

# Genetic Coefficients in the CROPGRO–Soybean Model: Links to Field Performance and Genomics

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## ABSTRACT

Crop growth models are tools with valuable uses in research synthesis and crop management. This paper discusses genetic coefficients in the CROPGRO–Soybean model in terms of definitions, implications for genetic improvement, relationships to field performance, and linkage to genomics. As used in crop models, genetic coefficients are mathematical constructs designed to mimic the phenotypic phenotypic outcome of genes under different environments to influence: (i) life cycle including fractional allocation to different phases, (ii) photosynthetic, (iii) vegetative, (iv) rooting, and (v) reproductive processes. Model sensitivity analyses was used to hypothesize genetic coefficients of soybean [*Glycine max* (L.) Merr.] and impact on field performance. Yield improvement from increased leaf photosynthesis was shown to be small if coupled to specific leaf weight. Yield improvement with longer seed filling duration was enhanced by traits such as slower N mobilization to sustain leaf photosynthesis or by genetic traits and management factors allowing adequate leaf area index before seed fill. Yield improvement under water-deficit appeared feasible from rate of root-depth increase, shift in root profile, and a slow senescence trait. Modeled genetic coefficients showed mostly additive effects on yield when evaluated in combinations; and combinations of minor changes gave yield increases of 13 to 17%, comparable to recent genetic improvement. More than additive effects occurred under good crop management or under projected rise in global CO<sub>2</sub>. Information from genomics, physiology, and yield performance trials can be used to derive genetic coefficients for crop models. Interaction of molecular geneticists, physiologists, and crop modelers is needed to facilitate the translation of genetic knowledge to modes of action, and finally to integrated field performance under multiple stress environments.

CROP GROWTH models integrate C, N, and water balances of growth processes over the entire life cycle, predicting growth and yield in response to management and environment. They account for climatic and resource limitations that may influence yield response to genetic traits. Increasingly, these tools are being used in research synthesis and decision support of crop management (e.g., Egli and Bruening, 1992; Hook, 1994; Boote et al., 1996, 1997b, 2001; Hammer et al., 1996; Jame and Cutforth, 1996; Sexton et al., 1998; Paz et al., 1999, 2001; Ruiz-Nogueira et al., 2001). With further improvement in definition and specificity of modeled genetic coefficients, crop models can also be used to

assess the value of genetic traits on crop performance under differing environments and management (Duncan et al., 1978; Landivar et al., 1983; Boote and Jones, 1986; Salado-Navarro et al., 1986a, 1986b; Elwell et al., 1987; Boote and Tollenaar, 1994; Hammer et al., 1996; Boote et al., 2001). Relative to crop models, genetic coefficients are mathematical constructs that are designed to mimic the phenotypic outcome of genes under different environments. The goal of this paper is to discuss genetic coefficients in crop models, to hypothesize effects of varying genetic traits on field performance, and to discuss linkage/derivation of modeled genetic coefficients from agronomic field trials, physiological measurements, and knowledge of gene structure. We propose cooperation among geneticists, physiologists, and modelers to derive these genetic coefficients from information coming from the rapidly developing field of genomics.

The framework for this paper is built around three perspectives of modeling genetic coefficients: (i) crop modeling, to identify the theoretical basis for specific beneficial traits, considering conservation of mass and energy; (ii) crop physiology/agronomy, to test and evaluate traits; and (iii) genetics/molecular biology, to identify genes. We suggest the need for spirited interactions between these three types of activities to make good progress. Shorter et al. (1991) proposed a collaborative role and a crop modeling approach, for breeders, physiologists, and modelers to select genotypes adapted for target environments. To adequately model a specific gene, the crop modeler must know the physiological mode of action (expression). This requires information or feedback from physiologists or molecular biologists. A geneticist may find many pieces of DNA (genes), but needs to know the physiological mode of action (when, what environments, interactions with other genes, etc.) to determine whether the gene is a desirable one to use in creating a better cultivar for multiple environments. Interaction of physiologists, and help from crop modelers, is needed to integrate effects of those traits to final performance over multiple environments considering limits of resources. The physiologist may be able to take a limited number of measurements of processes on a limited number of genetic strains, but needs the help of geneticists to know the genes involved, and advice from geneticists and modelers on where to focus limited measurement efforts.

**Abbreviations:** G × E, genotype by environment; HI, harvest index; LAI, leaf area index; MG, maturity group; PTD, photothermal day; QTL, quantitative trait loci; SLN, specific leaf nitrogen; SLW, specific leaf weight; SWFAC, ratio of root water uptake to crop transpirational demand; WUE, water use efficiency.

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### **Lessons from Physiology: Some Processes Are Common for All Crops and May Not Need Description of Genetic Coefficients**

Before discussing genetic coefficients, we need to consider which processes are common (unchanged or conserved) for all crops/species and which are not. Research on crop physiology and basic growth patterns can provide information about where we need to make genetic coefficients different among cultivars and where traits are common for all plants or at least within a species. The modeled crop should mimic those basic processes that are common and present in all crops or broad classes of crops. For example, the processes of photosynthetic electron transport, rubisco enzyme kinetics, and mitochondrial respiration are similar across crops (basic process is conserved). Membrane transport processes are mostly the same, except where changes in fatty acid composition cause differences in temperature sensitivity. Likewise, electron transport in mitochondria or chloroplast membranes is basically similar across all species. Rubisco enzyme functional traits are nearly similar in all terrestrial species, causing similar CO<sub>2</sub> compensation point behavior in all C<sub>3</sub> species, but altered in presence of the C<sub>4</sub> cell type/enzyme complex that concentrates CO<sub>2</sub> to rubisco (Farquhar et al., 1989). Thus, it may not be necessary to model genetic coefficients below a level where processes really are the same. We suggest that differences among species or cultivars in leaf-level photosynthesis, for example, are expressed in the more gross features, such as the amount of rubisco enzyme or amount of electron transport components per unit leaf area. These are associated with, and can be modeled primarily as, different leaf thickness (SLW, specific leaf weight) or N concentration.

### **Lessons from Crop Modeling: Genetic Coefficients Must Honor the Laws of Physics: Conservation of Mass and Energy**

The modeled (or real) crop must honor the physics of water, C, N, and energy balance at a process level, as well as pleiotropic costs related to physical structure or composition. All crop species, regardless of genetics, must honor physical aspects such as satisfying energy balance and water balance, i.e., trading CO<sub>2</sub> entry for water vapor escape. This puts limits on finding *the gene* for drought avoidance or high water-use-efficiency; because plants cannot fix CO<sub>2</sub> without transpiring water. A gene that would increase stomatal closure to decrease transpiration would also decrease CO<sub>2</sub> gain and productivity. Also, species taking this approach must withstand the higher foliage temperature associated with lower transpiration. Modifications on trading CO<sub>2</sub> entry for water vapor loss are possible, but they must be explainable, such as the C<sub>4</sub> pathway, which has a steeper gradient for CO<sub>2</sub> entry (concentrating shuttle that drops the intercellular CO<sub>2</sub>) while not changing the gradient for water vapor loss. In C<sub>3</sub> species, minor effects are possible, such as a slightly larger CO<sub>2</sub> gradient attributable to increased rubisco enzyme per unit area. Such increases may be caused by an explainable larger-scale

feature, such as higher leaf N concentration at the same SLW, increased SLW at same leaf N concentration, or shift to increased rubisco per unit of total leaf N. These features have their own costs, i.e., plants must take up more total N to increase leaf N concentration, or the increased SLW causes smaller leaves or smaller leaf area per plant, thus resulting in less light interception. Many times, seemingly desirable features come with a set of physical constraints. Crop modeling, assisted by physiology, can place resource limits on expected gain from a given genetic trait or multiple combinations of them, for a range of environments limited in resources such as water, light, temperature, and available N.

Cooperation and feedbacks between physiology and crop modeling activities can help us learn the lesson that the modeled (or real) crop must honor the laws of physics and mass balance, i.e., assimilate sent to the roots is not available for growing leaves or producing seed yield. Likewise, there are pleiotropic costs, i.e., a crop can make thick leaves or roots, but at the cost of less leaf area or less total root length. Thick leaves would increase leaf photosynthesis, but at the cost of smaller leaf area and light interception. The modeled crop must mimic seasonal dynamics of C balance, N accumulation, and C and N mobilization/senescence that are observed in physiologists' experiments. If the model does not do this, the basic processes or traits may not be modeled correctly. Testing by comparison of modeled to observed growth patterns of different cultivars is crucial. It may not be necessary to invoke highly mechanistic or enzymatic explanations of genetic variation if, for example, the determinacy of leaf area expansion is not modeled correctly, or if leaf senescence is predicted incorrectly.

Crop modeling is still in a juvenile stage, particularly relative to adequately assigning genetic coefficients (cultivar traits) within a species. Most crop modelers have chosen to limit the number of genetic coefficients for several reasons: convenience (lack of exposure of models to cultivar comparisons), more pressing issues (it is more important to first improve model ability to mimic process responses to environment), by design (keep it simple), and lack of information on how traits or processes may differ among genotypes. It is prudent to keep the modeled genetic coefficients initially relatively simple for the more important features, and to add more specific traits as evidence shows them necessary. Nevertheless, crop modelers generally recognize that present crop models inadequately address cultivar differences. Early efforts to link genetic coefficients of crop models to real genes were made by White and Hoogenboom (1996), Hoogenboom et al. (1997), and Yin et al. (1999).

### **Lessons from Genetics: What Genetic Coefficients are Needed**

Genetic research and genome mapping may be able to provide considerable information about when and where we need to create modeled genetic coefficients. In some cases there is research to document the principle of one gene-one product; for example, where one gene leads to one specific change in a structure, an enzyme,

or a specific event in time. A convenient example of this is the daylength-sensitive genes, where presence or absence of one allele of a gene causes a precise shift in the flowering or maturity date (Cober et al., 1996). Such a situation would give valuable information for modeling the trait. Unfortunately, with more integrative responses (such as final yield), multiple gene causes are the norm. Genetic mapping for relationships to yield may reveal groups of quantitative trait loci (QTLs) for yield, but the individual gene contributions may be low. This is not surprising because yield is a strong function of environment. A group of QTLs positive for yield in one environment (and experiment), may be neutral or negative in another. A general message from molecular genetics is that the regulation of gene expression may be more important than the actual gene itself.

Genotype  $\times$  environment interaction is a favorite topic of plant breeders. Considering the limitations of resources and environment (via crop modeling) and understanding the physiological mode of action for different environments may help explain why a trait enhances yield in one environment, but not in another. For example, plant membranes handle water and solute flow in similar manners, but there may be membrane traits that lead to different reactions depending on environment. A higher percentage of unsaturated fatty acids in membranes of one cultivar could cause a somewhat lower base temperature for many processes, causing that cultivar to be more active in a cool climate (this would lead to  $G \times E$  effect, i.e., causing no difference in performance under optimum temperature, but better performance in a cool climate). However, membrane composition suited for cool climates may not be as suitable when the crop is exposed to a hot climate. In a second example, the value of early flowering for yield may depend on environment. Early flowering may be a valuable trait for yield in seasons where terminal drought limits resources in late season, or where cold temperature limits seed fill. But early flowering (and associated short life cycle) may limit yield potential for environments that have good water supply or remain warm. A crop simulation model can project this situation for multiple years of weather, i.e., determine long-term probabilities of benefit from a given trait.

### MODEL SENSITIVITY ANALYSES TO HYPOTHEZIZE GENETIC COEFFICIENTS AND EFFECTS ON FIELD PERFORMANCE

Before addressing the question of how knowledge of genetics can be translated into the genetic coefficients used in crop simulation models, it is appropriate to have a better understanding of how coefficients in crop models are presently used to mimic cultivar differences. One of the best ways to do that is to conduct model sensitivity analysis and explore how present model features can be varied to mimic differential gene effects. As we conduct model sensitivity analyses, it is important to know the reasonableness of a model in representing a physiological trait or mode of action. Crop simulation can provide

a quantitative evaluation of the value of a given trait in a target environment only if the physiological basis of the trait action is known and if physiological connections and required feedbacks are present (Hammer et al., 1996, 1999). One of the problems with model sensitivity analysis, especially for fairly simple models with few genetic coefficients, is that one must make assumptions about how the model parameters represent genetic traits. One example of this is the use of a simple radiation-use-efficiency coefficient to represent the possibility that cultivars may vary slightly in leaf photosynthetic rate within a species. Is the change in photosynthesis associated with change in SLW, leaf N concentration, or increased rubisco per unit of leaf protein? Is there a feedback cost on the rest of the crop? Simple crop models lack the ability to look at individual causes, let alone the assumption that radiation use efficiency is a constant for the species. In studying cultivar variation within a species, it is better to use crop models that have a reasonable degree of mechanistic detail to mimic genetic traits.

