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Analysis of genetic improvement for soybean from 1950-2000

Charanjit Singh Kahlon

Louisiana State University and Agricultural and Mechanical College

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ANALYSIS OF GENETIC IMPROVEMENT FOR SOYBEAN FROM 1950- 2000

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
In partial fulfillment of the
Requirements for the degree of
Doctor of Philosophy
in

The School of Plant, Environmental and Soil Sciences

by

Charanjit Singh Kahlon

B.S. Ag. Guru Nanak Dev University, Amritsar, India 2001

M.S. (Agronomy) University of Agricultural Sciences, Bangalore, India 2005

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Abstract

Reasons for the gradual genetic yield improvement (21-31 kg ha⁻¹yr⁻¹) reported for soybean [*Glycine max* (L.) Merr.] during decades of cultivar development are not clearly understood. Identification of mechanisms for the yield improvement would aid in providing indirect selection criteria for streamlining cultivar development. Our objective was to identify yield components, growth parameters, phenological data, and/or other agronomic data responsible for yield improvement in 18 public southern cultivars released between 1952 and 2000. The study was done at the Ben Hur research farm near Baton Rouge, LA (30⁰N Lat) during 2007 and 2008. Experimental design was a randomized complete block with four replications and one factor (cultivar). Data were obtained on yield, seed per area, seed size, seed per pod, pod per area, pod per reproductive node, reproductive node number per area, percent reproductive nodes, node number per area, total dry matter (TDM) at R7 and harvest index (HI). Data were analyzed sequentially at primary (seed number per area and seed size affecting yield), secondary (pod number per area and seed per pod effecting seed number per area), tertiary (pods per reproductive node and reproductive node number per area affecting pod number per area) and quaternary levels (node number per area and percent reproductive nodes affecting reproductive node number per area). Yield improvement among these cultivars was not related to length of the seed filling period, or days from emergence to R5 or R7. Neither was lodging resistance involved. Greater yield in new vs. old cultivars was mainly due to greater TDM (R7) (71%) and secondarily to higher HI (29%). Yield components responding to greater dry matter accumulation to create more yield in new vs. old cultivars were node and reproductive node number per area, pod number per area and seed number per area. A possible indirect selection criterion for yield during cultivar development is reproductive node number per area.

Chapter 1

Introduction

1.1 Introduction

Across a 60-year period, cultivar development efforts by soybean breeders have resulted in a 21-31 kg ha⁻¹yr⁻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 responsible for higher yield in the cultivar development process. For example, in summarizing corn research by several authors (Liu and Tollenaar, 2009), erect leaf angle (allowing greater canopy light penetration) and extended leaf area during seed filling (to support greater kernel number) were identified as critical factors in explaining increased yield in new vs. old corn cultivars.

Yield, whether affected by genetic and/or environmental factors, is controlled by an interplay between growth dynamic and yield component parameters. Growth dynamic parameters are rates and levels of dry matter, leaf area, and light interception that characterize soybean's seasonal growing pattern (Loomis and Connor, 1992a). Yield components are morphological characteristics whose formation is critical to yield production (Egli, 1998). For soybean, examples are seed number per area, seed size, seed per pod, pod number per area, pod per reproductive node (reproductive nodes contain at least one pod having at least one seed), reproductive node number per area, fraction of nodes becoming reproductive (percent

reproductive nodes), and node number per area (Board and Modali, 2005). 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 number per area; seed number per area is controlled by secondary yield components seed per pod and pod number per area; pod number per area is controlled by tertiary yield components pod per reproductive node and reproductive node number per area; and reproductive node number per area is controlled by quaternary yield components node number per area and percent reproductive nodes.

Yield is basically a function of intercepted light (fraction of the sunlight intercepted by the crop), the dry matter produced from this light [which is controlled by radiation use efficiency (g of dry matter/units of light energy intercepted)], and the percentage of this dry matter transferred to the seed [harvest index (g of seed yield/g of total dry matter)] (Loomis and Connor, 1992a). Attainment of optimal yield is dependent on achievement of optimum dry matter accumulation by R5 (Board and Modali, 2005). This, in turn, is a function of the length of time to R5 and the crop growth rate ($\text{g m}^{-2}\text{d}^{-1}$) between emergence and R5. Crop growth rate is controlled by the leaf photosynthetic rate and the level of leaf area index [leaf area (m^2)/ground area (m^2)]. The majority of abiotic stresses affecting soybean, as well as some biotic stresses (weeds, defoliating insects and diseases, nematodes), influence yield through crop growth rate effects on seed number per area (Jiang and Egli, 1995; Egli, 1998). Consequently, farmer cultural practices aimed at optimizing yield (e.g. optimum planting date, reduced row spacing, irrigation, planting on raised beds, pesticide application, seeding rate, fertility, etc.) achieve better yield through the effects of these cultural practices on crop growth rate and seed number per area.

Thus, yield components are the vehicle through which crop growth rate and dry matter increases affect yield. Based on studies conducted on the environmental level, dry matter accumulation was shown to affect some yield components but not others (Board and Modali, 2005). Differences in row spacing, planting date, plant population, and waterlogging stress affected yield through the growth dynamic process described above. Dry matter accumulation affected yield through control of seed number per area, pod number per area, and reproductive node number per area (node containing a pod having at least one seed), and node number per area. In contrast, seed size, seed per pod, pod per reproductive node, and percent reproductive nodes appeared unrelated to the yield formation process.

Although recent studies comparing new vs. old soybean cultivars have indicated that dry matter levels and seed number per area help explain yield improvement (Kumudini et al., 2001; DeBruin and Pedersen, 2009; Kahlon and Board, 2010), no studies have clearly identified the growth parameters responsible for this greater seed and yield production. Thus, our general objective was to identify growth dynamic parameters responsible for greater yield in new vs. old cultivars. Elucidation of this issue will provide soybean breeders with potential indirect selection criteria for soybean cultivar development.

1.2 Review of Literature

1.2.1 Soybean as a Major Crop

Soybean is the most important oilseed crop grown in the world (56% of world oil seed production) and has been a major crop in the US since the end of World War II (Wilcox, 2004). Currently, soybean is grown on about 30 million hectares in the US with most of the production (82%) in the midwestern US. Louisiana only contributes to about 1% of the country's soybean production. Despite this small percentage, soybean makes a significant contribution to

Louisiana's economy (\$300 million in 2008) (Louisiana Agricultural Statistics, 2008). As a percentage, the US produces about 33% of the world's soybeans, followed closely by our main competitors, Brazil (28%) and Argentina (21%). Remaining producers are China, India, and a few other countries. The value of soybean to the US economy is attested to by the \$26.9 billion total value of the US soybean crop in 2006/2007 (Soyatech, 2008). Thus, soybean accounts for 16% of total US crop value (\$165 billion). This makes soybean second to corn (29% of total value) in its importance to the US economy.

Soybean is used as human food in East Asia, but is predominately crushed into meal and oil in the US; and then used for human food (as cooking oil, margarine, and livestock feed. 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 (Soyatech, 2008). 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.

Although once the dominant supplier for soybean sold in world trade, the US now contributes only to 40% of this market, followed by Brazil (32%) and Argentina (17%) (United Soybean Board, 2008). Most of the oil and meal crushed from soybean in the US stays within the country. Thus, our contribution to the world market is mainly as whole seed. Currently, our largest customers are China, Mexico, and the European Union.

1.2.2 Yield Enhancement from Cultivar Development

Reports of genetic gain from soybean cultivar development differ with region and the time period studied [10 to 30 kg ha⁻¹ yr⁻¹] (Specht et al., 1999). Using midwestern cultivars, Wilcox (2001) reported a genetic gain of 21 to 31 kg ha⁻¹ yr⁻¹ across a 60-year period. However, other studies also involving midwestern cultivars reported an annual gain of only 12 to 18.8 kg

ha⁻¹ yr⁻¹ (Specht and Williams, 1984). Boerma (1979) compared 18 southern cultivars released from 1942 to 1973 and reported an annual yield increase of 13.7 kg ha⁻¹ yr⁻¹. Canadian researchers working with very early maturing cultivars (MG 0, 00, and 000) showed no genetic gain in yield from 1934 to 1976. However, with the introduction of cold tolerant cultivars in 1976, yield gain from 1976-1992 was 30 kg ha⁻¹yr⁻¹ (Voldeng et al., 1997). Genetic yield gain from private cultivar development appears to be comparative to that for public cultivars discussed above. Specht et al. (1999) was able to overcome proprietary restrictions to test several MG II and III cultivars developed by Asgrow and Pioneer seed companies. The reported genetic gain in yield was 25 to 30 kg ha⁻¹ yr⁻¹. In an Indian study, Karmakar and Bhatnagari (1996) reported a yield increase of 22 kg ha⁻¹yr⁻¹. Chinese researchers reported a smaller increase of 12.1 kg ha⁻¹ yr⁻¹ for the 1950-1991 period (Hu, 1994)

In addition to reporting yield gains, researchers have also tried to identify factors responsible for greater yield in new vs. old cultivars. Among midwestern cultivars, Leudders (1977) attributed some of the yield increase to a 17% decrease in lodging score. Voldeng et al. (1997) also reported that in new vs. old Canadian cultivars, lodging was reduced. Wilcox et al. (1979) identified increased plant height, decreased lodging, reduced seed protein, and greater oil content as characterizing new vs. old cultivars, but did not think that any of these factors were necessarily related to the greater yield. Specht and Williams (1984), studying 19 cultivars released between 1924 to 1980, also reported decreased lodging, as well as improved seed quality.

1.2.3 Stress Tolerance in New vs. Old Cultivars

Research has also investigated the role of stress tolerance for explaining greater yield during the cultivar development process. Research with corn has indicated that new cultivars had

greater tolerance to stresses such as low night temperature, low soil moisture, low soil nitrogen, high plant population, and weed interference (Tollenaar and Wu, 1999). Results with soybean have been more mixed. In comparing new vs. old cultivars, the greater yield potential of the new cultivars was more expressed in a well-watered compared with drought conditions (Frederick et al., 1991). In contrast, Boyer et al. (1980) reported that older cultivars had leaf water potential levels slightly below that for newer cultivars in nonirrigated conditions. He concluded that greater root density for the newer cultivars was responsible for improved water status. Canadian researchers reported that new cultivars showed greatest yield superiority over older cultivars under the stressful conditions of ultra-high plant populations; suggesting that cultivar development resulted in greater ability for soybean to withstand stress (Cober et al., 2005).

1.2.4 Yield Components in New vs. Old Cultivars

Several studies have endeavored 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 MG VIII cultivars, and not in MG 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), in the study cited above, demonstrated a small, but in some cases significant, annual 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 MG 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 MG 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 much more strongly related to seed number per area than seed size (De Bruin and Pedersen, 2009). The authors also stated that greater seed number per area 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.

1.2.5 Growth Dynamics in New vs. Old Cultivars

In addition to yield components, researchers have also investigated growth dynamic parameters (e.g. dry matter level, leaf area index, light interception, harvest index, etc.) that may be related to yield improvement in new vs. old cultivars. Such factors are important to study because yield is a function of dry matter produced and the percentage of dry matter transferred into the seed (i.e. harvest index) (Loomis and Connor, 1992a). Dry matter accumulation is also important because yield components recognized as important in controlling yield on the environmental level (node number per area, pod number per area, and seed number per area) are responsive to dry matter accumulation (Egli and Yu, 1991; Board and Modali, 2005). Dry matter level is regulated by the interplay of crop growth rate (rate of dry matter accumulation per m^2 per day), light interception (% of sun light intercepted by the crop), and leaf area index (m^2 leaf area/ m^2 land area) (Loomis and Connor, 1992a). Crop growth rate is directly controlled by light interception up until canopy closure and by the level of ambient light afterwards. Maximal crop

growth rate is reached when light interception is about 95% (Shibles and Weber, 1966). Light interception (up until canopy closure) is largely controlled by leaf area index, although the leaf area index required for 95% light interception is smaller in narrow rows (3.0 to 4.0) compared with wide rows (5.0 to 6.0) (Board et al., 1990).

As with yield components, previous studies do not give a consistent picture of how dry matter accumulation and harvest index are related to yield increases during the cultivar development process. Salado-Navarro et al. (1993) examined 18 southern cultivars released from 1945 to 1982, but found no relationships between improved yield with either dry matter or harvest index. Gay et al. (1980) explained yield differences between new and old cultivars as governed more by increased harvest index rather than dry matter 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 dry matter were shown between new and old cultivars. These results are supported by Chinese studies which reported a greater role for harvest index vs. dry matter accumulation in explaining yield improvement in cultivar development programs (Cui and Yu, 2005).

In contrast, Frederick et al. (1991) reported little role for harvest index in explaining genetic improvement in soybean and attributed greater importance to dry matter accumulation. Cregan and Yaklich (1986) reported similar findings. These results were supported by Kumudini et al. (2001) who showed that dry matter accumulation contributed 78% to greater yield in new vs. old cultivars, whereas harvest index contributed only 22%. Greater dry matter accumulation entirely occurred during the seed filling period and was supported by the longer leaf area duration (leaf area index integrated over time) during the seed filling period 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.

1.2.6 Nitrogen Relationships in New vs. Old Cultivars

Since nitrogen accumulation and partition to the seed is considered to be an important yield-limiting factor (Sinclair and deWit, 1976; Frederick and Hesketh, 1994; Sinclair, 1998), nitrogen relationships have also been explored as a possible explanation for improved yield in new vs. old cultivars. According to the "self-destructive hypothesis" of Sinclair and deWit (1976) the high demand of the soybean seed for nitrogen (because of the seed's high protein content) depletes leaf nitrogen concentration (measured either on a weight or area basis), resulting in decreased photosynthetic capacity during seed filling. This consequently results in a shortening of the seed filling period which reduces yield potential. This theory has led some researchers to speculate that improved yield in new vs. old cultivars results from greater nitrogen uptake and/or partitioning of nitrogen to the seed. Evidence supporting this hypothesis can be found in studies demonstrating that newer cultivars have a longer seed filling period (Gay et al., 1980) and also have longer leaf area duration (Kumudini et al., 2001). However, further investigation revealed that the extended leaf area duration and greater yield for new vs. older cultivars was not correlated to differences in nitrogen concentration, thus undermining the "self-destructive hypothesis" (Kumudini et al., 2001). The authors reported that by early seed filling (R6) nitrogen concentrations for new cultivars were no different from the older cultivars; and that nitrogen partitioning was similar in both. The newer cultivars simply had more nitrogen

because of greater leaf area index associated with their greater biomass to meet the increased nitrogen demand for their greater yield. The authors concluded that leaf nitrogen concentration in older cultivars was not a barrier to yield enhancement. Kumudini's findings support previous research by Zeinaki-khanghah et al. (1993) that among 213 F₆-derived lines, yield showed no association with nitrogen content or concentration at R5. The "self-destructive hypothesis" has also been challenged by other research showing that seed growth was not closely related to nitrogen supply (Hayati, 1994). In this study, soybean seed was shown to maintain seed growth rate for 14 days across nitrogen concentrations ranging from 0 to 270 mM.

1.2.7 Photosynthesis in New vs. Old Cultivars

Because of the importance of dry matter accumulation in explaining yield in new vs. old cultivars, researchers have also endeavored to determine if leaf photosynthetic rate also plays a role, since it is the physiological process that contributes to most of the crop's dry matter (Gardner et al., 1985). Net CO₂ uptake in soybean mainly comes from leaves as little is fixed by pods or stems (Sambo et al., 1977; Spaeth et al., 1983; Quebedeaux and Chollet, 1975). The role of photosynthesis in explaining increased yield in new vs. old cultivars 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 compared with 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 reported 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 leaf area index 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 in the F₃ and F₄ 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.

1.2.8 Role of Phenology in Yield Improvement of New vs. Old Cultivars

Among developmental periods, the seed filling period (R5-R7) has received the greatest research attention. Early studies during the 1970's suggested an association of seed filling period with yield on the environmental level (Egli and Leggett, 1973). Dunphy et al. (1979) studied 119 midwestern cultivars at 10 locations and reported significant correlation ($r=0.51$) of yield with seed filling period. In contrast, no significant relationships were found in yield at any vegetative period. Similar empirical relationships between seed filling period and yield were reported by Boote (1981) in the southeastern US using indeterminate early maturing soybeans (MG IV and less).

Positive results from these early studies stimulated further research into the use of seed filling period as an indirect selection criterion for identifying high-yielding lines in a cultivar development crossing program. Smith and Nelson (1986) examined yield and seed filling period in F_4 and F_5 lines in a breeding program and concluded that seed filling period could be used as an indirect selection criterion for yield. Similar results were reported in the southeastern US using determinate cultivars (Hanson, 1985; Boerma and Ashley, 1988). However, in subsequent studies, the authors noted less gain for yield when using seed filling period as a selection criterion vs. direct selection for yield (Smith and Nelson, 1986). For research involving various lines from the USDA Soybean Germplasm Collection in the midwest, Nelson (1986) showed a very high genotypic correlation of seed filling period with yield ($R=0.93$). However, phenotypic correlations were lower, suggesting that environmental effects confounded the relationship of yield with seed filling period.

The inconsistency of the yield/seed filling period linkage across environments in a breeding program was corroborated in other studies (Pfeiffer et al., 1991; Hanson, 1992; Egli et

al., 1984). Salado-Navarro et al. (1986) conducted four field studies using over 100 late maturing (MG VII and VIII) determinate cultivars in Florida in order to come to some consensus over the use of seed filling period as an indirect selection criterion for yield. They concluded that although higher-yielding cultivars usually had a longer seed filling period, correlation between yield and seed filling period was generally nonsignificant and inconsistent; and that selection for seed filling period would not necessarily result in increased yield.

Although less researched, the lengths of other developmental periods have, in certain circumstances, been shown to be important in yield determination. Using data from diverse environmental backgrounds, attainment of optimal yield depended on achieving a dry matter level of 600 g m^{-2} by R5 (developmental stage where vegetative growth ceases) (Board and Modali, 2005). Since obtaining this dry matter level depends on the length of time between emergence and R5, as well as the crop growth rate during this period, it is reasonable to surmise that in some cases lengths of developmental periods prior to seed filling may be important to yield formation. When growing conditions are favorable to early canopy closure and optimal light interception, the longer vegetative period of later-maturing cultivars did not convey any yield advantage relative to earlier maturing cultivars (Egli, 1993). However, under conditions of a late planting date in which dry matter accumulation was limited, extended periods from emergence to R5 for late vs. earlier maturing cultivars contributed to the yield advantage for the former over the latter (Board et al., 1996).

1.2.9 Description of Soybean's Phenostages (Developmental Stages)

Development in soybean is described by a system of vegetative (V) and reproductive (R) stages (Fehr and Caviness, 1977). The vegetative stages describe development prior to first flowering (emergence to first flower). From first flower onwards (reproductive period),

developmental stage are characterized by R stages. Designation of V stages is based on the topmost leaf formed on the main stem. The topmost leaf is identified as such when the young leaf at the next node above it has just unfurled its leaflets. For example, the V4 stage is when the 4th leaf on the main stem has formed and at the node just above it the young 5th leaf has just unfurled its leaflets.

Soybean seed begins germination when it absorbs water equal to 50% of the seed's weight. The radical first emerges from the seed. Afterward, the hypocotyl emerges and grows toward the soil surface pulling the cotyledons with it. This hook-shaped hypocotyl straightens out once above the soil and then the cotyledons unfold. Emergence is when the cotyledons rise above the soil surface. This emergence process normally takes 5-10 days depending on temperature, moisture, cultivar and planting depth. The V1 stage is reached when the primary leaves are formed and the leaves at the next node have just unfurled. Subsequent V stages occur as more leaves are successively formed going up the main stem. As with most V and R stages, a plot is considered to be at that stage when 50% of the plants are at the stage.

The eight R stages are divided into four parts: R1 (first flowering) and R2 (full flowering) describe flowering; R3 (pod initiation) and R4 (pod elongation) describe pod development; R5 (seed initiation) and R6 (full seed stage) describe seed development; and R7 (end of seed filling, physiological maturity) and R8 (harvest maturity) describe plant maturation (Whigham, 1997). At R1, the soybean plant develops one open flower at any node on the main stem. The R2 stage (full flowering stage) is indicated by an open flower at the top two nodes on the main stem with a fully developed leaf. The appearance of new flowers peaks between R2 and R3. The R3 (pod initiation stage) stage is when at least one pod has emerged from the calyx (the pod is about 5 mm long at this stage) at one of the four topmost main stem nodes having a fully expanded leaf.

When at least one pod at one of the four topmost nodes has lengthened to 2cm the plant is considered to be at R4 (pod elongation stage) Pods continue to elongate past the R4 stage as small seeds start forming in the pod cavities. The R5 stage (seed initiation stage) is identified when at least one seed reaches 3 mm length at one of the four topmost nodes having fully expanded leaves. The young seed expands length-wise and width-wise to fill the pod cavity, and then starts lateral bulging. Once the bulging reaches its limit for one seed at the four topmost leaves, the plant is considered to be at the R6 stage (full seed stage). Seeds continue filling until physiological maturity (R7) (end of seed filling). This indicates dry matter accumulation into the seed has ceased. Attainment of final seed weight is indicated by the pod losing its green color. The R7 stage is when one pod anywhere on the plant has turned its mature brown color. The soybean seed at physiological maturity is at 60% moisture and contains all necessary plant parts to initiate germination. The R8 stage is harvest maturity and is indicated by 95% of pods reaching their mature brown color for all plants in a plot. Within a few days after R8, seed moisture content usually falls to 15% or less, at which time harvest is possible.

1.2.10 Environmental Factors Affecting Soybean Yield

Environmental stress is any factor affecting the crop in such a way that yield and/or quality are significantly reduced. Environmental stresses are categorized as either biotic (i.e. pests such as weeds, insects, nematodes, and diseases) or abiotic (i.e. physical factors such as drought, waterlogging, hail, lodging, temperature extremes, subnormal light, soil compaction, low soil pH, etc.). The soybean cultivar improvement process has involved selection for characteristics that ameliorate both kinds of stresses.

