, 1977; Ramseur et al., 1984; Pandey et al., 1984; Snyder et al., 1982; Neyshabouri and Hatfield, 1986; Cox and Jolliff, 1986; Ball et al., 2000). Based on these results, we conclude that reduced seed m^{-2} from drought stress is derived predominately from reduced pod m^{-2} rather than seed per pod. Because pod per node is not severely affected by drought (Elmore et al., 1988), reduced pod and seed m^{-2} caused by drought results mainly from decreased node m^{-2}, mainly resulting from reduced branch development (Taylor et al., 1982; Snyder et al., 1982; Frederick et al., 2001). In addition to reduced node m^{-2}, drought stress during the flowering period retards early ovary expansion because of reduced photosynthetic supply (Westgate and Peterson, 1993; Liu et al., 2004; Kokubun et al., 2001). The period from 10 days before R1 to 10 days after R1 is the critical period.

Drought stress occurring at the start of linear seed filling (R6) can also reduce seed number, but the main effect of drought initiated at this time or later is on reduced seed size (Sionit and Kramer, 1977; De Souza et al., 1997; Brevedan and Egli, 2003; Doss and Thurlow, 1974). In cases where drought stress is similar at different developmental periods, yield loss is generally twice as great for the R1-R6 vs. R6-R7 periods (Kadhem et al., 1985; Korte et al., 1983b; Shaw and Laing, 1966; Eck et al., 1987; Brown et al., 1985; Hoogenboom et al., 1987; Korte et al., 1983b). Some studies show that within the R1-R6 period, the most drought sensitive phase is R3-R5 (Kadhem et al., 1985; Korte et al., 1983a). This explains why most irrigation studies have identified parts or all of the seed formation period as the most drought prone period (Heatherly and Spurlock, 1993; Elmore et al., 1988; Kadhem et al., 1985; Hoogenboom et al., 1987; Eck et al., 1987; Korte et al., 1983a; Korte et al., 1983b; Brown et al., 1985; Morrison et al., 2006). These studies far outweigh early studies indicating that seed filling had the same or greater sensitivity to drought as the seed formation period (Shaw and Laing, 1966; Snyder et al., 1982; Sionit and Kramer, 1977). Irrigation during the vegetative period has consistently proven unnecessary for alleviating drought stress (Heatherly and Spurlock, 1993; Neyshabouri and Hatfield, 1986). Lack of irrigation response during the vegetative period is likely due to the limited water use during that period (Reicosky and Heatherly, 1990). In conclusion, based on yield component responses, the most drought prone period during soybean development is R1-R6. Drought effects on soybean yield formation are summarized in Table 4.

2.3 Light interception and yield

Because of the importance of canopy photosynthesis and CGR in affecting yield, the level of intercepted photosynthetically active radiation (commonly referred to as light) is one of the most important stresses affecting soybean yield (Loomis and Connor, 1992a). Although a very complicated process, photosynthesis can be simplified by viewing it as three basic parts: 1) Movement of CO_2 from the atmosphere to the chloroplasts; 2) Light reactions in which absorption of specific wavelengths of radiation (red and blue light) cause ionization (photoelectric effect) and result in production of the high-energy compounds ATP and NADPH; and 3) Carbon fixation reactions in which the ATP and NADPH produced in the light reactions is used to fix CO_2 into organic compounds (Fageria et al., 2006). The major environmental factors affecting canopy photosynthetic rate and CGR are atmospheric [CO_2],

temperature, water availability, and light level absorbed by the canopy. An understanding of how light affects canopy photosynthesis is critical for analyzing the effect of environmental stress on yield.

Physiological Disruptions	Affected Canopy Level Growth Processes	Affected Yield Components	Drought Parameters
Reduced cell expansion	Reduced LAI and LI. Reduced canopy photosynthesis and CGR.	Reduced seed m^{-2} or seed size depending on timing of stress	Decrease of leaf water potential to -0.80 MPa or less reduces turgor pressure and cell expansion.
Reduced nitrogen fixation	Reduced canopy photosynthesis and CGR.	Reduced seed m^{-2} or seed size depending on timing of stress	Decline starts at -0.2 to -0.4 MPa.
Reduced net assimilation rate	Reduced CGR	Reduced seed m^{-2} or seed size depending on timing of stress.	Water potential below -1.2 MPa
		Seed m^{-2} reduction mainly due to reduced node m^{-2} and pod m^{-2}. Reduced seed size due to reduced effective filling period.	Most drought prone period is the R1-R6 seed formation period. Irrigation recommended when soil at 50% available water. Drought sensitivity of rapid seed filling (R6-R7) is less than half that for R1-R6 period.

Table 4. Summary of drought stress effects on soybean physiology, growth, and yield components.

For soybean, as well as other C3 crop species, photosynthetic rates of individual leaves increase asymptotically to a light intensity of 500 micro moles m^{-2} s^{-1} (or 100 W m^{-2}) (Hay and Porter, 2006); an intensity equivalent to about 25% of full sun in many soybean-growing regions. However, this relationship does not transfer to the canopy level; largely because of uneven shading for leaves in the mid and lower canopy levels which do not receive saturating light intensities. Although top leaves do not increase their photosynthetic rates as light intensity increases above 25% of full sun, mid and lower canopy leaves would receive increased light within the responsive range; thus resulting in an overall increase in canopy photosynthetic rate (Hay and Porter, 2006). In cases of crops having erect leaves with low canopy light extinction coefficients such as ryegrass, canopy photosynthetic rate increases linearly with increasing intensity to the full-sun level (Hay and Porter, 2006). Although soybean canopies having LAI<4.0 [canopy cover (95%) (Shibles and Weber, 1965)] saturate the canopy photosynthetic rate at intensity levels less than full sun, those having LAI >4.0 show continual increase up to full-sun conditions (Shibles et al., 1987). The increased canopy photosynthesis responds to increased light intensity in an asymptotic rather than linear fashion (Jeffers and Shibles, 1969). At any given time, light intercepted by the canopy

depends on LAI and the intensity of ambient light. Prior to canopy closure (LAI of 3.0 to 5.0 depending on row spacing), CGR primarily is influenced by LAI (Shibles and Weber, 1965), whereas ambient light level mainly affects CGR after canopy closure. Major research aims have been to determine yield response to reduced LI across different developmental periods; to assess yield losses related to specific reductions in LI; and to determine if different stresses reducing LI (e.g. shade, nonoptimal row spacing, subnormal plant population, and defoliation) affect yield by similar mechanisms. In the current discussion, we will examine the effects of shade, row spacing, plant population, and defoliation on yield.