### A. Genetic Coefficients in the CROPGRO Model

In this paper, we conduct sensitivity analyses with the CROPGRO-soybean model to mimic cultivar differences. Yield consequences of cultivar variation in photosynthesis, life cycle allocation to different phases, vegetative and partitioning attributes, reproductive attributes, and rooting traits are illustrated. Table 1 lists genetic coefficients and definitions as used in CROPGRO V3.5 (Boote et al., 1998a). These listed traits are complex and influenced by many genes; thus, going to the level of true genomic analysis would require a more detailed approach than is presently used in CROPGRO. Cultivar differences in CROPGRO are created by 15 cultivar traits and by a subset of ecotype traits that vary less often. The cultivar traits in Table 1 include two daylength sensitivity traits (CSDL, PPSEN), five important life cycle "phase" durations (EM-FL, FL-SH, FL-SD, SD-PM, and FL-LF), light-saturated single leaf photosynthesis ( $P_{\max}$ , defined at a given specific leaf weight, N concentration, temperature, and  $CO_2$ ), some vegetative traits (SLAVR, SIZELF, XFRT), and some reproductive traits (WTPSD, SFDUR, SDPDV, and PODUR). There are 19 traits in the ecotype file; these were placed there because they vary less, such as thermal time to emergence and V1 stage. Table 1 includes five traits from the ecotype file that are used frequently to characterize cultivars (R1PRO, FL-VS, THRESH, SDPRO, and SDLIP). In addition, CROPGRO has a species file that contains traits characterizing each species, but are constant for cultivars within a species. For some hypothetical simulations, we varied some of these species traits as potential candidate cultivar traits, such as rate of root depth increase or rate of leaf N mobilization. See Boote et al. (1998a, 1998b) for further details on the CROPGRO model and how respective cultivar and ecotype coefficients work. The CROPGRO model has been widely evaluated for its ability to predict growth and yield of soybean under a wide range of conditions



**Table 1.** Cultivar coefficients for the CROPGRO model, value ranges typical for soybean.

Trait	Range	Definition of trait
ECO#	SB0301	Code for the ecotype to which this cultivar belongs
CSDL	14.6–11.8	Critical Short Day Length below which reproductive development progresses with no daylength effect (for short day plants) (h)
PPSEN	0.129–0.349	Slope of the relative response of development to photoperiod with time (positive for short day plants) (1/h)
EM-FL	15.5–23.5	Time between plant emergence and flower appearance (R1) (PTD) <sup>†</sup>
FL-SH	5.5–10.0	Time between first flower and first pod (R3) (PTD)
FL-SD	12.0–16.0	Time between first flower and first seed (R5) (PTD)
SD-PM	28.5–38.0	Time between first seed (R5) and physiological maturity (R7) (PTD)
FL-LF	15.0–26.0	Time between first flower (R1) and end of leaf expansion (PTD)
$P_{\max}$	0.92–1.17	Maximum leaf photosynthesis rate at 30°C, 350 vpm CO <sub>2</sub> , and high light (mg CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )
SLAVR	355–400	Specific leaf area of cultivar under standard growth conditions (cm <sup>2</sup> g <sup>-1</sup> )
SIZELF	140–200	Maximum size of full leaf (three leaflets) (cm <sup>2</sup> )
XFRT	1.00	Maximum fraction of daily growth that is partitioned to seed + shell
WTPSD	0.15–0.22	Maximum weight per seed (g)
SFDUR	20–25	Seed filling duration for pod cohort at standard growth conditions (PTD)
SDPDV	1.9–2.5	Average seed per pod under standard growing conditions (no. pod <sup>-1</sup> )
PODUR	8.0–14.0	Time required for cultivar to reach final pod load under optimal conditions (PTD)
Frequently used important traits from ECO file		
ATOP	1.0	Maximum shift of partitioning to roots under water deficit
SENDAY	0.06	Fraction leaf mass abscised per day under severe water deficit
R1PRO	0.189–0.549	Increase in daylength sensitivity after anthesis, CSDL decreases by this amount (h)
FL-VS	9.0–26.0	Time from first flower to last leaf on main stem (PTD)
THRESH	76–79	The maximum ratio of [seed/(seed+shell)] at maturity. Causes seed to stop growing as their dry weight increases until shells are filled in a cohort.
SDPRO	0.37–0.43	Fraction protein in seeds [kg (protein) kg <sup>-1</sup> (seed)]
SDLIP	0.18–0.22	Fraction oil in seeds [kg (oil) kg <sup>-1</sup> (seed)]

<sup>†</sup> PTD, photothermal days, comparable to calendar days if at optimum temperature and <CSDL.

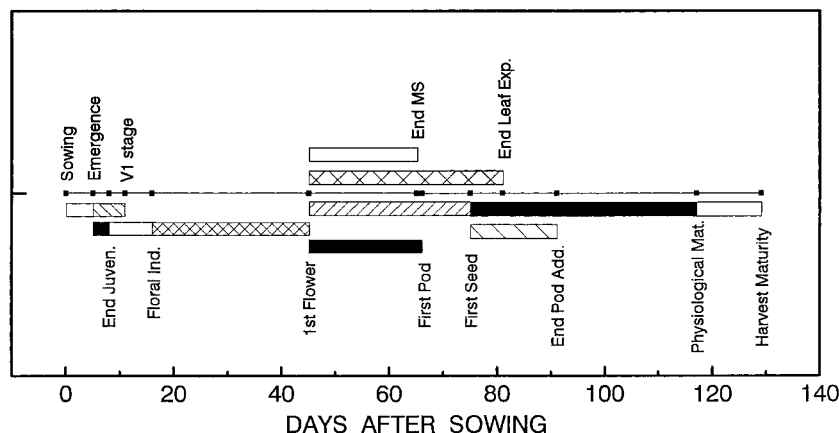
(Boote et al., 1997a; Sexton et al., 1998; Sau et al., 1999). It has been used to simulate effects of management (Boote et al., 1996, 1997a) and global climate change (Boote et al., 1997b).

## B. Yield Potential Associated with Best Fit of Life Cycle

Variation in life cycle and duration of different phases is perhaps the most important genetic variation contributing to yield potential of different cultivars. These cultivar features include the photothermal day durations of the different life cycle phases (defined under daylengths that allow most rapid progress), with consideration of daylength-sensitivity genes that slow the rate of progress. The CROPGRO-legume model considers 13 phases in the crop life cycle as shown in the timeline in Fig. 1. Some of these are only temperature-sensitive, but for soybean, most phases are sensitive to both temperature and daylength (Jones et al., 1991). Researchers have

frequently observed time to anthesis (first flower) and maturity as affected by daylength and temperature, but have often ignored intermediate phase durations. The daylength sensitivity is expressed in CROPGRO as two parameters: critical short daylength (CSDL), below which rate of progress is maximum; and PP-SEN, the slope of decline in rate of progress as daylength becomes longer than CSDL. There is a third parameter that describes a shift offset (up to 1 h) in critical short daylength after anthesis (R1PRO), proposed initially by Piper et al. (1996a, 1996b). Basically, this feature makes rate of development slower after anthesis than before anthesis, which these authors found necessary, especially for higher maturity group soybean.

These daylength-sensitivity and life cycle coefficients (in CROPGRO-soybean) have not yet been linked to specific genes because the mode of action is not completely understood; nevertheless, knowledge of the maturity genes in soybean ( $E_1$ ,  $E_2$ ,  $E_3$ ,  $E_4$ ,  $E_5$ , and their



**Fig. 1.** Timeline of life cycle phases as predicted by the CROPGRO model for MG 7 soybean sown 12 June 1984 at Gainesville, FL (29°40' N lat). Reprinted from Boote et al. (1998a) with permission.

**Table 2.** Effect of soybean maturity group (MG) and five genetic coefficients on days to maturity and yield for crops grown under rainfed conditions in Gainesville, FL, and Ames, IA.†

MG	Cultivar parameters used in model					Florida simulation		Iowa simulation	
	CSDL	PPSEN	EM-FL	FL-SD	SD-PM	Maturity	Yield	Maturity	Yield
	h	d h <sup>-1</sup>	PTD‡			d	kg ha <sup>-1</sup>	d	kg ha <sup>-1</sup>
00	14.35	0.148	16.0	12.0	30.0	70.5	842	93.3	1976
0	14.10	0.171	16.8	13.0	31.0	73.7	916	100.7	2395
1	13.84	0.203	17.0	13.0	32.0	77.2	984	108.8	2764
2	13.59	0.249	17.4	13.5	33.0	84.3	1108	121.1	3234
3	13.40	0.285	19.0	14.0	34.0	94.2	1398	134.7	3327
4	13.09	0.294	19.4	15.0	34.5	107.9	1984	151.1§	2994
5	12.83	0.303	19.8	15.5	35.0	120.0	2261	165.5¶	2215
6	12.58	0.311	20.2	16.0	35.5	132.7	2572	#	
8	12.33	0.320	20.8	16.0	36.0	145.0	2655	#	
8	12.07	0.330	21.5	16.0	36.0	159.3	2785	#	
9	11.88	0.340	23.0	16.0	36.5	170.2	2660	#	

† Crops were planted on Day 123 at 30 plants m<sup>-2</sup> and grown under rainfed conditions, using historical weather at each site (1978–1987 in Florida, and 1980–1996 in Iowa). Critical short daylength (CSDL), photoperiod sensitivity (PPSEN), and photothermal days (PTD) from emergence to flowering (EM-FL), flowering to first seed (FL-SD), and first seed to physiological maturity (SD-PM) are given for each MG, as used by the CROPGRO-soybean model. Photothermal day requirement to emergence is 3.6 d.

‡ PTD = photothermal days, comparable to calendar days if at optimum temperature and <CSDL.

§ Freeze damage in 2 of 17 years.

¶ Freeze damage in 7 of 17 years.

# Freeze damage in 17 of 17 years and maturity not reached.

recessive alleles) and *Dt*, *dt* genes for indeterminate and determinate growth habit may have advanced sufficiently (Cober et al., 1996) to allow this in the near future. Common bean (*Phaseolus vulgaris* L.) has a somewhat similar set of maturity genes. White and Hoogenboom (1996) and Hoogenboom et al. (1997) successfully demonstrated the ability of CROPGRO's cultivar coefficients to mimic specific combinations of four genes affecting photoperiod sensitivity (*Ppd/ppd*, *Hr/hr*), development rate before flowering (*Fd/fd*), and development rate to flowering, first pod, and first seed appearance as well as indeterminacy (*Fin/fin*) of common bean. This model explained 75% of the variation in days to flower and 68% of variation in days to maturity of common bean grown in 14 environments.

Soybean cultivars in the USA have been broadly classified into maturity groups (MG) from 000 to 12, based primarily on their time to harvest maturity in trials conducted at latitudes from north to south in the USA. Most of the effect on life-cycle duration is caused by differential sensitivity to photoperiod (Cregan and Hartwig, 1984; Grimm et al., 1993, 1994). Table 2 shows critical short daylength values, photoperiod sensitivity slopes, and photothermal day requirements to complete life cycles for MG 00-9 soybean cultivars as solved from experimental data (Grimm et al., 1993, 1994). Data on flowering and maturity dates were collected for cultivars within each MG class, all cultivars being grown at locations from Minnesota to Puerto Rico, to expose them to a wide range of daylengths and temperatures. Soybean cultivars in MG 00 have shorter basic life phases (EM-FL, FL-SD, SD-PM in Table 2) and are much less sensitive to daylength (higher CSDL, lower PPSEN in Table 2). These are grown at high latitudes such as Canada, while MG 10 to 12 are grown near the equator. Cultivars grown in the southern USA and the tropics have longer basic life cycle phases and greater daylength sensitivity. Photothermal days (PTD) in Table 2 can be thought of as comparable to calendar days, when the daylength is short (below CSDL) and temperature is optimum. For

MG 00 in Florida, calendar days nearly correspond to PTD, because temperature is warm and daylength is usually below 14.35 h (the CSDL for MG 00). Actual life cycle progress of all the cultivars is slower and days to maturity longer in Iowa because of both longer daylength and cooler temperatures (Table 2).

