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REGULAR ARTICLE

Predictive grain yield models based on canopy structure and structural plasticity

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ABSTRACT

Structural dimensions, digitally measured on stems and leaves of soybean plants during the first six reproductive growth stages (R1-R6), were used to assess the impact of five management strategies (combinations of cropping systems, tillage practices and crop rotations) on grain yield per plant. Stem and leaf dimensions, light penetration within the canopy [log (I/Io) x 100], fractal dimension of plant skeletal images (Do) multiplied by leaf area index (LAI), and midday differential canopy temperature (dT) explained 84.0% of variation among plant samples grown under five different management strategies, with 75-100% correct classification. Management strategies, growth stages and their interaction accounted for a total of 24-79% of variation in different structural dimensions and for 97%, 97% and 94% of variation in dT, LAI*Do, and log[(I/Io) x 100], respectively. Grain yield per plant can be predicted at R3, R4, R5 and R6 with increasing probability (R^2= 58, 64, 69 and 72%, respectively) while decreasing root mean square error of the validation models (from 2.33 at R3 to 2.1 g per plant at R6) using dT, LAI*Do, and [log(I/Io) x 100] as predictors.

Key Words: *plasticity; fractal dimension; light interception; structural dimension; grain yield.*

INTRODUCTION

Ontogenetically, crop plants react to environmental (Alados et al., 1998) and management (Weiner, 2004) factors in a complex, dynamic manner. Plant size and architecture are important factors in determining crop productivity (Vega et al., 2000); however, researchers are faced with the problem of developing reliable models for plant geometric structure and its relationship to yield and productivity, especially for plants with complex structures such as soybean (Foroutan-pour et al., 1999). One approach to solving this problem is to use fractal analysis to provide new avenues of understanding the functional implications of the branching patterns in relation to optimum space exploration by plants (Weiner, 2004). The fractal dimension (*Do*) is an effective tool for quantifying plant structure, measuring the structural response to cultural practices and modeling plant canopies (Foroutan-pour et al., 2000).

Soybean plant morphology and architecture are determined by branching and internode length (Pedersen and Lauer, 2004), whereas its growth and development are affected significantly by a cultivar-specific temperature regime (Pachepsky et al., 2004). Plant temperature will depend more on air temperature, but may differ from it due to canopy characteristics, thermal characteristics of plants and thermal conditions near the soil surface (Birch et al., 2003). It was speculated that temperature is a key environmental factor interacting with cultivars to influence yield (Pedersen and Lauer, 2003); the largest and smallest soybean grain yields were found to correspond well with the highest and lowest mean temperature during the growing season, respectively.

In the time-constrained cropping systems of the upper Midwestern USA, smaller soybean yields may be caused by longer time for the plants to reach full light interception; the lower rate of crop growth may be because of environmental stress during complete light interception or lower crop growth rate and incomplete light interception (Board, 2004). Several researchers (Singer, 2001 and references therein) showed that biomass and grain yield of soybean are significantly correlated with maximum light interception. Plastic responses of plants to light may involve a more efficient arrangement of leaf area to capture maximum available light (Semchenko and Zobel, 2005). The reproductive period, especially growth stages R1 through R5, (Pedersen and Lauer, 2004) is most sensitive to altered source strength and crop growth rate since it is the time during which important yield components are formed. The objectives of this 2-yr study were to (1) quantify the impact of management strategies on soybean's geometric distribution in space and time, and (2) predict grain yield per plant as a function of (a) midday differential canopy temperature (*dT*), fractal dimension (*Do*) and light penetration [Log(I/Io) x 100], and (b) stem and leaf structural dimensions.

MATERIALS AND METHODS

FIELD EXPERIMENT

A long-term field experiment was initiated in 2002 at the Swan Lake Research Farm located near Morris, MN (45° 41′ N, 95° 48′W, elevation 370 m) and was designed to address multiple agronomic, management, environmental, and economic objectives within the context of cropping system research. Field plots (6 x 12 m, total of 192 plots) were established in a randomized complete block design with four replications. Treatments include conventional and organic systems each with two crop rotations (corn-soybean, corn-soybean-wheat/alfalfa-alfalfa), two tillage treatments (conventional and strip-till), and two fertility treatments (no added fertilizer/manure, and fertilizer/manure applied according to soil test). A glyphosate-resistant soybean variety was used in the conventional system, whereas a non-genetically modified variety was used in the organic system. Five treatment combinations (Table 1) were selected from a total of 24 treatment combinations for this study. The CC2 management strategy represents the traditional system used by most farmers in the upper Midwestern USA (i.e., conventional system, conventional tillage, with N fertilizer as recommended by soil test and a 2-yr crop rotation). CC4 introduces wheat and alfalfa and extends the crop rotation to 4 years, CS4 replaces conventional tillage with strip tillage, OC4 is the organic system's equivalent of CC4, and OS4 is the organic system's equivalent of CS4. The land area was uniformly cropped with soybean prior to initiating the study to minimize any residual effects of any previous treatments. Historically, the site had been cropped in a corn-soybean-spring wheat rotation under conventional tillage.

Table 1. Observed level of significance in full (F), reduced (R) and single (S, with largest R^2 and smallest AIC values) variable regression models to predict (Y) midday differential canopy temperature (dT), light penetration [Log (I/Io)x100], and fractal dimension (Do) as a function of 10 plant traits (X) measured on soybean plants grown under five management strategies and sampled during six (R1-R6) growth stages.