2.3.1 Light interception and yield: Shade stress

Studies with heavy shade treatment (63%) demonstrated that the flowering/pod formation period (R1 to R6) was more sensitive to reduced LI than the period of linear seed filling (R6 to R7; rapid seed filling period) (Jiang and Egli, 1995; Egli, 1997). Application of shade during the seed determination period reduced yield by 52% (Jiang and Egli, 1995), whereas the same light interception reduction during rapid seed filling reduced yield by only 24% (Egli, 1997). Thus, within the reproductive period, the flowering/pod formation period was twice as sensitive to reduced LI as compared with the rapid seed filling period. Within the flowering (R1-R4) and pod formation (R4-R6) periods, yield responses to shade were similar (Jiang and Egli, 1993, 1995). Yield loss can occur with as few as 9 continuous days of heavy shade (80%) at any time during the flowering/pod formation period (Egli, 2010).

When shade stress is applied continuously across the reproductive period, yield losses occur with as little as 30% shade (22-31% yield loss) (Egli and Yu, 1991). Increasing shade stress to 50% resulted in a 55% yield loss. Yield losses were entirely due to reduced seed number rather than seed size. When faced with a reduced crop growth rate induced by shade stress starting at first flowering, soybean reduces its seed number so that when seed filling commences, seed size is unaffected. In such cases, yield is said to be "source restricted" during flowering and pod formation (i.e. yield reduction occurred due to lower CGR); whereas during seed filling yield was "sink restricted" (i.e. yield reduction occurred due to reduced seed number and was unaffected by changes in CGR). A summary of shade effects on yield is shown in Table 5.

2.3.2 Light interception and yield: Row spacing and plant population

Early studies which altered LI through row spacing and plant population demonstrated that optimizing light during the reproductive period (R1 to R7) was more important than during the vegetative period (emergence to R1) (Brun, 1978; Christy and Porter, 1982; Johnson, 1987; Tanner and Hume, 1978; Shibles and Weber, 1965). More recent studies suggest that reduced LI during the vegetative period can reduce yield if it results in a suboptimal CGR during the subsequent flowering/pod formation period (Board et al., 1992; Board and Harville, 1996). Row spacing and plant population have similar effects on LI, CGR, TDM, and yield component formation as do the aforementioned shade studies. Reducing row spacing from 100 to 50 cm increases LI and accelerates CGR during the vegetative, flowering/pod formation, and seed filling periods (Board et al., 1990). Greater CGR in narrow vs. wide rows was evident as early as 16 days after emergence (Board and Harville, 1996). During most of the vegetative and flowering/pod formation periods, accelerated CGR was due more to increased LAI than to net assimilation rate (Board et al.,

1990b). However, initial increases in CGR in narrow vs. wide rows during the vegetative period were influenced as much by increased net assimilation rate as increased LAI. This probably occurred due to greater interception of light per unit LAI in narrow vs. wide rows at this time (Board and Harville, 1992). Increased yield in narrow vs. wide rows is more evident in short-season soybean production, such as in late vs. normal planting dates or growing early vs. late maturing cultivars (Board et al., 1990a; Boerma and Ashley, 1982; Carter and Boerma, 1979).

Physiological Disruption from Shade Stress	Affected Canopy Level Growth Processes	Affected Yield Components	Shade Parameters
Reduced photosynthetic light reactions	Reduced canopy photosynthesis and CGR	Reduced seed number if shade applied during R1-R6 period. Reduced seed size if shade applied during R6-R7 period.	Most sensitive stress period is R1-R6. Reduced yield occurs (24% yield loss) with as few as 9 d of heavy shade (83%). Shade decreases yield as it decreases CGR < 16 $gm^{-2}d^{-1}$ during R1-R5 period. Moderate shade (30%) during R1-R6 period reduces yield 22-31%. Shade stress during linear seed filling period (R6-R7) has half the effect on yield vs. the R1-R6 period.

Table 5. Summary of shade effects on soybean physiology, growth, yield components, and yield.

Although narrow vs. wide culture enhances CGR at all three developmental periods, yield increases result entirely from increased pod and seed production (Egli and Yu, 1991; Board et al., 1990b, 1992). Seed per pod and seed size, yield components formed during the seed filling period (R5 to R7) were not affected by reduced row spacing. The dominant yield components controlling pod and seed production were node m^{-2} and reproductive node m^{-2}, which are formed during the vegetative period and part of the flowering/pod formation periods (emergence to R5) (Board et al., 1990b; 1992). Thus, greater LI and CGR in narrow vs. wide rows has its beneficial effect on yield between emergence and R6, with the main effect occurring from emergence to R5. In cases where wide rows achieve 95% light interception by first flowering, no yield loss occurs (Board et al., 1990a). Reduced yield in wide vs. narrow rows starts occurring when average LI across the R1 to R5 period is reduced by 14% (Board et al., 1992). In summary, changes in row spacing affected yield by a mechanism very similar to that reported for shade treatments applied throughout the reproductive period (Egli and Yu, 1991); i.e. pod and seed numbers produced during the emergence to R6 period were reduced by the lower CGR so that seed size (produced during the R5 to R7 seed filling period) could remain constant.