Cultivar development programs generally involve efforts at developing genotypic resistance to biotic stresses (Fehr, 1987). Research in the 1950's developed several cultivars

resistant to phytophthora rot, a disease associated with heavy poorly-drained soils, that results in premature plant death (Hartwig, 1973). Efforts to develop resistance to soybean cyst nematode, considered to be the worst biotic stress, also date back to the 1950's. Attempts at pest control through cultivar development have been hampered by the development of resistant pest races, and the difficulty of trying to incorporate the many genes necessary for achieving quantitative resistance.

Aside from yield improvement and pest resistance, cultivar development also has tried to reduce combine losses through raising the height to lowest pod and reduced pod shattering (Fehr, 1987). Much effort was also applied to lodging resistance. Lodging is an abiotic stress that reduces yield by disrupting canopy light relations. Early studies demonstrated that moderate lodging (2.6, plant leaning at a 45° angle) was sufficient to cause 13% yield losses (Weber and Fehr, 1966). Greater yield losses occur with more serious lodging. Generally, lodging needs to occur by R5 for yield to be reduced (Woods and Swearingin, 1977). Lodging resistance in indeterminate midwestern cultivars has been achieved by incorporation of the determinate growth habit (Cooper, 1971). This has reduced plant height with a corresponding reduction in lodging. Midwestern breeders have also developed cultivar tolerance to Fe-deficiency chlorosis, a common problem on the high-pH calcareous soils of the region (Fehr, 1982).

In addition to the aforementioned factors, greater yield has also been a major factor soybean breeders have strived to improve (Fehr, 1987); although explanations for this yield improvement are not apparent. Because temperature extremes, drought stress, and canopy light absorption are the major abiotic stress factors influencing soybean yield (Hollinger and Angel, 2009), it is possible that cultivar yield improvement across years may have been inadvertently selecting for resistance (either through avoidance and/or tolerance) to any one or combinations of

these potential stresses. Therefore, an understanding of all three is helpful for finding an explanation of yield improvement.

1.2.11 Temperature Effects on Soybean Physiology and Yield

Temperature extremes are one of the most common stresses in soybean as well as other crops. Internally, temperature controls the rate of biochemical processes. In some cases, reaction rate may double with an increase of 10°C. Temperature extremes can also affect yield through enzyme inactivation. Temperature effects on soybean are best characterized by relating them to a specific developmental period. When planting is conducted under potentially cool conditions (e.g. the midwest and the southeast USA in early Spring), temperature may have a large effect on stand establishment.

Seedling vigor (rapid germination and seedling emergence) involves two physiologically separate processes: germination and post-germination growth through the soil until emergence occurs. Hamman et al. (2002) concluded that the second process was probably more important than the first in affecting seedling vigor. Previous work has demonstrated that time from planting to emergence is best when soil temperature is in the range of 25 to 35°C (Hatfield and Egli, 1974). Days to emergence increase as temperature falls below this level. For example, at 30° C, emergence occurs in only 4 days, whereas at 15°C, it takes 21 days (Hatfield and Egli, 1974). For every one degree reduction in soil temperature from 18 to 8°C, days to emergence was delayed by two days (Muendel, 1986). Days to emergence at an Alberta, Canada location decreased from 27 to 13 days at an early compared with late planting date. Similar studies in the midwestern US showed days to emergence increasing from 6 days at an 11 May planting date to 19 days at a 13 April date (Andales et al., 2000). Delayed emergence induced by cold temperature increases the chances for seedling death, largely because it enhances microbial infection of the seedling

(Woodstock, 1973; Hamman et al., 2002). This increases solute leakage as membranes are degraded (Leopold, 1980) and/or halts the continued development of the seedling (Helms et al., 1996). Consequently, cold-impaired seedling vigor can result in a plant population that is too low for optimal yield, even when farmers plant at the recommended seeding rates. Thus, farmers wishing to achieve the minimal optimal plant population must increase their seeding rate to compensate for increased seedling death when planting is conducted under cool conditions. Studies conducted in the midwestern USA demonstrated cultivar differences in seedling vigor under cool conditions, and suggested the need to avoid cultivars having poor vigor when planting under these conditions (Unander et al., 1986; Littlejohn and Tanner, 1976; Pinthus and Kimel, 1979; Bramlage et al., 1979; Hopper et al., 1979).

Temperature continues to influence soybean growth and development from stand establishment through maturity. Understanding the influence of temperature on soybean requires knowledge of factors controlling crop temperature and how temperature influences physiological and phenological events. Leaf temperature is controlled by the difference between absorbed radiation and energy released through emission of radiation, sensible heat flux, and evapotranspiration (latent heat flux) (Paulsen, 1994). Absorbed radiation comes from short wave solar radiation received during the day plus long wave radiation continually received from the atmosphere and other objects. Absorption of radiation is influenced by leaf size, shape, orientation, and color, as well as cloudiness, solar radiation input and proximity of other objects. Dissipation of this absorbed radiation through the three processes described above (emission of radiations sensible heat flux evapo-transpiration) is affected by leaf emissivity (influencing radiation loss from the leaf); difference between air and leaf temperature, leaf boundary layer thickness, wind speed, leaf size, and atmospheric mixing (affecting sensible heat loss). Other

important factors are water availability, canopy cover, relative humidity, leaf temperature, solar radiation and wind speed (affecting evapotranspiration) (Loomis and Connor, 1992a). If these three processes balance absorbed radiation, leaf temperature is unchanged. If the energy lost is less than that absorbed, then leaf temperature increases. However, if energy lost is greater than that absorbed, leaf temperature will fall.

Understanding the radiation balance provides a basis for predicting plant/air temperature interactions. Since it is the top leaves of a soybean crop that receive most of the sun's short wave radiation, it is these leaves that become the hottest part of the canopy during the day (Loomis and Connor, 1992a). Temperature at the bottom of the canopy can be as much as 3⁰ C cooler than temperature at the top. Unrestricted transpiration from these top leaves, as well as exposure to cooler air temperature will promote energy loss through latent and sensible heat, respectively; and keep temperature of the top leaves at or below the air immediately above it. Any restriction of these processes will have the reverse effect, raising temperature of the top leaves above ambient air temperature. Harris et al. (1984) demonstrated how leaf temperature varied from air temperature depending on transpiration. In a year of high evaporative demand, irrigated soybean showed leaf temperatures 2.19⁰ C below air temperature, whereas nonirrigated plots had leaf temperature of only 0.8⁰ C below air temperature. In contrast, in a year of low evaporative demand, leaf temperature was 1.08 C above air temperature for both irrigated and nonirrigated conditions.

Canopy profile temperatures change with the coming of night fall. No short wave radiation is present to increase the energy load of the top leaves, and only long wave radiation from the atmosphere and other objects impinge on the top leaves. At the same time the crop is emitting long wave radiation itself. Being the most exposed part of the canopy, the top leaves

(relative to other leaves) emit more radiation than is absorbed and therefore their temperature falls below that of leaves in the middle and lower canopy. Lower canopy temperature can be as much as 4⁰ C greater than leaves at the top of the canopy (Loomis and Connor, 1992a). Depending on microclimatic relationships, temperature of the top leaves can be several degrees C lower than air temperature. In summary, it is the top leaves of the canopy that experience greater diurnal fluctuations in temperature compared with any other leaves or organs in the crop. Thus, the top leaves have the greatest probability of being damaged by temperature extremes. In addition, depending on microclimatic conditions near the canopy (evapotranspiration, leaf boundary layer thickness, leaf morphology and physical properties, and atmospheric conditions), temperature of the top leaves may diverge several degrees C above or below ambient air temperature.

Instances of heat resistance in plants may result from heat avoidance where the plant uses microclimatic temperature relationships described above to reduce leaf temperature (Hall, 1992). Mechanisms include increased transpirational cooling, altered leaf orientation and movement, changes in leaf reflectivity, and leaf shading. Heat resistance can also be accomplished through heat tolerance, that is, ability of physiological processes to maintain normal functioning in the presence of temperature extremes. However, attempts at breeding heat tolerance into crop plants through incorporation of genes controlling photosynthesis, chlorophyll fluorescence, membrane thermostability, or heat shock protein has not been promising (Hall, 1992).

Temperature stress in soybean is manifested through effects on photosynthesis and crop growth rate (Paulsen, 1994), reproductive abnormalities (Salem et al., 2007), phenological events (Huxley and Summerfield, 1974), and seed quality (i.e. germination and seedling vigor) (Gibson and Mullen, 1996). Photosynthesis is frequently the first physiological process affected by

suboptimal or supraoptimal temperatures (Paulsen, 1994). 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). Crop growth rate and dry matter production, as well as concomitant yield component formation, are closely linked with canopy photosynthetic rate (Imsande, 1989; Board and Modali, 2005). Effects of temperature on physiological events are characterized by an optimal temperature response range falling between minimal and maximal optimal temperatures (Hollinger and Angel, 2009), and suboptimal and supraoptimal temperatures falling below and above the optimal range, respectively.

Paulsen (1994) reported that for C3 species such as soybean, optimum temperature for photosynthesis is 30⁰ C, and that the process is inhibited at 40⁰ C. Studies by Jeffers and Shibles (1969) reported an optimal range of 25-30⁰ C for canopy photosynthetic rate. However, later studies using daytime temperatures of 26, 31, and 36⁰ C showed no effect on photosynthetic rates of top leaves (Campbell et al., 1990). These findings were confirmed by Jones et al. (1985) who reported that temperature within the 28-35⁰ C range did not affect canopy photosynthetic rate. Gesch et al. (2001) concluded that the optimal temperature for soybean photosynthesis was 32⁰ C. However, Vu et al. (1997) reported only a 10% decrease in photosynthetic rate when temperature was increased from 32 to 36⁰ C. However, a further increase of day time temperature to 40⁰ C resulted in a 38% decline in photosynthetic rate.

The aforementioned studies were all conducted under constant day time temperatures where temperature remained at a high level for several hours (12-16 hours) across a series of days. Thus, application of these results to natural growing conditions where a crop is exposed to episodic high temperature for a relatively short period (1-2 hours, climatic data, Louisiana State University Agricultural Center) may be problematic. Ferris et al. (1998) concluded from short-

term heat stress studies that temperature had to be raised to 42-43⁰ C (about 108⁰ F) to have deleterious effects on soybean photosynthesis. These results are corroborated by Fitter and Hay (1987) who stated that for plants from most climatic regions, temperatures of 45-55⁰ C for 30 minutes were sufficient to cause irreversible damage to the photosynthetic apparatus. Based on the previous discussion, it appears that the maximal optimal temperature for soybean canopy photosynthesis under prevailing conditions for Louisiana and other mid South states is approximately 40⁰ C (104⁰ F). Minimal optimal temperature appears to be 25/26 C (77-79⁰F) (Sionit et al., 1987; Jeffers and Shibles, 1969). In conclusion, the optimal temperature range for soybean canopy photosynthetic rate appears to be 25-40⁰ C (77-104⁰ F). A five-year (2004-2009) survey of Louisiana temperature patterns revealed that in south Louisiana there were no days during the typical reproductive period (R1-R7) where maximal temperature ever reached 40⁰C (Louisiana Agriclimate Information Service). A similar survey in North Louisiana revealed only 1 day in which temperature reached 40⁰C. Thus, the possibility of heat stress affecting soybean production in Louisiana is very remote.

Although canopy photosynthetic rate and dry matter accumulation are closely linked (Imssande, 1989), in some crops (e.g. wheat) temperature effects on the two processes are not similar (Paulsen, 1994). An optimum day time temperature of 25-30⁰ C for dry matter accumulation has been reported (Sato and Ikeda, 1979; Raper and Kramer, 1987). Sato and Ikeda (1979) suggested that optimal dry matter production occurred when day time temperatures were 10⁰C above night time temperature. However, subsequent research showed no deleterious effects of high night time temperature on plant growth (Hewitt et al., 1985; Raper and Kramer, 1987). Season-long studies by Sionit et al. (1987) showed greater dry matter production and yield for soybean grown at a day time temperature of 26⁰ C vs. lower temperatures of 22⁰ C or 18⁰ C.

Subsequent studies by Baker et al. (1989) reported no change in yield as seasonal day time temperature was increased from 26 °C to 31° C, and then to 36° C. They concluded that 36° C was near or above the maximal optimal temperature for soybean growth. These results were supported by Hofstra (1972) who reported maximal dry matter accumulation at a day time temperature of 36° C compared with lower temperatures. Based on these results, minimal and maximal temperature for optimal soybean growth appear similar to those for photosynthesis, 26 C to 36° C (79 F to 97° F). In South Louisiana the probability of temperatures going above 36° C during the reproductive period are very slight (1.6%) (Louisiana Agriclimatic Information Service). The possibility increases to 7.7% in North Louisiana. However, for days when temperatures rise above 36° C, the interval is usually very short (lasting from a few minutes to a few hours) and therefore would not be expected to have the same adverse effect on growth as for plants subjected to continuous daily (12 hours or more) heat treatments above 36° C. Based on this analysis, it does not appear that heat stress effects on soybean growth are a significant production problem in Louisiana. The few studies that have been done comparing heat stress tolerance of old and new soybean cultivars have not reported any differences (Frederick et al., 1989).

Although temperatures in Louisiana and other southeastern states do not appear to be greater than the maximal optimal temperature for optimal photosynthesis and crop growth, temperatures during the early growing season frequently fall below the minimal optimal level. This problem has become more prevalent with the advent of the early season production system (ESPS) in the southeastern US (Heatherly, 1999). Average temperature in northeastern Louisiana (the state's main soybean growing region) during the last half of March is 15° C, well below the minimal optimal level of 26° C. Growing temperatures are considerably better the last half of

April (21⁰C) and the last half of May (22⁰C). Thus, soybean planted in the early Spring may well receive temperatures too low for optimal crop growth rate.

In addition to photosynthesis and growth, reproductive events such as floral bud development, seed and fruit set, as well as embryo, seed, and fruit development can also be affected by heat stress (Hall, 1992). Salem et al. (2007) reported an optimal range for pollen germination and pollen tube growth of 25 to 35⁰C. Koti et al. (2004) also reported abnormal flower morphology, decreased pollen germination, and reduced pollen tube growth at 38⁰ C vs. 30⁰ C. Since anther dehiscence occurs at 8-10 AM, it is doubtful that heat stress (>35⁰C) affects these processes. Another potential stress factor pertinent to soybean production is adverse effect of heat stress during seed filling on germination and seedling vigor for seed developing on the mother plant (Gibson and Mullen, 1996). Reports have demonstrated that temperatures of 32-35⁰ C during the seed filling period result in substantial reductions of seed germination and seedling vigor (Keigley and Mullen, 1986; Dornbos and Mullen, 1991; Gibson and Mullen, 1996). Introduction of the early season production system in the southeastern US has subjected soybean to temperatures within the harmful range. Consequently, poor germination and vigor of seed produced from these plants is a recognized problem (Smith et al., 2008). A final potential temperature factor adversely affecting yield is the interaction of temperature with photoperiod in affecting soybean phenology (Hadley et al., 1984). Because this interaction predominately affects development between emergence and the start of seed filling (R5) (Board and Settini, 1986), warm temperature can reduce this period resulting in a suboptimal level of vegetative dry matter for optimal yield (Board and Modali, 2005). When photoperiod is below the critical level for hastening phenological development [which frequently occurs for soybean in Louisiana and other southeastern states (Board and Hall, 1984)], warmer temperature accelerates phenological

development even more. Since vegetative growth stops at the start of seed filling (Egli and Leggett, 1973), this curtailment of vegetative growth may impact yield. In the case of late-planted soybean, it has been implicated in yield losses (Board and Settini, 1986).

1.2.12 Canopy Light Effects on Photosynthesis and Yield

The importance of the photosynthetic reactions in crop growth and yield formation cannot be overestimated. Among crop plant species, as well as other members of the plant kingdom, 90-95% of dry weight is derived from CO₂ fixed through photosynthesis (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. It also supplies the chemical energy for metabolism (Loomis and Connor, 1992a). Although a very complicated process, photosynthesis can be simplified by viewing it as three basic parts: 1) Movement of CO₂ 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 CO₂ into organic compounds (Fageria et al., 2006). The major environmental factor affecting the photosynthetic rate (the rate of net CO₂ uptake by the leaf or crop) are atmospheric [CO₂], temperature, water availability, and light level absorbed by the canopy. Light level, in turn, is affected by the percentage of ambient light intercepted by the crop and light intensity (light flux). An understanding of how light affects canopy photosynthesis is critical for analyzing genotypic yield differences.

For soybean, as well as other C₃ crops 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 at Baton Rouge during the summer growing season. 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 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). However, increased canopy photosynthesis responds to increased light intensity in an asymptotic rather than linear fashion (Jeffers and Shibles, 1969). Seasonal crop growth rate patterns closely follow seasonal canopy photosynthetic rates (Imsande, 1989). Both parameters increase slowly after emergence and then increase exponentially until early reproductive development (R1-R3). Plateau rates are maintained until R5 and then fall as the seed filling period progresses. At any given time, radiation absorbed by the canopy depends on the leaf area index (LAI affecting light interception) and the intensity of ambient light. Prior to canopy closure (LAI of 3.0 to 5.0 depending on row spacing), crop growth primarily is influenced by LAI (Shibles and Weber, 1965), whereas ambient light level mainly affects crop growth rate after canopy closure.

A major aim of research has been to determine the temporal importance of light for soybean yield determination. Early studies which altered light interception 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). Identification of periods within reproductive development where yield is most responsive to altered light interception and level has shown conflicting results. Understanding temporal yield component relationships aids this objective. Yield is determined by the following yield component relationships (Board and Modali, 2005):

Yield: determined by seed number per area and seed size (g per 100 seed).

Seed number per area: determined by pod number per area and seed per pod.

Pod number per area: determined by pod per reproductive node and reproductive node number per area. A reproductive node is defined as any node that has at least one pod containing one seed that contributes to yield.

Reproductive node number per area: determined by fraction of nodes becoming reproductive and node number per area.

Node number per area: related to dry matter accumulation (R5) in an asymptotic fashion (Board and Modali, 2005).

By understanding when yield components are formed and identifying which yield components are affected by altered light interception and/or level, one can identify when optimal canopy light relations are required for best yield (Board et al., 1995). Seed number per area is determined by the sequential influences of node number per area, reproductive node number per area, and pod number per area; all of which are formed during the R1-R6 period (Board and Tan, 1995; Andrews, 1966; Pigeaire et al., 1986). Even drastic reductions in light level after R6 have little effect on pod number per area (Board et al., 1994). Seed size determination occurs during

the R3 to R7 period, encompassing the production of cotyledonary cells (R3 to R6) and the seed filling period (R5 to R7) (Egli, 1994; Peterson et al., 1992). The overwhelming weight of research evidence indicates that environmental and cultural factors affecting light level (through light interception and intensity) (e.g. row spacing, plant population, defoliation, and shading) affect yield through seed number per area rather than seed size (Carpenter and Board, 1997; Egli and Yu, 1991; Egli, 1998; Board and Tan, 1995; Board and Modali, 2005). These studies show that enhancements or reduction in light level initiated during the R3 to R6 period when both seed number per area and seed size are being determined have usually affected seed number per area and not seed size. The only exceptions are for very severe light reductions such as are caused by total defoliation (Board et al., 2010). Whereas incremental reductions in seed number per area occur when light is incrementally reduced during the R1 to R6 seed formation period, drastic reductions are required during the R6 to R7 period (rapid seed filling) to reduce seed size. This analysis aids in making recommendations to growers for many management decisions involving light interception and light level such as use of narrow vs. wide row spacing (Board et al., 1992), optimal plant population (Carpenter and Board, 1997), and control of defoliating insect pests (Board et al., 1997).

One aspect of genetic improvement in soybean related to light relationships has been incorporation of genes to reduce lodging (Cooper, 1981). Lodging is a common problem for growing soybean, as well as other crops (Cooper, 1971; Noor and Caviness, 1980). Early studies with naturally-induced lodging demonstrated yield losses of 14-23% (Weber and Fehr, 1966; Cooper, 1971). Most of the yield loss (91%) was caused by physiological reductions in pod and seed production, with only 9% of yield decline due to combine losses (Weber and Fehr, 1966). Yield losses from lodging are greatest when it occurs at R5 (Woods and Swearingin, 1977). A

summary of several reports concluded that significant yield losses could be expected when lodging occurred between R4 to R6 (Noor and Caviness, 1980), but were relatively minor at other stages. For significant yield losses to occur, lodging must be greater than 45° (Noor and Caviness, 1980). Reduced light penetration into the middle and lower canopy levels of lodged plants has been clearly implicated in the yield losses which occur (Shaw and Weber, 1967; Johnston and Pendleton, 1968).

Soybean breeders endeavored to reduce lodging by incorporating genes from southern determinate cultivars (dt_1 homozygous recessive) that reduced plant height. This resulted in shorter statured determinate cultivars that were resistant to lodging and well adapted to midwestern growing conditions. Later studies by Cober and Tanner (1995) suggested that combinations of the $dt_1 dt_1$ determinate gene pair with certain E genes controlling maturity ($E_1E_1 e_3e_3 e_4e_4$) resulted in high-yield determinate cultivars well adapted to areas having short growing seasons. Besides plant height and maturity, stem resiliency was also identified as a trait conducive to lodging tolerance (Mancuso and Caviness, 1991).

Another research area related to soybean genetic improvement through alteration of canopy light relationships is leaf morphology. This has occurred mainly through alterations in leaf angle and shape that increase canopy light penetration resulting in greater canopy photosynthesis and crop growth rate (Monsi and Saeki, 1953). Such relationships can be analyzed by using the Bouguer-Lambert Law (also known as Beer's Law) that uses ambient light level, light level within the canopy at some point, and the leaf area between the two to derive the canopy extinction coefficient (k). The equation is shown below:

$I = I_0 \exp^{-KL}$ where: I = light intensity at some point within the canopy; I_0 = ambient light intensity; K = canopy light extinction coefficient; L = LAI between I and I_0 .