Y	X	CC2			CC4			CS4			OC4			OS4		
		Model			Model			Model			Model			Model		
		F	R	S	F	R	S	F	R	S	F	R	S	F	R	S
		Level of significance (p) based on F-statistic (i.e., variance ratios)														
dT	SA[a]	0.12	0.03		0.73			0.77			0.05	0.05		0.02	0.01	
	SP	0.81			0.20			0.30	0.02	0.01	0.93			0.15	0.05	
	SW	0.53	0.01		0.51		0.04	0.03	0.02		0.30			0.90		
	SH	0.22	0.02		0.03	0.05		0.01	0.05		0.90			0.42		
	SC	0.25			0.03	0.02		0.52			0.20			0.26	0.03	
	LA	0.13	0.01		0.10	0.01		0.80			0.02	0.03		0.20		0.04
	LP	0.33			0.83			0.15			0.41			0.20		
	LW	0.12	0.01		0.44			0.20			0.65			0.05		
	LL	0.02	0.05		0.50			0.80	0.04		0.10	0.02		0.90		
	LC	0.02		0.03	0.02	0.05		0.65			0.05	0.02	0.02	0.90		
	R^2	74	78	39	98	98	81	81	83	61	63	66	32	71	72	28
	AIC	36	30	57	36	29	183	36	28	49	36	29	45	36	28	58
Log(I/Io)	SA	0.35			0.02	0.02		0.12	0.02		0.05	0.02	0.05	0.02	0.02	
	SP	0.30			0.85			0.35			0.05	0.01		0.45		
	SW	0.60	0.04		0.02	0.03		0.75	0.05		0.03	0.01		0.05	0.01	
	SH	0.54			0.02	0.03		0.70			0.50			0.02	0.01	
	SC	0.90			0.17			0.24	0.03		0.02	0.05		0.02	0.05	
	LA	0.44			0.03	0.05		0.15			0.15	0.04		0.03	0.03	0.02
	LP	0.57			0.03	0.04		0.53			0.46			0.05	0.05	
	LW	0.40	0.05		0.44		0.01	0.02			0.88			0.48		
	LL	0.72	0.01		0.78	0.01		0.01			0.02	0.02		0.01	0.01	
	LC	0.30	0.01	0.03	0.02	0.01		0.15		0.15	0.02	0.02		0.02		
	R^2	69	75	28	94	94	48	73	73	32	97	98	77	97	97	69
	AIC	36	26	54	36	34	210	36	29	58	36	32	232	36	34	248
Do	SA	0.30			0.03	0.03		0.44	0.02		0.05	0.03		0.02	0.02	
	SP	0.61			0.82	0.02		0.75			0.30			0.02	0.02	
	SW	0.70		0.05	0.02	0.03	0.02	0.12	0.02	0.03	0.15		0.02	0.44		
	SH	0.30			0.85			0.02	0.01		0.54	0.02		0.50		
	SC	0.14	0.01		0.25			0.33			0.98			0.75		
	LA	0.30			0.05	0.01		0.85			0.36			0.02	0.01	0.05
	LP	0.95			0.29			0.85			0.02			0.02		
	LW	0.50	0.01		0.72			0.45	0.05		0.70			0.01	0.03	
	LL	0.10			0.23	0.01		0.52	0.02		0.40	0.02		0.45		
	LC	0.05	0.03		0.55			0.02	0.04		0.05	0.01		0.83	0.05	
	R^2	90	91	76	86	88	39	75	81	46	87	87	67	84	84	46
	AIC	36	27	58	36	28	93	36	27	52	36	30	58	36	32	77
Correct classification, %		100			83.3			75.0			95.8			100		

[a] SA=stem area, SP=stem perimeter, SW, stem width, SH=Stem height, SC=Stem circularity (i.e., minimum axis/maximum axis), LA=Leaf area, LP= leaf perimeter, LW=Leaf width, LL=Leaf length, LC=Leaf circularity.

PLANT SAMPLING AND MEASUREMENTS

Five random soybean plants were sampled at each of the R1 to R6 reproductive growth stages from two replicates per management strategy in 2003 and 2004. Digital imagery procedures (Rasband, 2004) were used to capture, process, and measure images of single stems and detached leaves. Single stems were positioned on a white background so that all branches were visible, and whenever possible a 1:1 JPEG image was captured. A scale (in cm) was attached to each object (stem or leaves per plant) on a white background, and the generated image was saved with a resolution of 300 pixels. The JPEG images were processed with ImajeJ, a public domain image processing software by W. Rasband of the National Institute of Health, Bethesda, MD (http://rsb.info.nih.gov/ij/) as follows: images were first saved as TIF, background was subtracted to eliminate any noise, files were converted to 1-bit black and white using the threshold command, skeletal images were developed, then all measurements were adjusted based on the pixel-to-cm conversion scale using built-in algorithms (Rasband, 2004). The fractal analysis procedure employed the box count concept as outlined by Mandelbrot (1983) and applied by Foroutan-pour et al. (2000). Each plant or leaf image was covered by a sequence of grids made of squares decreasing in size. Two values were recorded per grid, these were: the number of squares intersected by the image, $N(s)$, and the side length of the square (s). The regression slope (Do) of the straight line formed by plotting $\log[N(s)]$ against $\log(1/s)$ in the equation: $\log[N(s)=\log(C) + Do*\log(1/s)$, where log is the natural log, C is a constant, and $N(s)$ is proportional to $(1/s)^{Do}$ (Mandelbrot, 1983), is constrained to be in the range of $1.0 \leq Do \leq 2.0$; a value of 1.0 indicates that the image is completely differentiable and that of 2.0 indicates that the image is very rough and irregular.

Biomass and grain yield were estimated at each growth stage on a per plant basis. Plant variables (area, perimeter, length, width and circularity of each leaf and stem) and fractal dimension (Do) were automatically measured by the ImageJ software and collected on a per plant basis, whereas midday differential canopy temperature (dT, i.e., the difference between midday canopy and air temperature measured by an infrared thermometer; Isla et al., 1998), leaf area index, and canopy light penetration [$\log(I/Io)$ x 100] were estimated on plot basis. Light penetration was determined according to Board (2004) by a 1-m LI-COR Line Quantum Sensor (LI-COR, Lincoln, NE) connected to a LI-1000 data logger. The extinction coefficient (k'), which is the fraction of light intercepted per LAI unit, was calculated according to Foroutan-pour et al. (2001) using the equation:

$$\log[(I/Io) \times 100] = -k' (\mathrm{LAI} \times Do)$$

to improve the description of proportional light penetration through the crop canopy (Critten, 2003). The expression $\log[(I/Io) \times 100]$ will be referred to in the rest of the article as $\log(I/Io)$.

STATISTICAL ANALYSES

Homogeneity of variances of data collected during 2003 and 2004 was confirmed using the Bartlett test before conducting statistical analyses on the normalized pooled data collected on both soybean varieties (StatSoft Inc., 2005b). Patterns of morphological similarities or dissimilarities were analyzed by analysis of variance and multivariate statistical methods (Hair et al., 1998). All subset regression models with full, reduced and single independent variables were developed to estimate dT, $\log(I/Io)$ and Do as a function of stem and leaf structural variables of plants grown under each of the five management strategies. Model selection was based on the largest R^2 and smallest Akaike Information Criterion (AIC) values calculated by the regression procedure (Payne et al., 2006). General linear models (GLM) were developed to quantify variance components in all variables due to management strategies, growth stages and their interaction. The principal components regression (PCR) analysis was used to analyze morpho-metric patterns of individual plants and to quantify possible differences among plants grown under different management strategies. PCR is a two-step method comprised of principal components analysis (PCA) and multiple linear regression (MLR) analysis. PCA is carried out on the independent variables to develop the smallest number of orthogonal principal components (PCs) that account for as much of the variation in the raw data as possible. PCs are then used in multiple linear regression of the form

$$\mathbf{Y} = \mathbf{XB}+\mathbf{E},$$

where **Y** is an '**n**' cases by '**m**' variables response matrix, **X** is an '**n**' cases by '**p**' variables predictor matrix, **B** is a '**p** x **m**' regression coefficient (β) matrix, and **E** is an error term for the model that has the same dimensions as Y. The models developed in this analysis were cross-validated by successively leaving out data one at a time, and a model was built using the remaining data points. Then, the model created was used to predict the dependent variables. Calibration and validation models were developed to predict grain yield per plant as a function of *dT*, LAI**Do* and log(*I*/*Io*) or as a function of stem and leaf structural variables at each reproductive growth stage. Root mean square errors (RMSE) and coefficients of determination (R^2) were calculated for each growth stage. RMSE was used to compare the prediction and validation errors of different PCR regression models and was based on the differences between the predicted and actual values after all the samples were held-out once. RMSE was calculated as:

$$\text{RMSE} = \sqrt{\sum_{i=1}^{n}\frac{(\hat{y}_i - y_i)^2}{n}}$$

where $\hat{y}_i$ and y_i are predicted and measured *Y*, and '*n*' is the number of samples. Statistical analyses were performed on normalized mean data values (Hair et al., 1998) for each variety and reproductive growth stage, pooled over years and replicates, then back-transformed after statistical analyses were conducted. Statistical analyses were performed using the relevant modules in STATISTICA (StatSoft Inc., 2005a), GenStat (Payne et al., 2006), and the Unscrambler v 9.6 (Camo ASA, Oslo, 2006; Esbensen, 2005) software packages.