Plant population studies conducted under short-season conditions also have outlined a yield-control mechanism very similar to those described for narrow vs. wide row spacing and shade (Ball et al., 2000, 2001; Purcell, 2002). Increasing plant population above the

normal recommendation of 25-35 plant m^{-2} increased LI early in the vegetative period [similar to the findings for narrow vs. wide row spacing (Board and Harville, 1996)] resulting in an accelerated CGR during the R1 to R5 period, greater dry matter accumulation, and yield (Ball et al., 2000). Purcell et al. (2002) determined that increased yield responded linearly to increased photosynthetically active radiation accumulated across the emergence to R5 period. Thus, the period during which increased LI benefitted yield in high vs. normal plant population was the same as that described for narrow vs. wide rows (Board et al., 1990a; Board et al., 1992). Yield increases were shown to be caused by increased node m^{-2} and pod m^{-2} (Ball et al., 2001), similar to findings by Board et al. (1990b, 1992) for narrow vs. wide row spacing. Data indicate that subnormal plant populations can achieve yields similar to those of normal populations if average light interception across the R1 to R5 period is 90% (Carpenter and Board, 1997). Yield losses started occurring when average light interception across this period falls 14% below that for full-coverage canopies. This yield response to reduced light interception corresponds very closely to that shown by Board et al. (1992) for wide vs. narrow row spacing. Row spacing and plant population effects on yield, growth and yield components are summarized in Table 6.

2.3.3 Light interception and yield: Defoliation

Several biotic and abiotic stresses such as hail, insect leaf feeders, and diseases affect yield through defoliation. Potential physiological responses to defoliation include effects on canopy photosynthesis, TDM, altered partitioning of TDM to plant parts, leaf abscission, delayed leaf senescence, delayed crop maturity, changes in leaf specific weight, and reduced nitrogen fixation, as well as others (Welter, 1993). Convincing evidence has shown that insect defoliation reduces yield through LI effects on canopy photosynthetic activity and/or CGR. Ingram et al. (1981) infested soybean with velvetbean caterpillar during the reproductive period to study effects on physiological processes and yield. The treatments resulted in a 50% reduction in LAI resulting in LI falling to 83% of the control level during the seed filling period. Corresponding to reduced LI, canopy photosynthetic activity declined to 85% of control and yield was reduced to 86% of control. Yield loss occurred through reduced seed size caused by reduced seed growth rate which was entirely attributed to decreased photosynthetic supply. Similar results were found by Board and Harville (1993) for partial defoliation treatments made to create a LI gradient during the reproductive period. Yield loss occurred only when defoliation was severe enough to reduce LAI below 3.0 and light interception below 95% for extended periods. Although these studies involved manual defoliation, rather than insect defoliation, research has shown that yield responses from either manual or insect defoliation are similar if applied during the same growth period and if leaf removal rates are similar (Higgins, et al., 1983; Turnipseed and Kogan, 1987). The connection between LI and soybean yield response to defoliation has been reinforced by research showing that photosynthetic rates in leaves damaged by defoliation are similar to undamaged controls (Peterson and Higley, 1996). Thus, leaves remaining after defoliation cannot compensate photosynthetically for lost leaf material and the reduced LI directly decreases the photosynthetic rate and yield. Browde et al. (1994) using a combination of defoliating insects, nematodes, and herbicide damage, concluded that light interception was the "unifying explanation for yield losses". Similar conclusions were reached by Board et al. (1997) who reported a linear relationship between yield and LI at the temporal midpoint of the seed filling period.

Previous defoliation studies have indicated that yield response is affected not only by the severity of insect infestation, but also the timing of the attacks. Defoliation during the vegetative period (emergence to first flowering) usually has shown little effect on yield, largely due to leaf regrowth potential at this time. Since defoliation during the vegetative period usually does not have a long-term depressing effect on LI and CGR, little effect on yield has been reported (Haile et al., 1998a,b; Weber, 1955). These results are similar to those of Jiang and Egli (1995) where shade during the vegetative period did not reduce yield if crop growth rate during the R1 to R5 period was unaffected. Fifty percent defoliation between appearance of the first trifoliate leaf and full flowering had little effect on yield (Weber, 1955). Significant yield losses (20%) occurred in this study only when 100% defoliation was applied during this period. Pickle and Caviness (1984) reported no yield loss when soybean received 100% defoliation at the fifth leaf stage.

Greater yield responses to defoliation have been reported during the reproductive period with greatest effect near the start of seed filling (R5). Yield losses from 100% defoliation at R2 were only 25%, but rose sharply as defoliation was delayed to R3, R4, and R5 (see Table 1 for definitions of R stages) (Fehr et al., 1977). Increased defoliation tolerance at early reproductive stages (near first flower) were later determined to be caused by rapid leaf regrowth (Haile et al., 1998a,b). Greatest yield loss (75-88%) occurred at R5 (Fehr et al., 1977), a finding substantiated by later studies (Fehr et al., 1981; Gazzoni and Moscardi, 1998; Goli and Weaver, 1986). Delay of total defoliation to R6.6 resulted in only a 20% yield loss (Board et al., 1994), supporting the view of greater tolerance to defoliation as seed filling progresses.

Partial defoliation treatments initiated at R1 and terminated at R3, R4, R5, and R6.5 resulted in significant yield loss (approximately 15%) when average LI during the R1 to R5 period was reduced at least by 17-20% (Board and Harville, 1993; Board and Tan, 1995). Although these partial defoliations resulted in decreased LI during seed filling, yield losses were almost entirely due to reduced pod m^{-2} and seed m^{-2} rather than seed size. These results are similar to shade responses shown by Egli and Yu (1991). In summary, shade, defoliation, wide row spacing, and subnormal plant population affect yield through reduced CGR during all or part of the period between emergence and R6. Stresses that operate during the entire emergence to R6 period (wide row spacing, subnormal plant population), cause these reductions to pod and seed numbers through lower production of node m^{-2} and reproductive node m^{-2}. However, in cases where CGR is reduced only during the flowering/pod formation period (e.g. defoliation stress initiated at R1), lower pod and seed numbers can also be affected by decreased pod per reproductive node.