Thus, once canopy cover is achieved, crops having lower K (i.e. greater light penetration into the canopy) would have greater canopy photosynthesis and crop growth rate relative to those with higher K values (Loomis and Connor, 1992a). This explains why photosynthetic light saturation levels for C3 crops having erect leaves (i.e. low K) such as wheat, are greater than those for C3 crops such as soybean having more horizontal leaves (i.e. high K). Because 90% of incident light is intercepted by leaves at the top and edges of the soybean canopy (Sakamoto and Shaw, 1967), interest developed in improving soybean yield through greater light penetration. This issue is related to the ability of soybean leaves to translocate photosynthate to pods at other nodes. Since most pods are contained at middle and lower canopy levels that receive little light, it is hypothesized that greater light penetration would be beneficial to yield, especially if leaves only feed pods at their own or nearby nodes as claimed in some reports (Blomquist and Kust, 1971; Stephenson and Wilson, 1977). However, other research has demonstrated that when source/sink relationships are sufficiently altered, long-distance transfer of photosynthate from source leaves to sink pods does occur (Gent, 1982). Yield restriction caused by light absorption at the top of the canopy has also been questioned by the finding that some top leaves are connected by their petioles to lower nodes containing pods in the middle of the canopy (Willcott et al., 1984). Further evidence suggesting that pod position has little effect on yield was reported by Weil et al. (1990). Yields were similar in determinate and indeterminate isolines, even though the determinate lines had more pods in low canopy positions. In summary, studies by Willcott et al (1984), Weil et al. (1990), and Gent (1982) imply that high K values for soybean may not be as yield limiting as originally thought.

Application of greater canopy light penetration (i.e. lower K) to yield improvement has been demonstrated by Shaw and Weber (1967) by creating greater light interception through

moderate lodging which resulted in greater light penetration and increased yield. Other mechanisms for increasing canopy light penetration have been explored. Bunce (1990) reported an inverse relationship between leaf size and photosynthetic rate per unit leaf area which he attributed to lesser mutual shading by smaller leaves. However, Sung and Chen (1989) reported that greater photosynthesis per unit leaf area for narrow vs. normal leaves was related to increased chloroplast number. Smaller leaf size with greater light penetration has resulted in higher yield (Metz et al., 1984; Moraghan, 1970), although the reported trends were not conclusive. Haile et al. (1998) reported that narrow vs. wide leaflet isolines demonstrated greater defoliation tolerance; largely due to greater light interception per unit LAI. Thus, when moderate manual defoliation was applied, light interception was decreased less for the narrow-leaflet isolines. Consequently, these lines did not suffer a yield loss while the wide-leaflet types did. In contrast to these aforementioned findings, others have reported no yield gain using isogenic narrow- vs. broad-leaved genotypes (Mandel and Buss, 1981; Hiebsch et al., 1976; Wells et al., 1993). In summary, the benefit of increased canopy light penetration on soybean yield has shown inconsistent yield effects and it would be unwise to consider this research approach as a guarantee for yield improvement.

1.2.13 Drought as a Stress Factor in Soybean Production

Drought stress is recognized as the most damaging abiotic stress for soybean production in the US (Heatherly, 2009). Evidence for this statement is supported by the 48% average yield increase shown by soybean in irrigated vs. dry land conditions. Drought stress is a climatic term referring to an unusually long rainless period for a given area (Loomis and Connor, 1992b). A crop is considered to be under drought stress when the dry period extends long enough to

adversely affect yield. In agronomic conditions, drought can be characterized by two typical patterns:

1. Situations where rainfall is adequate for the initial and subsequent periods of crop growth; but later becomes limiting resulting in death unless irrigation is applied.
2. Situations where seasonal rainfall is usually adequate for optimal yield but variability sometimes occurs resulting in drought stress.

The first situation applies to areas having Mediterranean climates such as the countries bordering the Mediterranean Sea, California, Western Australia, Chile, and South Africa. It also includes cropping areas subjected to monsoon weather such as India. The second situation characterizes drought problems in the soybean-growing areas of the midwestern and southeastern US.

Despite the general recognition of drought stress as a major problem in US soybean production, only 8% of the entire acreage (5.8 million acres out of 72 million acres) is irrigated (Heatherly, 2009). In the main part of the midwestern 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. Irrigation in the state is recommended only on atypical sandy or claypan soils.

Irrigated acreage is concentrated in the drier areas of the soybean growing region (western Midwest or Great Plains states) such as Nebraska where 46% of soybean acreage is irrigated (Pore, 2009). Irrigation is also common in some southeastern states where shallow-rooted soils combined with erratic rainfall make drought stress a potential threat. In Arkansas,

75% of the soybean acreage is irrigated (J. Ross, personal communication) and for Mississippi the figure is 25-30% (Thomas and Blaine, 2009). Irrigated soybean acreage is less in Louisiana compared with Arkansas and Mississippi. Based on 1998 information, only 8.6% of state's soybean land was irrigated. (<http://nimss.umd.edu/homepages/home.cfm?trackID=4575>). Although hard data is lacking, it is currently estimated that about 20% of Louisiana soybean acreage is irrigated (personal communication R. Levy).

Increased irrigation in the Great Plains and mid South states has been stimulated by research showing large yield increases in irrigated vs. nonirrigated conditions. Specht et al. (1999) concluded that across a 26-year period (1972-1997) soybean yielded 800 kg ha^{-1} more than nonirrigated plants and had greater yield stability. Yield increases from irrigation are also well documented in Arkansas ($672\text{-}1,344 \text{ kg ha}^{-1}$, University of Arkansas Coop. Ext., 2006) and Mississippi ($1490\text{-}2020 \text{ kg ha}^{-1}$, Heatherly and Elmore, 1986). Similar to its sister mid South states, typical yield increases from irrigation in Louisiana are about 672 kg ha^{-1} , although such yield stimulations vary greatly with soil type, year, and location (Paxton, 2009). Most irrigation studies have demonstrated that irrigation under drought stress conditions increases yield through greater seed number (seed m^{-2}) rather than seed size (g per 100 seed) (Ashley and Ethridge, 1978; Heatherly, 1983; Huck et al., 1986; Ramseur et al., 1984). However, drought stress occurring only during seed filling can also reduce seed size and yield if severe enough (Doss et al., 1974).

Thus, drought stress affects yield mainly through lower seed number, similar to the case for most abiotic stresses (Board and Modali, 2005). Because seed number is largely determined during the R1 to R6 period (Board and Tan, 1995), it is expected that this would also be the most drought prone period. This supposition is supported by irrigation timing studies in the mid South

and other areas (Reicosky and Heatherly, 1990). Once a stand is established, little benefit results from irrigation prior to R1. Under drought conditions, irrigation commencing at R1 is recommended and should be continued through R6 unless rainfall occurs. In response to drought stress problems in the southeastern US, the early soybean production system (ESPS) in which early maturing cultivars (Maturity Group IV vs. Maturity Group V or VI) are planted early (in April vs. May) has received wide acceptance in the mid South (Heatherly, 2009). The purpose of this system is to avoid drought by placing more of the growing season before typical mid-summer moisture deficits occur (Heatherly and Spurlock, 1999).

Drought stress problems in soybean can be better understood by knowing how the hydrologic cycle affects the soil water content on which the crop survives (Loomis and Connor, 1992b):

Soil water content= (rainfall) + (irrigation)-(evapotranspiration)-(surface runoff)-(drainage below root zone)

The occurrence of “drought stress” (i.e. soil water too low for optimal yield) is not just determined by the drought period (prolonged lack of rain) but by evapotranspiration from the soil/plant system, rooting depth and proliferation, and how much rainfall gets into and stays in the rooting zone. Thus, in addition to rainfall, other factors also determine if drought stress occurs: tillage systems (conservation tillage reduces runoff), plant genetic factors (rooting characteristics, stomatal control, leaf reflectance, osmotic adjustments, etc.), and climatic factors (relative humidity, temperature, wind). This explains why regions such as the mid South have greater drought stress problems than many midwestern states, even though seasonal rainfall may be greater in the former compared with the latter.

Loss of water from the leaves to the atmosphere, and its replacement with water flowing into the roots from the soil is controlled by water potential (Loomis and Connor, 1992b). Water potential is the energy of water measured as a force in bars or pascals (1 bar=0.1 MPa). 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 evaporation 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 content (volume of water per volume of soil) of 0.6 and 0.35 for a clay and sand soil, respectively. At night, water potentials for soil, root, 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). Volumetric soil water content at the wilting point for clay and sand soils are 0.2 and 0.1, respectively. The difference between volumetric water content at field capacity and wilting point represents plant available water (0.4 and 0.25 volumetric water content for clay and sand soils, respectively). In order to avoid yield loss, or even possible plant death, irrigation must be started before leaf water potential reaches -1.5 MPa. It is generally recommended in the mid South to start irrigation when plant available water falls to 50% (volumetric water content of 0.4 and 0.23 for clay and sand soils, respectively) (Univ. of Ark. Coop. Ext., 2006). This corresponds to 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 (http://www.aragriculture.org/soil_water/irrigation/crop/soybeans.htm)

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). Relative to other crop seeds, soybean must imbibe a large amount of water (50% of fresh weight) to successfully germinate. 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 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.

The most sensitive physiological process 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). In contrast, 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. Drought stress effects on photosynthesis become irreversible once water potential falls below -1.6 MPa. Thus, in a drying soil where leaf water potential fell into the -0.8 to -1.2 MPa range for extended periods, reduced cell expansion would result in short low-yielding soybean plants without any effect on photosynthetic rate per unit leaf area.

Another physiological process sensitive to drought stress is nitrogen fixation (Purcell and Specht, 2004). 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 Midwest 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 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 will reduce photosynthetic rate and possibly affect yield. Ample evidence indicates that nitrogen fixation is

more sensitive to drought than photosynthesis, dry matter accumulation, transpiration, and soil nitrogen uptake (Purcell and Specht, 2004).

Genetic attempts to improve soybean drought tolerance reflect the physiological factors discussed above. Introduction of early maturing cultivars (Maturity Groups III and IV compared with V and higher) planted at an early date positions critical phenological periods (R1-R6) into a time where drought stress is less likely compared with traditional cropping systems (Heatherly, 2009). Breeding genotypes have been developed that maintain nitrogen fixation during drought stress relative to standard cultivars (King and Purcell, 2006). Also, two soybean plant introductions have been identified that have greater ability to maintain leaf water potential under stress (slow-wilt trait, Carter et al., 2006). Comparisons of old vs. new cultivars has shown greater water conservation by older cultivars during drought stress (Frederick et al., 1990). However, the yield advantage of new vs. old cultivars was more evident under irrigated compared with nonirrigated conditions. This suggests that the cultivar development process may have resulted in greater genetic potential to benefit from more optimal growing conditions.

1.2.14 Breeding Methods in Soybean Related to Cultivar Development

The goals of soybean breeders are to improve cultivars through higher yield, altered maturity, resistance to lodging and pests, improved oil and protein seed composition, altered amino acid and fatty acid composition of the seed, greater seed size, and pesticide tolerance, as well as other factors (Fehr, 1987). A breeding program of genetic improvement begins with choosing the parents to create segregating populations. These segregating populations are then inbred (i.e. selfed) with or without selection to produce relatively homozygous genotypes that are then selected for whatever trait of interest (e.g. yield, pest resistance, etc.). The evaluation starts when parental plants are selected for crossing to develop segregating progeny which develop into

homozygous genotypes (i.e. inbred lines) after several generations of selfing. The process ends with inbred lines being either discarded or selected for testing as potential future commercial cultivars. The amount of selection during cultivar development depends on the type of environment, heritability of the trait, and available work resources. (Fehr, 1987)

Although many plant characteristics may be evaluated, paramount importance is always given to yield. Yield is usually not measured until after desirable homozygosity is reached and is initially assessed by visual observations. Actual yield testing using combine-harvested yield occurs only after a lower number of lines have been selected for further testing. Other characteristics commonly identified by visual assessments are maturity, plant height, and lodging. Kwon and Torrie (1964) concluded that low yielding plots were more readily identified than high yielding ones. Byth et al. (1969) rated lines at maturity with scores ranging from 1 to 5, with 1 for least desirable and 5 for most desirable phenotype.

Because of the need to better identify yield potential (relative to that resulting from visual observations) for progeny in a breeding program, extensive research to identify characteristics as indirect selection criteria for yield has been conducted. The goal is to find factor(s) highly correlated with yield that is rapid, easy, and cheap to use. Efforts at linking yield to single leaf photosynthetic rates (photosynthetic rate per cm^2 leaf area), harvest index, and length of the seed filling period have not been successful (Ford et al., 1983; Schapaugh and Wilcox, 1980; Salado-Navarro et al., 1986). Canopy apparent photosynthesis (photosynthetic rate per m^2 crop land) was correlated with yield, but this method was not practical to use in a breeding program (Harrison et al., 1981). Possible candidates for indirect selection criteria are phenological data (e.g. days to R5 and R7), yield components, and total dry matter at important phenological stages such as R5 and R7 (Dunphy, 1979; Board and Modali, 2005; Board et al., 2003). Some of these

factors can be easily and rapidly determined and, if proved useful in cultivar development, would reduce the time, money, and work required.

Various breeding methods are used in soybean cultivar development programs. These include the pedigree, single seed descent, bulk, and early-generation methods. Every breeding method has its own advantages and disadvantages; and method selection is based on suitability, effectiveness, and available resources.

1.2.14.1 Pedigree Method

The pedigree method is used for both self and cross pollinated crops. The term was first applied to single plant selections from heterogeneous landraces of self pollinated species. This was a modification over the mass selection method where desirable plants were selected and seed bulked to grow the next generation (Fehr, 1987). In the pedigree breeding method, two parents are crossed to produce the F₁ generation. One seed from each cross were taken and bulked. These seeds gave rise to the F₂ generation from which desirable types are selected (Luedders et al, 1973). These bulked seeds are then grown in F₃ and F₄ generations with 200 plants were selected in each bulk. These plants were grown in rows during the F₅ generation and the best looking 20 rows were selected for yield testing in the F₆ and F₇ generations. Lines having desirable characteristics and higher yield potential are harvested and bulked during F₆ and F₇ generations during yield testing. (Luedders et al, 1973). The pedigree method is very useful if selection can be practiced in each generation. It is especially useful for discarding inferior lines and making selection of superior inbred homozygous lines easier. Because selection in each generation involves different environments, better genetic selection occurs. Records are kept that provide genetic relationships of lines. Disadvantages are the requirements for an experienced

person for plant selections, a relatively large land and labor requirement, and the inability to use green houses or winter nurseries for rapid generation advance.

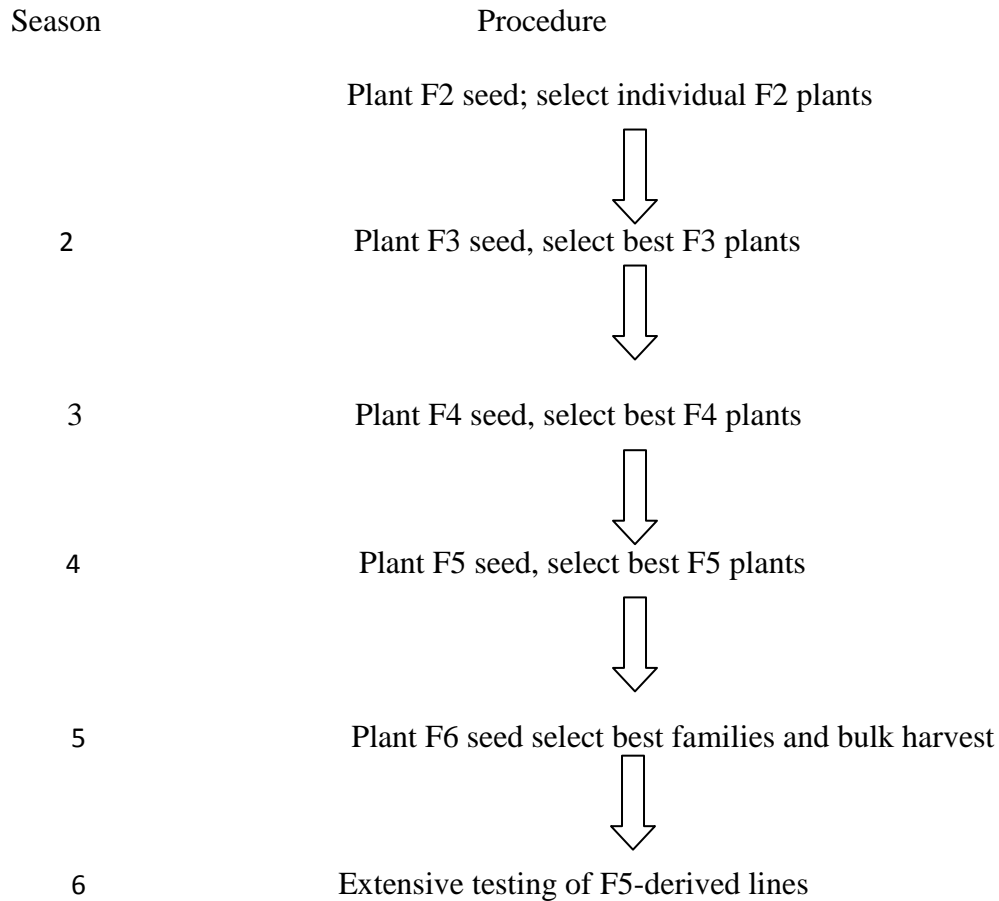


Fig. 1.1. Pedigree method

1.2.14.2 Single Seed Descent Method

Another common method used in soybean breeding programs is the single seed descent method. This method (Brim, 1966) is a modified pedigree method and is well suited for winter nurseries in tropical environments and green houses where selection is not possible for important agronomic characters. This allows for more rapid genetic advance. However, it precludes selection within the natural environment where future cultivars will be grown. Single seed descent is divided into two categories: 1) Development of homozygous lines from segregating populations; and 2) Selection of desirable plants within homozygous lines. Because some

generations are grown in winter nurseries and/or green houses, development of inbred lines can occur in two years rather than the normal five to six years when using the pedigree method. The classic procedure of single seed descent is to select one seed from each plant in a specific generation, bulk these, and then grow this entire sample in the next generation (Fig 2). As in the pedigree method, the F_2 plants of a population are grown in season 1. One F_3 seed is harvested from all the plants and bulked. A second seed is also harvested from each plant as reserve seed. The F_3 seed are planted in the second season to produce F_4 plants. As in the previous generation, one seed per plant is again harvested and bulked. This process is repeated until the desired homozygosity is achieved. (Fehr, 1987). At this point, selection of desirable plants for testing inbred lines commences. There is some reduction in population size during each generation due to lack of seed germination or failure of plants to produce seed.

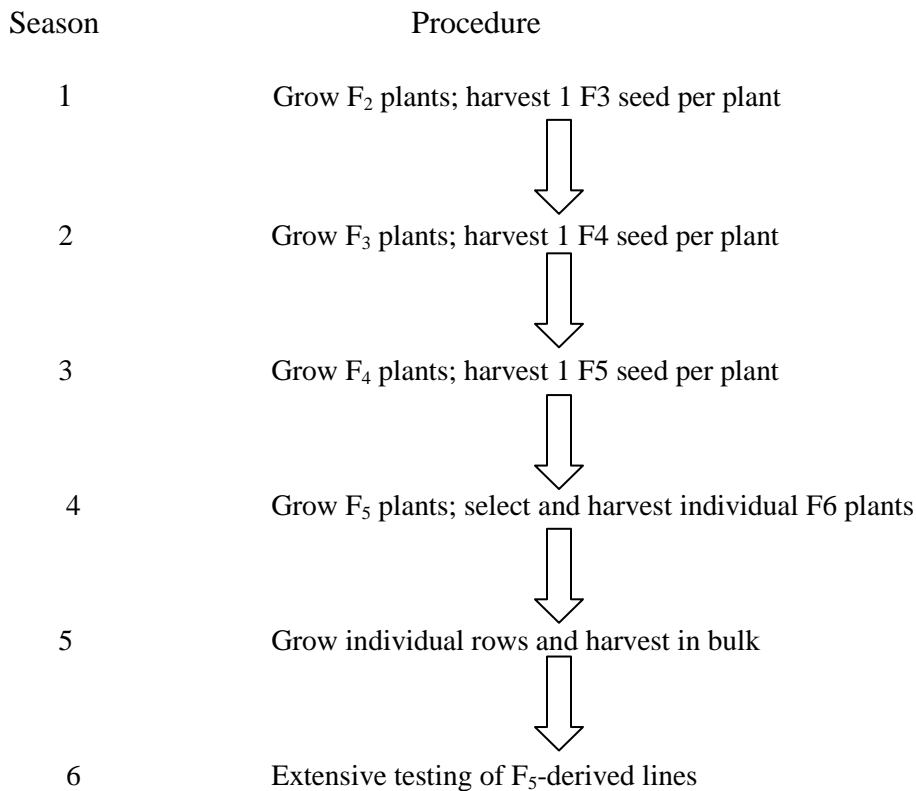


Fig. 1.2. Single-Seed Descent Method

One problem with the single seed descent method is that some F_2 families are eliminated because seed fail to germinate or plants do not produce seed. Thus, alternative methods of single seed descent which involve harvest of more than one seed per plant have been developed. These are called the single hill and multiple seed method. In both methods, several seed are harvested from each plant with some being planted and the rest held in reserve. If planted together in hills, the method is called single hill; but, if planted separately it is called the multiple seed method. Once homozygosity is reached, individual lines are selected for further development as potential cultivars.

1.2.14.3 Bulk Method

This procedure is used for inbreeding a segregating population until the desired level of homozygosity is reached. Prior to homozygosity, no selection is practiced. Seeds used for planting in each generation are those harvested and bulked in the previous generation. In the first season, F_2 plants are grown and F_3 seeds are harvested and bulked (Fig 3). In the second season, some of the F_3 seeds are planted and F_4 seeds are again harvested in bulk. This process is repeated until the desired level of homozygosity is achieved. At this point, selection of inbred lines is done for potential future cultivars. Lines having desired characteristics and showing visual yield potential are harvested and bulked. Further testing and selection ensures. Once a number of lines is derived and sufficient seed is available, yield trials are conducted (Fehr, 1987). The bulk method allows rapid development of an inbred population. Since inbreeding occurs in the same environment intended for future cultivars, natural selection operates to maintain better lines. However, this method cannot be used in green houses or winter nurseries, thus lengthening the inbreeding process relative to the single seed descent method.