RESULTS

MODELING CANOPY CHARACHTERISTICS

Table 1 presents levels of significance in full (F), reduced (R) and single variable (S, with largest R^2 and smallest AIC values) best regression models to predict midday differential canopy temperature (*dT*), canopy light penetration [log(*I*/*Io*)], and fractal dimension (*Do*) as functions of 10 stem and leaf structural variables. The goodness-of-fit (i.e., R^2 values) for the reduced (R) models was equal to or larger than the R^2 values for the corresponding full (F) models for all three dependent variables. Largest and smallest R^2 values for *dT*, log(*I*/*Io*), and *Do* were found in plants grown under CC4 and OC4, OC4 and CC2, and CC2 and CS4, respectively. These R^2 values were associated with the smallest AIC values as compared to the corresponding full models. Forty, 56 and 46% of all stem and leaf structural variables had a significant ($p<0.05$) impact on the variation in full models of *dT*, log(*I*/*Io*), and *Do*, respectively. For all five management strategies, more stem (12) than leaf (8) structural variables contributed to variation explained in *dT*; the respective numbers for log(*I*/*Io*) and *Do* were 15 and 13 and 11 and 12 structural variables.

Management strategies differed as to the minimum and maximum amount of variation in each of the three dependent variables explained by structural variables in the R models. For example, area, length and width of stems and leaves of plants grown under CC2 explained 78.0% of total variation in *dT*, whereas 91.0% of variation in *Do* was explained by stem circularity, leaf width and leaf circularity. Stem width was the single most important independent variable (i.e., in the S model), with the largest R^2 and smallest AIC values, in predicting *Do* of plants grown under four of the five management strategies. Leaf circularity, stem perimeter and stem width were significant, independent variables in predicting *dT*, whereas leaf width and leaf circularity were significant independent variables in predicting log(*I*/*Io*). Single stem or leaf structural variables (i.e., S models) explained significant variation in all three dependent variables; however, the R^2 values were associated with AIC values larger than those associated with the F or the R models. Plants grown under CC2 and OS4 were 100% correctly classified on the basis of their structural variables, *dT*, *Do* and log(*I*/*Io*), whereas 83.3, 75.0 and 95.8% of plants grown under CC4, CS4 and OC4 were correctly classified, respectively (Table 1).

TEMPORAL CANOPY CHARACHTERISTICS

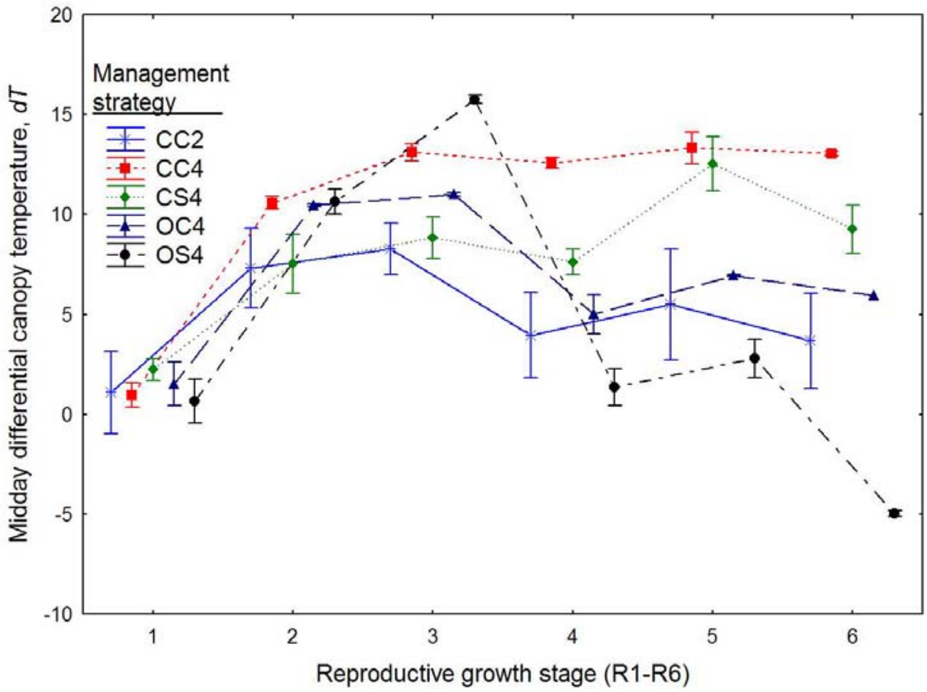
The dynamics of *dT*, log(*I*/*Io*) and LAI**Do* estimated for soybean plots and for each management strategy (Figure 1A-D) provide insights into the nature and magnitude of structural responses of plants to different cultural practices. Means (± 95.0% confidence intervals) of *dT* (Figure 1A) estimated during the six reproductive growth stages indicate that plants maintained lower midday temperatures than the air temperature between R2 and R6; however, plants grown under OS4 failed to maintain positive *dT* values between R4 and R6. Most *dT* estimates fluctuated during the R2 to R6 period, whereas plants grown under CC4 maintained steady *dT* values above 10°C. There were significant differences among *dT* estimates between R2 and R6; however, the magnitude of these differences increased with time, especially between R5 and R6. The joint estimates of LAI**Do* (Figure 1B) suggest that there was a gradual decline during most of the reproductive growth period, especially between R4 and R6. Differences among most LAI**Do* means were significant at each of the reproductive growth stages. Plants grown under the conventional system (CC2, CC4 and CS4) generally had larger LAI**Do* estimates, whereas plants grown under the organic system (OC4 and OS4) had significantly smaller LAI**Do* values, especially between R5 and R6. Canopy light extinction coefficient (*k*', Figure 1C) and light penetration, expressed as log(*I*/*Io*) (Figure 1D), represent two different quantitative descriptors of light interception by soybean plants grown under different management strategies and estimated at different reproductive growth stages. Canopy light extinction coefficient, but not log(*I*/*Io*), is proportional to LAI, hence the different dynamics expressed by both statistics. Canopy extinction coefficient ranged from a little over 0.25 to about 0.70. There were fewer significant differences among mean *k*' estimates for management strategies than those for growth stages (see below). Differences among mean log(*I*/*Io*), whether comparing management strategies or growth stages, were less dynamic as compared with mean *k*' estimates.