Table 2 illustrates how daylength-sensitivity traits affect maturity and soybean yield potential for two diverse sites (Iowa and Florida). Physiologists and breeders are well aware that the most important aspects of yield potential are coupled with life cycle differences that optimize the use of the season available at a given location (relative to limits of cold temperature in early spring and killing frost in fall in temperate regions, and relative to rainy season in all regions). Table 2 gives a practical illustration of how these daylength-sensitivity traits and phase durations lead to highly different simulated days to maturity and yield performance for MG 00-9 soybean cultivars grown in Florida and Iowa. The low-number MGs mature much too early in Florida and yield poorly. The optimum MGs in Florida for yield and most effective use of the season are MGs 6-9 (both in simulations and in actual production practice). In Iowa, the low-number MGs have a longer simulated life cycle and higher yield potential because of longer daylength and cooler temperature. The optimum MGs for Iowa for yield and effective use of the season are MGs 2-3, again corresponding to actual practice. The simulated MG 4 was reasonably high in yield, but suffered freeze damage in 2 of 17 seasons and MG 5 suffered freeze damage in 7 of 17 yr. It is important to note that freeze damage would be more frequent for later sowing dates, which occur in some years, thus mostly ruling out MG 4 for this site as well. MGs 5-12 are not suited for Iowa because they have shorter critical daylength and greater daylength-sensitivity, which prevents them from completing their life cycle before fall frost. While the CSDL and PP-SEN are the dominant traits affecting cultivar fit to latitude zones, notice that the basic photothermal day requirement for emergence to flowering (EM-FL),

flowering to beginning seed (FL-SD), and beginning seed to physiological maturity (SD-PM), also increase with successively higher MG classes. For example, when grown in Puerto Rico, a MG 4 cultivar will have a longer life cycle than MG 1, even though the daylength in Puerto Rico is below the 13.09 h critical value of MG 4.

### C. Yield Potential Related to Shifting of Phases within a Fixed Life Cycle

There are also yield potential differences among cultivars within a maturity-group class (having the same maturity date) that are attributed to other genetic traits. Such variations in yield potential may come from higher photosynthesis, better maintenance of photosynthesis during seed fill, and shift of life cycle phases from vegetative toward reproductive. There is evidence that yield improvement in soybean and other crops has come from longer reproductive phase durations, which lead to higher seed harvest index (Dunphy et al., 1979; Gay et al., 1980; Nelson, 1986; Smith and Nelson, 1986a, 1986b).

The CROPGRO genetic coefficients can be modified to shift a portion of the life cycle from vegetative to the reproductive phase. First, we can increase the phase from beginning seed to physiological maturity (SD-PM) to increase the phase allocated to seed filling. However, to have maturity be on the same date, we need to concurrently cause earlier flowering and earlier podset. To do this requires either increasing CSDL or decreasing the EM-FL phase to cause slightly earlier flowering (and earlier termination of vegetative expansion, which is linked to anthesis date). In addition, the third change is to shorten the time from first flower to first pod (FL-SH) and first seed (FL-SD) so pods are added sooner, and to shorten the period for pod addition (PODUR) to add pods more rapidly. While extending the phenological time from beginning seed to physiological maturity (SD-PM), we also need to ensure that single seed fill duration (SFDUR) is long enough to provide the capacity to use the whole growth phase.

We tested these possibilities with CROPGRO-soybean simulations at Ames, IA, using 17 yr of weather data (1980–1996), and starting with standard coefficients for the Williams 82 cultivar. As life cycle was shifted from vegetative to reproductive, soybean yield initially increased rapidly, but the response slowed and became nearly asymptotic at long filling periods (Fig. 2). While yield improvement above the standard seems possible, there is an asymptotic or limiting effect that occurs not too far above the cultivar standard genetic values. There are several reasons for this saturating or limiting effect. First, the earlier onset of reproductive growth causes lower LAI, which becomes progressively more limiting to photosynthesis and light interception (maximum LAI declined steadily from 7.2 to 3.8 over the range of filling periods shown in Fig. 2). This limitation to genetic improvement can be offset by narrow row spacing and higher plant population, as discussed later. Second, the longer reproductive phase causes the crop to rely on its existing (somewhat older) foliage for a longer period; thus, the leaf N concentration may be declining too

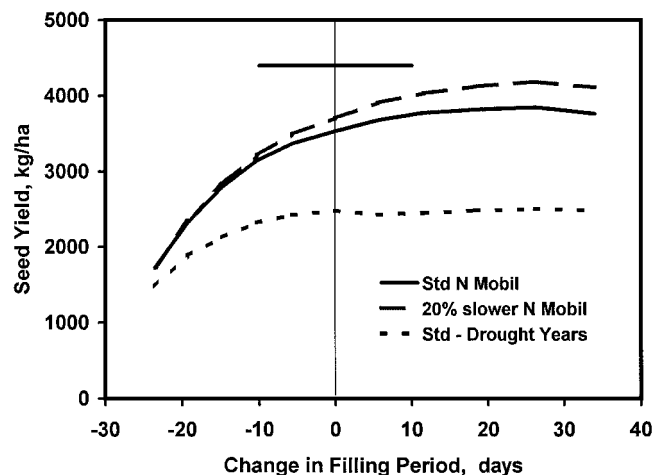


Fig. 2. Simulated soybean seed yield response to varying the filling period duration (beginning seed, R5, to physiological maturity) at Ames, IA, for 1980–1996 rainfed weather. Treatments include standard N mobilization and 20% slower N mobilization (both with 11 adequate rainfall years) and standard N mobilization (with 6 drought-prone years). Horizontal bar represents feasible genetic range for filling period duration. Reprinted from Boote et al. (2001) with permission.

much and decreasing photosynthesis. Creating a *stay-green* leaf trait (slower N mobilization) allowed better yield response to lengthening the reproductive phase (Fig. 2). We did this by slowing down leaf N mobilization rate, but a stay-green phenomena could possibly come from enhanced  $N_2$  fixation, or better disease/nematode resistance. Breeders, while selecting for higher yield, would likely already have selected for slow N mobilization (more stay-green) along with longer filling period as shown by Boerma and Ashley (1988). The simulated yield response per day increase from R5 to R7 is 27.4 and 36.8 kg ha<sup>-1</sup> for normal N mobilization and 20% slower N mobilization, respectively. This agrees closely with reported yield increase of 35 kg ha<sup>-1</sup> for each day increase in time from R4 to R7, averaged over 119 cultivars at 10 site-years in the midwestern USA (Dunphy et al., 1979). There appears to be a genotype × environment interaction with the longer filling period trait. In the 6 more drought-prone years between 1980 and 1996 at the same site, longer filling period had no advantage over the midrange cultivar, and was less advantageous because earlier podset resulted in less simulated root growth, less soil water extraction, more water stress, and greater drought-reductions of biomass and seed yield.

Shifting life cycle from vegetative to reproductive clearly increased final seed harvest index (HI) as shown in Fig. 3 and as simulated previously using SOYGRO (Boote and Tollenaar, 1994). Sometimes HI is represented as an independent genetic trait; however, these simulations suggest otherwise and illustrate the real origins of HI. These simulations show that HI is the outcome of many traits (up to 10 or more) associated with shifting the timing of life cycle allocation toward reproductive growth. Importantly, notice that seed HI increases asymptotically with increased reproductive duration and appears to achieve an asymptote at about

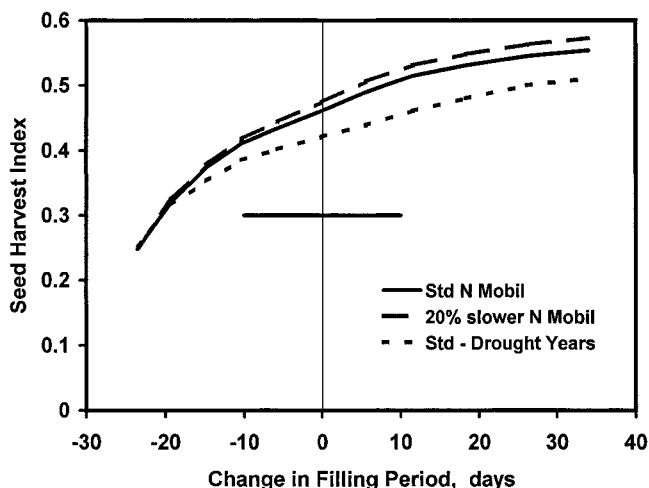


Fig. 3. Simulated soybean seed harvest index in response to varying the filling period duration (beginning seed, R5, to physiological maturity) at Ames, IA, for 1980–1996 rainfed weather. Treatments include standard N mobilization and 20% slower N mobilization (both with 11 adequate rainfall years) and standard N mobilization (with 6 drought-prone years). Horizontal bar represents feasible genetic range for filling period duration. Reprinted from Boote et al. (2001) with permission.

0.6; however, traits such as slower N mobilization appear to push the asymptote up somewhat. Notice, also, that water deficit limits the degree of increase in HI that can be obtained from increased filling period.

How much of the simulated increase in yield in Fig. 2 is feasible? To correctly interpret the value of this cultivar trait (or any other trait) to improve yield, we need to know the feasible range of genetic variation for that trait. The line bar in Fig. 2 and 3 illustrates the feasible range for varying seed filling period; this range is 10 d shorter to 10 d longer than the Williams 82 cultivar used here, based on literature review of Boote and Tollenaar (1994), Egli et al. (1984), and Swank et al. (1987).

#### D. Increasing Crop Assimilation

Increased canopy assimilation can be caused by increased photosynthesis per unit leaf area and by increased light interception [depending on whether leaf area index (LAI) is limiting for light capture]. Leaf angle distribution has only minor effects via light distribution to leaves within the canopy. Canopy LAI is affected by vegetative phase duration, crop management, and by canopy specific leaf weight (SLW) pattern over the season. Increasing canopy assimilation from increased single leaf photosynthesis may be associated with either increased SLW, increased leaf N concentration, or increased allocation of total leaf protein to rubisco enzyme (intrinsic rate). Model simulations demonstrate that there is considerable feedback between SLW effects on leaf photosynthesis and SLW effects on LAI. Leaf photosynthesis is a relatively conservative trait among adapted cultivars within a given crop. Within soybean, there is cultivar variation for light-saturated leaf photosynthesis ( $P_{\max}$ ) from 0.82 to 1.39 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, although the major variation falls within 0.92 to 1.17 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, with a mean of 1.05 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (see

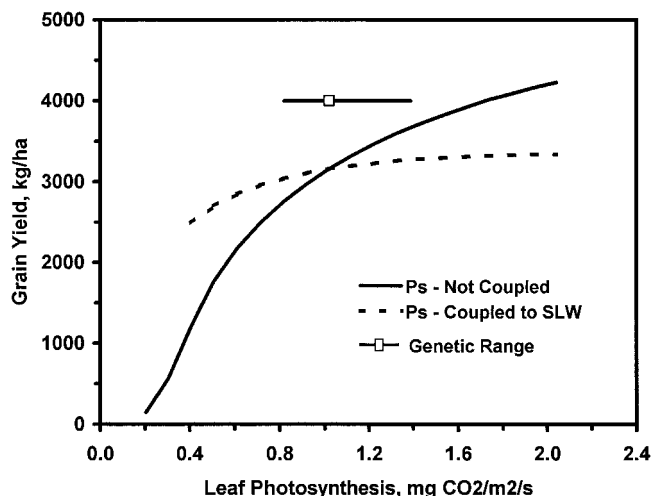


Fig. 4. Simulated soybean yield as a function of variation in leaf  $P_{\max}$ , attributed to inherent rate (no change in SLW), or attributed (coupled) only to SLW. Simulated over 17 rainfed seasons at Ames, IA. Horizontal bar represents feasible genetic range for  $P_{\max}$  about the mean of reported literature values.

Boote and Tollenaar, 1994; Dornhoff and Shibles, 1970, Sinclair, 1980). More recently released cultivars have higher light-saturated leaf photosynthesis than older cultivars, which is associated primarily with increased SLW (Dornhoff and Shibles, 1970; Buttery et al., 1981; Wiebold et al., 1981; Bhatia et al., 1996; Morrison et al., 1999).