As defoliation is delayed past the start of initial seed filling (R5), yield losses attenuate and yield components causing the yield loss change. By the time seed number is determined and soybean starts rapid seed filling (R6), yield losses from 100% defoliation are half that compared with 100% defoliation at R5 (Goli and Weaver, 1986). Thus, similar to findings with shade stress (Egli and Yu, 1991), yield was twice as sensitive to defoliation stress during the flowering/pod formation period compared with the rapid seed filling period. Defoliation during seed filling affects yield mainly through reduced seed size, although seed number is also affected if defoliation occurred at or before R6 (Board et al., 2010). Every 0.1 unit delay in developmental stage from R5 to R7 (e.g. 5.4 to 5.5 or 6.2 to 6.3) resulted in a 5% reduction in yield loss caused by 100% defoliation. Throughout early and mid seed filling (R5 to R6.2), defoliation had to be sufficient to reduce light interception by about 20% to decrease yield (Board et al., 2010; Ingram et al., 1981; Board et al., 1997). Once soybean

Physiological Disruptions from Wide vs. Narrow Row Spacing	Affected Canopy Level Growth Processes	Affected Yield Components	Row Spacing Parameters
Reduced LAI and LI efficiency results in lower canopy LI.	Growing at nonoptimal wide row spacing reduces canopy photosynthesis and CGR during emergence-R6 period.	Reduced node and reproductive node numbers, pods and seeds.	Sensitive stress period is emergence to R6. Wide vs. narrow rows reduces yield whenever LI falls enough to reduce average CGR (R1-R5) below 15 gm^{-2} d^{-1}. Seed filling period is unaffected by LI in wide vs narrow rows .
Physiological Disruption From Subnormal Plant Population	**Affected Canopy Level Growth Processes**	**Affected Yield Components**	**Plant Population Parameters**
Reduced LAI results in lower canopy LI	Reduced canopy photosynthesis and CGR during emergence-R6 Period	Reduced node and reproductive node numbers, pods and seeds.	Sensitive period is emergence-R6. Yield losses occur when average CGR (R1-R5) falls below 15 g m^2 d^{-1}. Seed filling period is unaffected.

Table 6. Summary of row spacing and plant population effects on soybean physiology, growth, yield components, and yield.

passes into the last half of the seed filling period, defoliation must be at or close to 100% (resulting in a 50% relative LI reduction) to cause yield loss (Board et al., 2010; Board et al., 1997). The effects of defoliation stress on yield formation are summarized in Table 7.

Physiological Disruption from Defoliation	Affected Canopy Level Growth Processes	Affected Yield Components	Defoliation Parameters
Reduced LAI and canopy LI	Reduced canopy photosynthesis and CGR.	Defoliation during R1-R6 period reduces node and reproductive node numbers, pod per reproductive node, pods and seed. Defoliation during R6-R7 reduces seed size.	Vegetative period is not sensitive to defoliation stress unless at 100% level. Period most sensitive to defoliation stress is R1-R6.2. Significant yield losses start occurring when light interception across this period falls 17-20% and CGR falls below 15 g m^{-2} d^{-1} . During R6.2-R7 period must have total defoliation to get significant yield loss; i.e. 50% reduction in relative LI. Thus, yield is half as sensitive to defoliation during R6.2- R7 as during R1-R6.2.

Table 7. Summary of defoliation effects on soybean physiology, growth, yield components, and yield.

3. A general mechanism for explaining stress effects on yield

Our discussion on temperature, drought, and light interception has outlined a paradigm of how these factors cause yield loss (Fig. 4). Despite differences in initial physiological disruptions, environmental stress first affected canopy photosynthesis and CGR. Coupled with length of the emergence to R5 period (related to maturity group), these growth dynamic rates influence TDM(R5), the dry matter level at which vegetative TDM, node m^{-2}, reproductive node m^{-2}, and pod per reproductive node are maximized (Board and Harville, 1993; Board and Tan, 1995) (Fig. 3). These yield components, in turn, regulate pod m^{-2} and seed m^{-2} which mediate stress effects on yield. Thus, TDM(R5) serves as a benchmark indicator for yield potential. Because yield component production per unit dry matter (yield component production efficiency) differs with environmental (Board and Maricherla, 2008) and genotypic factors (Kahlon and Board, 2011), final yield component number is also affected by this factor (Fig.4). Seed size usually plays a much smaller role in explaining environmental influences on yield. Support for this paradigm can be seen in data for a single cultivar grown across a wide environmental range (Fig. 5). Yield is highly correlated with seed m^{-2} (R^2=0.83), but shows no relationship with seed size. Because of the paramount importance of nodes, pods, and seeds in regulating environmental effects on yield, the most stress-prone period is between emergence and R5, the predominant period in which these yield components are formed.
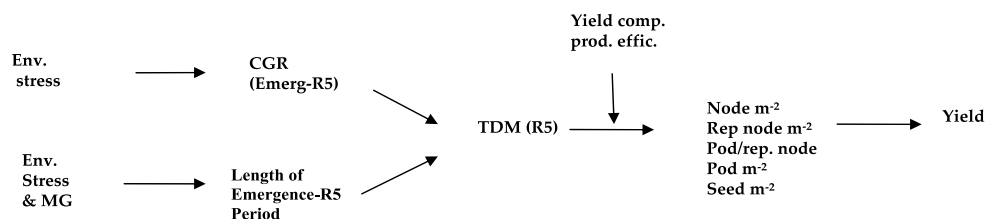
Fig. 4. Paradigm for explaining how environmental stresses affect growth, yield components, and yield. MG=Maturity Group.