STRUCTURAL PLASTICITY

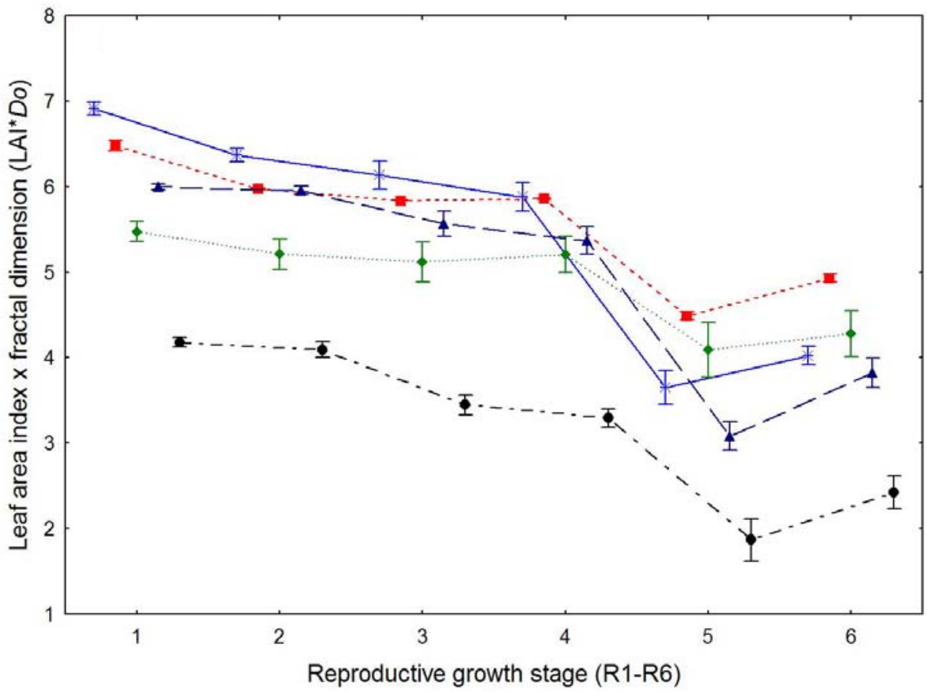
Management strategies, growth stages, and their interaction accounted for different and relatively small variances in plant structural components (R^2 ranged from 24 in stem length to 79% in stem width; Table 2) when compared to the large (94-97%) portion of variance explained in *dT*, LAI**Do*, and log(*I*/*Io*). Large and significant portions of variation in stem and leaf structural variables were accounted for by differences among management strategies (34-69%), whereas growth stages (4-34%) and their interaction with management strategies accounted for much smaller (5-17%), albeit significant, portions of this variation. Growth stages did not account for any significant variation in leaf structural variables. Leaf circularity, but not stem circularity, was stable and did not show any plasticity in response to management practices.

Management strategies, growth stages, and their interaction explained most variation (93-97%) in *dT*, LAI**Do*, and log(*I*/*Io*). Differences among management strategies accounted for the largest portion in LAI**Do* (47%) and log(*I*/*Io*) (59%). Differences among growth stages accounted for an equally large (46%) portion of variation in LAI**Do* and relatively smaller portions in *dT* (37%) and log(*I*/*Io*) (32%), whereas the interaction component between systems and growth stages accounted for a large portion (45%) of variation in *dT*. Single plant dry weight, measured throughout the reproductive growth phase, has 73 and 12% of its variance accounted for by management practices and growth stages, respectively.

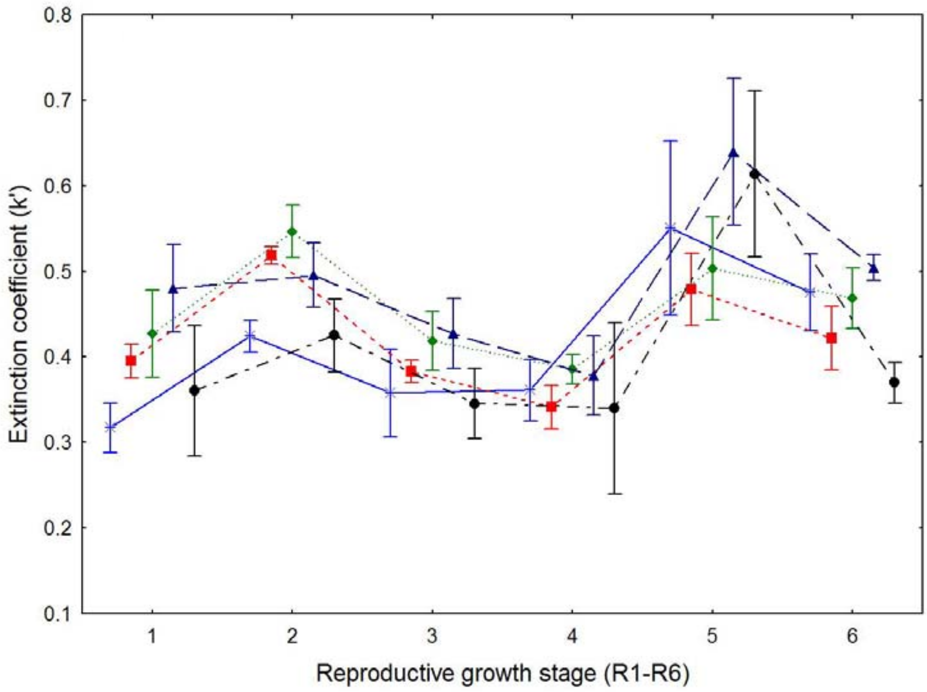
A


Management strategy
CC2
CC4
CS4
OC4
OS4
Midday differential canopy temperature, dT
Reproductive growth stage (R1-R6)
20
15
10
5
0
-5
-10
1
2
3
4
5
6

B


Leaf area index x fractal dimension (LAI*Do)
Reproductive growth stage (R1-R6)
8
7
6
5
4
3
2
1
1
2
3
4
5
6