If we assume there is coupling between increased SLW and leaf photosynthesis as reported by Dornhoff and Shibles (1970), then yield response to increasing leaf photosynthesis (via SLW) rapidly becomes limiting and asymptotic (Fig. 4), because there is a negative feedback of increased SLW to decrease LAI and light interception. Indeed, there is a practical plateau or optimum for  $P_{\max}$  at 1.6 to 2.0 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. On the other hand, if there is no coupling, seed yield continues to increase with increasing  $P_{\max}$ , although there is a clear trend for less response as  $P_{\max}$  increases above the present genetic range. Under either case, the seed yield response to increasing leaf photosynthesis is less than proportional to the percent increase in  $P_{\max}$ . Where the increase in leaf photosynthesis is not coupled to SLW change, seed yield is increased about 3 to 4% for each 10% increase in  $P_{\max}$  above the midpoint (Boote and Tollenaar, 1994), or about 5.1% in the simulations shown in Fig. 4. When increase in  $P_{\max}$  derives only from increased SLW, then the increase in seed yield is small (1–2%) for each 10% increase in  $P_{\max}$  (Boote and Tollenaar, 1994; also in Fig. 4). These simulations of canopy assimilation, which account for light distribution over all canopy leaves and which consider diurnal and seasonal irradiance, show why the great promise implied by physiologists for single leaf photosynthesis did not work out. The above analyses assume that the method of computing canopy assimilation from leaf-level inputs is realistic in CROPGRO. This sunlit and shaded leaf photosynthesis approach, the rubisco kinetics method, and the method of scaling from leaf to canopy assimilation were tested and shown to work well (Boote and Pickering,



1994). DePury and Farquhar (1997) used similar procedures for scaling from leaf to canopy assimilation and documented their validity. Canopy assimilation in CROPGRO considers vertical gradients in  $P_{\max}$  caused by vertical gradients in SLW and leaf N concentration vs. LAI depth (Boote and Pickering, 1994). Reynolds et al. (1992) confirmed the value of using sunlit-and-shaded leaf photosynthesis methods and vertical distribution of leaf  $P_{\max}$  in models that scale from leaf to canopy assimilation.

Beyond the interactions between SLW,  $P_{\max}$ , and LAI, there is also the possibility of higher inherent photosynthetic capacity per unit of leaf mass attributed to increased leaf N concentration or increased allocation of total leaf protein to the rubisco enzyme (intrinsic rate). There is reported variation in leaf N concentration among soybean cultivars (Young et al., 1979; Sexton et al., 1998). Over its entire life cycle, the Tracy cultivar had higher leaf N concentration than the Forrest cultivar for upper leaves (53 vs. 50 g N kg<sup>-1</sup>) and lower leaves (also higher by about 3 g N kg<sup>-1</sup>) as reported by Young et al. (1979). The Tracy cultivar was higher yielding in their study. Model simulations show that increased leaf N concentration has a clear benefit to leaf photosynthesis, but at a slight cost early in the season to provide the additional energy to assimilate the N. Later in the season, higher leaf N concentration also provides a different advantage attributed to greater leaf N available to mobilize to seeds. When leaf N concentration is increased 10% above our model default (from 57.0 to 62.7 g kg<sup>-1</sup>), the simulated yield is increased 3.0% and seed HI increased too. An increase of 3 g N kg<sup>-1</sup>, from 50 to 53 g N kg<sup>-1</sup> as reported above, gives a yield increase of 3.3%. Another aspect of leaf N concentration on photosynthesis is not necessarily the higher initial N concentration, but slower N mobilization (stay-green) during seed filling, which serves to maintain photosynthesis longer during grain filling of improved cultivars vs. older ones (Wells et al., 1982). In their study, the Tracy cultivar maintained canopy photosynthesis longer during seed-filling than other cultivars in its maturity class, consistent with higher leaf N concentration and slower N mobilization. Boerma and Ashley (1988) reported that improved soybean cultivars maintained higher leaf and canopy photosynthesis during grain filling than did old soybean cultivars. Simulating this as a 10% slower N mobilization resulted in 2.6% higher yield for the Iowa example. This also resulted in slightly higher seed HI.

### E. Vegetative Vigor and Early Season Partitioning

Vegetative vigor could be defined generally as rapidity of early leaf area expansion during the seedling and early expansive phase. How can crop models mimic genes that influence vegetative growth? All crop models initialize the leaf area per plant at emergence or a given stage after emergence. Modeling seedlings to start with greater initial leaf area per plant will provide a slight initial advantage. We mimic this by linking initial leaf

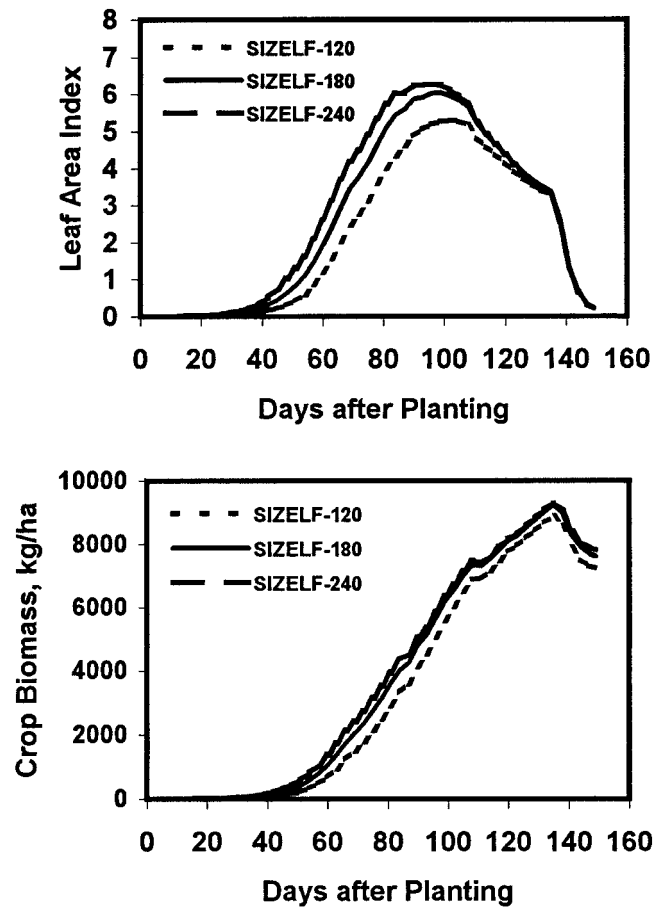


Fig. 5. (a) Simulated leaf area index, and (b) simulated biomass accumulation, as affected by varying early vegetative vigor of soybean (by varying a parameter called SIZELF) for the 1980 season at Ames, IA, when sown on Day 122 in 0.91-m rows at 30 plants m<sup>-2</sup>.

area per seedling to the seed mass because the initial leaf area bears a relationship to the amount of reserves in the seed and the initial embryo size at germination. Research also has shown that the first five or so leaves are pre-formed before germination. It appears as if the number of cells and the size of leaf cells for these pre-formed leaves may provide a strong limit to the leaf area that forms for up to the first five leaves. In addition, the rate of successive leaf appearance (trifoliolates per day) and leaf area expansion is temperature-dependent, and possibly varies with cultivar. During early development, SLW will also vary depending on light (decrease in low light) and temperature (decrease at more optimum temperature). Figure 5a illustrates how early leaf area development is affected when a parameter called SIZELF is varied; SIZELF affects the potential area per leaf for the first five leaves. Increasing SIZELF is like increasing vegetative expansion vigor but without necessarily increasing leaf photosynthesis. The question here is: what really causes increased vegetative vigor? Vegetative growth vigor is possibly related to leaf area partitioning (fraction dry matter partitioning to leaf multiplied by specific leaf area) as reported by Potter and Jones (1977). Regardless of the actual mechanism, increasing the size of early leaves on the plant up to the V5 stage increases



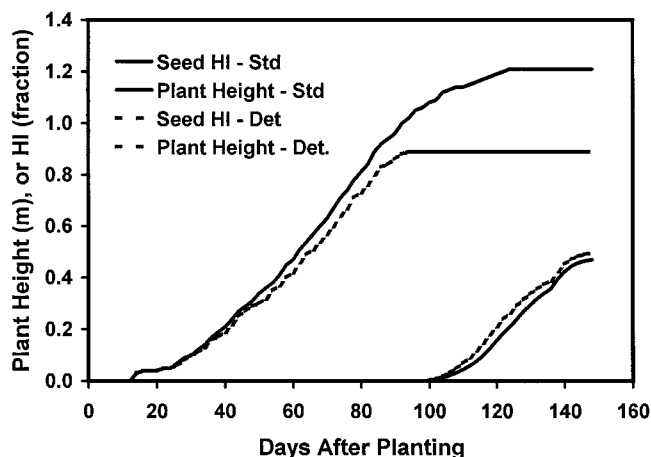


Fig. 6. Simulated plant height and seed harvest index (HI) for hypothetical determinate and indeterminate soybean cultivars grown in a nonstressed year (1981) at Ames, IA.

not only early LAI but increases biomass growth, particularly shortening the apparent lag phase of early growth (Fig. 5b). Yield is increased because of the higher LAI and biomass formed before seed-fill; however, the effect on yield is much less dramatic than the effect on early LAI and dry matter growth. A twofold range of SIZELF of 120, 180, and 240 cm<sup>2</sup> resulted in minor variation in seed yield of 3092, 3160, and 3189 kg ha<sup>-1</sup>, respectively.

#### F. Determinate versus Indeterminate Leaf Area Expansion

The termination of main stem node expression and end of leaf area expansion are features in crop models that can be used to mimic cultivar differences. This is important for canopy height, LAI, and light interception. In highly determinate cereal crops, the termination of leaf area expansion is closely related to date of anthesis, and occurs when the grain head is the terminal raceme. For the grain legumes, there are different degrees of determinacy. For indeterminate grain legumes, the first flower occurs in axillary buds, allowing the main stem to express more main axis leaves and leaf area after anthesis. Even for determinate grain legumes, the first flower may occur in the axillary buds, allowing several (2–4) additional nodes to be expressed on the main axis, and even more nodes on branches before cessation of leaf area expansion. The end of main stem node expression and the end of leaf expression are predicted separately in CROPGRO (Fig. 1), both being coupled to the predicted date of anthesis, plus an additional phase that varies in length for determinate vs. indeterminate types. A single gene (Dt vs. dt) causes these two effects in soybean, but is possibly also affected by genetic background. We have had experience with coefficients for determinant soybean cultivars in the South vs. indeterminate cultivars in the Midwest, as well as cultivars in MG 4 and 5 in the Mississippi delta where both determinate and indeterminate cultivars are grown. For determinate cultivars, the photothermal days for FL-VS (see Table 1 for definition) is much shorter (9 vs. 26 PTD), resulting in fewer main stem nodes, and shorter plants as simulated in Fig. 6. Photothermal days

from flowering to end of leaf area growth (also on branches), FL-LF, is about 18 for determinant vs. 26 for indeterminate, causing somewhat lower LAI (5.40 vs. 5.96). For the example simulation in Fig. 6, we assumed the same dates of flowering, podset, and maturity, but allowed the determinate cultivar to have 33% faster pod addition (8 vs. 12 PTD), shorter FL-LF (18 vs. 26 PTD), and shorter FL-VS (9 vs. 26 PTD). Simulating these three changes together as determinacy, resulted in 14.9 vs. 20.3 main stem nodes, 79 vs. 108 cm height, and 9.4% less LAI in Ames, IA. Seed yield was increased 2.4% and HI increased from 0.447 to 0.466 (Fig. 6), primarily because pods were added faster.

#### G. Traits to Improve Production under Drought

Drought can be described by duration of water deficit and as intermittent or terminal. In agriculture, drought tolerance of a cultivar or crop is best defined as its ability to survive and yield satisfactorily or better than other cultivars or crops. Drought tolerance traits that may be beneficial in one environment may not be beneficial in another. Crop modeling has the potential for evaluating the benefits of given traits in different weather conditions, particularly to find the best cultivar choice over long-term weather for a given locality (Chapman et al., 2000).

Following the systems modeling point of view proposed by Passioura (1994), there are three primary means for increasing yield in a water-limited environment: (i) increasing water uptake (from deeper rooting and/or more prolific rooting patterns), (ii) increasing water-use-efficiency (aspects discussed below), or (iii) improving HI. These means can be achieved by management and genetic improvement. We will not further discuss HI improvement under drought, as genetic traits improving HI are generally similar in irrigated and rain-fed environments. There are, however, cases where higher HI may be obtained by a better fit of life cycle to the rainfall availability, and where that same life cycle shift does not optimize yield or HI under irrigation as shown in Fig. 2 and 3.

