Phenotypic Plasticity and Fractal Dimension are Strong Determinants of Grain Yield in Soybean

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Abstract

We measured growth and development variables on single soybean [Glycin max (L.) Merr.] plants under five management strategies in the upper Midwestern USA. Plants grown under different management strategies differed significantly in their geometric structures, and were classified into their proper categories with 75 to 100% correct classification, based mainly on differences in their fractal dimension (Do), midday differential canopy temperature (dT), and canopy light penetration [Log(I/Io)]. A conventional system with moldboard tillage created the most ideal microenvironment for single soybean plants to develop complex geometric structures, with significantly larger Do (1.477) values and grain yield (11.2 g per plant) as compared to plants grown under an organic system with strip tillage (Do =1.358, and grain yield = 2.32 g per plant). Knowledge of how plants respond to single and multiple management strategies will help agronomists develop better predictive models and will help farmers refine management practices to optimize yield.

Introduction

Plant size and architecture are important factors in determining crop productivity [1]; 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 [2, 3]. 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 [1]. The fractal dimension (*Do*) is considered [2] an effective tool for quantifying plant structure, measuring the structural response to cultural practices and modeling plant canopies. The reproductive period, especially growth stages RGS1 through RGS5, [4] is most sensitive to altered source strength and crop growth rate since it is the time during which important yield components are formed. Changes in fractal dimension of several crops (e.g., corn and soybean) were found to be highly significant over time [2] reflecting the level of complexity in skeletal structure of single plants as the growth stages advanced. Several methods were used to quantify the relationships between soybean growth and development using growth analyses; however, limited information exists on the response of soybean's fractal dimension to management strategies. The objectives of this 2-yr study were to quantify the impact of management strategies on soybean's geometric distribution in space and time, and to predict grain yield (gm^{-2}) as a function of fractal dimension.

Materials and methods

Digital imagery [5] and analysis procedures [2, 6] were used to capture, measure, and statistically analyze several morphological traits of individual soybean plants grown under five combinations of conventional (C) or organic (O) cropping system, conventional (C) or strip (S) tillage, recommended fertilizer rate (Y) and 2- or 4-yr crop rotation (Fig.1); for example, CCY4 is the management strategy with conventional cropping system (C), conventional tillage (C), with N fertilizer based on soil analysis (Y) and 4-yr crop rotation. Light interception by plant canopy [log(*I/Io*)] and midday differential canopy temperature (*dT*) were estimated as described by Jaradat et al. [7]. The fractal analysis procedure employed the box count concept as outlined by Foroutan-pour et al. [2], where the fractal dimension (*Do*) is constrained to be in the range of $1.0 \leq Do \geq 2.0$. A value of 1.0 indicates that the image is completely differentiable and that of 2.0 indicates that the image is irregular. The principal components (PC) option in the Nonlinear Iterative Partial Least Squares module and canonical discriminant (CD) analyses were used to analyze standardized morphometric patterns of individual plants [8]. The impact of plant variables on *Do* and grain yield gm^{-2} was studied using artificial neural networks (ANNs), then the models were subjected to sensitivity analysis to evaluate the relative importance of each variable in explaining *Do* or grain yield gm^{-2}. In this analysis, each predictor was treated in turn as if it were not available in the ANN model and the average value of that predictor was used. A sensitivity ratio was calculated by dividing the total ANN error when the predictor was treated as "not available" by the total ANN error when the actual value of the predictor was used. If the ratio is >1.0, then the predictor made an important contribution to *Do* or grain yield gm^{-2}. The higher the ratio, the more important is the predictor [9].

Results

Discriminant analyses and principal components regression

Discrimination among plant samples grown under five management strategies (Fig. 1) was clearly achieved using plant structural dimensions and three derived statistics (i.e., *dT*, *Do* and log(*I/Io*). Two canonical discriminant roots (CAN) accounted for a total of 92% of total variation and discriminated among plant samples with 75.0 (CSY4) to 100.0% (CCY2 and OSY4) correct classification. CAN1 was dominated by leaf circularity (i.e., ratio of minor to major axes), leaf area, log(*I/Io*), *Do* and *dT*, accounted for the majority of variation (84%) and totally separated samples grown under organic system (i.e., OCY4 and OSY4, with 95.5 and 100.0% correct classification, respectively) from those grown under conventional system (CCY2, CCY4 and CSY4, with 100.0, 83.3, and 75.0% correct classification, respectively).