C



D

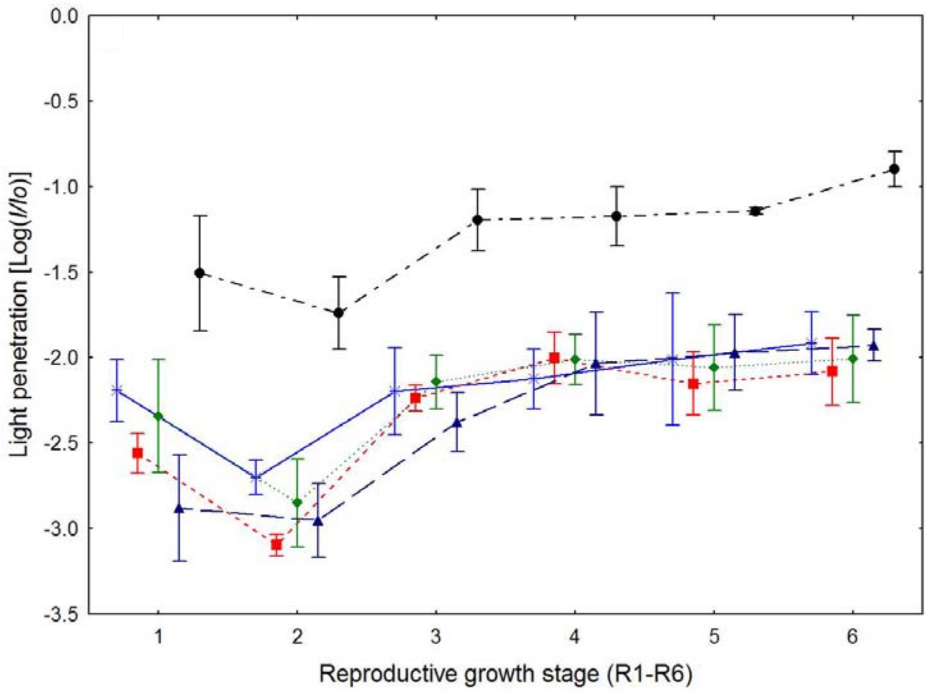


Figure 1(A-D). Mean (± 95% CI) of (A) midday differential canopy temperature, (B) leaf area index x fractal dimension, (C) extinction coefficient, and (D) light penetration measured during six reproductive growth stages (R1 to R6) on soybean plants grown under five management strategies.

Table 2. Percent significant (p<0.05) variance in 10 stem and leaf structural variables and three derived statistics accounted for by differences among five management strategies, reproductive growth stages of soybean, and their interactions.

Variable		Source of variation			Adjusted R^2
		Management strategy (MS)	Growth stage (R)	MS*R	
		Significant variance component at p<0.05			
Stem	height	35.0	4.0		24.0
	width	47.0	18.0	17.0	79.0
	area	41.0			26.0
	perimeter	67.0	13.0		75.0
	circularity	4.0	34.0		32.0
Leaf	length	45.0			33.0
	width	69.0		7.0	75.0
	area	49.0		5.0	38.0
	perimeter	47.0			47.0
	circularity				
Differential midday canopy temperature, dT		16.0	37.0	45.0	97.0
Leaf area index * fractal dimension, LAI*Do		47.0	46.0	6.0	97.0
Extinction coefficient, k'		9.0	58.0	20.0	85.0
Light penetration, log[(I/Io) x 100]		59.0	32.0	4.0	93.0
Dry weight per plant		73.0	12.0		79.0
Grain yield per plant		79.0			75.0

Grain yield per plant measured at harvest has only 69% of its variance accounted for by management strategies.

Average grain yield per plant was 7.32 g, with plants grown under CC4 producing the largest (11.2 g) and plants grown under OS4 the smallest (2.32 g) yield (Figure 2A). The combined effect of all management strategies, structural components, and derived variables explained 43.0% of variation in grain yield per plant. Larger loadings of most structural components on the (x) axis were associated with plants grown under the conventional system regardless of tillage method or length of the crop rotation, whereas negative loadings were associated with plants grown under the organic system.

The first PC accounted for 33.0 and 71.0% of total variation in the predictors (X) and predicted (Y) variables, respectively, and separated plants grown under OC4 and OS4 from those grown under the remaining three management strategies. The second PC accounted for 18 and 16% of total variation in the X and Y variables, respectively, and it resulted in little separation among plants grown under management strategies or among plants based on their structural variables as compared to PC1. On average, dT was positively (r=0.55, p<0.05) and negatively (r=–0.23, p<0.05) correlated with LAI*Do and log(I/Io), respectively, whereas a strong, negative correlation (r=–0.77, p<0.01) was found between log(I/Io) and LAI*Do, and the three-way correlation between dT and LAI*Do, log(I/Io) was positive and highly significant (r=0.56, p<0.001). Most stem and leaf structural variables, especially of plants grown under CC2, were associated with both dT and LAI*Do on PC1.

Plants grown under the traditional management strategy (CC2, Figure 2B) averaged 7.84 g per plant, with 48.0% of variance in this yield being explained by the predictors. Log (I/Io) and LAI*Do loaded on opposite sides of PC2 were significantly and negatively correlated with dT and were associated with leaf structural variables, whereas stem structural variables except stem width were associated with dT. Plants grown under CC4 produced the largest grain yield (11.22 g per plant; Figure 2C), and a much larger cumulative variance (77%) in this yield was explained by the predictors as indicated by the large loadings of most predictors on PC1. LAI*Do was negatively and significantly correlated with dT (r=–0.68, p<0.01) and with log(I/Io) (r=–0.48, p<0.05); the last two variables were positively and significantly correlated (r=0.48, p<0.05).

Grain yield per plant grown under CS4 averaged 7.89 g, with a cumulative variance of 57% being explained by the independent variables (Figure 2D). Leaf and stem structural variables except for leaf perimeter were associated with log(I/Io) and marginally with dT, whereas leaf structural variables were associated with LAI*Do. Bivariate correlations among dT, LAI*Do and log(I/Io) were similar to those found in CC4. Plants grown under the organic system with conventional (Figure 2E) or strip (Figure 2F) tillage produced the smallest grain yield per plant (5.37 and 2.23 g, respectively). Under OC4 and OS4, 50 and 60% of cumulative variance in this yield was accounted for by the independent variables, respectively; however, most of this variation was accounted for by variation among stem and leaf structural variables. A small amount of variation in grain yield per plant was accounted for by dT, LAI*Do, and log(I/Io) as measured by their loadings on PC1.

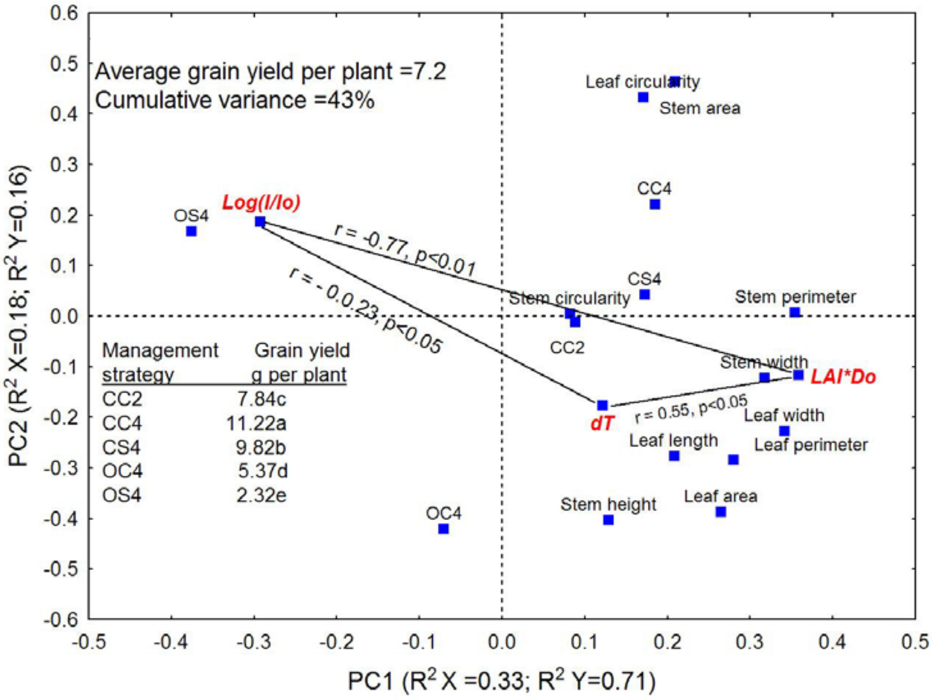
GRAIN YIELD PREDICTION

Calibration and validation regression models for grain yield (g per plant) of soybean as a function of dT, LAI*Do, and log(I/Io) (Model I) or as a function of 10 stem and leaf structural variables (Model II) measured on plants sampled during six (R1-R6) growth stages and grown under five management strategies are presented in Table 3.