##### 1. Increased Root Water Extraction (Increased Supply)

Increased water uptake is one of the candidate mechanisms contributing to yield advantage among cultivars during drought conditions. In a review of drought tolerance mechanisms among soybean cultivars, E.L. Piper (personal communication, 1999) concluded that there were only a few traits where cultivar differences were documented, and they usually related to enhanced rooting and water extraction. Reports of differentially delayed wilting or less negative water potential among soybean cultivars can also be generally hypothesized to result from increased water extraction. Boyer et al. (1980) and Frederick et al. (1990) reported that new, higher yielding soybean cultivars in the midwestern USA had less negative water potential at midday than lower yielding, older cultivars. This would imply better water extraction, consistent with the report by Boyer

**Table 3.** Yield response to hypothetical variation in genetic traits of soybean affecting response to water deficit simulated for 17 weather years for crops sown 2 May under rainfed conditions on a Nicollet soil at Ames, IA.

Cultivar trait	Seed yield	% Change	Final biomass	Seed HI	Seasonal Et	Standard deviation yield
	kg ha <sup>-1</sup>	%	kg ha <sup>-1</sup>	frac.	mm	kg ha <sup>-1</sup>
Wm-82 std†	3160	—	7011	0.451	529.8	688
10% slower root depth prog.	3003	-5.0	6737	0.446	523.5	769
10% faster root depth prog.	3236	+2.4	7176	0.451	532.8	672
-10% less RLD below 0.6 m	3075	-2.7	6839	0.450	526.0	726
+10% more RLD below 0.6 m	3174	+0.4	7064	0.449	530.8	704
-10% root length/mass	3123	-1.2	6926	0.451	528.4	713
+10% root length/mass	3182	+0.7	7066	0.450	530.7	685
Partition to root (+0.02)	3131	-0.9	6929	0.452	529.7	677
ATOP, 0.0 shift to root	3032	-4.1	6876	0.441	522.5	785
ATOP, 0.5 shift to root	3115	-1.4	7000	0.445	527.6	727
ATOP, 1.0 shift to root†	3160	—	7011	0.451	529.8	688
SENDAY, 0.04 d <sup>-1</sup>	3184	+0.8	7055	0.451	529.9	661
SENDAY, 0.08 d <sup>-1</sup>	3144	-0.5	6983	0.450	529.6	703
Accelerate R7, 0.2†	3160	—	7011	0.451	529.8	688
Accelerate R7, 0.8	3106	-1.7	6968	0.446	526.5	746
Accelerate R7, 1.4	3063	-3.1	6938	0.441	523.9	809

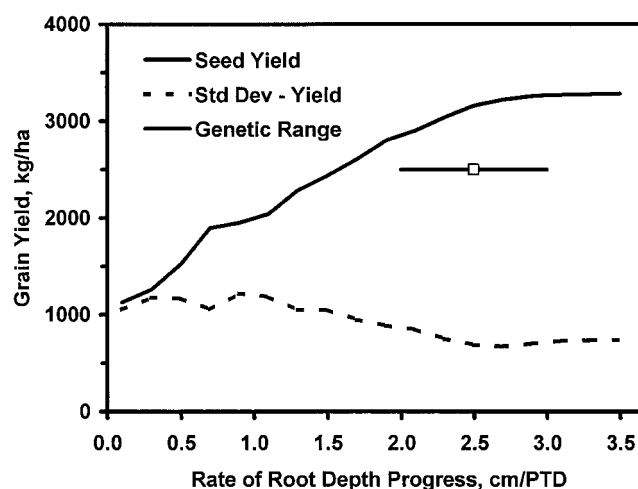
† Default values: rate of root depth increase = 2.50 cm PTD<sup>-1</sup>, root length per unit mass = 7500 cm g<sup>-1</sup>, ATOP = 1.0, SENDAY = 0.06 d<sup>-1</sup> under maximum water deficit, and 0.2 is the coefficient to accelerate maturity as function of soil water deficit (SWFAC).

et al. (1980) of greater root length density for the newer, higher yielding cultivars, especially at the 1.0- to 1.4-m soil depth.

What are some of the “genetic” traits that could enhance rooting to increase water extraction, assuming that we are concerned with grain yield rather than survival, and that the mechanism is not avoidance, i.e., we are not changing the length of crop life cycle or sowing date? Enhanced rooting for water extraction can come from: (i) increased rate of root-depth progression, (ii) increased root length per unit of root mass, (iii) a better shape of rooting profile within a fixed depth of maximum rooting, (iv) increased assimilate allocation to root growth within a fixed root growth duration before seed growth, and (v) increased duration of rooting growth (later onset of seed growth to allow greater root depth and/or greater total rooting density). Relative to the 5th trait, it is important to recognize that later flowering and seed growth would allow greater root depth and greater root length density, mechanisms for greater water extraction. Most crop models address this as an emergent property of their modeled phenology and assimilate partitioning, because the amount of modeled root growth is drastically reduced as the crop diverts assimilates to reproductive growth. Indeed, model simulation (Fig. 2) shows that later flowering and seed set (within a fixed season length) did increase root growth and reduce water deficit, but at the expense of lower yield potential.

There is evidence for variation in rate of root depth increase and in root depth by the R4 stage among soybean genotypes (Kaspar et al., 1978). Based on a study of 104 genotypes in root tubes in the greenhouse, Kaspar et al. (1984) reported variation in root depth increase among cultivars within MG I, II, and III, with range of variation up to 37% of the mean value. A set of four rapid rooting-depth cultivars compared with four slower rooting-depth cultivars in a Castana silt loam soil, had 9 to 11 cm deeper rooting depth, with much greater

rooting density below 1.0 m, twofold more at 1.5 m, and threefold more at 2.0 m. Under field conditions, root depth progression of the fast cultivars was 7% faster (2.41 vs. 2.25 cm d<sup>-1</sup>). Simulated yield advantage for 10% faster rooting depth averaged 2.4% over 17 weather years at Ames, IA (Table 3). Grain yield initially increased rapidly with increasing rate of root depth progression; but the response became asymptotic as the rate of root depth increase approached 3.0 cm PTD<sup>-1</sup> (Fig. 7). Yield variation was also reduced as rooting depth increased. The default value of 2.5 cm PTD<sup>-1</sup> used with the model (developed by comparison to field data) is almost optimized, as 10% faster root depth increase gives only 2.4% yield increase, whereas 10% slower rooting causes 5.0% less yield. The feasible range of genetic variability (in Fig. 7) for rate of root depth increase for soybean under field conditions is based on



**Fig. 7.** Simulated soybean yield and SD for yield as affected by rate of root depth progression (cm PTD<sup>-1</sup>), averaged over 17 rainfed seasons at Ames, IA. Horizontal bar represents feasible genetic range for rate of root depth progression about the default reference point.

Kaspar et al. (1984), and assumed between 2.0 to 3.0 cm  $\text{PTD}^{-1}$  with a range of 40%.

Another way to increase soil water uptake is with a rooting profile shift, i.e., to increase the fraction of roots below 0.6 m (18% more in 0.6–0.9 m depth, twofold more in 0.9–1.50 m depth) with no change in total root length density or rooting depth. This simulation, designed to be comparable to that reported by Kaspar et al. (1984), increased yield by 0.4%. Variation in root length per unit mass has also been observed among soybean genotypes (Pantalone et al., 1996). If root length per unit mass decreases or increases 10% around its nominal value of  $75000 \text{ m kg}^{-1}$ , the simulated yield decreases 1.2% or increases 0.7% (Table 3). One concern with changing root length per unit mass in the model, is the present assumption of no feedback impact of root diameter on water uptake, whereas influence may exist in reality.

Pantalone et al. (1996) proposed that drought-tolerance of 'PI416937' (Sloane et al., 1990) was primarily attributable to its large fibrous root system. However, the drought tolerance of PI416937 is substantially assisted by the tolerance of its roots to Al (Carter and Ruffy, 1993). The Al tolerance would be a clear advantage for regions with acid subsoils. However, the lateness and short seed-filling duration of this cultivar that allowed longer root growth and greater water extraction, was also detrimental to its yield potential (K.J. Boote and R.P. Patterson, unpublished crop model simulations, 1998). While breeders hoped to cross the trait of extended root growth duration into a high yielding line, model simulations showed this was a less promising approach, where yield was traded for drought tolerance. Aluminum tolerance is an exception to this issue of trading yield for tolerance, as it could be beneficial on soils high in Al. A number of soils in the southern USA and in tropical/subtropical regions of the world have subsoils high in Al.

Increased assimilate partitioning to root growth could be hypothesized to increase yield if it sufficiently increased water extraction relative to the diversion of assimilate to roots. We simulated increased partitioning to root growth before rapid seed growth as two different traits: first as a continuous constitutive trait, and second, as a trait induced only under perception of water deficit. The first constitutive case of continuously partitioning 2% more to root before rapid seed growth did not improve yield (gave 0.9% less yield, Table 3) under drought conditions because the same feature caused 1% less allocation to stem and 1% less to leaf area (thus less light interception) as reported by Boote and Jones (1986). Once pods and seeds are formed, they have priority for all assimilate; thus, the effect is via decreased LAI. For the second case, a partitioning shift from shoot to root was allowed to be induced by water deficit, dependent on a scalar named ATOP. A value of 1.0 for ATOP shifts all new assimilate from the vegetative shoot to the roots if water deficit is so severe that no water is transpired ( $\text{SWFAC} = 0.0$ ) ( $\text{SWFAC}$  in the model is the soil water factor, based on ratio of actual root water uptake to crop evaporative demand). This

function linearly shifts partitioning to roots as  $\text{SWFAC}$  decreases from 1.0 (no stress) to 0.0 (maximum stress). A 4.1% grain yield increase occurs (Table 3) for an ATOP of 1.0 (present default) compared with 0.0 (no shift). Inducible (or adaptative) responses would be best as they cost the plant nothing when there is no water deficit. There is evidence in the literature that such root/shoot shift occurs under water deficit. It is important that crop modelers consider realistic feedbacks or pleiotropic costs, i.e., increased assimilate allocation to root results in less shoot growth (unless compensated by the water extracted), and that longer vegetative growth to sustain root growth results in less time for grain growth.

There is a feed-forward signal sent from roots to shoots when the soil dries or is compacted, that acts to decrease growth and photosynthesis (Tardieu et al., 1992; Turner, 1997). This effect has been attributed to abscisic acid coming from roots in regions of drying soils, even though water uptake may be adequate from the remainder of the root system (Davies and Zhang, 1991). Indeed, the abscisic acid signal can override apparent good plant turgor to cause partial stomatal closure, decreased photosynthesis, and decreased leaf expansion (Davies and Zhang, 1991). This trait may vary with genotype. During intermittent drought, genotypes with less of this signal trait may benefit during seed fill. This could be one explanation for the observation by Frederick et al. (1990) that older soybean cultivars had higher stomatal resistance than new cultivars during a drought. The other possibility is that new cultivars have deeper rooting per se.

Water deficit during seed-fill is known to accelerate rate of seed maturation, causing 2 to 10 d earlier maturity in soybean depending on genotype (Desclaux and Roumet, 1996; Frederick et al., 1991; Ray, 1987; Ruiz-Nogueira et al., 2001; de Souza et al., 1997; Specht et al., 1986; Rose et al., 1992). Frederick et al. (1991) reported that old cultivars had a greater drought-induced acceleration of reproductive growth than did modern cultivars. CROPGRO-soybean allows for acceleration of reproductive development after beginning seed (R5) as a function of decrease in  $\text{SWFAC}$  (ratio of root water uptake to crop transpirational demand). Recent work by Ruiz-Nogueira et al. (2001) concluded that the scalar constant for this acceleration had to be 1.4 to produce the 10 d earlier maturity observed under severe terminal water deficit (the original default of 0.2 was inadequate). If a given cultivar can avoid acceleration (maintain a value of 0.2 compared with 1.4), then its yield would be 3.1% higher than one that accelerates seed maturation (Table 3). The modeled mechanism for yield loss is that acceleration shortens the grain-filling phase. The physiology of the acceleration mechanism is not well understood, but we believe it is more than heat unit accumulation. Another tolerance trait could be the ability to maintain leaves (slower abscission) despite severe water deficit. Decreasing this function ( $\text{SENDAY}$  from 0.06 to  $0.04 \text{ d}^{-1}$ ) increased yield 0.8%, because LAI was maintained better for subsequent light capture, after the drought is subsequently relieved by rainfall.