We acknowledge that some abiotic and biotic stresses do not follow the paradigm outlined above. Stresses that directly impair reproductive structures (i.e. flowers, pods, and seeds) without acting through CGR fall into this category. Examples are the southern green stink bug [*Nezara viridula* (L.)] which punctures the soybean seed; temperatures that are sufficiently hot or cold during or near to fertilization to disrupt pod development (Salem et al., 2007; Koti et al., 2004); and diseases such as pod and stem blight [*Diaporthe phaeseolorum* (var. sojae)] which enter pods through abrasions, cracks, or other injuries (Athow and Laviolette, 1973). Although these exceptions exist, analyses of many environmental stresses indicates that the mode of action for yield reduction at the canopy level is similar to that described for temperature extremes, drought, and reduced light interception; and that such stresses affect yield through the paradigm explained in Fig. 4. Although it is impossible to cover all the possible abiotic and biotic environmental stresses affecting soybean in a single chapter, a few of them will be described.

Nitrogen deficiency is a common limiting factor for soybean yield (Tolley-Henry and Raper, 1986). Optimal growth and yield of soybeans, as well as other crops, requires a greater input of N than any other nutrient. Soybean obtains its N either directly from the soil or from symbiotic N_2 fixation by the bacteria *Bradyrhizobium japonicum.* Deficiency symptoms
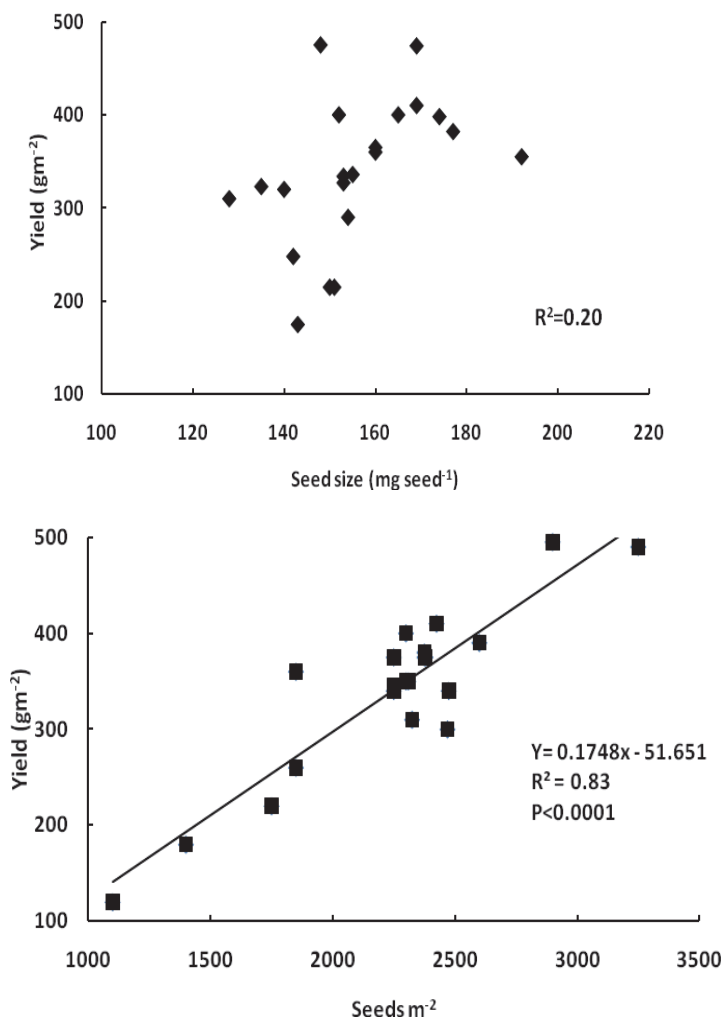
Fig. 5. The relationship of soybean yield with seed m^{-2} and seed size for cultivar Iroquois grown across 21 locations in the Midwestern US, 1996 (USDA, Unpublished data).

are manifested as decreased photosynthetic rate, reduced initiation and expansion of leaves, and lower growth rates for stems and roots (Tolley-Henry and Raper, 1986). Approximately 50% of soybean's leaf N is in rubisco, the enzyme involved in CO_2 carboxylation onto Ribulose di Phosphate (Sinclair, 2004). This enzyme is recognized as the rate-limiting step for photosynthesis. Thus, when N becomes deficient, the entire photosynthetic cycle declines, as evidenced by high correlation of leaf photosynthetic rate with [N] (Tolley-Henry et al., 1992) and soluble protein (Ford and Shibles, 1988; Sung and Chen, 1989). Thus, any stress which adversely affects N_2 fixation (e.g. inadequate inoculation, low pH soils, drought, etc.) can create N deficiency and yield loss in soybean. When a N deficiency results in leaf [N] falling below 5%, photosynthetic rate starts declining (Tolley-Henry et al., 1992).

Unavailability of N for 10 or more d results in cessation of dry matter accumulation (Tolley-Henry and Raper, 1986). Associated with this, leaf initiation and expansion stops. Consequently, LAI, LI, and CGR are greatly reduced during the emergence-R5 period, resulting in decreased seed m^{-2} and yield (Koutroubas et al., 1998). Thus, on the canopy level, N deficiency affects yield in a manner similar to that shown for temperature extremes, drought, and deficient light interception.

Several biotic stresses of soybean show a similar mechanism of yield loss. Among biotic stresses, farmers in the Southeastern US spend the greatest amount of money for weed control. Weeds reduce yield through competition with soybeans for water, light, and nutrients (Hoeft et al., 2000). Depending on weed species, weed population, and environmental conditions, there is a "critical period" early in soybean development when weeds must be controlled to maintain yield (Hoeft et al., 2000). Failure to control weeds in the critical period results in reduced soybean vegetative TDM(R5) and yield (Hagood et al., 1980, 1981). As with drought, reduced light interception and N deficiency, yield loss occurred through reduced pod and seed numbers.