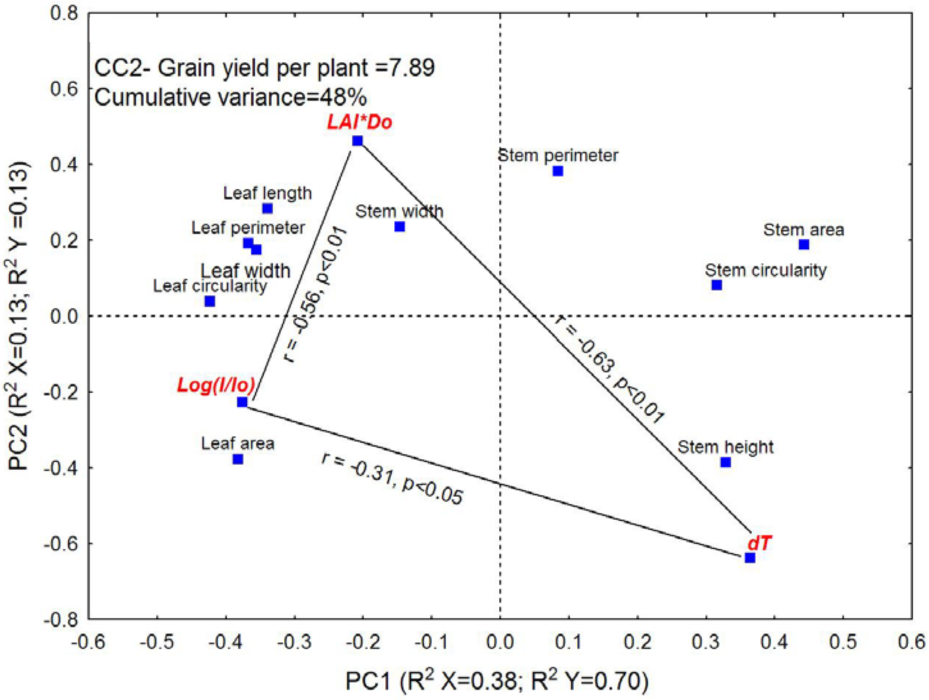
Table 3. Calibration and validation regression models to predict grain yield (g per plant) of soybean as a function of dT, LAI*Do, and log(I/Io), and stem and leaf variables measured on plants grown under five management strategies and sampled during six (R1- R6) reproductive growth stages.

Predictor	Growth stage	Calibration model				Validation model				
		r	a	β	RMSEc	R	α	β	RMSEv	R^2
Model I	R1	0.72	3.49	0.52	2.47	0.65	3.85	0.48	3.20	0.52
dT, LAI*Do	R2	0.70	3.32	0.52	2.53	0.64	3.79	0.48	2.98	0.53
and Log(I/Io)	R3	0.76	3.00	0.58	2.66	0.72	3.27	0.55	2.33	0.58
	R4	0.80	2.67	0.63	2.30	0.76	2.79	0.61	2.50	0.68
	R5	0.85	2.07	0.73	2.09	0.82	2.20	0.70	2.10	0.69
	R6	0.85	1.98	0.72	1.87	0.81	2.10	0.71	2.10	0.72
Model II	R1	0.37	6.29	0.13	3.32	0.16	8.58	0.12	4.90	0.41
Stem and	R2	0.73	3.43	0.53	2.45	0.65	3.88	0.46	2.73	0.63
leaf variables	R3	0.80	2.56	0.64	2.48	0.68	3.20	0.55	2.76	0.65
	R4	0.81	2.50	0.65	2.50	0.68	3.10	0.56	2.79	0.66
	R5	0.83	2.30	0.68	2.56	0.70	3.00	0.58	2.87	0.66
	R6	0.85	2.07	0.72	2.63	0.73	2.74	0.62	2.97	0.70

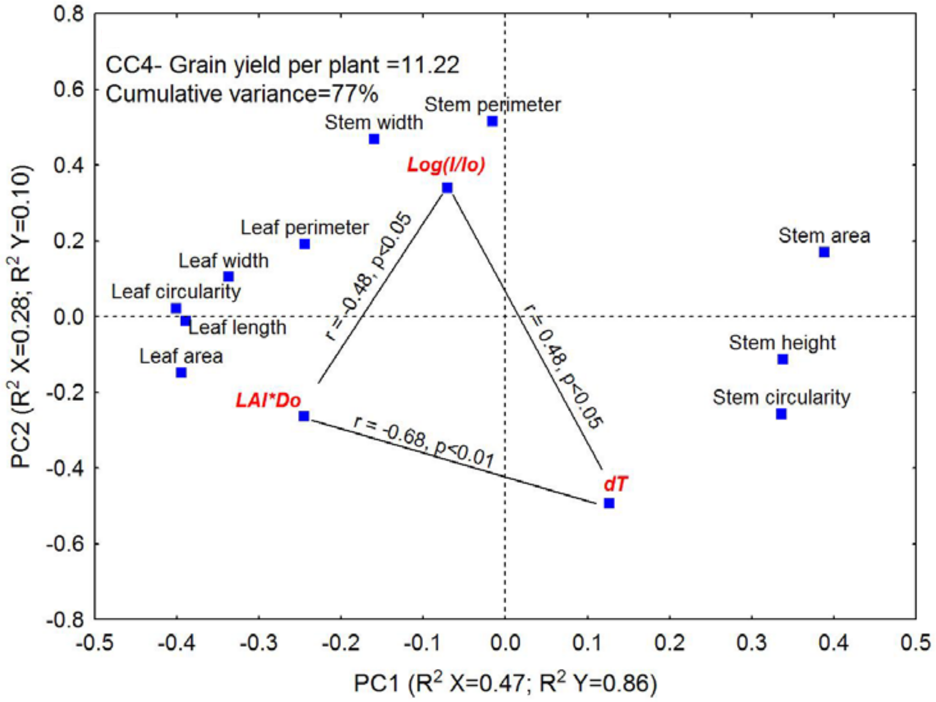
A


Average grain yield per plant =7.2
Cumulative variance =43%
Leaf circularity
Stem area
CC4
OS4
Log(I/Io)
r = -0.77, p<0.01
r = - 0.23, p<0.05
CS4
Stem circularity
Stem perimeter
CC2
Stem width
LAI*Do
dT
r = 0.55, p<0.05
Leaf width
Leaf length
Leaf perimeter
Leaf area
Stem height
OC4
Management strategy
Grain yield g per plant
CC2 7.84c
CC4 11.22a
CS4 9.82b
OC4 5.37d
OS4 2.32e
PC2 (R2 X=0.18; R2 Y=0.16)
PC1 (R2 X =0.33; R2 Y=0.71)