In summary, most of the rooting, assimilate parti-



tioning shift, and water deficit signal traits that improved grain yield and biomass (Table 3) did so by causing more seasonal evapotranspiration (faster rooting, increased root length per mass, altered rooting profile, inducible shift in assimilate partitioning to root, slower leaf abscission, and slower reproductive maturation). Generally, these beneficial traits also caused less yield variability and slightly higher seed HI (range was 0.441–0.451). As expected, yield variation decreased substantially as rate of rooting-depth progression was increased (Fig. 7). The strongest evidence of genetic variation is for rate of root-depth progression, but there is also evidence of genetic differences in acceleration of maturity and shift in rooting profile.

## 2. Water-Use Efficiency

Water-use efficiency (WUE) is a trait of interest for water-limited environments. Increasing WUE would result in increased dry matter accumulation for a given amount of water transpired. Small but significant differences in WUE have been found among cultivars within a given  $C_3$  species, and increased WUE is generally associated with lower C isotopic discrimination (Farquhar and Richards, 1984; Wright et al., 1988), lower leaf ash concentration (Masle et al., 1992), and increased SLW and SLN (Wright et al., 1988; Nageswara Rao and Wright, 1994). Farquhar and Richards (1984) showed, based on theory and experimentation, that the lower isotopic discrimination (and increased WUE) originated from the lower intercellular  $CO_2$  concentration of leaves ( $C_i$ ). The lower  $C_i/C_a$  ratio ( $C_a$  is ambient  $CO_2$  concentration) and less isotopic discrimination can be attributed to increased SLW and SLN (Makino et al., 1988; Wright et al., 1988), which cause a greater sink for  $CO_2$ , yet the gradient for water vapor loss is dependent on energy balance and is not increased. Mian et al. (1996) found four and six molecular markers for WUE and lower leaf ash, respectively, in a soybean cross of 'Young' (high WUE line) with 'PI416937' (high water uptake, but relatively low WUE). They found a negative correlation of WUE with lower leaf ash, and also that two of the quantitative trait loci (QTL) were associated with both WUE and lower leaf ash. In a cross of 'S100'  $\times$  'Tokyo', Mian et al. (1998) reconfirmed one of the common QTLs for WUE and identified an additional one (which would not have shown previously if homozygous in the 'Young'  $\times$  'PI416937' cross). A modeling analysis can potentially assist such molecular marker methodology by helping these and other researchers explore the possible mechanisms that lead to improved WUE. Crop growth models can help understand these connections, if the models are sufficiently mechanistic and are able to simulate canopy energy balance, leaf rubisco kinetics, specific leaf mass, and specific leaf N traits.

Williams and Boote (1995) used an hourly energy balance version of CROPGRO-peanut to show that WUE could be increased 42% by increasing the average canopy SLW from 15 to 60  $g\ m^{-2}$ . Their simulations assumed that the ratio of  $C_i/C_a$  was a function of SLW, from  $C_i/C_a$  of 0.9 at SLW = 0.0, to 0.5 at SLW = 90  $g\ m^{-2}$ .

The relationship between  $C_i/C_a$  and SLW was based on the theory of  $C_i/C_a$  to C isotopic discrimination (Farquhar et al., 1982, 1989), observed isotope discrimination and SLW of peanut genotypes (Wright et al., 1988; Nageswara Rao and Wright, 1994), as well as the isotope discrimination and observed WUE of peanut genotypes (Hubrick et al., 1986, 1988). Makino et al. (1988) found for wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.), that the ratio of  $C_i/C_a$  during photosynthesis was linearly related to SLN, declining from 0.9 at 0.4  $g\ m^{-2}$  to 0.6 at 2.5  $g\ m^{-2}$ . There are two ways to increase SLN: increasing leaf N concentration at constant SLW or increasing SLW at constant N concentration. We evaluated the extent of WUE improvement that would occur for an improved soybean cultivar with 10% greater SLW (26.7 vs. 24.2  $g\ m^{-2}$ ) and 10% higher leaf N (57.0 vs. 51.8  $g\ kg^{-1}$ ) compared with an unimproved cultivar, where photosynthetic capacity per unit of SLN was constant. With this combination, grain yield was increased 5.89%, with the first 4.27% coming from increased N concentration and 1.62% from the increased SLW. The WUE for grain yield (per unit evapotranspiration) was improved 5.95%.

## COMBINATIONS OF GENOTYPIC TRAITS AND ADDITIVITY VS. INTERACTION IN TWO TYPES OF MANAGEMENT

So far, we have considered simulated effects of single trait changes. In reality, breeders' primary selection for yield would likely encourage multiple combinations of improved traits. Are these traits additive or are there negative or positive interactions? Also, is there a situation where certain traits, alone or in combination, are only advantageous in high level management (0.18-m row spacing and 30 plants  $m^{-2}$ )? Table 4 compares simulations of single traits and combinations of traits, under low management (0.91-m row spacing and 25 plants  $m^{-2}$ ) and also under high management. Many, but not all, of the traits give more yield enhancement under high management. For example, yield increase with determinate or 10% longer filling period (within same life cycle) was 2.26 and 1.43% in the low management case, but 4.24 and 2.51% in the high management case. The reason is simply that narrow row spacing and higher density offset the negative feedback effect of lower LAI caused by determinate or longer filling period. Likewise, the combination of determinate plus longer filling period gave only 4.04% yield increase in the low management case, but 6.98% yield increase under high management, again because of the effect on LAI. Response to determinate and long filling period is about 2 and 1% greater, respectively, in the high management, and all combinations having both determinate and longer filling period are about 3% greater under high management (Table 4). These simulation findings are in agreement with the strategy of Cooper (1977, 1981), who developed semidwarf soybean cultivars for narrow-row, high-yielding environments in the midwestern USA.

What about combinations of traits within a given management? Based on these simulations, it appears that

**Table 4. Simulating single and multiple combinations of traits in low and high management to evaluate additivity or enhancement under high management. Yield response to hypothetical variation in genetic traits of soybean was simulated for 17 weather years for crops sown 2 May under rainfed conditions on a Nicollet soil at Ames, IA, under either low management (0.91-m row spacing at 25 plants m<sup>-2</sup>) or high management (0.18-m rows at 30 plants m<sup>-2</sup>).**

Cultivar trait or combination	Seed yield	% Change	Enhanced by management	Final biomass	Seed HI
	kg ha <sup>-1</sup>	%	%	kg ha <sup>-1</sup>	fraction
<b>Low management</b>					
Standard	3140			6970	0.450
Determinate	3211	2.26		6792	0.473
10% EFP	3185	1.43		6691	0.476
10% slow Nmob†	3224	2.69		7047	0.458
10% SLW	3176	1.15		7087	0.448
10% P <sub>max</sub>	3306	5.29		7321	0.452
Det + EFP	3267	4.04		6521	0.501
Det + EFP + Nmob	3375	7.48		6632	0.509
Det + EFP + SLW	3304	5.25		6601	0.501
Det + EFP + P <sub>max</sub>	3453	9.98		6882	0.502
Det + EFP + Nmob + SLW	3423	9.03		6716	0.510
Det + EFP + Nmob + P <sub>max</sub>	3563	13.48		6994	0.509
<b>High management</b>					
Standard	3247			7251	0.448
Determinate	3385	4.24	1.98	7194	0.471
10% EFP	3329	2.51	1.08	6984	0.477
10% slow Nmob	3322	2.30	-0.39	7318	0.454
10% SLW	3288	1.25	0.10	7381	0.445
10% P <sub>max</sub>	3421	5.34	0.05	7631	0.448
Det + EFP	3474	6.98	2.94	6945	0.500
Det + EFP + Nmob	3591	10.58	3.10	7068	0.508
Det + EFP + SLW	3520	8.38	3.13	7058	0.499
Det + EFP + P <sub>max</sub>	3681	13.35	3.37	7337	0.502
Det + EFP + Nmob + SLW	3638	12.03	3.00	7179	0.507
Det + EFP + Nmob + P <sub>max</sub>	3795	16.87	3.39	7459	0.509

† Nmob, fraction available protein mobilized from vegetative tissue per photothermal day.

effects are mostly additive, with a tendency for a small synergistic interaction. For the combination of determinate plus longer filling period, the individual effects nearly add up under either management case (in low management, 2.26 + 1.43 = 3.69%, compared with 4.04%; and in high management, 4.24 + 2.51 = 6.75% compared with 6.98%). The same trend occurred for the three- and four-way combinations as well.

How realistic are the combinations in Table 4? We believe the ranges selected and the possible combinations are feasible and generally conservative. Determinate vs. indeterminate cultivars are available, 10% longer filling period is much less than the genetic range, slower N mobilization is present, while SLW and leaf P<sub>max</sub> can vary in the ranges described. Putting four-way combinations together would increase yield 13 to 17%, which is in the range of genetic improvement over the past 20 to 30 yr. There are certainly other multiple combinations we have not considered. We believe this analysis illustrates the reason that selection for single traits per se is less likely to give statistically significant yield increases (if the field variance threshold requires about 5.0% difference to be significant), whereas breeder selection for yield has allowed yield improvement to come from multiple combinations of traits, sufficient to improve yield by a much higher percentage over a period of years. The 13 to 17% yield increase hypothesized here is very close to the yield increase (12–23%) observed during a 20-yr period of genetic improvement as shown by comparisons of old vs. new cultivars studied by growth analyses and model simulation during 2 yr at 11 sites in Iowa, Illinois, and Wisconsin in an Iowa–Illinois Soybean Promotion Board project (Boote et al., 1999,

2001). In those studies, growth observations in conjunction with model analyses attributed that yield improvement to the same type of traits (earlier podset, more rapid pod addition, longer grain filling period, slower N mobilization, higher leaf photosynthesis). Genetic improvement in seed HI in that study was comparable to the simulated increase in seed HI with four-way combination improvements in Table 4.

### BREEDING FOR GLOBAL CLIMATE CHANGE, TECHNOLOGY TREND, GENOTYPE × ENVIRONMENT INTERACTIONS

One of the questions asked of plant breeders is whether genetic improvement can keep pace (both adapt to climate change and increase yield potential) as the global climate changes. We will consider this issue with recent history from 1958 (beginning of continuous recording of CO<sub>2</sub>) to the year 2000, during which time the atmospheric CO<sub>2</sub> concentration [CO<sub>2</sub>] increased from 315 to 370 μmol mol<sup>-1</sup>, and soybean producers gradually shifted from wide to narrow row spacing (0.91–0.18 m) and increased sowing density about 20% (from 25 to 30 plants m<sup>-2</sup>). Is it possible that a shift in environment can affect the type of traits that would give a yield advantage? Figure 8 shows how the year 2000 environment (increased [CO<sub>2</sub>], narrow row spacing, higher plant population) favors selection for a longer filling period more than the 1958 environment did. All three factors (increased [CO<sub>2</sub>], narrow row spacing, higher plant population) enhance the amount of LAI and biomass produced early in the season, and thus offset the lower

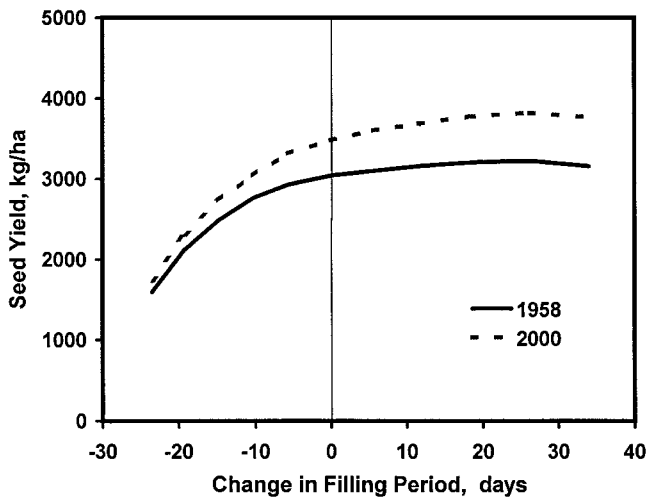


Fig. 8. Simulated soybean yield response to varying the filling period duration (beginning seed, R5, to physiological maturity) at Ames, IA, for 1980–1996 rainfed weather under two scenarios (Year 1958: 315  $\text{CO}_2$   $\mu\text{mol mol}^{-1}$ , 0.91-m row spacing, 25 plants  $\text{m}^{-2}$ ; Year 2000: 370  $\text{CO}_2$   $\mu\text{mol mol}^{-1}$ , 0.18-m row spacing, 30 plants  $\text{m}^{-2}$ ).