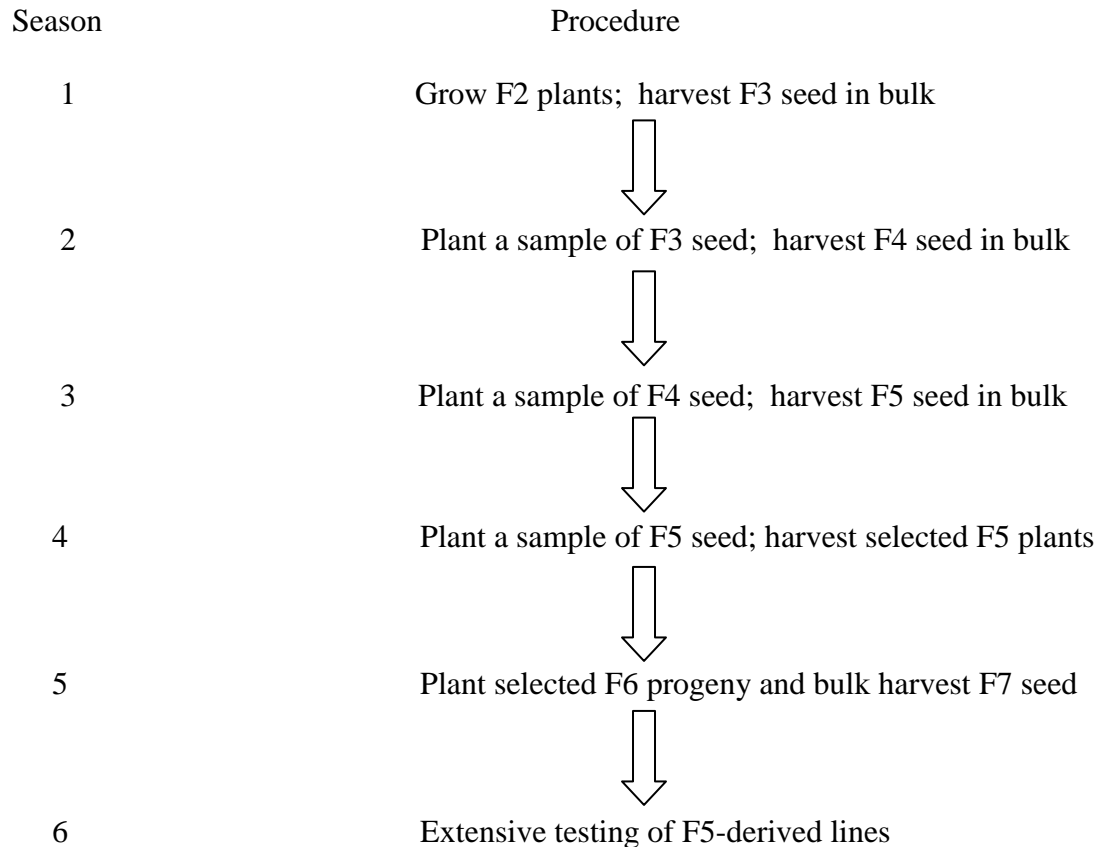


Fig. 1.3. Bulk Method

1.2.14.4 Early Generation Method

The early generation method is used to estimate the potential of an individual plant, line or population during the early stages of inbreeding. Early generation testing is done by conducting replicated tests of segregating populations in the F₂ and F₃ generations to determine performance of various F₂ families (Fig 4) instead of later stages as is done in the pedigree methods (Fehr, 1987). Yield potential is based on visual observations. Selected populations are inbred by the bulk method until homozygosity is reached. In the first year, the F₂ generation is grown and plants with desirable characteristics are selected and harvested individually from each population. In the second season, harvested seed from the previous season is grown, evaluated for desired characteristics and bulked. In the third season, selected F_{2:4} lines are evaluated in

replicated yield tests and those having inferior performance discarded. In the fourth and fifth seasons, the same process is repeated resulting in $F_{2:5}$ and $F_{2:6}$ lines. In the sixth season, selection and testing of inbred lines commences (Fehr, 1987). The advantages of the early generation method is discarding of inferior individuals, lines or populations early in the breeding process. At the same time, the process results in a relatively smaller number of inbred lines for final evaluation.

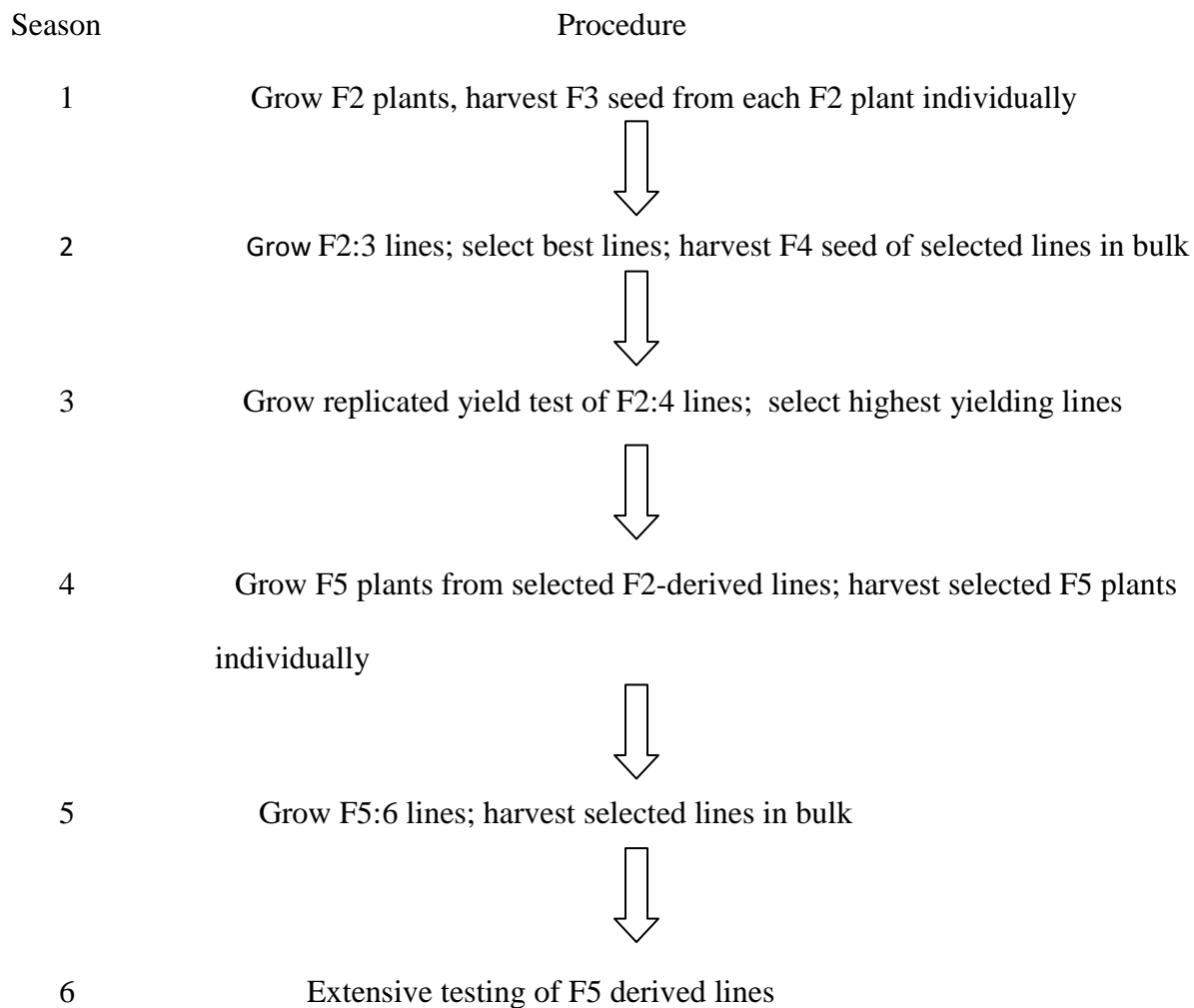


Fig. 1.4. Early-generation testing

All methods have their relative advantages and disadvantages. Torrie (1958) compared bulk and pedigree methods for six soybean crosses and found no difference in yield, plant height,

lodging index, bacterial blight reaction, oil and protein content of the seed. However, Raeber and Weber (1953) found the pedigree procedure to be more effective than the bulk method in isolating high-yielding soybean lines. The comparison between bulk, pedigree and early generation methods made by Voigt and Weber (1960) showed that the lines selected by the early generation method were superior in yield vs. the other two methods. Boerma and Cooper (1975) also found effectiveness of modified early generation testing procedure in identifying superior yielding soybean lines. In contrast, Luedders et al. (1973) indicated no significant difference in lines derived by these same three methods.

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Chapter 2

Yield and Agronomic Characteristics of Old and New Soybean Cultivars

2.1 Introduction

Soybean is the most important oilseed crop grown in the world (56% of world oil seed production) and has been a major crop in the US since the end of World War II (Wilcox, 2004). Currently, soybean is grown on about 30 million hectares in the US with most of the production (82%) in the midwestern US. Louisiana only contributes to about 1% of the country's soybean production. Despite this small percentage, soybean makes a significant contribution to Louisiana's economy (\$300 million in 2008) (Louisiana Agricultural Statistics, 2008). Yield is an important trait that has been continuously improved over the last fifty years. Reports of genetic gain from soybean cultivar development in the US differ with region and the time period studied [$10\text{-}30 \text{ kg ha}^{-1} \text{ yr}^{-1}$] (Specht et al., 1999).

Canadian researchers working with very early maturity group cultivars (MG 0, 00, and 000) selected from 1934 to 1992 showed a genetic yield gain of only $11 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Voldeng et al., 1997). From 1934 to 1976 the yield enhancement was barely above zero, while from 1976 to 1992 it increased to $30 \text{ kg ha}^{-1} \text{ yr}^{-1}$. This was attributed to the introduction of cold-tolerant cultivars from Hokkaido, Japan. In an Indian study, Karmakar and Bhatnagar (1996) reported a yield increase of $22 \text{ kg ha}^{-1} \text{ yr}^{-1}$. Chinese researchers reported a smaller increase of $12.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for the 1950-1991 periods (Hu, 1994).

In addition to reporting yield gains, researchers have also tried to identify factors responsible for greater yield in new vs. old cultivars. Among midwestern cultivars, Leudders (1977) attributed some of the yield increase to a 17% decrease in lodging score. Voldeng et al. (1997) also reported that in new vs. old Canadian cultivars, lodging was reduced. Specht and Williams (1984), studying 19 cultivars released between 1924 to 1980, also reported decreased

lodging, as well as improved seed quality. Among developmental periods, the seed filling period (R5-R7) has received the greatest research attention as a possible factor explaining yield gains across years. Early studies during the 1970's suggested an association of seed filling period with yield on the environmental level (Egli and Leggett, 1973). Dunphy et al. (1979) studied 119 midwestern cultivars at 10 locations and reported significant correlation ($R=0.51$) of yield with seed filling period. In contrast, no significant relationships were found of yield with any vegetative period.

Similar empirical relationships between seed filling period and yield were reported by Boote (1981) in the southeastern US using indeterminate early maturing soybeans (MG IV and less). Days to R5 and R7 also were significantly correlated with yield. Investigations between yield, lodging, seed filling period, and days to R5 and R7 have not been conducted among public southern cultivars; nor have the roles of these factors in yield improvement been shown. Such understanding would be very helpful to plant breeders for use as indirect selection criteria. Thus, the objective of this research was to determine the roles of lodging, days to R5 and R7, and length of the seed filling period (R5-R7) on yield improvement for 18 soybean cultivars representing the southeastern USA released between 1950 and 2000.

2.2 Materials and Methods

2.2.1 Culture

Eighteen soybean cultivars released between 1950-2000 (Table 1) were planted on 20 April, 2007 and 9 May 2008 at the Ben Hur Research Farm near Baton Rouge, LA (30⁰N Lat). These cultivars represent the Southern public germplasm collection and included Maturity Groups V-VIII cultivars (MG V-VIII). The study was conducted on a commerce silty clay loam soil (fine-silty, mixed, superactive, nonacid, thermic Fluvaquent Endo aquepts). The test site had tile drainage and access to irrigation. Based on soil test recommendations, the site was fertilized

at the rate of 0-34-67-33 kg ha⁻¹ (N-P-K-S). Planting was done on raised beds with a 95-cm row spacing and a 7.2 m row length. Plots consisted of four rows. Seed were sown at the rate of 30 seed m⁻² to achieve a final plant population of 180,000- 225,300 plants ha⁻¹, considered optimal for Louisiana conditions. Recommended pesticides were used to control weeds, diseases, and insects.

2.2.2 Experimental Design and Data Obtained

The test was planted as a randomized complete block experimental design with four replications and two years as blocking factors. The study had one factor, cultivars. Eighteen southern public soybean cultivars released from 1950 to 2000, representing MG V-VIII were selected (Table 1). Data were obtained for yield, lodging, plant stand and three phenological parameters: days to R5 (start of the seed filling period), days to R7 (end of the seed filling period or physiological maturity), and length of the seed filling period (R5-R7) (developmental stages according to Fehr and Caviness, 1977). Yield was determined at maturity by the following method:

1. Machine cutting a 4-m² section of interior plot area and determining fresh weight of the entire sample using a field scale.
2. At the same date as in step 1, a 0.5-m² sample was harvested for determination of the percent dry weight of the plant material (oven-dried at 60⁰ C for 4 days), the percent dry weight of remaining leaf/petiole material, and the harvest index [HI=seed dry weight/total dry weight (exclusive of leaf/petiole material)]. Total dry matter (R7) was determined by removing any remaining leaf/petiole material and weighing the sample after oven-drying at 60°C for four days.
3. Parameters measured in steps 1 and 2 were then used to calculate yield dry weight as follows:
[(total fresh wgt.) (fraction dry wgt./fresh wgt.)- leaf/petiole dry wgt.]xHI(fraction)

4. Yield dry weight was then adjusted to 130 g kg⁻¹ moisture content.

Lodging scores (leaning or falling over of plants) were based on visual ratings from one to five according to the method of Mancuso and Caviness (1991): 1=almost all plants erect; 2=either all plants leaning slightly or only a few plants prostrate; 3=either all plants bending moderately (45° angle) or 25-50% of the plants prostrate; 4=either all plants leaning considerably (45-90° angle) or 50-80% of the plants prostrate; 5=all plants prostrate.

2.2.3 Statistical Analyses

Correlation and regression analyses were done with SAS PROC MIXED in which linear, quadratic, and cubic components were successively tested for significance and included if the residual sum of squares was significantly reduced ($p < 0.05$). The tests for homogeneity of regression equations between 2007 and 2008 were also done with SAS PROC MIXED. If homogeneity was present, a single regression equation representing both years was presented; otherwise, data were regressed separately by year. Analysis of variance (ANOVA) was also performed with SAS PROC MIXED ($P < 0.05$). Mean separation was according to Tukey's test ($P < 0.05$). Years and replications were random factors and cultivars were fixed.

2.3 Results

Cultivar had a highly significant effect on yield ($P < 0.001$). Yield varied from a low of 1909 kg ha⁻¹ for Hardee (released in 1962) to a high of 3978 kg ha⁻¹ for Graham (released in 1996). Cultivars yielding similar to Graham ($P < 0.05$ according to Tukey's test) were Anand (3814 kg ha⁻¹), Pace (3669 kg ha⁻¹), Musen (3529 kg ha⁻¹), TN-5-95 (3506 kg ha⁻¹), and Clifford (3335 kg ha⁻¹), all of which were among new cultivars. The only cultivar released in the 1990's not to be among this top-yielding group was Lyon (released 1993). Among top-yielding

Table 2.1. Yield and agronomic characteristics of 18 soybean cultivars, released between 1950-2000, averaged across 2 years and grown near Baton Rouge, LA, 2007 and 2008.

Cultivars	Year of release	Yield Kg ha ⁻¹	Days to R5 days	Days to R7 days	Seed filling period days	Lodging 1-5†	Plant pop. no. m ⁻²
Graham (V)	1996	3978‡	71	129	59‡	1.2	21
Anand (V)	1999	3814‡	65	128	61‡	1.4	17
Pace (V)	1996	3669‡	78	136	58‡	2.8‡	17
Musen (VI)	1997	3529‡	90	136	44	1.4	19
TN-5-95 (V)	1997	3506‡	75	128	53‡	1.4	18
Clifford (V)	1994	3335‡	71	127	56‡	1.4	18
Ransom(VI)	1970	3079	93	146	52‡	1.6	16
Bragg (VII)	1963	2955	106	158	52‡	2.2	19
Mack(V)	1971	2759	82	125	44	1.8	19
Lyon (VI)	1993	2733	88	141	53‡	1.8	19
Hutton(VIII)	1972	2592	82	126	44	1.8	14
Essex (V)	1972	2536	78	129	51‡	2.0	17
Jackson(VII)	1953	2494	106	160‡	55‡	1.6	14
Semmes VII)	1965	2445	112	163‡	51‡	1.8	15
Lee (VII)	1954	2392	88	147	60‡	1.4	20
Tracy (VI)	1973	2295	83	140	57‡	1.8	20
Dyer (V)	1967	2273	78	127	49	2.4‡	21
Hardee (VIII)	1962	1909	128‡	172‡	44	3.0‡	17
CV(%)		15.0	2.0	1.0	4.1	16.7	18.7

‡ Indicates cultivars means are similar according to Turkey's test at the .05 probability level.

† Lodging score using a scale of 1-5 where 1 = all plants erect and 5 = all plants lodged

cultivars (released 1994-1999), average yield was 3639 kg ha⁻¹. All other cultivars, which were released from 1952 to 1973, showed yields significantly less than Graham. Average yield for cultivars released between 1950 and 1970 was only 2411 kg ha⁻¹ and those released during the 1970's showed a mean yield of 2652 kg ha⁻¹. Yield and year of release were significantly correlated in a linear relationship ($P < 0.0001$, Fig. 1). Across the 40-year period from 1950 to 2000, yield increased about 30.4 kg ha⁻¹ annually.

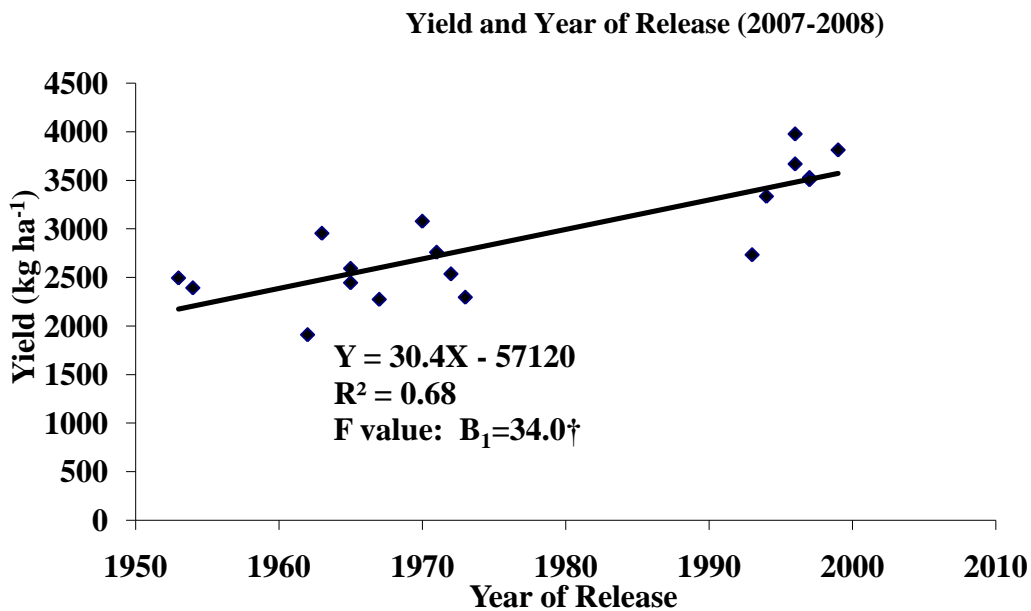


Fig. 2.1. Regression of yield on year of release for 18 soybean cultivars released from 1950-2000 and averaged across two years, grown near Baton Rouge, LA, 2007 and 2008. † Significant at the 0.0001 probability level.

Yield and days to R5 were negatively correlated in a linear relationship ($R^2 = 0.56$, $P < 0.01$) (Fig. 2) resulting from data pooled across years (regression equations were homogenous). Yields tended to be greater for those that had a relatively short time to R5 (60-70 d > emergence), such as Anand (65 d), Clifford (71 d), and TN 5-95 (75 d), all of which were

among the new cultivars released during the 1990's. In contrast, most cultivars released during 1952 to 1973 had days to R5 greater than 80 (Table 1). In particular, older low-yielding cultivars belonging to MG VII and VIII had very long periods to R5: Hardee (128 d), Semmes (112 d), Jackson (106 days) and Bragg (106 days).

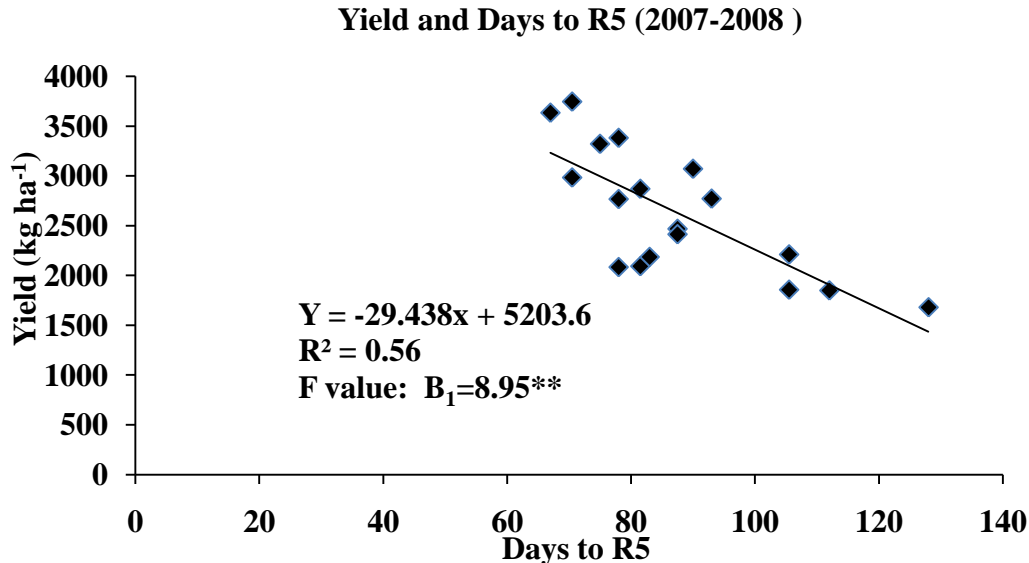


Fig. 2.2. Regression of yield (kg ha⁻¹) on days to R5 for 18 soybean cultivars released from 1950-2000 and averaged across two years, grown near Baton Rouge, LA, 2007 and 2008.