4. Development of yield-loss prediction tools for diagnosing environmental stress problems

A major barrier to improved yield is correct identification of environmental stresses causing yield losses. During any given growing season, a soybean crop can be faced with a series of potential yield-limiting stresses. For example, an early-season drought stress may have slowed CGR during the vegetative period. This might be followed by a waterlogging stress during the flowering/pod formation period (R1-R6) which left standing water on the field for 2-3 d (sufficient to slow CGR, Scott et al., 1989). Finally, a late-season attack of defoliating insects during rapid seed filling (R6-R7) may have decreased LAI enough to cause significant yield loss. Correct identification of which factor(s) caused the yield loss aids in devising remedial strategies to improve yield. If the entire yield loss was due to early-season drought stress, then the farmer may consider irrigation when a similar future stress occurs. On the other hand, if the early-season drought stress was shown not to play a role in yield loss, the farmer would know that his crop could tolerate such drought periods without suffering yield loss. If waterlogging was identified as the causative factor of yield loss, then the farmer may wish to consider planting on raised beds or sloping the field in a given direction so that water runs off the field rather than ponding. If the yield loss was caused by the late-season insect defoliation, the farmer should consider more vigilant monitoring and control of whatever pest was infesting the field.

Using the paradigm outlined in Fig. 4 for explaining environmental stress effects on yield, yield-loss prediction tools can be identified which aid farmers in making decisions such as those described above. Because CGR during the emergence to R5 period plays a critical role in stress effects, TDM levels at developmental stages that are easily identifiable could be used as putative yield-loss prediction tools. Since vegetative growth ends near R5 (Egli and Leggett, 1973), TDM(R5) serves as an integrative measure of growing conditions during the emergence to R5 period. Total dry matter (R5) also has value in predicting yield (Fig. 6). The R5 stage is easy to identify by the appearance of fully-elongated pods at the top four main stem nodes. Total dry matter at R1 (also an easily identifiable developmental stage) could be used to indicate growing conditions at an intermediate stage of the vegetative growth period. Based on an analyses of studies conducted across 1987-1996 near Baton Rouge, LA

involving a wide range of environmental conditions (years, planting dates, row spacings, plant populations, and waterlogging stress) achievement of optimal yield was shown to be associated with a TDM(R1) level of 200 g m^{-2} and a TDM(R5) level of 600 g m^{-2} (Fig. 6) (Board and Modali, 2005). Dry matter levels below these resulted in a curvilinear decline in yield, while increases above this level gave only small insignificant yield increases. Yield components identified as important for yield formation (seed m^{-2}, pod m^{-2}, reproductive node m^{-2}, and node m^{-2}) demonstrated similar curvilinear responses to TDM(R1) and TDM(R5) as did yield.
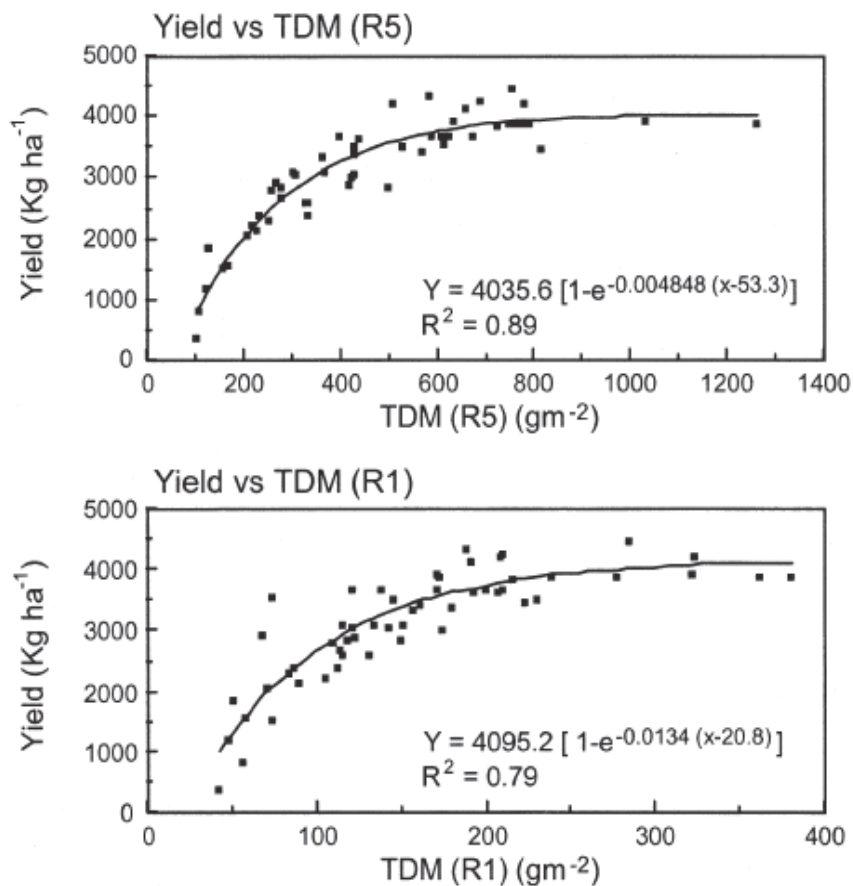

Fig. 6. Yield response to total dry matter at R1 [TDM (R1)] and total dry matter at R5 [TDM (R5)] for soybean grown across a range of environment conditions near Baton Rouge, LA, 1987 through 1996.

Use of TDM(R1) and TDM(R5) as yield-loss prediction tools can be illustrated by analyzing the aforementioned case of decreased yield resulting from three possible stresses across the growing season: drought during the vegetative period, waterlogging during the flowering/pod formation period, and insect defoliation during rapid seed filling.