LAI, which was one of the feedback limitations of longer filling period. These three nongenetic factors are estimated to jointly result in 14.4% yield increase for soybean in Iowa over 42 yr. The increase in  $[\text{CO}_2]$  is predicted to have increased yield by 9.1%, decreased evapotranspiration by 1.5%, and improved WUE (grain basis) by 10.7%. One of the points to be made here is that part of the upward yield trend in soybean during the past 42 yr can be attributed to the increase in  $[\text{CO}_2]$  in addition to management and genetic improvement. Management effect (here, row spacing and population only) contributed 5.3% to yield increase. Adding a single genetic improvement of 11.3 d longer effective filling period would give a 5.95% yield increase for 2000, compared with a 3.91% yield increase in 1958. If genetic improvement of 11.3 d longer filling period were combined with improved management and  $\text{CO}_2$  increase from 1958 to 2000, soybean yield would have increased by 21.2 or 0.5% per year, or 15.9  $\text{kg ha}^{-1} \text{yr}^{-1}$ , starting with a mean of 3140  $\text{kg ha}^{-1}$ .

How much of the trend in soybean yield increase can be attributed to genetic improvement vs. technology or  $\text{CO}_2$  increase? Soybean yield in USA has increased by 22.6  $\text{kg ha}^{-1} \text{yr}^{-1}$  from 1928 to 1998, and more rapidly at 31.6  $\text{kg ha}^{-1} \text{yr}^{-1}$  during the past 25 yr, from all causes. Genetic improvement contributed 14.8  $\text{kg ha}^{-1} \text{yr}^{-1}$  over the longer 50 to 60 yr time period, contributing about two-thirds of the yield enhancement (See Table 1 of Specht et al., 1999). Based on our analyses above and ignoring slightly different mean starting points, the  $\text{CO}_2$  and row-spacing/population management effects would have contributed increases of 6.8 and 4.0  $\text{kg ha}^{-1} \text{yr}^{-1}$  or about 34% to the more recent trend of 31.6  $\text{kg ha}^{-1} \text{yr}^{-1}$ , again leaving genetic improvement to contribute about two-thirds of the effect. Regardless, our point is that better management and elevated  $\text{CO}_2$  have made it easier for recent genetic improvement via interaction effects.

While the above examples have shown additivity of

traits in a good environment, we believe there are times when genotype  $\times$  environment ( $G \times E$ ) interactions will occur, as seen from a crop modeling viewpoint. When exposed to two different environments (whether season-length, drought, temperature, soil type, etc.),  $G \times E$  interaction can occur if cultivars have different life cycles and fractional allocation to phases, which exposes the crop to different environmental conditions during the phases. This would include increased root growth and water extraction ability if the cultivar is late to set pods and seeds, as discussed earlier. These types of interactions are emergent properties and part of the modeling outcome with current genetic traits. There may be specific cases where one cultivar may have a different process response to environment than another cultivar. For example, one cultivar may have a more rapid rate of root depth penetration (inherent) or more rapid penetration into the subsoil (from Al tolerance) or an altered profile distribution. Under this situation, the  $G \times E$  interaction can show up if one environment is neutral (no water deficit) and the trait expression in the other environment allows enhanced water uptake. We need to know if there is a negative feedback of the trait in the good environment (possibly a C cost). Having a process such as photosynthesis or pod addition with different sensitivity to temperature (because of different membrane composition) could give a  $G \times E$  interaction, but only where the temperature shift was part of the environmental differences. Genotypic differences in pest resistance may, in fact, be the dominant situation that causes  $G \times E$  interaction, particularly if the resistance vs. susceptible traits are neutral in a low pest density field, but the resistance trait gives improved crop performance in a pest-infested field.

### HOW CAN GENETIC COEFFICIENTS BE DERIVED FOR DIFFERENT CULTIVARS?

So far we have given our view of genetic coefficients, shown crop model sensitivity of the yield potential to variation in hypothesized genetic coefficients (one or several at a time) within limits of known physiological range, and discussed the interactions needed between geneticists, physiologists, and crop modelers. How can we use this information to derive genetic coefficients for different cultivars? What are the data sources for information on different cultivars? There are several possible data sources and starting places.

1. Genetic knowledge—Geneticists have some of the genes defined (or possibly entire maps of DNA), but there still is the problem of knowing the mode of action of each section of DNA, when integrated together in the whole plant, and integrated over the entire season in multiple environments. Can molecular geneticists help translate these to modeled genetic coefficients? We believe they will need more physiological and biochemical assistance, plus interactions with whole-plant crop growth modelers.

2. Physiological knowledge available from laboratory



or field screening trials is another information source—Can physiologists define and measure physiological processes determined by those genes that geneticists indicate are present, and then translate these into modeled genetic coefficients? The task is overwhelming, because the number of cultivars and number of traits for defining mode of action are too many. What process traits should be measured and in what environment?

3. Crop Performance Trials are routinely available data sources—Can the standard performance trials of plant breeders/agronomists be used to good advantage? In this case, the numbers game is already being played with many cultivars grown in many environments. Unfortunately, these trials record only a few measurements including final grain yield, and sometimes also maturity date, height, and seed size. From such data, it would appear to be difficult to arrive at any sophistication in defining modes of action or physiological trait differences sufficient to be called modeled genetic coefficients. The problem is that there are many genes, many modes of actions, and many ideas of modeled genetic coefficients to be solved for, against only final yield. This leads to statistical problems of which trait (s) and how they contributed to the final yield, even if done over many environments of the yield trials.

We propose the solution should begin with current knowledge of gene structure, knowing the range of processes/enzymes/actions possible in the genetics, but then asking how these function in a framework that the modeler can help integrate. For example, how do the genes influence C balance, N balance, life cycle, canopy geometry, rooting, cold tolerance, heat tolerance, pest resistance, and in what environments? Physiologists must be in the middle of this to help maintain reality in the translations, despite the limitation of being able to evaluate fewer genetic materials than a geneticist can. Because presently modeled genetic coefficients are a complex result influenced by many genes, there is a need to become more detailed in the modeled genetic coefficients, or to develop a translator whereby several genes create one modeled genetic coefficient, much as White and Hoogenboom (1996) did for dry bean.

### Learning about Genetic Coefficients from Cultivar Performance Trials

We propose that standard performance trials of plant breeder/agronomists can be efficiently used for extracting some genetic coefficient information using the crop model in an optimization mode (Mavromatis et al., 2001, 2002). Performance trials are routine, with large numbers of cultivars being grown in many environments, usually with recorded weather and cultural practices. These trials include only a few measurements, such as final grain yield, maturity date, height, seed composition, and seed size. This makes it difficult to be specific in defining modes of action or physiological trait differences sufficient to be called modeled genetic coefficients. Despite this limitation, the process has led to interesting insights and has the advantage of providing information on an extended number of cultivars and

estimating genetic coefficients for recent cultivars as they come on the market, with no additional data collection required.

In the approach described by Mavromatis et al. (2001, 2002), the crop model helps by accounting for nongenetic factors affecting yield, such as site-specific factors of soil water holding capacity, fertility, and impact of weather on yield. The approach requires minor calibration of soils traits to reproduce the site-specific mean yield of each yield trial. Then the approach solves for genotypic variation in yield, maturity, plant height, or seed size among cultivars that may be attributed to modeled genetic coefficients. This process requires careful forethought as to the appropriate model genetic coefficients to influence a given yield trial measurement, because in cases such as yield, there many genetic coefficients that may affect measured variables. This is less difficult for maturity date, plant height, and seed size. For harvest maturity date, we commonly solve on just two traits: CSDL and a linked phase duration (FL-SD + SD-PM). However, for yield, the CROPGRO model has five to eight cultivar traits that can create yield differences, even after solving for the correct maturity date. These traits are not all equal in importance; therefore, we combined certain of these traits into fewer aggregated traits (Irmak et al., 2000; Mavromatis et al., 2001, 2002). For example, leaf photosynthesis and threshing percentage were linked and placed into a productivity enhancer category. A second combined trait was comprised of life cycle shifting and reproductive traits that either increase (or decrease) yield, including shorter FL-SH, shorter FL-SD, shorter PODUR, longer SD-PM, and longer SFDUR. The latter five traits were linked in a fixed fashion to create one trait. They act to increase final seed HI with little effect on total biomass. Using this approach for 15 cultivars in the Northern Uniform Regional Test for 3 yr at 11 sites in the midwestern USA, resulted in  $P_{\max}$  values ranging from 0.93 to 1.11 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (the default starting point was 1.03) among cultivars, and a range in fraction of the total flowering to maturity phase allocated to seed fill (SD-PM/FL-PM) from 0.65 to 0.78 (Table 5). Similarly, Mavromatis et al. (2002) found that estimated  $P_{\max}$  varied from 0.96 to 1.11 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, and the ratio SD-PM/FL-PM varied from 0.71 to 0.80. In both studies, the solved values of CSDL and total FL-PM reasonably represented the different maturity groups.

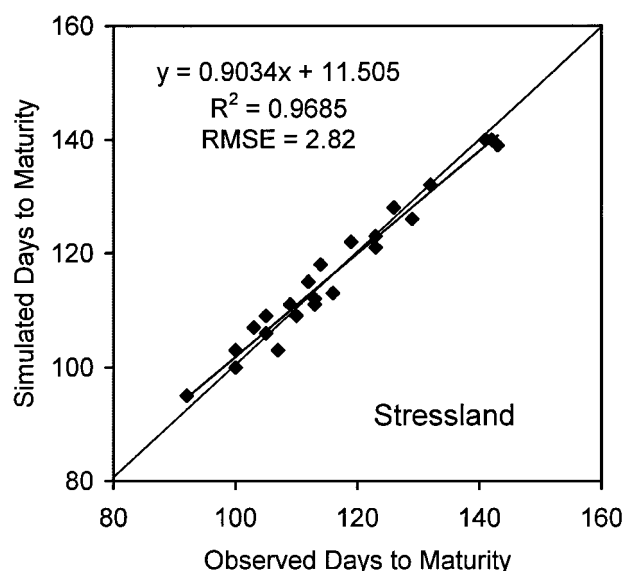
To estimate phenological and yield-potential traits requires 20 to 30 site-year combinations of trials, preferably over locations that differ in latitude, sowing date, and weather. This approach has been quite successful in solving for stable and repeatable values for CSDL and phenological phase durations (Grimm et al., 1993, 1994; Mavromatis et al., 2001, 2002). Figure 9 gives an example of the ability to predict harvest maturity date for the Stressland cultivar, estimated with data from the Northern Uniform Regional Soybean Trials. Root mean square error was 2.82 d. Mavromatis et al. (2002) found that the estimated phenological traits such as CSDL were quite repeatable ( $r^2 = 0.96$ ), even when solved with data from one region (Georgia) and used for pre-

**Table 5. Solved traits of 15 cultivars in Northern Uniform Regional Test, based on yield and maturity records for 1995, 1996, and 1997 in Illinois, Indiana, Ohio, Michigan, Kentucky, and Missouri. Root mean square error (RMSE) of maturity and yield associated with the optimized genetic coefficients.**

Cultivar	MG	CSDL	FLPM	FLSD	SDPM	SDPM/ FLPM	$P_{\max}$	Thresh	RMSE maturity	RMSE yield
		h	PTD	PTD	PTD	fraction	$\text{mg m}^{-2} \text{s}^{-1}$	%	d	$\text{kg ha}^{-1}$
A94-674017	2	13.47	44.10	12.00	32.10	0.73	1.010	76.5	4.51	650
IA2021	2	13.52	42.50	9.94	32.56	0.77	0.930	74.5	4.50	589
SD93-522	2	13.72	45.70	14.07	31.63	0.69	0.950	75.0	4.14	585
A94-774021	3	13.56	45.60	14.10	31.50	0.69	1.110	79.0	3.73	418
Charleston	3	13.56	47.20	13.77	33.43	0.71	1.030	77.0	4.43	468
U94-3412	3	13.56	45.60	14.10	31.50	0.69	1.070	78.0	4.09	468
KS4694	4	13.25	47.90	15.32	32.58	0.68	1.010	76.5	4.01	244
Stressland	4	13.30	45.50	13.79	31.71	0.70	1.090	78.5	2.62	275
HC90-196	4	13.35	45.50	11.39	34.11	0.75	1.030	77.0	3.26	240
HS93-4118	4	13.35	45.50	9.79	35.71	0.78	1.050	77.5	2.48	226
LS92-3660	4	13.35	45.50	13.79	31.71	0.70	0.950	75.0	1.96	328
LS92-4173	4	13.25	47.10	16.67	30.43	0.65	1.010	76.5	2.74	337
Md92-5850	4	13.35	45.50	9.79	35.71	0.78	0.970	75.5	2.79	322
Ripley	4	13.35	46.30	14.03	32.27	0.70	0.950	75.0	3.30	240
SS91-7138	4	13.25	45.50	12.99	32.51	0.71	1.050	77.5	2.72	276

diction in a new region (North Carolina). The approach with the yield-potential traits was able to provide reasonably good predictions of yield potential and cultivar yield ranking with independent data, but the two traits (photosynthesis-enhancing and HI-shifting traits) were less stable than phenological traits, when moved from one region to another. It is not surprising that yield prediction is more difficult than life cycle, because of the influence of soil, weather, and management factors. Indeed, the latter factors have much more impact on yield than do genetic yield potential traits, unless faced with a particular disease situation. Figure 10 illustrates predicted grain yield for the Stressland cultivar across a range of these trials. Factors contributing to the excellent predictions of grain yield in Fig. 10 come from the model's ability to account for weather effects, adjusting for soil water-holding and soil fertility traits, as well as estimating traits of life cycle phenology and genetic yield potential.