**** Significant at the 0.01 probability level.**

Regression of yield on days to R7 differed between years (regression equations were not homogenous across years) and therefore was presented separately for 2007 and 2008 (Figs. 3 and 4). During 2007 there was no relationship between yield and days to R7 ($R^2 = 0.015$, NS). In contrast, an inverse relationship between yield and days to R7 occurred in 2008 ($R^2 = 0.44$, $P < 0.001$). Generally, the top-yielding cultivars released in the 1990's had fewer days to R7 compared with older cultivars. For example, new cultivars Anand, TN5-95, and Graham had 121-126 d to R7, whereas older cultivars like Hardee, Jackson, and Bragg had 148-158 d.

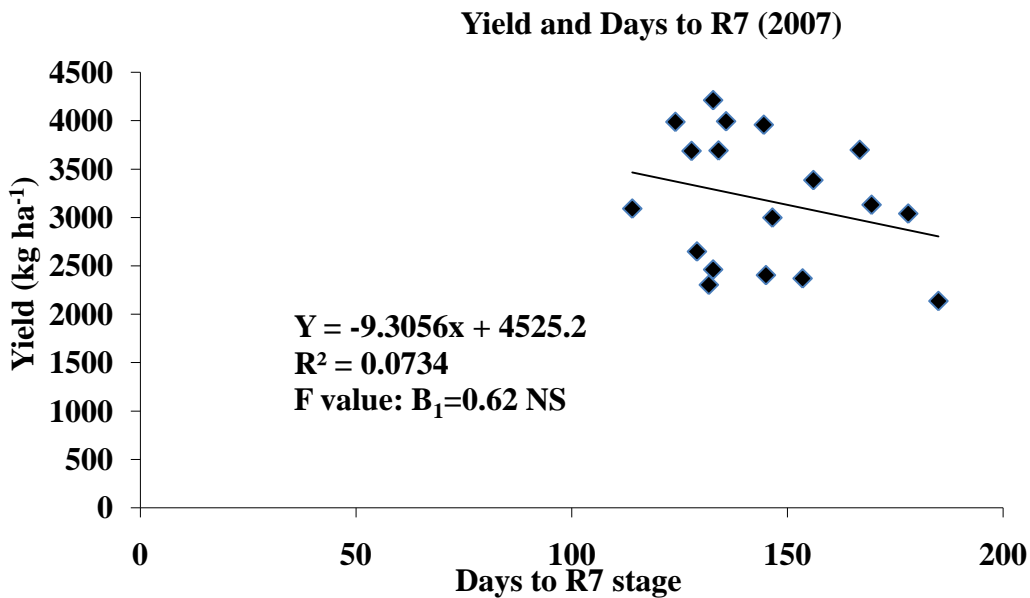


Fig. 2.3. Regression of yield on days to R7 for 18 soybean cultivars released from 1950-2000, grown near Baton Rouge, LA, 2007. NS=Not Significant.

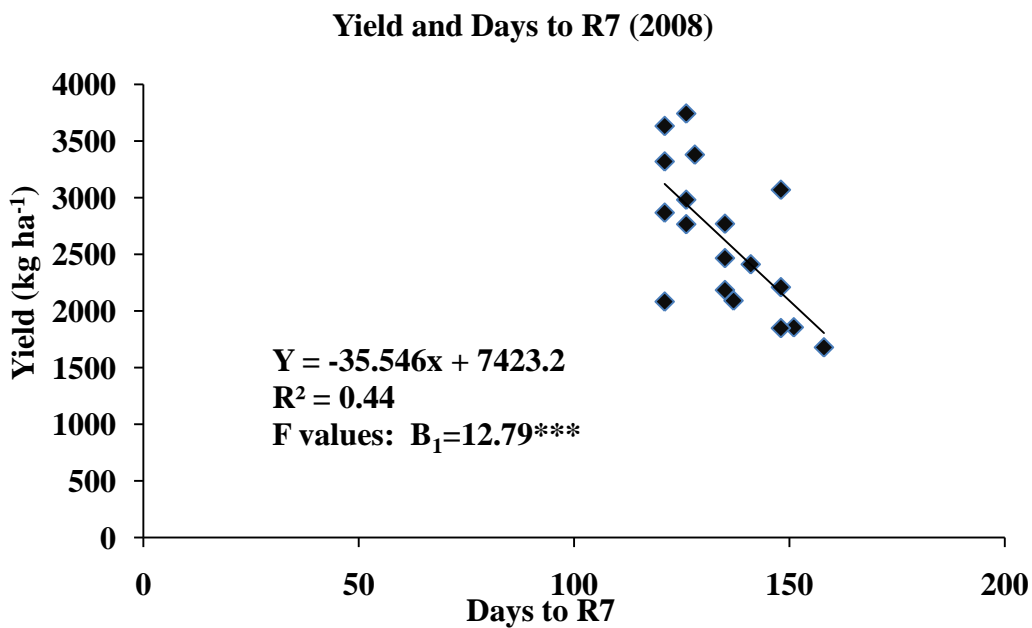


Fig. 2.4. Regression of yield on days to R7 for 18 old and new soybean cultivars grown near Baton Rouge, LA, 2008. * Significant at the 0.001 probability level.**

The regression of yield on lodging also differed between years and could not be pooled. In 2007 there was no relationship between yield and lodging score ($R^2=0.04$) (Fig. 5). Lodging was not very evident in 2007 with most cultivars showing scores of less than 2, a level recognized as having no yield effect (Noor and Caviness, 1980). In contrast, lodging was greater in 2008, most likely due to hurricane Gustav in early September. Over half the cultivars had scores above 2.0. There was an inverse relationship between yield and lodging in 2008 ($R^2=0.43$, $P<0.001$) (Fig. 6). Greatest lodging scores occurred for old cultivars such as Hardee (3.5), Pace (2.7), Davis (2.6), and Essex (2.4) which had taller plant height relative to newer cultivars such as Anand (1.5), Graham (1.3), Clifford (1.1) and TN5-95 (1.4). Because of earlier maturity, the newer cultivars flowered earlier resulting in reduced plant height. Reduced plant height is recognized as a main factor for reducing lodging (Wilcox and Sedyama, 1981).

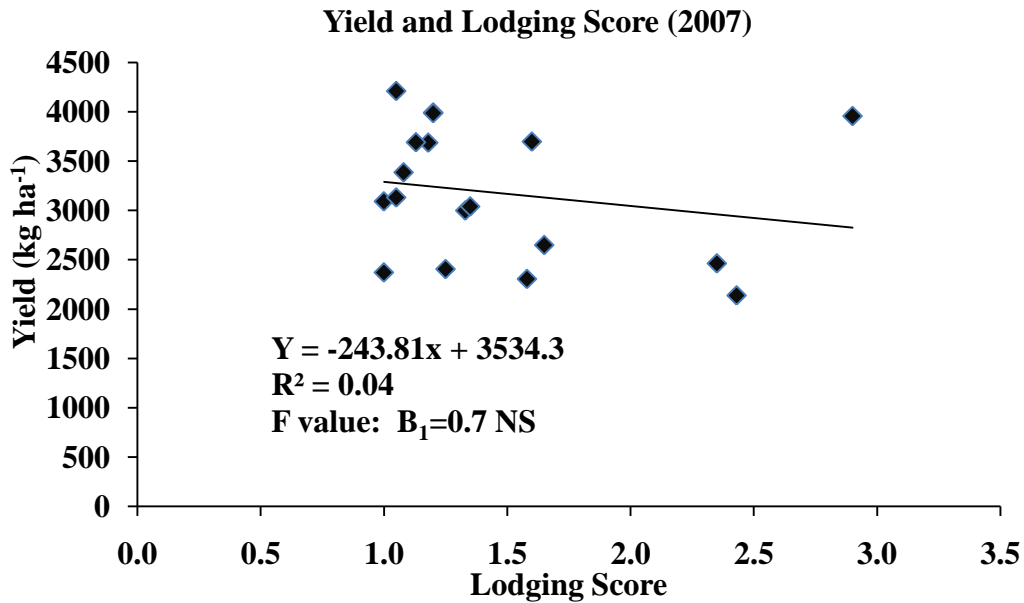


Fig. 2.5. Regression of yield on lodging score for 18 old and new soybean cultivars grown near Baton Rouge, LA, 2007.
 NS =Not Significant

Yield and Lodging Score (2008)

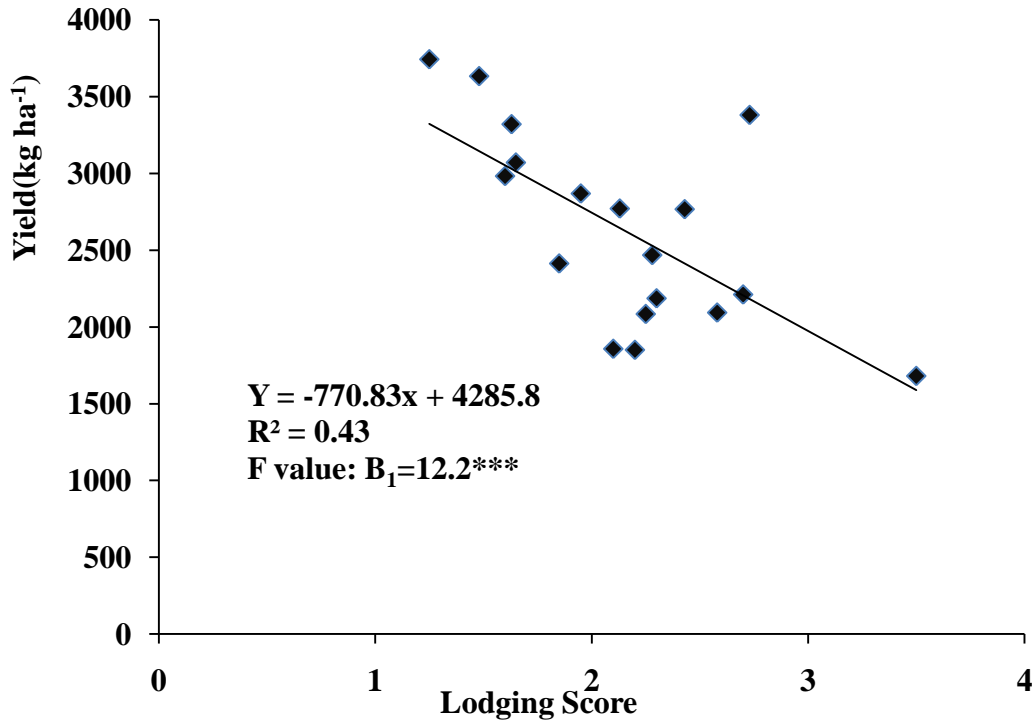


Fig. 2.6. Regression of yield on lodging score for 18 old and new soybean cultivars grown near Baton Rouge, LA , 2008.

***** Significant at the 0.001 probability level.**

Regression of yield on length of the seed filling period (days R5-R7) differed between years and therefore could not be pooled. In 2007 there was no significant relationship of yield with days R5-R7 ($R^2 = 0.009$, NS) (Fig. 7). In contrast, a weak linear relationship between yield and length of seed filling occurred in 2008 ($R^2 = 0.28$, $P < 0.01$) (Fig. 8). During 2008, the seed filling periods of new cultivars [Anand (56 days) , Pace (56 days) and Graham (54 days)] were more than 48 days except TN 5-95 (42 days) and seed filling period of older cultivars ranged from 35 to 48 days with lowest being for Ransom (35 days) and highest for Musen (48 days) and Bragg (48 days).

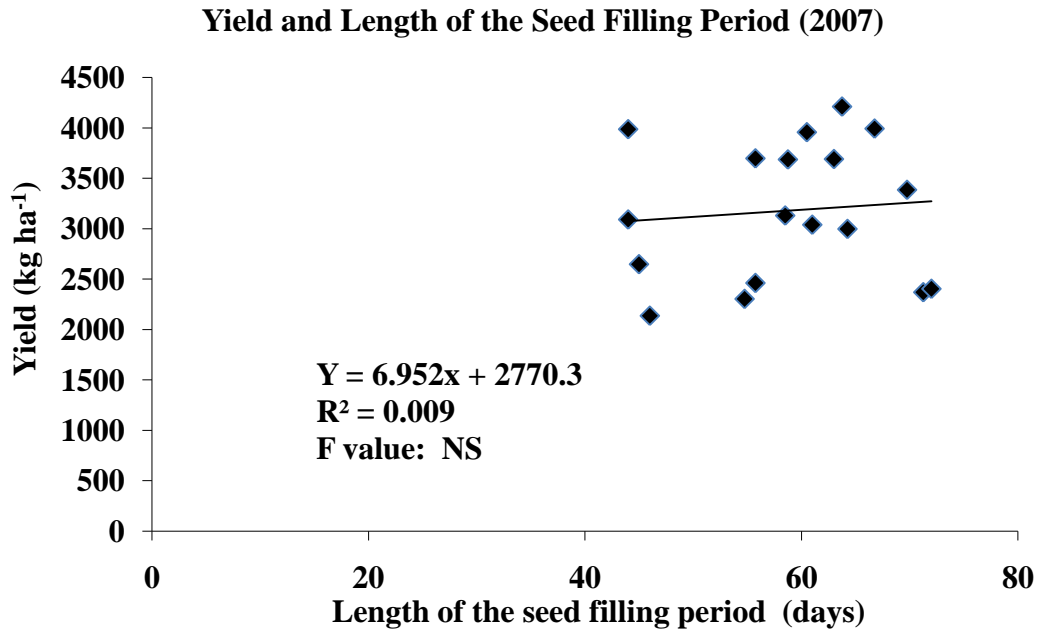


Fig. 2.7. Relationship between yield and length of the seed filling period for 18 soybean cultivars released between 1950-2000 grown near Baton Rouge, LA, 2007. NS= not significant.

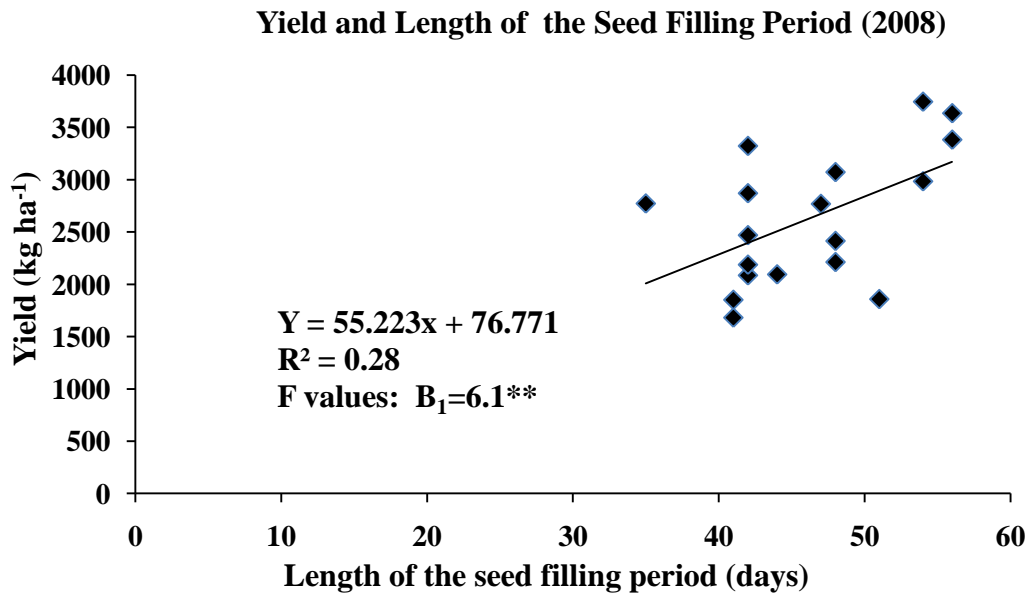


Fig. 2.8. Relationship between yield and length of the seed filling period for 18 soybean cultivars released between 1950-2000 grown near Baton Rouge, LA, 2008.

**** Significant at the 0.01 probability level.**

2.4 Discussion

Increased yield through cultivar development in our study ($30.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$) fell within the general range found in other studies ($10\text{-}30 \text{ kg ha}^{-1} \text{ yr}^{-1}$, Specht et al., 1999). This occurred despite the fact that most new cultivars were MG V, whereas old cultivars were mainly from later MG VI-VIII (Table 1). Thus, genetic improvement occurred despite reduction in growing period. When averaged within new and old cultivars, growing period (days emergence to R7) fell from 147 d in the latter to 136 d in the former. Despite this, yield rose from 2521 kg ha^{-1} for old cultivars to 3509 kg ha^{-1} for new cultivars, a 39% increase. This explains the negative correlation of yield with days to R7 shown in Fig. 4. Lower yield was not being caused by the later maturity, but the later maturity was simply associated with the lower-yielding older cultivars.

A key factor in soybean yield formation is accumulation of sufficient vegetative dry matter by R5 to optimize seed number per area (Board and Modali, 2005). Since dry matter (R5) is controlled by length of the emergence-R5 period, as well as crop growth rate during this period, it is interesting that the newer cultivars were able to achieve greater yields while at the same time reducing the number of days to R5. Days to R5 dropped from 94 d for old cultivars to 77d for new cultivars. Since all cultivars were being grown under the same conditions, there are only three possible explanations for greater yield in the new vs. old cultivars: 1) greater seed size (g per seed); 2) greater seed number production per unit of dry matter; and/or 3) faster crop growth rate during the emergence-R5 period. Answers to these questions will appear in subsequent chapters.

Yield was weakly correlated with length of the seed filling period in one year of the study. This substantiates previous studies indicating length of seed filling had little use as an indirect selection criterion for yield (Nelson, 1986; Pfeiffer et al., 1991; Hanson, 1992; Egli et

al., 1984; Salado-Navarro et al., 1986). The relative importance of seed number per area and seed size in explaining yield increases from cultivar development (discussed in a chapter 4) will help elucidate this issue.

Similar to the case for length of the seed filling period, lodging showed little connection with yield increases during the cultivar improvement process. Yield and lodging were significantly negatively correlated in 2008 (Fig. 6). However, this was probably more a correlative effect rather than a cause-and-effect relationship. Lodging in that year was mainly due to the arrival of hurricane Gustav late in the growing season after physiological maturity. This is long past the time at which lodging has a negative effect on yield (Woods and Swearingin, 1977). Thus, the lodging itself had little effect on yield. The negative correlation of yield with lodging in 2008 probably occurred because the low-yielding old cultivars were taller than the higher-yielding new cultivars and therefore lodged more.

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Chapter 3

Dry Matter Accumulation and Harvest Index

3.1 Introduction

Soybean is the most important oilseed crop grown in the world (56% of world oil seed production) and has been a major crop in the US since the end of World War II (Wilcox, 2004). The US produces about 33% of the world's soybeans, followed closely by our main competitors, Brazil (28%) and Argentina (21%). Remaining producers are China, India, and a few other countries. The value of soybean to the US economy is attested to by the \$26.9 billion total value of the US soybean crop in 2006/2007 (How the Global Oilseed and Grain Trade Works, 2008). Most of the oil and meal crushed from soybean in the US stays within the country. Thus, our contribution to the world market is mainly as whole seed. Currently, our largest customers are China, Mexico, and the European Union.

Previous research showed that yield increases from soybean cultivar development varied from 10 to 30 kg ha⁻¹ yr⁻¹ (Specht et al., 1999). This genetic gain basically occurs either through increased total dry matter (TDM) or greater partitioning of TDM into yield [i.e. harvest index (HI)] (Loomis and Connor, 1992). Total dry matter accumulation affects yield through development of yield components, morphological features on the plant which potentially influence yield: nodes per area, reproductive nodes per area (nodes bearing at least one viable pod that contributes to yield), pod per reproductive node, pod number per area, seed per pod, seed number per area, and seed size (Board and Modali, 2005). Among these, node and reproductive node numbers per area, pod number per area, and seed number per area are most responsive to TDM accumulation (Egli and Yu, 1991; Board and Modali, 2005). Total dry matter level is regulated by the interplay of crop growth rate (g m⁻² day⁻¹ gain in dry matter), light

interception (% of sun light intercepted by the crop), and leaf area index (m^2 leaf area m^{-2} land area) (Loomis and Connor, 1992).

Previous studies do not give a consistent picture of how TDM accumulation and HI have been related to yield increases during the cultivar development process. Salado-Navarro et al. (1993) examined 18 Southern cultivars released from 1945 to 1982, but found no relationships between improved yield with either TDM or HI. Gay et al. (1980) explained yield differences between new and old cultivars as governed more by increased HI rather than TDM accumulation. More recent studies involving new vs. old cultivars in Canada (Morrison et al., 1999), Japan (Shiraiwa and Hashikawa, 1995) and China (Cui and Yu, 2005) have also reported the greater importance of HI vs. TDM for explaining genetic yield improvement. In the case of the Canadian study, no differences in TDM were shown between new and old cultivars. In contrast, Frederick et al. (1991) reported little role for HI in explaining genetic improvement in soybean and attributed greater importance to TDM accumulation. Cregan and Yaklich (1986), Kumudini et al. (2001), and De Bruin and Pedersen (2009) reported similar findings in midwestern research. Thus, it appears the relative importance of HI vs. TDM in explaining yield increases due to cultivar development vary with region and/or germplasm pool. Since no study of this nature has been done within the Southern germplasm pool, our objective was to determine the relative importance of HI vs. TDM in yield improvement between 1950 to 2000.