Determination that TDM(R1) was optimal (200 g m^{-2} or greater), but TDM(R5) was suboptimal (<600 g m^{-2}) would indicate that the waterlogging stress contributed to the yield loss, but the drought stress did not. Such a result would be manifested in a reduction in seed m^{-2}. If TDM levels at R1 and R5 were both optimal, then the yield loss probably resulted from the insect defoliation. This would be reflected by a reduction in seed size, but no reduction in seed m^{-2}. Seed size can be determined from a field by random sampling of 100-seed samples. Seed m^{-2} can then be easily calculated by dividing seed size into seed yield (as dry matter). Thus, a knowledge of when stresses occur, developmental stage timing, TDM(R1) and TDM(R5), and seed size and seed m^{-2} data, greatly aid in diagnosing yield-limiting stresses.

Because of the large size of many commercial soybean farms, it is not practical to determine TDM(R1) and TDM(R5) by conventional sampling methods. However, simple regression methods have been developed that allow easy, rapid, and accurate determination of these parameters. Total dry matter (R5) can be predicted from a multiple regression equation using canopy closure (CC) date (achievement of 95% light interception) and days to R5 (R5days) [TDM(R5)= -20.1-(5.9 x CC)+(13.7 x R5days)] (R^2=0.81). The regression model was verified using independent data (R^2=0.90). Both canopy closure date and days to R5 are parameters that can easily, rapidly, and accurately be determined in commercial soybean fields.

Because of the relationship between TDM, LAI, and LI (Loomis and Connor, 1992a), TDM(R1) can be predicted from LI. Determination of light interception under field conditions can now be done rapidly and accurately for commercial soybean farms using digital photographic methods developed by Purcell (2000). When grown in narrow-row culture (50 cm or less), a light interception of 92% at R1 is associated with a dry matter level of 200 g m^{-2} (Board et al., 1992; Board and Harville, 1996). In the case of wide rows (75-100 cm), light interception of 68% at R1 is associated with a dry matter of 200 g m^{-2}. The greater light interception value for narrow rows occurs because LAI in narrow rows intercepts more light per unit LAI (Board and Harville, 1992). In conclusion, TDM(R1) and TDM(R5) are robust yield-loss prediction tools that can be used in conjunction with seed m^{-2} and seed size data to efficiently analyze environmental stress problems in soybean.

5. Genetic strategies for yield improvement

Across a 60-year period, cultivar development efforts by soybean breeders have resulted in a 21-31 kg ha^{-1}yr^{-1} increase in soybean yield (Wilcox, 2001). Selection for yield during this process has been done through empirical yield trials across a range of different environments (Fehr, 1987; Frederick and Hesketh, 1994). Desirable lines are selected as future cultivars based on high and stable yields across years and locations. Thus, factors responsible for this yield improvement have not been clearly identified. In an effort to identify indirect yield criteria for streamlining cultivar development, scientists have endeavored to determine the pertinent factors related to genetically-induced yield enhancement in the cultivar development process.

Several studies have sought to explain yield improvement in the cultivar development process through greater production of specific yield components. However, results have been mixed. Boerma (1979) reported that yield improvement was attributed to greater pod production, although this was apparent only in maturity group VIII cultivars, and not in maturity group VI and VII. Frederick et al. (1991) also demonstrated that increased yield in new compared with old cultivars was related to increased pod number. In contrast, Specht and Williams (1984) demonstrated a small increase in seed size averaging 0.1 g/year. Other

research indicated that the relative importance of seed number and seed size in explaining greater yield in the cultivar development process may depend on cultivar comparisons being made. Gay et al. (1980) demonstrated that within indeterminate maturity group III cultivars, the newer cultivar Williams yielded more than the older cultivar Lincoln because of greater seed size. On the other hand, in comparing determinate maturity group V cultivars, the newer cultivar Essex yielded more than the older cultivar Dorman because of greater seed number. More recent studies comparing old and new Midwestern cultivars clearly indicated that yield improvement was more strongly related to seed m^{-2} than seed size (De Bruin and Pedersen, 2009). The authors also stated that greater seed m^{-2} appeared to be related to greater seed per pod, although other yield components were not examined. Comprehensive research from China involving determinate and indeterminate soybeans in four areas of the country showed that greater yield occurred through differential increases of pods per plant, seed per pod, and seed size (Cui and Yu, 2005). Based on the diversity of results from different researchers, countries, and germplasms, it appears that yield improvement with cultivar development can occur through different yield component mechanisms. However, for the Southeastern and Midwestern US soybean-growing regions, most studies conclude that cultivar yield improvement in new vs. old cultivars has been more controlled by changes in seed m^{-2} than seed size. Recent studies involving Southeastern US cultivars indicated that genetic differences in new vs. old cultivars were sequentially controlled by node m^{-2}, reproductive node m^{-2}, pod m^{-2}, and seed m^{-2} (Kahlon et al., 2011).

Because of its importance in crop production, researchers have also tried to determine if leaf photosynthetic rate plays a role in explaining yield improvement during cultivar development. This objective has been studied by comparing carbon exchange rates (CER) per unit leaf area in new vs. old cultivars and also between parents and progeny in a breeding program. Results have been mixed. Early studies by Larson et al. (1981) involving cultivars released between 1927 to 1973 found no correlation between yield and leaf photosynthetic rate. Gay et al. (1980) also found little change in CER between two new and two old cultivars. Similar results were reported by Frederick et al. (1989). In contrast, Dornhoff and Shibles (1970) compared 20 cultivars released across time and demonstrated a general trend between CER and yield, although exceptions occurred. More recent studies by Morrison et al. (2000) with new and old Canadian cultivars did report a 0.52 % per yr increase in the photosynthetic rate, a level very similar to the annual yield increase shown by these cultivars. However, an inverse relation of photosynthetic rate per leaf with LAI may have negated some of the positive effect of increased photosynthetic rate. The increase in photosynthetic rate was related to an increase in stomatal conductance.