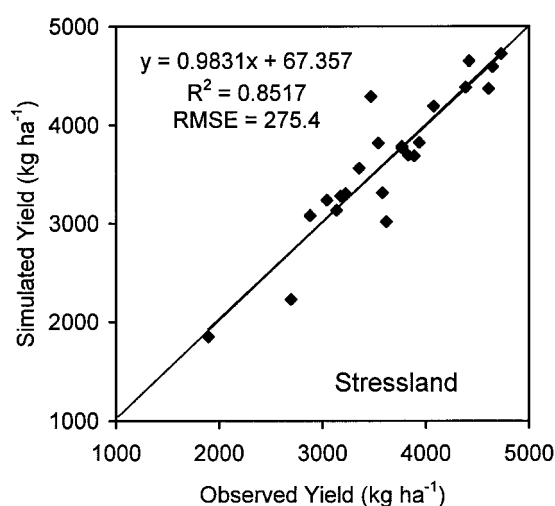
How realistic is the above approach? Except for the



**Fig. 9. Comparison of simulated vs. observed days to maturity for the Stressland soybean cultivar, grown at 11 sites for 3 yr in the Northern Uniform Regional Soybean Trials. The 1:1 line is also shown.**

phenology parameters, which were repeatable from region to region, we need to be cautious in attributing variation in yield potential to the specific modes of action or physiological traits solved for. There is too much possibility of compensation, and there are many genes and many modes of actions solved for, against only final yield. This creates questions of which trait(s) contributed and how they contributed to the final yield. More confidence could be gained if there were additional knowledge on HI (in the same trial) or measurements of leaf photosynthesis to verify whether this really varied among the set of cultivars. Of course, this requires more measurements by the agronomists/physiologists.

Additional information can be provided by detailed crop growth analyses of different cultivars, to determine causes for yield improvement of new vs. old cultivars. Growth analyses can be assisted by interactive use of crop growth models, to determine those differences in modeled cultivar traits required to mimic observed growth differences (Duncan et al., 1978; Salado-Navarro et al., 1986a, 1986b). We recently undertook such a modeling-growth analyses comparison of new vs. older soybean



**Fig. 10. Comparison of simulated vs. observed seed yield for the Stressland soybean cultivar, grown at 11 sites for 3 yr in the Northern Uniform Regional Soybean Trials. The 1:1 line is also shown.**

cultivars in studies over 2 yr at 11 sites in Iowa, Illinois, and Wisconsin (Boote et al., 1999, 2001). We systematically solved for genetic coefficients, as presently available in CROPGRO-soybean, to account first for phenology/life cycle, followed by traits affecting partitioning, determinacy, photosynthesis, and N mobilization. Yield advantage of 12 to 23% existed for the newer soybean cultivars. With detailed growth analyses (leaf, stem, pod, seed, computed HI), we concluded that yield improvement was attributed to genetic coefficients that created earlier podset (by 4–5 d), 14 to 30% faster pod addition, 8 to 17% longer grain filling, 5 to 11% increased leaf photosynthesis, and 10% slower N mobilization. Yield improvement did not come from not just one trait, but a number of traits acting together, particularly for those that shifted life cycle from vegetative to reproductive to increase HI. Moreover, the story of yield improvement repeated its pattern with several different sets of cultivar comparisons.

Detailed physiological screening for variation in traits/processes such as leaf photosynthesis rate, tissue composition, particular structures, enzymes, is feasible only on small numbers of lines at a time. However, molecular markers can be used concurrently to the physiological study of limited numbers of lines to establish connection of function to genome. Then later, molecular markers can be used to screen large numbers of cultivars, thus verifying presence or absence of a desirable trait, and even tighter constraints could be placed on which traits would be allowed to vary in a model search for genetic coefficients affecting yield in regional yield trials.

An added avenue to assist the yield-trial approach in searching for genetic coefficients of cultivars would be to include evidence of parent–progeny relationships and genetic relatedness, either based on crossing pedigree or from molecular genetic screening. We could presume that cultivars with high similarity of parentage (or with exactly the same set of QTLs) should have a greater probability of having similar coefficient values (for CSDL, photosynthesis, or life-cycle allocation to reproductive). Thus, constraints would be placed on the model optimization procedure with cultivar trials, to encourage selection of traits based on genetic relatedness, provided the root mean square error for that cultivar is not substantially increased.

### **Pest Tolerances as Genetic Coefficients: A Missing Part of the Puzzle**

Some of the genetic improvement in soybean yield clearly derives from genetic improvement in pest resistance. This is apparent from all the breeding work to improve tolerance to pests, from molecular screening emphasis for genes for pest resistance, and from observations of variety trials or farmer fields where it is obvious that certain cultivars perform poorly. Pest tolerances have not been represented well by crop physiologists or in this modeling analysis, but nematode resistance or disease resistance could give an apparent response that would appear as enhanced photosynthesis, stay-

green effect, or longer grain-filling period, which a crop physiologist might say was the cause of yield improvement. The modeling community has been slow to tackle the pest tolerance issue for several reasons. For example, in our evaluation of variety trial data, we recognized that cultivar yield differences were partially attributable to differential cultivar pest tolerances, but the requisite information on pest pressures at specific site-years was not collected, thus preventing a good evaluation and assignment of modeled pest resistance traits. Second, we would also need information for each cultivar on stated levels of pest tolerance, to then make any attribution of pest effects on yield. Breeders usually have such information. Lastly, we would need to predict the effect of the pest on crop growth and yield.

### **BRIDGING THE GAP: LINKING GENETIC COEFFICIENTS TO QTLs, FUNCTIONAL GENOMICS, AND GENOME MAPPING**

The ultimate approach will be to use information from genome-mapping projects presently underway in given species. The question or problem is knowing what part of the field performance can be attributed to a given section or pattern of DNA and whether that stated field performance applies to all environments. The actual knowledge of what a given DNA pattern means for field performance is poorly understood, particularly when it comes to its mechanism or physiological mode of action, but these topics will certainly be the subject of investigation over the next few decades, possibly with some of the approaches suggested above. One of the top priority research areas listed in a 2000 meeting of soybean breeders was to identify QTLs for yield, sequence the yield genes, and then determine their function (Anonymous, unpublished report, 2000). We interpret this statement and emphasis on functional genomics as a recognition of the need for understanding the mechanism or function of the individual genes contributing to yield. Likewise, before we can really use these QTLs in a meaningful way in mechanistic crop models, we will need to understand the mechanism behind each of these QTLs. We highlight the *all environments* statement because we believe that the genes will express one way in a given environment, but differently in another.

We give several examples to illustrate the need to move beyond knowing just the QTLs or sections of DNA involved. A paper by Mian et al. (1996) illustrated that four QTLs were associated with WUE and six with leaf ash of soybean, coming from a cross of Young by PI416937. Water-use-efficiency was negatively correlated with leaf ash concentration and two of the QTLs were common. However, this study did not uncover the mechanism or the intermediate causal traits. Physiologists know that WUE (and decreased ash concentration) is associated with lower  $C_i/C_a$  ratio, caused by greater leaf internal  $CO_2$  depletion caused by more rubisco activity per unit leaf area (this could come from increased leaf N concentration, increased SLW at constant leaf N concentration [leaf N], increased allocation of total protein to rubisco or other critical enzymes). The QTLs



for WUE may act jointly on just one or two intermediate traits. Also disconcerting is the probability that the trait, SLW or [leaf N], is not constant but is life-cycle dependent and environmentally dependent. For example, SLW in soybean is known to increase progressively from early flowering to beginning seed stage, and also increases with high light, drought stress, and cool temperature. Likewise, [leaf N] may be environmentally dependent and declines during seed filling in most species; however, there may be genes that cause partial stay-green. The message here is that we need to know the mechanisms involved, so we can understand when a response should also be environmentally determined.

Molecular markers will increasingly be identified for pest resistance (Lewers et al., 1999). Modeling of different cultivars may be made easier, because the presence of markers would clearly identify a given cultivar as falling into a given resistance or susceptibility group. However, the exact effect of a pest on growth in the mechanistic crop growth model still needs to be worked out. Decreases in a plant function relative to a given disease pressure are not constant, but are a function of environment and plant growth conditions (Batchelor et al., 1993; Boote et al., 1993). Fallick et al. (2002), for example, tested which of several processes should be mimicked to be affected by soybean cyst nematode.

Grain yield is probably the most complex agronomic trait, because it is the integrated result of all the physiological processes and genetic contributions. For this reason, one should expect low contribution from any given set of QTLs for yield, considering that contribution of any given QTL may vary depending on the season, location, and environment. Orf et al. (1999) attempted to evaluate QTLs for yield and interactions between QTLs for yield in soybean. In some cases, QTLs for yield were independent of environment and did not affect maturity date or plant height. In other cases, the QTLs were stated to interact with each other (i.e., lack of additivity), the interaction being environment-specific. Lark et al. (1995) discovered that, of several loci affecting final height of soybean, variation was conditional on presence of a particular allele at a second locus that itself explained no trait variation. This implicates the action of several genes interacting. Stated another way, the phenotypic response of a given gene is influenced by the genetic background into which that trait is moved. This type of action makes it very difficult for a modeler to simply assign a certain offset for the presence of one gene when the presence or absence of a second gene determines its effect also. Specht et al. (2001) conducted analyses of QTLs associated with the slope of soybean yield response to water applied (*Beta*) and the carbon isotope discrimination (CID) ratio over a range of water regimes. The major QTLs for *Beta* and CID coincided with maturity and determinancy QTLs. Although there was a QTL for CID, it had no effect on *Beta*; thus, the authors concluded that it was best to have high sensitivity of yield to water applied, i.e., overall grand mean yield.

## THE FUTURE OF CROP MODELING RELATIVE TO CULTIVAR VARIATION

There is much potential for collaboration between crop modelers, physiologists, and plant breeders to study effects of genetic improvement in traits as simulated by crop models. Crop modelers' view of genetic coefficients must adapt to accommodate increased availability of genetic information. One of the current hot areas in molecular genetics is functional genomics. Crop modelers would benefit from such information collected by geneticists and physiologists, because the impact of a given section of DNA is not particularly predictable until the function (physiological, enzymatic, developmental, etc.) is known. We propose the molecular genetics and physiology community also needs feedback from crop modelers as well, to help them focus on the most likely plant traits to improve performance in a given environment. As modelers await further interactions and progress in functional genomics, they need to use the information that is presently available to learn about genetic improvement from past growth analyses studies, from physiological comparisons, and variety trials. Variety trials can be useful in optimization techniques to calculate coefficients to predict crop life cycle and yield potential. Crop models must continue to improve, to consider the complexity among cultivars, to consider natural feedbacks, and to fully honor the conservation and balance of energy, water, and crop C and N mass. Physiological processes need to be simulated with correct modes of action for processes, and the pleiotropic connections between traits should be honored.

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