3.2 Materials and Methods

3.2.1 Culture

Eighteen soybean cultivars released between 1950-2000 (Table 1) were planted on 20 April, 2007 and 9 May 2008 at the Ben Hur Research Farm near Baton Rouge, LA (30°N Lat). The cultivars were from different Maturity Groups (MGV-VIII). The study was conducted on a

commerce silty clay loam soil (fine-silty, mixed, superactive, nonacid, thermic Fluvaquent Endoaquepts). The test site had tile drainage and access to irrigation. Based on soil test recommendations, the site was fertilized at the rate of 0-34-67-33 kg ha⁻¹ (N-P-K-S). Planting was done on raised beds with a 95-cm row spacing and a 7.2 m row length. Plots consisted of four rows. Seed were sown at the rate of 30 seed m⁻² to achieve a final plant population of 225,300 plants ha⁻¹. Recommended pesticides were used to control weeds, diseases, and insects.

3.2.2 Experimental Design and Data Obtained

The test was planted as a randomized complete block experimental design with four replications and two years as blocking factors. The study had one factor, cultivars. Eighteen southern public soybean cultivars released from 1950 to 2000, representing MG V-VIII, were selected (Table 1). Data were obtained for yield, dry matter accumulation at R7 and Harvest Index (partitioning of dry matter into the economic part) Yield was determined at maturity by the following method:

1. Machine cutting a 4-m² section of interior plot area and determining fresh weight of the entire sample using a field scale.
2. At the same time as step 1, a 0.5-m² sample was harvested for determination of the percent dry weight of the plant material (oven-dried at 60⁰ C for 4 days), the percent dry weight of remaining leaf/petiole material, and the harvest index [HI=seed dry weight/total dry weight (exclusive of leaf/petiole material)]. Total dry matter (R7) was determined by removing any remaining leaf/petiole material and weighing the sample after oven-drying at 60°C for four days.
3. Parameters measured in steps 1 and 2 were then used to calculate yield dry weight as follows:
[(total fresh wgt.)(fraction dry wgt./fresh wgt.)- leaf/petiole dry wgt.]xHI(fraction)
4. Yield dry weight was then adjusted to 130 g kg⁻¹ moisture content.

3.2.2 Statistical Analysis

Correlation and regression analyses were done with the PROC GLM procedures of the SAS system. Regression analyses of yield vs. HI and TDM, as well as HI and TDM vs. year of release were done using SAS regression (PROC GLM) in which linear, quadratic, and cubic components were successively tested for significance and included if the residual sum of squares was significantly reduced ($p < 0.05$). The tests for homogeneity of regression equations between 2007 and 2008 were also done with SAS PROC MIXED. If homogeneity was present, a single regression equation representing both years was presented; otherwise, data were regressed separately by year. Analysis of variance (ANOVA) was also performed with SAS PROC MIXED ($P < 0.05$). Years and replications were considered random factors and cultivars was fixed.

3.3 Results

The ANOVA revealed a significant cultivar effect on yield ($P < 0.001$). Yield varied from a low of 1909 kg ha⁻¹ for Hardee (released in 1962) to a high of 3978 kg ha⁻¹ for Graham (released in 1996) (Table 1). Cultivars yielding similar to Graham ($P < 0.05$ according to Tukey's test) were Anand (3814 kg ha⁻¹), Pace (3669 kg ha⁻¹), Musen (3529 kg ha⁻¹), and TN-5-95 (3506 kg ha⁻¹), all of which were among new cultivars released in the 1990's. All cultivars released from 1950 to 1975 showed yields significantly less than Graham. Average yield for cultivars released during the 1990's was 3509 kg ha⁻¹. In contrast, average yield for cultivars released between 1950 and 1975 was only 2521 kg ha⁻¹. This represents a 39% yield increase between old and new cultivars. Within both years of the study, regression of yield on year of release was highly significantly correlated ($P < 0.0001$) and the regression equations were homogenous. Therefore, the data were pooled across years into a single regression equation

Table 3.1. Yield, harvest index, and total dry matter at R7 [TDM(R7)] for 18 public southern soybean cultivars released between 1950-2000, grown near Baton Rouge, LA, averaged across two years, 2007 and 2008.

Cultivars	Maturity Group	Year of release	Yield	Harvest Index	TDM (R7)
			Kg ha ⁻¹	%	
Graham	V	1996	3978 [‡]	49.1 [‡]	737 [‡]
Anand	V	1999	3813 [‡]	49.9 [‡]	695 [‡]
Pace	V	1996	3669 [‡]	39.8	844 [‡]
Musen	VI	1997	3528 [‡]	41.5	774 [‡]
TN-5-95	V	1997	3506 [‡]	39.3	815 [‡]
Clifford	V	1994	3335 [‡]	47.1 [‡]	643
Ransom	VII	1970	3079	42.1	666
Bragg	VII	1963	2955	38.8	693 [‡]
Mack	V	1971	2759	47.2 [‡]	532
Lyon	VI	1993	2733	37.8	659
Hutton	VIII	1972	2592	40.5	576
Essex	V	1972	2536	45.7 [‡]	505
Jackson	VII	1953	2494	39.0	570
Semmes	VII	1965	2445	34.6	633
Lee	VI	1954	2392	42.0	518
Tracy	VI	1973	2296	31.5	662
Dyer	V	1967	2273	40.0	513
Hardee	VIII	1962	1909	28.8	607
CV (%)			15.0	9.4	12.0

[‡] Indicates cultivar means are similar to the top-ranking cultivar for that parameter. Significant differences were based on Tukey's test at the 0.05 probability level.

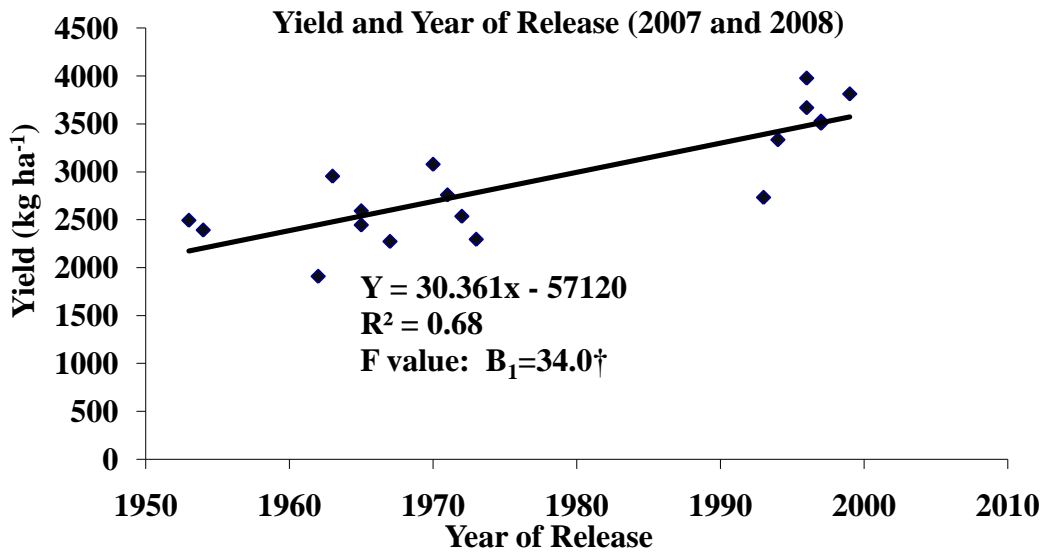


Fig. 3.1. Regression of yield on year of release for 18 public southern soybean cultivars released between 1950-2000, and grown near Baton Rouge, LA, 2007 and 2008.
 † Significant at the 0.0001 probability level.

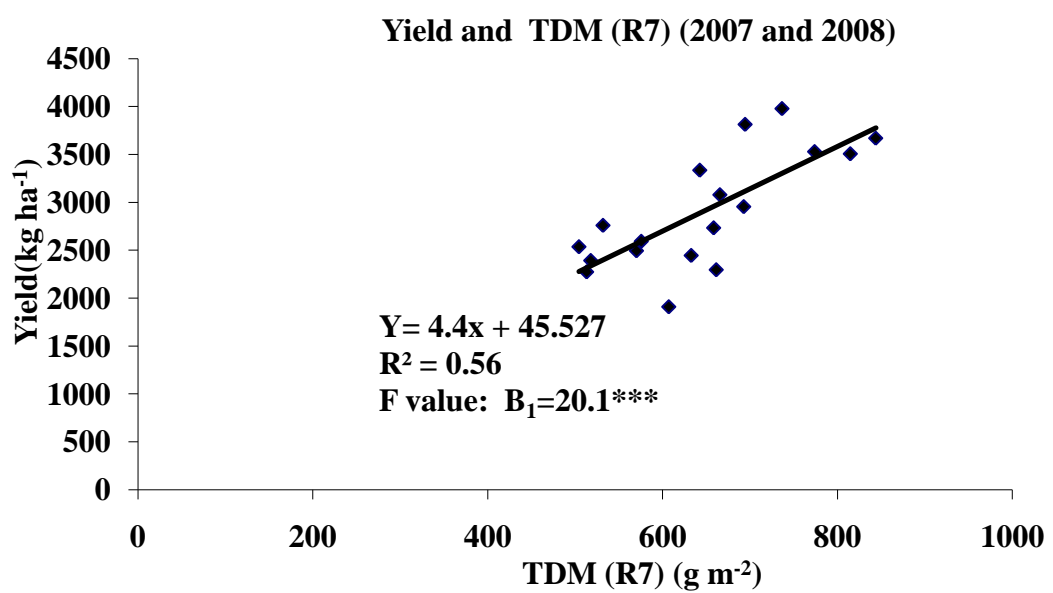


Fig. 3.2. Regression of yield (kg ha⁻¹) on total dry matter at R7 [TDM (R7)] of 18 soybean cultivars grown near Baton Rouge,LA, during 2007 and 2008.
 *** Significant at the 0.001 probability level.

(Fig.1). Yield and year of release were significantly correlated in a linear relationship ($P < 0.0001$). Across the 40-year period from 1950 to 2000, yield increased about $30.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$.

Total dry matter (R7) was also significantly affected by cultivar at $P < 0.001$, ranging from 505 g m^{-2} for old cultivar Essex to 844 for new cultivar Pace (Table 1). Among the six cultivars that had TDM (R7) similar to Pace, five of them were top-yielding new cultivars. Differences in TDM (R7) between old and new cultivars are more apparent when averaged within the two groups. For cultivars released between 1950-1975, TDM (R7) was 594 g m^{-2} , whereas for those released in the 1990's it was 751 g m^{-2} . This represents a 26% increase, a level considerably less than the 39% yield increase experienced by these same groups. Yield was highly significantly correlated with TDM (R7) within both years and regression equations were homogenous. Combined data are shown in Fig. 2 ($R^2 = 0.56$, $P < 0.001$). Total dry matter (R7) was also significantly correlated with year of release in both years. Because of homogeneity of regression equations, the data were pooled across years into one equation ($R^2 = 0.53$, $P < 0.001$) (Fig. 3). On average, cultivar development across the 1950-2000 period resulted in a TDM (R7) increase of $4.5 \text{ g m}^{-2} \text{ yr}^{-1}$. Thus, a general trend of increasing TDM (R7) with increasing yield occurred over this period of cultivar development, although the level of TDM (R7) increase between old and new cultivars did not appear great enough to explain the entire yield enhancement between the two groups.

Harvest index was also significantly affected by cultivar, differing from 31.5% for old cultivar Tracy to 49.9% for new cultivar Anand (Table 1). Among the five cultivars having the greatest HI, three were from the top-yielding new cultivars and two were from the lower-yielding old cultivars. Regression equations for relating yield with HI were not homogenous across years, and were therefore presented separately for 2007 (Fig. 4) and 2008 (Fig.56).

Year of Release and TDM(R7) (2007 and 2008)

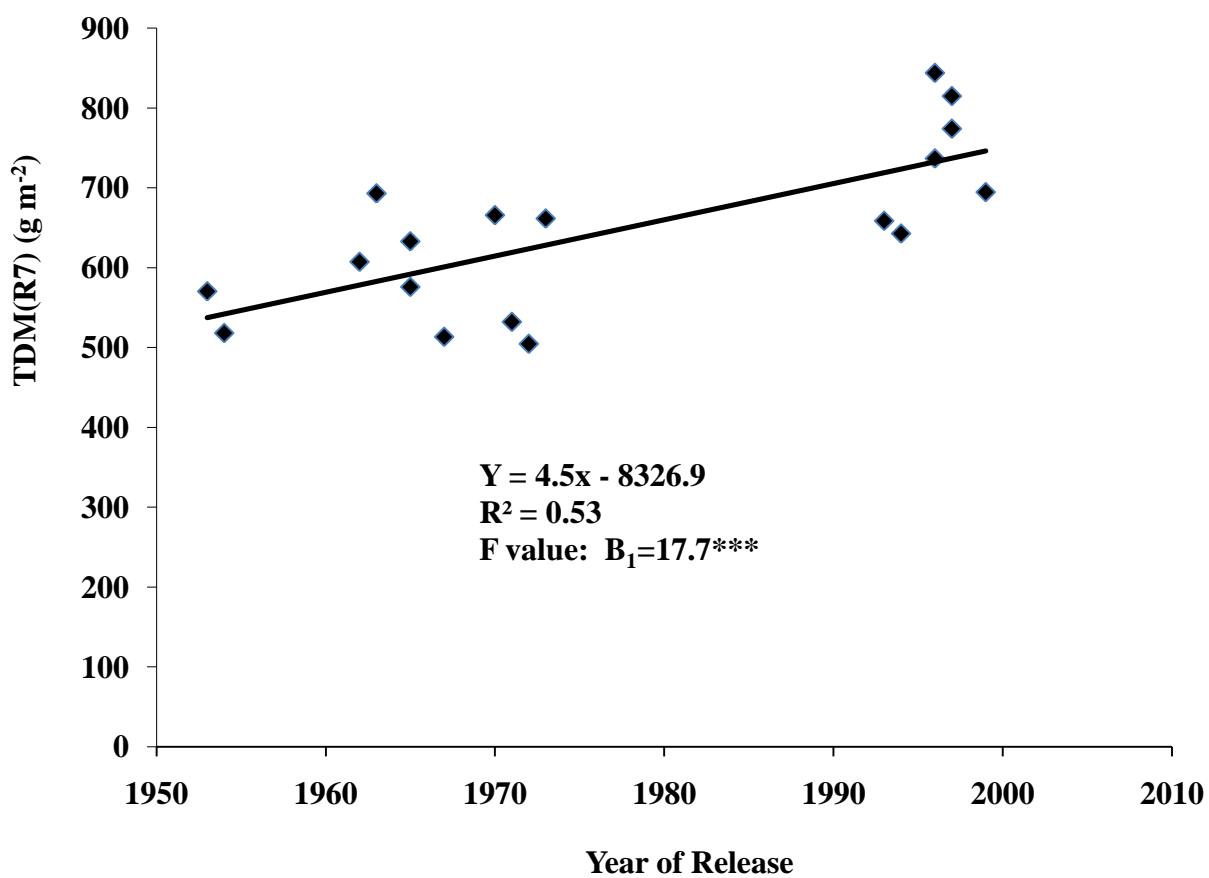


Fig. 3.3. Regression of total dry matter at R7 TDM(R7) on year of release for 18 soybean cultivars grown near Baton Rouge, LA, during 2007 and 2008. * Significant at the 0.001 probability level.**

In 2007, the two parameters were not significantly correlated, whereas in 2008 they were ($R^2=0.56$, $P<0.001$). Regression equations relating harvest index to year of release were homogenous and were therefore pooled across years (Fig. 6). In contrast to TDM(R7) and yield which showed significant upward trends with year of release (Figs. 1 and 3), HI showed no such trend, and remained relatively flat across the 1950-2000 period. When averaged within old cultivars (released 1950-1975) and new cultivars (released in 1990's), HI was 39.1 and 43.5%, respectively. This represents an 11.3% increase between the two groups, a level considerably below that for TDM(R7) (28% increase). Increases in TDM(R7) and HI between old and new cultivars added to 39%, the same % increase shown for yield enhancement between new vs. old cultivars.

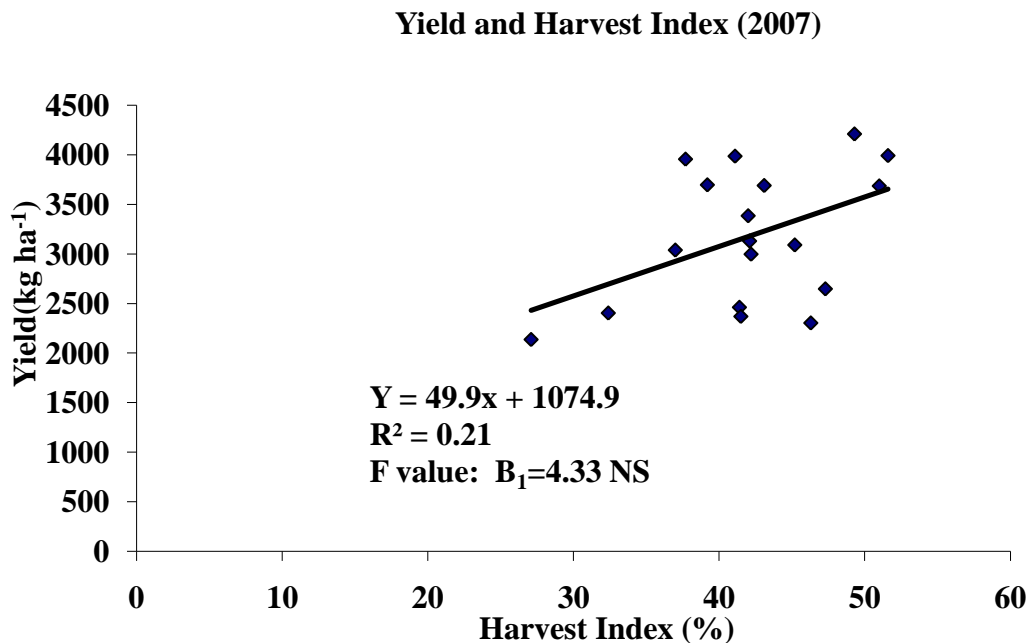


Fig. 3.4. Regression of yield on Harvest Index for 18 public southern soybean cultivars released between 1950-2000, and grown near Baton Rouge, LA in 2007. NS=not significant

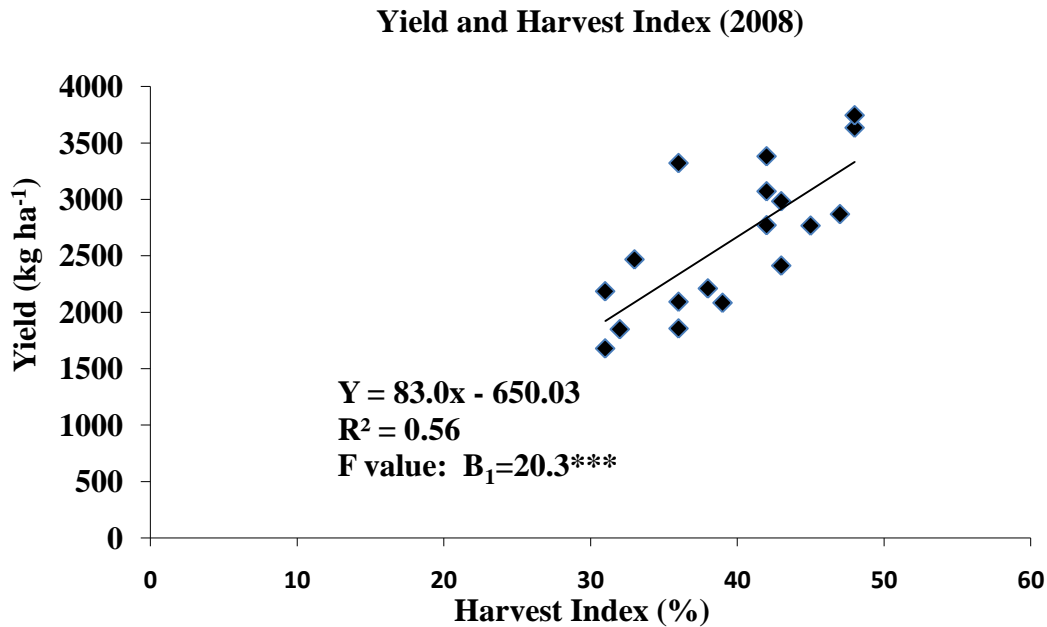


Fig. 3.5. Regression of yield on harvest index for 18 public southern soybean cultivars released between 1950-2000, and grown near Baton Rouge, LA in 2008. * Significant at the 0.001 probability level.**

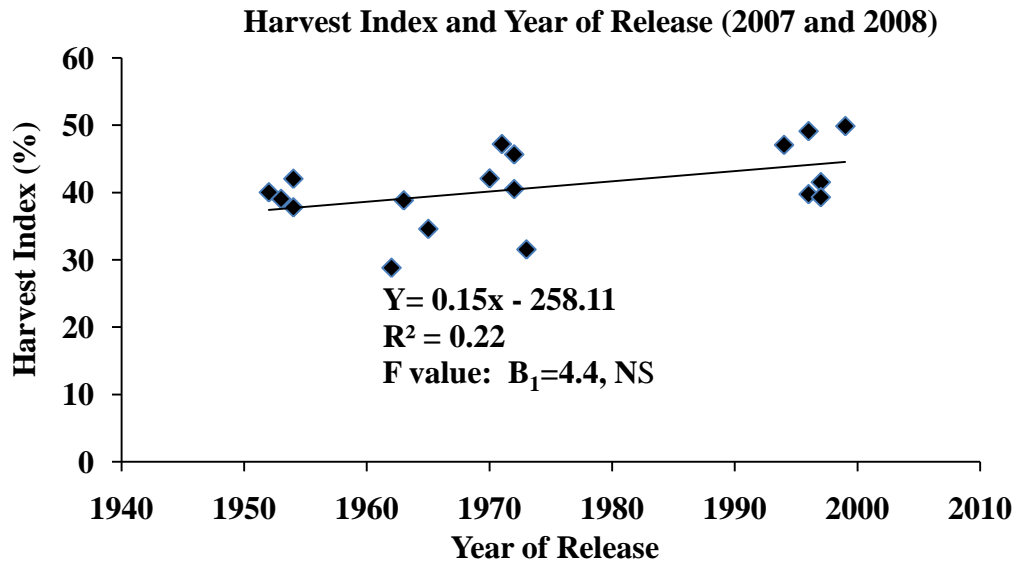


Fig. 3.6. Regression of harvest index on year of release for 18 public southern soybean cultivars released between 1950-2000, and grown near Baton Rouge, LA across two years, 2007 and 2008. NS=not significant

3.4 Discussion

Yield increases with cultivar development in this study ($30.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$) fell within the top range for yield increases reported in similar studies ($10\text{-}30 \text{ kg ha}^{-1} \text{ yr}^{-1}$, Specht et al., 1999). Previous studies involving southern cultivars released from 1942-1973 reported a smaller increase ($13.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$, Boerma, 1979). This difference may be due to the shorter time period used in the previous study, as well as cultivar changes associated with the different eras of cultivar development. In our study, new cultivars had greater yield and TDM(R7) (Table 1) compared with old ones, despite having a reduced growing period of 136 vs. 147 days (chapter 3). Such a result suggests new cultivars have a greater canopy photosynthetic rate and/or crop growth rate than do old cultivars. This suggestion is made stronger by our finding that large differences in HI did not occur in new vs. old cultivars. Harvest index did not move upward with year of release as TDM(R7) did (Figs. 3 and 6). Although yield and harvest index were significantly correlated in 2008 (Fig. 5), such was not the case in 2007 (Fig. 4). When averaged across years and within old and new cultivars, HI increased 11.3% from 39.1 to 43.5%; a modest increase, but sufficient to have a significant impact on yield.