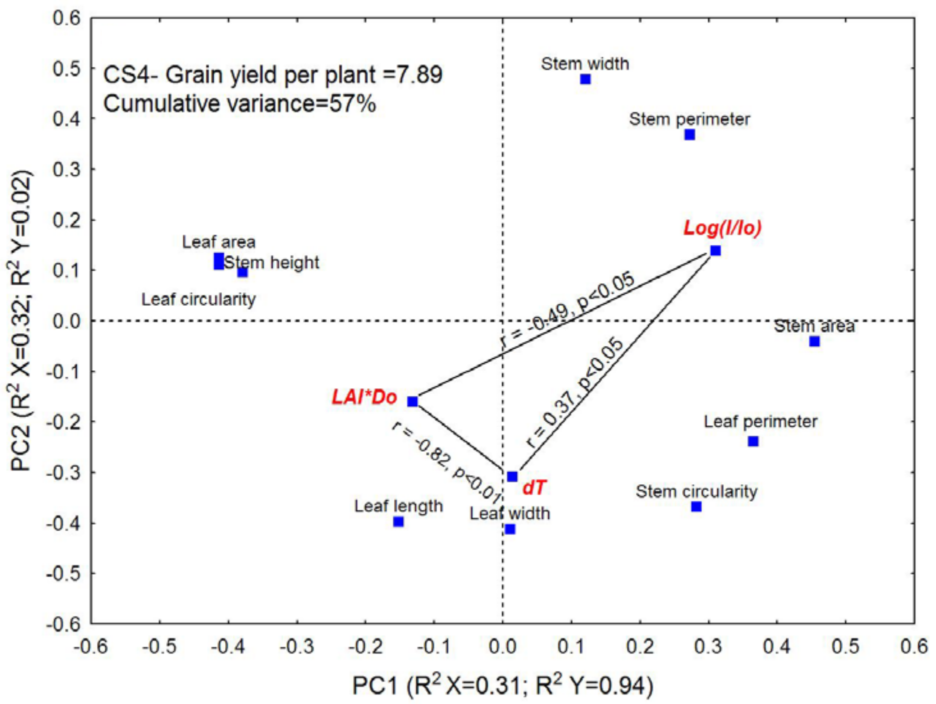
B


CC2- Grain yield per plant =7.89
Cumulative variance=48%
LAI*Do
Stem perimeter
Leaf length
Stem width
Stem area
Leaf perimeter
Leaf width
Leaf circularity
Stem circularity
r = -0.56, p<0.01
r = -0.63, p<0.01
Log(I/Io)
Leaf area
Stem height
r = -0.31, p<0.05
dT
PC2 (R2 X=0.13; R2 Y =0.13)
PC1 (R2 X=0.38; R2 Y=0.70)

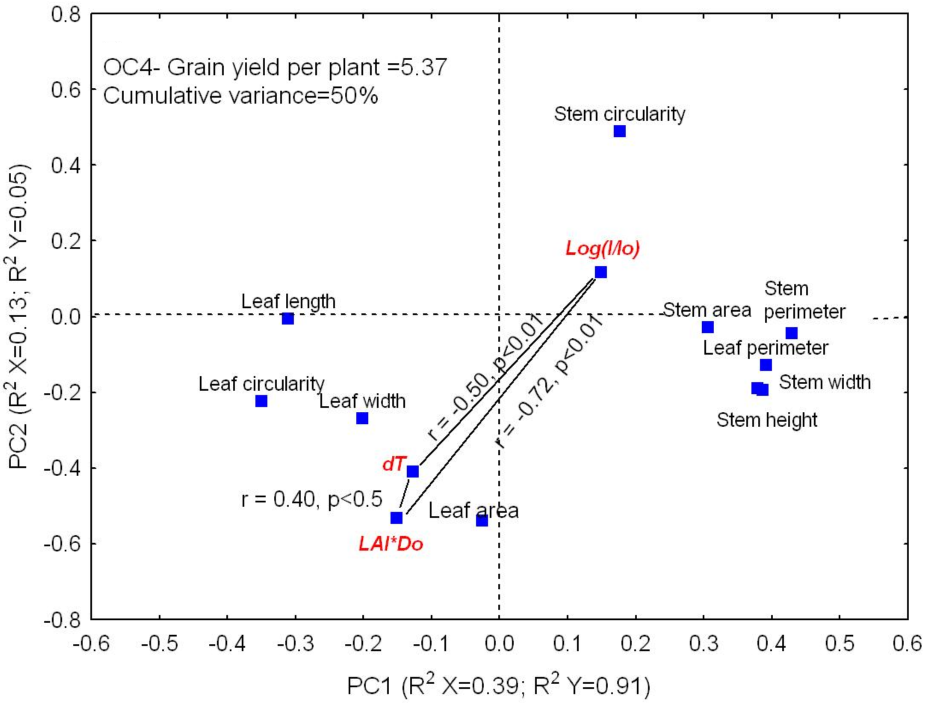
C


CC4- Grain yield per plant =11.22
Cumulative variance=77%
Stem perimeter
Stem width
Log(I/Io)
Leaf perimeter
Leaf width
Leaf circularity
Leaf length
Leaf area
Stem area
Stem height
Stem circularity
LAI*Do
dT
r = -0.48, p<0.05
r = 0.48, p<0.05
r = -0.68, p<0.01
PC2 (R2 X=0.28; R2 Y=0.10)
PC1 (R2 X=0.47; R2 Y=0.86)

D


CS4- Grain yield per plant =7.89
Cumulative variance=57%
Stem width
Stem perimeter
Log(I/Io)
Leaf area
Stem height
Leaf circularity
Stem area
LAI*Do
Leaf perimeter
dT
Stem circularity
Leaf length
Leaf width
r = -0.49, p<0.05
r = 0.37, p<0.05
r = -0.82, p<0.01
PC2 (R2 X=0.32; R2 Y=0.02)
PC1 (R2 X=0.31; R2 Y=0.94)