Results of studies looking at CER in progeny of a breeding program have also been mixed. Buttery and Buzzell (1972) determined that over 60% of cultivars developed from breeding programs had CER greater than their parent cultivars. Ojima (1972) also was successful in demonstrating increased CER in early progeny lines vs. parental cultivars. However, other research has not demonstrated positive results. Wiebold et al. (1981) crossed two parental cultivars with contrasting high and low CER and could not find improved CER by the F_3 and F_4 generations. Ford et al. (1983) found similar disappointing results. The current general consensus is that using CER as an indirect selection criterion in a breeding program has limited value (Frederick and Hesketh, 1994).

Measurement of photosynthesis on the canopy level (canopy apparent photosynthesis, CAP) has shown greater association with final yield compared with CER (Harrison et al., 1981;

Wells et al., 1982). However, the degree of correlation was not high (r=0.5). Using cultivars and plant introductions differing in CAP and seed filling period, Boerma and Ashley (1988) showed positive partial correlations of yield with CAP (averaged during the reproductive period) (r=0.63) and seed filling period (r=0.54). The product of CAP x seed filling period was even more closely related to yield (r=0.78). However, the inherent difficulties involved in measuring CAP (variable light and temperature conditions; tedious equipment set-up) preclude its use as an indirect selection tool in a breeding program.

The roles of TDM accumulation and harvest index in explaining yield improvement during cultivar development have also shown mixed results. Salado-Navarro et al. (1993) examined 18 Southeastern cultivars released from 1945 to 1982, but found no relationships between improved yield with either TDM or harvest index. Gay et al. (1980) explained yield differences between new and old cultivars as governed more by increased harvest index rather than TDM accumulation. More recent studies involving new vs. old cultivars in Canada (Morrison et al., 1999) and Japan (Shiraiwa and Hashikawa, 1995) have also supported the importance of harvest index for explaining greater yield. In the case of the Canadian study, no differences in TDM were shown between new and old cultivars. These results are supported by Chinese studies which reported a greater role for harvest index vs. TDM accumulation for explaining yield improvement in cultivar development programs (Cui and Yu, 2005).

In contrast, Frederick et al. (1991) (US cultivars) reported little role for harvest index in explaining genetic improvement in soybean and attributed greater importance to TDM accumulation. Cregan and Yaklich (1986) reported similar findings. These results were supported by Kumudini et al. (2001) who showed that TDM accumulation contributed 78% to greater yield in new vs. old cultivars, whereas harvest index contributed only 22%. Greater TDM accumulation occurred entirely during the seed filling period and was supported by the longer leaf area duration (leaf area index integrated over time) for the new cultivars. De Bruin and Pedersen (2009) supported Kumudini's findings and attributed yield enhancement in new vs. old Midwestern cultivars as entirely due to dry matter and not harvest index. However, this more recent study differed from Kumudini in concluding that the greater dry matter accumulation was partly due to greater crop growth rate (R1-R5.5) prior to seed filling.

6. Summary and conclusion

Because of soybean's importance in meeting world food needs, increased demand for agricultural commodities fueled by global economic development, and the limited potential for expansion of arable land, it is imperative that strategies be developed for coping with the effects of environmental stress on crop yields. Accurate identification and correction for environmental stress problems potentially can increase yield from 25-66%, with increases being greater in the developing compared with developed world. Environmental stresses can be divided into either abiotic stresses (atmospheric and soil factors) or biotic stresses (pest problems). Because such a high proportion of crop dry matter is derived from either current or previous photosynthesis, the vast majority of environmental stresses affect yield through the canopy photosynthetic rate and CGR. The majority of soybean research has conclusively demonstrated that environmental stress affects yield through control of seed m^{-2}, which, in turn, is controlled by sequential formation and growth of node m^{-2}, reproductive node m^{-2}, and pod m^{-2}. Since formation of these yield components occurs across the

emergence to R6 period, this is the period where stresses depressing crop growth rate have their greatest effect on yield. Although yield is less sensitive to stress during the rapid seed filling period (R6-R7), stresses during this period can also reduce yield if sufficiently severe. Correct advice to soybean farmers concerning correction of environmental stresses depends on accurate identification of which potentially damaging biotic and abiotic factors occurring in any growing season significantly reduce yield (i.e. act as stresses). Development of TDM levels at R1 and R5 as yield-loss prediction tools facilitates this process. Both developmental stages are easy to identify and yield has shown robust asymptotic relationships of TDM(R1) and TDM(R5) with yield reaching plateau levels at 200 g m^{-2} TDM(R1) and 600 g m^{-2} TDM(R5). Accurate and rapid regression methods were outlined for indirect calculation of these parameters. Thus a farmer having knowledge of TDM(R1) and TDM(R5), the timing of potential stress events, and knowledge of seed m^{-2} and seed size, would be able to identify which potential stresses actually cause yield loss.

On the genetic level, the majority of yield formation studies indicate that seed m^{-2} plays a larger role in yield improvement than seed size. However, exceptions to this exist and it must be realized that alternative mechanisms of yield improvement are possible between different germplasm pools and geographic regions. Although little research has been done beyond the primary yield component level, studies that have been conducted indicate that genetic influences on seed m^{-2} are mediated by node m^{-2}, reproductive node m^{-2}, and pod m^{-2}. Genetic studies involving old and new soybean cultivars indicate that both TDM accumulation and harvest index play roles in explaining yield improvement. However, the evidence is so conflicting at this point in time that definitive statements are not possible. Although much research has been done on the subject, there is little evidence to suggest that improved yield has resulted from improved photosynthetic rate per unit leaf area, canopy photosynthesis, or CGR.

7. Acknowledgements

8. References

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