In contrast, TDM(R7) was strongly correlated with yield (Fig. 2) and significantly trended upwards with year of release (Fig. 3). Based on the percentage increases between new vs. old cultivars for TDM(R7) (28%), HI (11.3%), and yield (39%), about 71% of the yield enhancement for new vs. old cultivars came from increased TDM(R7) and 29% from increased HI. This calculation is similar to that reported by Kumudini et al. (2001) where TDM and HI explained 78% and 22% of the yield increase, respectively. Our results agree with those reporting a greater role for TDM in explaining yield increases in new vs. old cultivars (Frederick et al., 1991; Cregan and Yaklich, 1986; Kumudini et al., 2001; DeBruin and Pedersen, 2009); but

disagree with those reporting a greater role for HI (Gay et al., 1980; Morrison et al., 1999; Shiraiwa and Hashikawa, 1995; Cui and Yu, 2005). Although TDM at the beginning of seed filling (R5) was not directly measured in our studies, it can be calculated from allometric relationships determined in previous studies (Board and Modali, 2005). By subtracting yield dry matter from TDM(R7), stem dry matter (R5) [maximal stem dry weight is determined at R5 (Board and Settimi, 1986)] is calculated. Since stem dry matter (R5) and leaf dry matter (R5) are strongly linearly correlated [$R=0.79$, $P<0.0001$; leaf weight (R5) = $0.183(\text{stem dry weight at R5}) + 33$], leaf dry matter (R5) can be calculated from stem dry matter (R5). The two values can then be added to determine TDM (R5). Based on these calculations, TDM (R5) for new and old cultivars was determined as 532 and 461 g m⁻², respectively. New vs. old cultivars were closer to the TDM (R5) level required for optimum yield (600 g m⁻²; Board and Modali, 2005). Thus, greater TDM (R7) for new vs. old cultivars was caused by increased TDM (R5) [despite less days to R5 (chapter 3)] and the increased pod load resulting from more TDM(R5). These results disagree with Kumudini et al. (2001) who found increased TDM (R7) in new vs. old cultivars to be entirely due to increased dry matter accumulation during seed filling.

The importance of TDM for explaining yield increases in our study suggests that crop photosynthetic rate and/or crop growth rate may be greater in new compared with old cultivars. Measurement of photosynthesis on the canopy level [canopy apparent photosynthesis (CAP)] has shown association with final yield (Harrison et al., 1981; Wells et al., 1982). However, the degree of correlation was not high ($R^2=0.25$). Boerma and Ashley (1988) reported stronger correlations of canopy apparent photosynthesis with yield, but they did not compare old vs. new cultivars. Studies involving photosynthesis rate per unit leaf area have shown mixed results. Early studies by Larson et al. (1981) involving cultivars released between 1927-1973 found no

correlation between yield and photosynthetic rate. Gay et al. (1980) and Frederick and Hesketh (1994) reported similar findings. In contrast, Dornhoff and Shibles (1970) compared 20 cultivars released across time and demonstrated a general trend between leaf photosynthetic rate and yield, although exceptions occurred. More recent studies by Morrison et al. (2000) reported an increase in leaf photosynthetic rate in new vs. old cultivars sufficiently large to explain yield increases with cultivar development. In regard to crop growth rate, Kumudini et al. (2001) demonstrated greater TDM accumulation during the seed filling period in new vs. old cultivars. However, this may have been due to a longer seed filling period rather than increased crop growth rate. In contrast, recent studies by De Bruin and Pedersen (2009) suggested increased yield in new vs. old cultivars was due to increased crop growth rate during flowering and pod set (R1-R5.5).

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Chapter 4

Yield Components and Their Relationship to the Yield Formation Process During Cultivar Improvement

4.1 Introduction

Cultivar development efforts by soybean [*Glycine max* (L.) Merr.] breeders have resulted in a 21-31 kg ha⁻¹yr⁻¹ increase in 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 soybean cultivar development process.

Yield, whether affected by genetic and/or environmental factors, is controlled by an interplay between growth dynamic and yield component parameters. Growth dynamic parameters are rates and levels of dry matter accumulation, leaf area, and light interception that characterize soybean's seasonal growing pattern (Loomis and Connor, 1992). Yield components are morphological characteristics whose formation is critical to yield production (Egli, 1998). For soybean, examples are seed number per area, seed size, seed per pod, pod number per area, pod per reproductive node (reproductive node contains at least one pod having at least one seed), reproductive node number per area, percentage of nodes becoming reproductive (percent reproductive nodes), and node number per area (Board and Modali, 2005). 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 number per area; seed number per area is controlled by secondary yield components seed per pod and pod number per area; pod

number per area is controlled by tertiary yield components pod per reproductive node and reproductive node number per area; and reproductive node number per area is controlled by quaternary yield components node number per area and percent reproductive nodes (percentage of all nodes that become reproductive).

Yield is basically a function of intercepted light (fraction of the sunlight intercepted by the crop), the dry matter produced from this light [which is controlled by radiation use efficiency (g of dry matter/units of light energy intercepted)], and the percentage of this dry matter transferred to the seed [harvest index (g of seed yield/g of total dry matter)] (Loomis and Connor, 1992). Attainment of optimal yield is dependent on achievement of optimum dry matter accumulation by R5 (Board and Modali, 2005). This, in turn, is a function of the length of time to R5 and the crop growth rate ($\text{g m}^{-2} \text{d}^{-1}$) between emergence and R5. Crop growth rate is controlled by the leaf photosynthetic rate and the level of leaf area index [leaf area (m^2)/ground area (m^2)]. The majority of abiotic stresses affecting soybean, as well as some biotic stresses (weeds, defoliating insects and diseases, nematodes), influence yield through crop growth rate effects on seed number per area (Jiang and Egli, 1995; Egli, 1998). Consequently, farmer cultural practices aimed at optimizing yield (e.g. optimum planting date, reduced row spacing, irrigation, planting on raised beds, pesticide application, seeding rate, fertility, etc.) achieve better yield through the effects of these cultural practices on crop growth rate and seed number per area.

Thus, yield components are the vehicle through which dry matter increases affect yield. Based on studies conducted on the environmental level, dry matter accumulation was shown to affect some yield components but not others (Board and Modali, 2005). Differences in row spacing, planting date, plant population, and waterlogging stress affected yield through the growth dynamic process described above. Dry matter accumulation affected yield through

control of seed number per area, pod number per area, and reproductive node number per area (node containing a pod having at least one seed), and node number per area. In contrast, seed size, seed per pod, pod per reproductive node, and percent reproductive nodes appeared unrelated to the yield formation process.

Because previous data presented in chapter 4 indicated that yield increases in new vs. old cultivars mainly resulted from greater TDM (R7) rather than increased harvest index (HI), we hypothesized that the same yield components responsible for increased yield on the environmental level, also operated on the genetic level. Previous studies involving new and old cultivars have provided ambivalent results, with some reporting yield increases caused by more pods and seeds (Frederick et al., 1991; DeBruin and Pedersen, 2009), while others have reported greater importance for seed size (Speeth and Williams, 1984; Gay et al., 1980; Cui and Yu, 2005). Thus, our objective was to identify yield components responsible for greater yield in new vs. old cultivars. Elucidation of this issue will provide soybean breeders with potential indirect selection criteria for soybean cultivar development

4.2 Materials and Methods

4.2.1 Culture

Eighteen soybean cultivars released between 1950-2000 (Table 1) were planted on 20 April, 2007 and 9 May, 2008 at the Ben Hur Research Farm near Baton Rouge, LA (30⁰N Lat). The cultivars were from different Maturity Groups (MGV-VIII). The study was conducted on a commerce silty clay loam soil (fine-silty, mixed, superactive, nonacid, thermic Fluvaquent Endoaquepts). The test site had tile drainage and access to irrigation. Based on soil test recommendations, the site was fertilized at the rate of 0-34-67-33 kg ha⁻¹ (N-P-K-S). Planting was done on raised beds with a 97-cm row spacing and a 7.2 m row length. Plots consisted of

four rows. Seed were machine-planted at the rate of 30 seed m⁻² to achieve a final plant population of 225,300 plants ha⁻¹. Recommended pesticides were used to control weeds, diseases, and insects.

4.2.2 Experimental Design and Data Obtained

The test was planted as a randomized complete block experimental design with four replications and two years as blocking factors. The study had one factor, cultivars. Years and replications were fixed factors while cultivar was random. Eighteen southern public soybean cultivars, released from 1950 to 2000, representing MG V-VIII were selected (Table 1). Yield was determined at maturity by the following method:

1. Machine cutting a 4-m² section of interior plot area and determining fresh weight of the entire sample using a field scale.
2. At the same date as in step 1, a 0.5-m² sample was harvested for determination of the percent dry weight of the plant material (oven-dried at 60⁰ C for 4 days), the percent dry weight of remaining leaf/petiole material, and the harvest index [HI=seed dry weight/total dry weight (exclusive of leaf/petiole material)]. Total dry matter (R7) was determined by removing any remaining leaf/petiole material and weighing the sample after oven-drying at 60⁰C for four days.
3. Parameters measured in steps 1 and 2 were then used to calculate yield dry weight as follows: [(total fresh wgt.) (dry wgt./fresh wgt.)- leaf/petiole dry wgt.] x HI4. Yield dry weight was then adjusted to 130 g kg⁻¹ moisture content.
5. Seed size (g per 100 seed) was determined by counting 300 seed from each yield sample with an automatic seed counter, drying the seed for 4 days to constant weight at 60⁰C in a forced-air dryer, weighing the sample, and then dividing the weight by three.

6. Seed number per area (no. m^{-2}) was determined by dividing dry yield by seed size (as g per seed). Thus, $g\ m^{-2}$ (dry yield)/ $g\ seed^{-1}$ (individual seed size) calculates seed number per area (no. m^{-2}).
7. Seed per pod (no. per pod) was determined from a second $0.5\ m^2$ sample. The pods were removed from all the plants and 50 pods were randomly selected and the number of bulging locules was counted to determine seed per pod (no. per pod).
8. Pod number per area (no. m^{-2}) was calculated by dividing seed number per area (no. m^{-2}) by seed per pod (no. m^{-2} /no. per pod).
9. Pod per reproductive node number (no. per reproductive node) was calculated from the same sample used for determination of seed per pod. All reproductive nodes (a reproductive node is defined as a node bearing at least one pod having at least one seed) and pods in the samples were counted and pod per reproductive node determined by dividing pod number by reproductive node number.
10. Reproductive node number per area (no m^{-2}) was determined by dividing pod number per area (no. m^{-2}) by pod per reproductive node (no. per node).
11. Percent reproductive nodes (%) was also determined from the second $0.5\ m^2$ sample. Reproductive and total node numbers were determined and the percentage of nodes becoming reproductive determined as (reproductive nodes/total nodes) X 100.
12. Node number per area (no. m^{-2}) was calculated by dividing reproductive node number per area (no. m^{-2}) by the fraction of nodes becoming reproductive.

4.2.3 Statistical Analysis

Regression analyses of growth, yield and yield components were done using SAS regression (PROC MIXED) in which linear, quadratic, and cubic components were successively

tested for significance and included if the residual sum of squares was significantly reduced ($p < 0.05$). Tests for homogeneity of regression equations between 2007 and 2008 were also done using SAS PROC MIXED at $P < 0.05$. Homogenous equations across years were pooled (cultivar means averaged across years) while those that were not were presented separately by year. Mean separation was done according to Tukey's test ($P < 0.05$). For a given parameter, all cultivars having a level similar to that of the top-ranked cultivar were marked with an “‡”.

Correlation and path analyses at the phenotypic and genotypic levels were applied using all data observations within years. The phenotypic level involves correlation and path analyses that include both genotypic and environmental factors, whereas genotypic analyses exclude environmental factors and focus strictly on genetic effects. Thus, the genotypic correlations and path analyses define more clearly what factors affect yield genetically than do the phenotypic analyses. Both analyses were applied to the data within primary, secondary, tertiary, and quaternary yield components. Primary predictor variables seed m^{-2} and seed size affected the primary response variable yield; secondary predictor variables seed per pod and pod m^{-2} affected the secondary response variable seed m^{-2} ; tertiary predictor variables reproductive node m^{-2} and pod per reproductive node affected the tertiary response variable pod m^{-2} ; and quaternary predictor variables node m^{-2} and percent reproductive nodes affected the quaternary response variable reproductive node m^{-2} . A diagram describing the path analyses for the various yield components is shown in Fig. 1. This diagram indicates direct and indirect pathways of influence for predictor variables on a response variable. Within each trait level, simultaneous equations were solved for direct path coefficients by a PROC IML (SAS Inst., Cary, NC) version of a computer program given by Kang (1994). Indirect path coefficients were determined by multiplying appropriate r (correlation coefficient) and path coefficient values. The unaccounted

for residual effect and coefficient of determination were computed in accordance with Kang (1994). The path analyses were done additively. Our criteria for identifying the importance of a specific trait in affecting its response variable were:

1. Positive correlation between the trait and the response variable.
2. Large positive direct effect by the trait on the response variable.
3. Small or nonexistent negative indirect effects by the trait on the response variable via other traits (i.e., lack of yield component compensation).

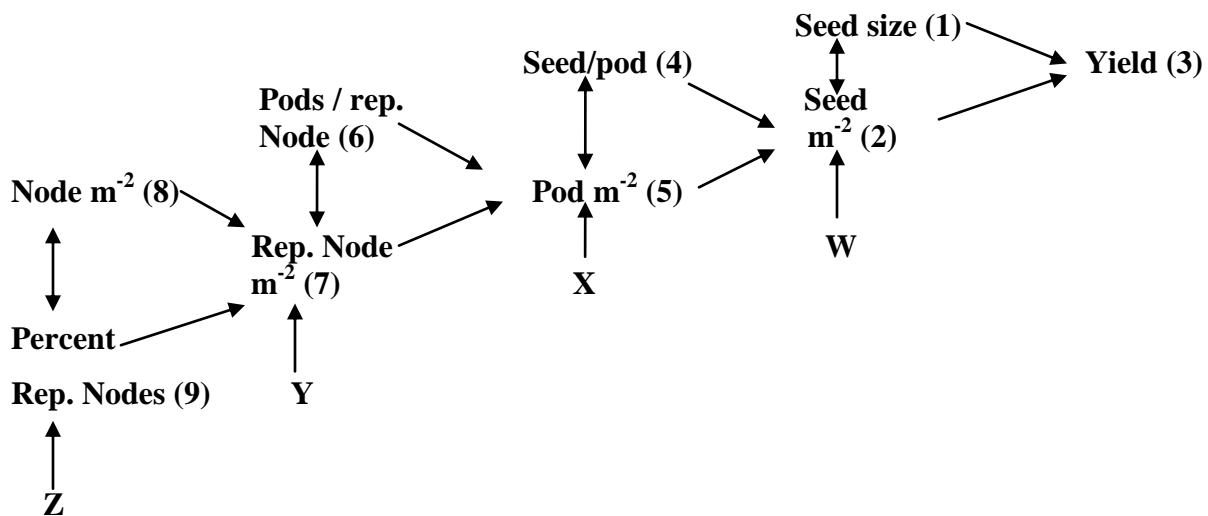


Fig. 4.1. Path diagram showing interrelationships among primary level traits (traits 1, 2 → 3), secondary level traits (traits 4, 5 → 2), tertiary level traits (6, 7 → 5) and quaternary traits (traits 8, 9 → 7). W, X, Y, and Z represent residual effects in the primary, secondary, Tertiary, and Quaternary levels, respectively.

4.3 Results

Yield was significantly affected by cultivar ($P < 0.001$). As described in previous chapters, yield increased at a steady gradual pace of $30.4 \text{ kg ha}^{-1}\text{yr}^{-1}$ across the 1950-2000 period (Table 3). Highest yielding cultivars in the study [i.e. those having yield similar to top-ranking cultivar

Graham according to Tukey's ($P < 0.05$) were Graham, Anand, Pace, Musen, TN-5-95, and Clifford. All top-ranking cultivars were among new cultivars released in the 1990's. Between seed number per area and seed size (the primary yield components affecting yield), seed number per area showed much greater linkage with yield than seed size (Table 1). Among the aforementioned top-ranking cultivars for yield, five of them also had the greatest seed number per area. In contrast, none of the old cultivars released from 1950-1975 had seed number per area similar to top-ranking cultivars (Table 1).

Although seed number per area was strongly related with yield, seed size was not (Table 1). Cultivar did not have a significant effect on seed size ($P < 0.05$) and there was little distinction between new (12.5 g per 100 seed) and old (13.6 g per 100 seed) cultivars. Observations concerning the relative effects of seed number per area and seed size on yield are supported by regression analyses. Yield and seed number per area were strongly related (Fig. 2, $R^2 = 0.84$, $P < 0.0001$) in a linear regression, whereas yield showed no significant correlation with seed size in either year (Table 3). Supporting these trends, seed number per area and year of release were in a strong linear regression relationship (Table 2; $R^2 = 0.69$, $P < 0.0001$), indicating that the cultivar development process resulted in a steady rise in this yield component across the 1950-2000 period. In contrast, seed size showed no response to year of release (Table 2).

Pod number per area was related to yield in a manner similar to that for seed number per area (Table 1). Among the six cultivars having the greatest level of pod number per area, five of them were also top-ranking for seed number per area and yield. Seed per pod, the other

Table 4.1. Yield and yield components of 18 public southern soybean cultivars released between 1950-2000 grown near Baton Rouge, LA, and averaged across two years, 2007 and 2008.

Cultivars	Mat. group	Year of release	Yield kg ha ⁻¹	Seed number no. m ⁻²	Seed size g per 100 seeds	Pod number no. m ⁻²	Seed per pod no. m ⁻²
Graham	V	1996	3978 [‡]	2835 [‡]	12.84 [‡]	1404 [‡]	2.02
Anand	V	1999	3813 [‡]	2712 [‡]	12.82 [‡]	1260 [‡]	2.20 [‡]
Pace	V	1996	3669 [‡]	2604 [‡]	13.04 [‡]	1334 [‡]	1.95
Musen	VI	1997	3529 [‡]	2774 [‡]	11.73 [‡]	1106 [‡]	2.51 [‡]
TN-5-95	V	1997	3506 [‡]	2948 [‡]	11.00	1331 [‡]	2.26 [‡]
Clifford	V	1994	3335 [‡]	1912	14.02 [‡]	1023 [‡]	2.18 [‡]
Ransom	VII	1970	3079	2303	12.65 [‡]	8.72	2.29 [‡]
Bragg	VII	1963	2954	2081	13.36 [‡]	955	2.19 [‡]
Mack	V	1971	2759	1804	14.14 [‡]	751	2.42 [‡]
Lyon	VI	1993	2733	2152 [‡]	11.60	898	2.39 [‡]
Hutton	VIII	1972	2593	1595	14.55 [‡]	763	2.15
Essex	V	1972	2536	2109	10.94	1011 [‡]	2.11
Jackson	VII	1953	2494	1690	13.78 [‡]	871	2.06
Semmes	VII	1965	2445	1582	13.39 [‡]	835	2.06
Lee	VI	1954	2392	1784	11.88 [‡]	790	2.27 [‡]
Tracy	VI	1973	2295	1847	11.48	932	2.01
Dyer	V	1967	2273	1674	12.19 [‡]	681	2.46 [‡]
Hardee	VIII	1962	1909	1281	13.43 [‡]	694	1.83
CV (%)			15.0	16.1	9.3	19.3	7.2

[‡] Indicates cultivar means are similar according to Turkey's test at the 0.05 probability level.

Table 4.2. Yield and yield components of 18 public southern soybean cultivars released between 1950-2000 grown near Baton Rouge, LA, and averaged across two years, 2007 and 2008.