E



F

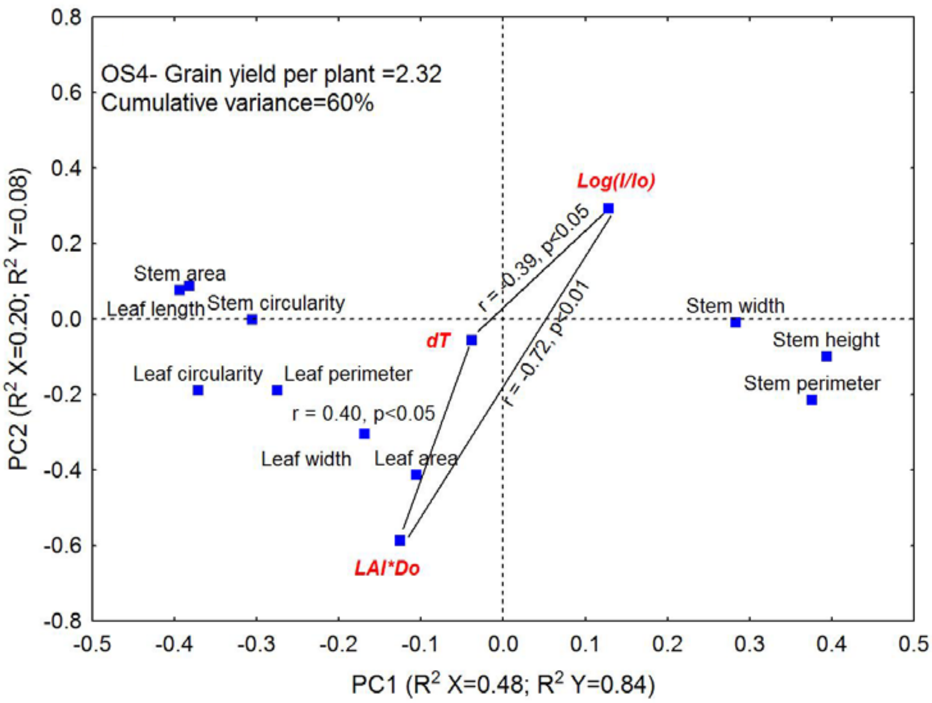


Figure 2A-F. Cumulative variance in grain yield (g per plant) and loadings on the first two principal components (PC) in a PC regression to predict grain yield per plant as a function of *dT*, LAI**Do*, log(*I*/*Io*), and 10 structural variables of soybean plants.

Correlation coefficients between measured and predicted grain yield for the calibration stage of Model I increased from 0.72 (R1) to 0.85 as the plants approached maturity (R6); the respective R values for the validation stage were smaller (0.65 to 0.81), albeit significant ($p<0.05$). Similarly, correlation coefficients for the calibration and validation stages of Model II were significant ($p<0.05$), except for the validation stage at R1 which was associated with a large root mean square error (RMSEv=4.9). RMSE values for the validation stage (RMSEv) of both models were always larger than those for the calibration stage (RMSEc), and this was reflected on the model fit as expressed by the R2 estimates (Table 3). Additionally, RMSEc and RMSEv estimates decreased as the plants approached maturity and were almost always smaller than the intercept of their respective regression models. Moreover, the slope of the regression models (i.e., the rate of grain yield increase per unit increase in the predictors) increased steadily as the crop approached maturity. The R2 estimates suggest that either model can be used to predict grain yield per plant, and that the reliability of this prediction increases as plants approach maturity.

DISCUSSION

The dynamic temporal interrelationships among stem and leaf structural variables were successfully used in developing reliable models for plant geometric structure and its relationship to yield in soybean plants, an objective considered difficult, especially for plants with complex structures (Foroutan-pour et al., 1999). Different management practices create different micro-environments where a genotype is capable of giving rise to different phenotypes (Pachepsky et al., 2004; Weiner, 2004). This environment-dependent phenotypic expression (i.e., phenotypic plasticity; Weiner, 2004) was expressed by soybean at different hierarchical levels of complexity (Table 1; Figure 2). The stem and leaf structural variables responded quantitatively in different manners to changes in management practices, impacted *dT*, LAI**Do* and log(*I*/*Io*), and provided insights into how single plants adjust their architecture, interact with their environment, and determine grain yield. Plant architecture has been shown to impact grain yield in many crops (Cheplick, 2002) including soybean (Foroutan-pour et al., 2000). Soybean plants in this study displayed a large level of structural plasticity that was expressed by all stem and leaf structural variables, but mainly by stem area and stem width. These two variables are expressions of different branching patterns and are quantified as *Do* estimates.

Large percentages of correct classification (75.0-100.0%) of plants into their original categories (i.e., management strategies under which they were grown) indicate that plants differed in both the magnitude and direction of phenological responses to contrasting cropping systems, tillage and crop rotations. Additionally, these phenotypic responses triggered significant differences among *dT*, LAI**Do*, and log(*I*/*Io*) estimates of plants grown under different management strategies. Differences among *dT* and among log(*I*/*Io*) estimates were mainly due to cropping systems, whereas differences among LAI**Do* estimates were mainly due to tillage.

Changes in *dT*, LAI**Do* and log(*I*/*Io*) were significant over time, reflecting changes in plant development. Thus, the level of complexity in skeletal structure of soybean plants increased as the stage of growth advanced. Additionally, *dT*, LAI**Do* and log(*I*/*Io*) provided a meaningful and effective tool for quantifying plant structure, measuring the structural response to cultural practices, and modeling plant canopies and grain yield. It was speculated (Pedersen and Lauer, 2003) that temperature may interact with soybean cultivars to influence grain yield; however, in this study, it was the midday differential canopy temperature (*dT*) in addition to LAI**Do* and log(*I*/*Io*) that significantly impacted grain yield, especially towards the end of the reproductive growth phase. The value of *dT* depends on air temperature, but may differ from it due to canopy characteristics, thermal characteristics and thermal conditions near the soil surface. Reliability of the predictive equations (expressed as

R^2-values) increased as the plants grew and changed the microenvironment within the canopy, and with time as suggested by Birch et al. (2003). Further evidence on how grain yield responded to adjustments in plant architecture, which in turn responded to components of different management practices, is quantified in Figure 2A. The larger grain yields per plant (7.84-11.22 g) were positively associated with LAI**Do*. The increased complexity of branch structure, which was measured by LAI**Do*, is expected (Alados et al., 1998) to enhance energy flow and nutrient cycling in plants, eventually increasing grain yield. This phenotypic plasticity is known (Semchenko and Zobel, 2005) to optimize the capture of different resources in a manner that maximizes plant growth. Trait loadings on PC1 accounted for >70% of variation in grain yield (Figure 2A-F). Cumulative grain yield variance accounted for by these traits and correlation coefficients among *dT*, LAI**Do*, and log(I/Io) provided quantitative comparisons among different management strategies. Additionally, their impact on phenotypic plasticity can be visually deduced. For example, the only difference between CC4 (Figure 2C) and CS4 (Figure 2D) is the use of strip tillage in CS4 instead of conventional tillage. Strip tillage failed to create the same "microenvironment" for single plants to fully develop as can be seen by comparing mean *dT*, (Figure 1A) and LAI**Do* (Figure 1B) of plants grown under CC4 and CS4. As a result, grain yield per plant was reduced by about 30.0%, and the cumulative variation in grain yield per plant accounted for by all variables was reduced from 77 to 60% due to strip tillage.

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