Cultivars	Mat. Group	Year of release	Yield kg ha ⁻¹	Rep. node number no. m ⁻²	Pod per rep. node no. m ⁻²	Node number no. m ⁻²	Percent rep. node number %
Graham	V	1996	3978 [‡]	474 [‡]	3.0	569 [‡]	83.2 [‡]
Anand	V	1999	3813 [‡]	391 [‡]	3.3	473 [‡]	82.7 [‡]
Pace	V	1996	3669 [‡]	500 [‡]	2.7	618 [‡]	81.2 [‡]
Musen	VI	1997	3529 [‡]	396 [‡]	2.8	571 [‡]	70.7
TN-5-95	V	1997	3506 [‡]	491 [‡]	2.7	564 [‡]	87.7 [‡]
Clifford	V	1994	3335 [‡]	242	3.6	290	84.1 [‡]
Ransom	VII	1970	3079	314	3.4	447 [‡]	75.9 [‡]
Bragg	VII	1963	2954	342 [‡]	2.8	484	69.9
Mack	V	1971	2759	300	2.5	373	80.9 [‡]
Lyon	VI	1993	2733	320	3.1	397	83.1 [‡]
Hutton	VIII	1972	2593	277	3.0	415 [‡]	67.4
Essex	V	1972	2536	321	3.2	373	86.5 [‡]
Jackson	VII	1953	2494	249	3.6	347	72.1
Semmes	VII	1965	2445	337	2.6	473 [‡]	73.6
Lee	VI	1954	2392	285	3.2	351	82.2 [‡]
Tracy	VI	1973	2295	408 [‡]	2.5	538 [‡]	78.8 [‡]
Dyer	V	1967	2273	246	2.8	322	77.2 [‡]
Hardee	VIII	1962	1909	265	2.7	345	74.5 [‡]
CV (%)			15.0	20.3	19.1	21.4	7.2

[‡] Indicates cultivar means are similar according to Turkey's test at the 0.05 probability level.

secondary yield component, was not significantly affected by cultivar, and was not significantly correlated with seed number per area, year of release or yield (Table 3). In contrast, seed number and pod number per area were strongly linearly correlated ($R^2=0.88$, Table 3, $P<0.0001$). Pod number per area was linearly correlated with year of release ($R^2=0.60$, $P<0.001$, Table 3) and was significantly correlated with yield ($R^2=0.78$, $P<0.0001$, Table 3).

Among tertiary yield components affecting pod number per area (reproductive node number per area and pod per reproductive node), and quaternary yield components affecting reproductive node number per area (node number per area and percent reproductive nodes), reproductive node number per area and node number per area were most important in affecting yield increases (Tables 2 and 3). Among the six top-yielding cultivars, five also showed greatest levels for reproductive node and/or node number per area. In contrast, pod per reproductive node and percent reproductive nodes were not linked with the higher-yielding cultivars (Table 2). Pod number per area was strongly correlated with reproductive node number per area ($R^2=0.81$, $P<0.0001$; Table 3), but was not significantly correlated with pod per reproductive node (Table 3). Reproductive node number per area was also related to year of release ($R^2=0.52$, $P<0.001$, Table 2), but not as strongly compared to seed and pod number per area. Reproductive node number per area, in turn, was regulated much more strongly by node number per area ($R^2=0.89$, $P<0.0001$, Table 3) than percent reproductive nodes (Table 3, NS). In addition, node number per area was significantly correlated with yield ($R^2=0.46$, $P<0.01$) and year of release ($R^2=0.41$, $P<0.01$, Table 3), whereas percent reproductive nodes was not linked with either parameter.

Table. 4.3. Linear correlations between yield with yield components, year of release with yield and yield components, and between yield components themselves for 18 southern public soybean cultivars released between 1950-2000 and grown near Baton Rouge, LA across two years, 2007 and 2008.

Dependent variable	Independent variable	R ²	F value	P value
Yield	Seed no. per area	0.84	86.2	†
Yield	Seed size (2007)	0.04	0.72	NS
Yield	Seed size (2008)	0.37	9.54	NS
Yield	Pod no. per area	0.78	60.07	†
Yield	Seed per pod	0.009	0.16	NS
Yield	Rep. node no. per area	0.53	18.1	***
Yield	Pod per rep. node	0.03	0.46	NS
Yield	Node no. per area	0.46	14.0	**
Yield	Percent rep. node	0.10	1.89	NS
Year of release	Yield	0.68	34.0	†
Year of release	Seed no. per area	0.69	37.1	†
Year of release	Seed size	0.15	2.97	NS
Year of release	Pod no. per area	0.60	24.0	***
Year of release	Seeds per pod	0.02	0.34	NS
Year of release	Rep. node no. per area	0.52	17.7	***
Year of release	Pods per rep. node	0.01	.01	NS
Year of release	Node no. per area	0.41	11.3	**
Year of release	Percent reproductive nodes	0.21	4.39	NS
Seed no. per area	Pod no. per area	0.88	118.9	†
Seed no. per area	Seed per pod	0.04	0.41	NS

(Table 4.3 continued)

Pod no. per area	Rep. node no. per area	0.81	69.8	†
Pod no. per area	Pod per reproductive node	0.01	0.07	NS
Rep. node no. per area	Node no. per area	0.89	134.1	†
Rep. node no. per area	Percent reproductive node	0.17	3.29	NS

** , *** , † Indicate significance at the 0.01, 0.001, and 0.0001 probability levels, respectively.
NS=not significant

Because phenotypic and genotypic path analyses were similar (Tables 4 and 5), only the genotypic analyses will be described. Genotypic path analyses support the importance of node number, pods, and seed in the yield formation process described above. The direct genotypic path effect for seed m^{-2} on yield was over twice as great compared with that for seed size (1.22 vs. 0.47). Indirect genotypic path analyses revealed a strong negative effect of seed size on yield through seed m^{-2} (-0.74) which negated any beneficial direct path effect of seed size on yield. In contrast, seed m^{-2} had only a moderate indirect negative effect (-0.29) on yield through seed size. This accounted for the high genotypic correlation between seed m^{-2} and yield. The direct genotypic path effect of pod m^{-2} on seed m^{-2} was three times greater than that for seed per pod (0.97 vs. 0.32). Negative genotypic indirect effects between the two yield components on seed m^{-2} were small indicating little yield component compensation.

The genotypic direct path effect for reproductive node m^{-2} on pod m^{-2} was almost three times greater compared to that for pod per reproductive node (Table 5). Whatever beneficial effect of pod per reproductive node on pod m^{-2} was negated by a negative indirect effect of pod per reproductive node on pod m^{-2} through reproductive node m^{-2} . Thus, genotypic correlation between reproductive node m^{-2} and pod m^{-2} was much greater (0.92, $P < 0.0001$) compared with pod per reproductive node (0.05, NS). The genotypic direct path effect of node m^{-2} on reproductive node m^{-2} was three

Table 4.4. Phenotypic correlations (r), direct path coefficients, and indirect path coefficients between (a) primary traits and yield; (b) secondary traits and seed m⁻²; (c) tertiary traits and pod m⁻²; and (d) quaternary traits and reproductive nodes for 18 soybean cultivars released between 1950 to 2000 and grown near Baton Rouge, LA for two years, 2007 and 2008.

(a) Primary trait	Phenotypic correlation (r) with yield	Phenotypic direct path effect of primary trait on yield	Phenotypic indirect path effect of primary trait on yield via:	
			Seed m ⁻²	Seed Size
Seed m ⁻²	0.89	1.15	–	-0.30
Seed size	-0.16	0.47	-0.63	–
Coefficient of determination R ² = 0.95		Residual effect=.05		
(b) Secondary trait	Phenotypic correlation (r) with seed m ⁻²	Phenotypic direct path effect of secondary trait on seed m ⁻²	Phenotypic indirect path effect of secondary trait on seed m ⁻² via:	
			Seed per pod	Pod m ⁻²
Seed per pod	0.14	0.35	–	-0.21
Pod m ⁻²	0.93	1.00	-0.07	–
Coefficient of determination R ² =0.98		Residual effect=.017		
(c) Tertiary trait	Phenotypic correlation (r) with pod m ⁻²	Phenotypic direct path effect of tertiary trait on pod m ⁻²	Phenotypic indirect path effect of tertiary trait on pods m ⁻² via:	
			Pod per rep. node	Rep. node m ⁻²
Pod per rep. node	0.15	0.47	-	-0.32
Rep. node m ⁻²	0.86	1.01	-0.15	–
Coefficient of determination R ² = 0.94		Residual effect=0.059		
(d) Quaternary trait	Phenotypic correlation (r) with rep. node m ⁻²	Phenotypic direct path effect of quaternary trait on rep. node m ⁻²	Phenotypic indirect path effect of quaternary trait on node m ⁻² via:	
			Node no. m ⁻²	Percent rep. node
Node no. m ⁻²	0.94	0.94	–	-0.003
Percent rep. node	0.30	0.31	-0.01	–
Coefficient of determination R ² =0.98		Residual effect=0.02		

Table. 4. 5: Genotypic correlations (r), direct path coefficients, and indirect path coefficient between (a) primary traits and yield; (b) secondary traits and seed m⁻²; (c) tertiary traits and pod m⁻²; and (d) quaternary traits and reproductive nodes for 18 soybean cultivars released between 1950 to 2000 and grown near Baton Rouge, LA for two years, 2007 and 2008.

(a) Primary Trait	Genotypic correlation (r) with yield	Genotypic direct path effect of primary trait on yield	Genotypic indirect path effect of primary trait on yield via:	
			Seed m ⁻²	Seed Size
Seed m ⁻²	0.93	1.22	–	-0.29
Seed Size	-0.28	0.47	-0.74	–
Coefficient of determination R ² = 0.99		Residual effect=0.01		
(b) Secondary Trait	Genotypic correlation (r) with seed m ⁻²	Genotypic direct path effect of secondary trait on seed m ⁻²	Genotypic indirect path effect of secondary trait on seed m ⁻² via:	
			Seed per pod	Pod m ⁻²
Seed per pod	0.24	0.32	–	-0.08
Pod m ⁻²	0.94	0.97	-0.03	–
Coefficient of determination R ² = 0.99		Residual effect=.004		
(c) Tertiary Trait	Genotypic correlation (r) with pod m ⁻²	Genotypic direct path effect of tertiary trait on pod m ⁻²	Genotypic indirect path effect of tertiary trait on pod m ⁻² via:	
			Pod per rep. node	Rep. node m ⁻²
Pod per rep. node	0.05	0.38	–	-0.33
Rep. node m ⁻²	0.92	1.03	-0.11	–
Coefficient of determination R ² = 0.98		Residual effect=0.024		
(d) Quaternary Trait	Genotypic correlation (r) with rep. node m ⁻²	Genotypic direct path effect of quaternary trait rep node m ⁻²	Genotypic indirect path effect of quaternary trait on node m ⁻² via:	
			Node m ⁻²	Percent rep. node
Node m ⁻²	0.95	0.90	–	0.05
Percent rep. node	0.47	0.31	0.16	–
Coefficient of determination R ² =0.99		Residual effect=0.006		

times greater than that for percent reproductive nodes. Since little yield component compensation occurred between these components, the genotypic correlation of node m^{-2} with reproductive node m^{-2} was much greater (0.95, $P < 0.0001$) relative to that for percent reproductive nodes (0.47, $P < 0.05$).

4.4 Discussion

Increased yield through cultivar development for entries in this study was controlled by the following yield components: node and reproductive node number per area, pod number per area, and seed number per area. The remaining yield components studied (seed size, seed per pod, pod per reproductive node, and percent reproductive node) showed little involvement in yield formation. Evidence for this conclusion rests on three bodies of evidence: correlation analyses between yield with individual yield components; correlation of yield components with year of release; and sequential genotypic correlation and path analyses between yield and yield components at the primary, secondary, tertiary, and quaternary yield formation levels. Yield was significantly linearly correlated with seed number per area, pod number per area, reproductive node number per area, and node number per area (Table 3). In contrast, yield was not correlated with seed size, seed per pod, pod per reproductive node, or percent reproductive node.

Similarly, the four yield components correlated with yield also were significantly linearly correlated with year of release, indicating that, along with yield, plant breeders were indirectly selecting for these parameters as they selected for higher yielding cultivars. Lastly, when yield formation is analyzed from the primary to quaternary levels, genetic correlations and path effects clearly demonstrate the greater importance of seed, pod, reproductive node, and node numbers relative to the other yield components (Table 5). These four yield components had greater genotypic correlations and direct path effects on the response variable relative to that for the

corresponding yield component at the same level of yield formation. Furthermore, such effects occurred without significant yield component compensation. That is, as genetic factors increased these yield components, there was little negative effect on the corresponding yield component. In contrast, positive direct effects of seed size and pod per reproductive node on response variables was negated by yield component compensation for seed m^{-2} and reproductive node m^{-2} , respectively.

The four yield components important in the yield formation process of this study have been recognized as responsive to dry matter accumulation and canopy photosynthetic activity (Board and Modali, 2005; Egli and Yu, 1991; Egli and Bruening, 2006). Yield components not demonstrating linkage to yield formation in the current study have also not demonstrated responses to either dry matter accumulation or canopy photosynthetic activity (Board and Modali, 2005). Coupled with results from chapter 4 showing the importance of dry matter for yield enhancement in cultivar development, yield formation in this study was controlled as shown in fig.4.6.

In summary, our results indicate that during the 1950-2000 periods, breeders involved with yield improvement of southern public cultivars have been inadvertently selecting for greater dry matter production and the associated increases in nodes, pods, and seeds which result in the greater yield. Our results agree with reports that yield enhancement through cultivar development is linked to greater seed number per area (Frederick et al., 1991; DeBruin and Pedersen, 2009). Results from the current study help explain how seed number is enhanced during cultivar development, a finding not previously reported. Our findings disagree with those reporting seed size to be more important for yield increases during cultivar development (Specht and Williams, 1984; Gay et al., 1980; Cui and Yu, 2005). This divergence of results could

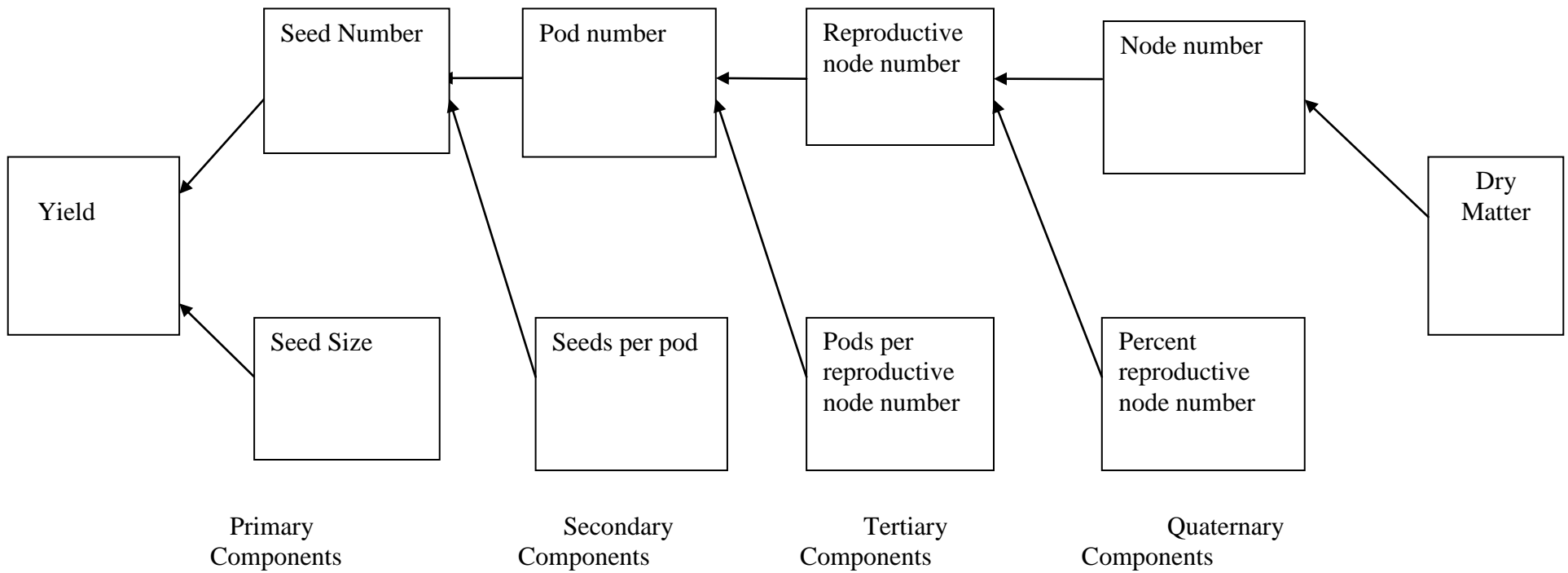


Fig.4.2. Diagram describing relationships between dry matter accumulation and yield components contributing to yield improvement during the cultivar development process for selected southern public cultivars released during the 1950-2000 period.

possibly be due to different inadvertent selection methods for greater yield operating in different germplasms and/or regions.

The aforementioned mechanism for yield enhancement during cultivar development is strikingly similar to environmentally-induced changes in soybean yield outlined in Board and Modali (2005). In that study, yield variation induced by changes in planting date, row spacing, plant population, and waterlogging stress were also shown to be regulated by dry matter accumulation. Node number per area, reproductive node number per area, pod number per area, and seed number per area all responded to increasing dry matter in an asymptotic relationship that plateaued at about 600 g m^{-2} [dry matter (R5)]. Similar to findings in the current study, yield was linked with these same four yield components. Thus, similar yield formation mechanisms were shown to operate on both environmental and genetic levels.

Total dry matter and/or yield components identified in this study as controlling yield formation are potential indirect selection criteria for cultivar improvement. Such criteria would facilitate identifying desirable inbred lines for further evaluation. Because of the many lines involved in breeding programs, such criteria would need to be rapid, as well as accurate. Since yield increases with cultivar development were linked with dry matter accumulation, one possible criterion would be vegetative dry matter (R5). This measures the maximum level of vegetative dry matter accumulated by the crop, and has been shown to be a reliable yield predictor (Board and Modali, 2005). The conventional method for determination of dry matter (R5) involves harvesting plants at R5, removing pods, drying the sample, and then weighing. Such a method is too time consuming and arduous to use as an indirect selection criterion.

However, vegetative dry matter (R5) can be accurately predicted using a multiple regression equation using days to R5 and days to canopy closure (95% light interception) (Board, unpublished data):

$$\text{Dry Matter (R5)} = -20.1 - 5.89(\text{days to canopy closure}) + 13.66(\text{days to R5})$$

High R^2 (0.91, $P < 0.0001$) between predicted and observed dry matter (R5) have been demonstrated in a 1:1 (y-intercept=0) linear regression. Both parameters can be easily, rapidly, and accurately obtained for a large number of inbred lines. Canopy closure is when the row area subtending an individual plant row (area extending from the plant row to the interrow midpoints in both directions) is covered by leaves. The R5 date is easily recognized by 50% of the plants in the row having a seed 3 mm long among the top 4 main stem nodes (Fehr and Caviness, 1977).

Other parameters identified as possible indirect selection criteria are pod and seed number per area. Because determination of these yield components is time consuming, they would not be suitable candidates as indirect selection criteria. Estimates of pod load are used as a selection criterion for space-planted F_4 progeny in some cultivar development programs (Tanner et al., 2001). However, objective determination of pod number is not done. Rather, progeny are rated visually by numerical scores that provide a subjective comparative estimate of pod number (personal communication, D.J. Hume). Reproductive node number is a possible candidate as an indirect selection criterion. Reproductive node number per plant is not large, averaging about 25 per plant for soybean grown at a normal plant population under optimal conditions. (Board and Modali, 2005). Also, they are easily observable and can be tabulated with an electronic counter. Assuming inbred lines were grown at similar plant populations to avoid confounding [greater plant population results in fewer reproductive nodes per plant (Carpenter and Board, 1997)], recordings could be made directly in the field on a sample of plants from each inbred line.

Another advantage for reproductive node counts is that selection can be done at mid season without waiting until maturity. In conclusion, results from the study do provide potential indirect selection criteria for assessing yield potential of inbred lines in a cultivar development breeding program.

4.5 References

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Chapter 5 Summary and Conclusion

The results of the study clearly indicated yield components and growth dynamic parameters responsible for yield improvement during the cultivar development process of the last five to six decades among southern public soybean cultivars. The following conclusions were made:

1. Across the 18 cultivars in our study, the average gain from genetic selection was 30.4 kg ha⁻¹yr⁻¹.
2. Although newer cultivars (those released during the 1990's) had fewer days from emergence to physiological maturity (R7) compared with the older cultivars (those released 1953-1973), their yield was 39% greater (3509 vs. 2521 kg ha⁻¹).
3. Yield increases in new vs. old cultivars were not strongly related to any phenological parameter (days to R5 or length of seed filling period) or lodging.
4. Most of the yield increase was due to greater TDM (R7) accumulation (71%) and the remainder to increased HI (29%). About 2/3 of the greater TDM (R7) for new vs. old cultivars was caused by greater seed yield, and the remainder 1/3 was due to greater dry matter accumulation by R5.
5. Based on numerical values, correlation and regression analyses, and path analysis, yield increases due to cultivar development were caused by greater node and reproductive node numbers per area, pod number per area and seed number per area. In contrast, seed size, seed per pod, pod per reproductive node, and percent reproductive node number showed little involvement in yield formation among the cultivars in this study.

Results can aid plant breeders by providing indirect selection criteria for progeny selection in a breeding program. Use of such criteria can make cultivar development more

efficient through greater accuracy for identifying promising genotypes, as well as reduced time, labor, and resources. Among the parameters identified as important in the yield formation process, TDM (R5) and reproductive node number per area are the most practical to use as putative indirect selection criteria. Both parameters can be determined quickly and accurately. Also, they can be assessed at mid season (50-60 days after emergence) without having to grow field trials until maturity.

VITA

Charanjit Singh Kahlon was born in Gurdaspur, Punjab, India. He attended the St. Thomas, Baring and Senior Secondary School, India. He studied at the Guru Nanak Dev University, India, and graduated with a bachelor of agriculture from 1997 to 2002. He went to the University of Agricultural Sciences, Bangalore, for a master's in agronomy from 2002-2005. He was admitted into the doctoral program in the School of Plant, Environmental and Soil Sciences at Louisiana State University, during fall 2006. He was married to Amandeep Kaur on 28th December, 2007. He completed graduate studies in July, 2010, and will receive the degree of Doctor of Philosophy in December 2010.