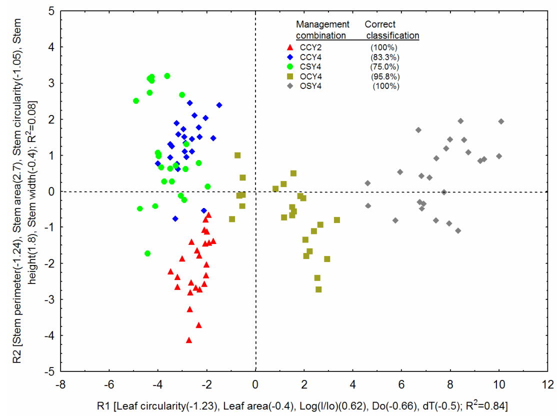

Fig. 1. Canonical discriminant analysis and percent correct classification of soybean plants grow under five management strategies and based on plant architecture.

Separation between the latter three groups along CAN2, with 8% of total variation, ranged from 75 (CSY4) to 83.3% (CCY4). CAN2 was dominated by stem-related variables and there was clear overlap between plants grown under CCY4 and CSY4, on one hand, and those grown under CCY2. The three derived statistics (i.e., *Do, dT* and log(*I/Io*) were closely associated with leaf circularity and leaf area, whereas stem structural dimensions were independent.

Slightly more than 50% of total variation in the whole data set was explained by the first two principal components (PCs; Fig. 2). Distinct separation between plants grown under organic and conventional systems was achieved on the basis of single plant characteristics, most of which were positively associated with conventional cropping system, conventional tillage and fertilizer application. Thousand-seed weight was the only variable associated with organic cropping system, strip tillage and no fertilizer treatment. Leaf area loaded on the third PC and accounted for additional 10% of total variance (data not presented). Grain yield m^{-2} was positively and closely associated with the fractal dimension, pods m^{-2}, and stem circularity, and to a lesser extent with the remaining plant structural dimensions on PC1 which explained 33% of total variation.

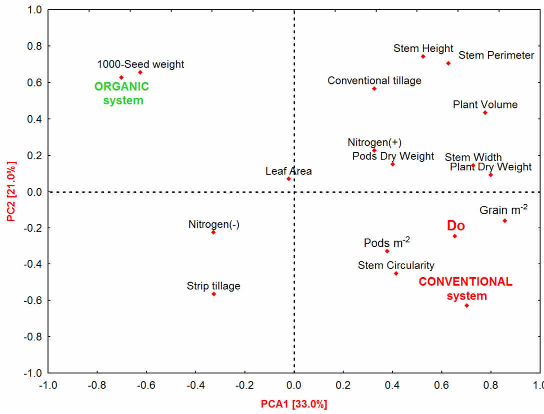

Fig. 2. Joint plot of six components of management strategies, ten soybean characteristics and the fractal dimension on the first two principal components in PC analysis.

Larger *Do* values, especially when multiplied by leaf area index (LAI), were positively associated with conventional cropping system and conventional tillage; whereas large values of *dT* and log(*I/Io*) (i.e., less light interception by plant canopy) were associated with organic cropping system (Fig. 3). The large *Do* values were loaded positively on PC1 along with most stem and leaf characteristics; however, stem width, leaf width, leaf perimeter, and stem perimeter were more closely associated with *Do* than the remaining stem and leaf structural dimensions. A cumulative variance of 43% was explained by all independent variables in the PC regression (Fig. 3).

A total of 51% of total variation in the dependent variables, accounted for by the first two PCs, explained 87% of total variation in grain yield per plant, which ranged from 2.32 (OSY4) to 11.2 g (CCY4) with significant differences among all management strategies. There were significant differences in grain yield per plant due to the tillage component, whether associated with conventional or organic systems, and due to crop rotation (2- vs. 4-yr) whether associated with conventional or strip tillage. Plants grown under CCY4 produced the largest grain yield (11.2 g), followed by CSY4 (9.82 g); whereas those grown under OCY4 and OSY4 produced the least (5.37 and 2.32 g per plant, respectively).

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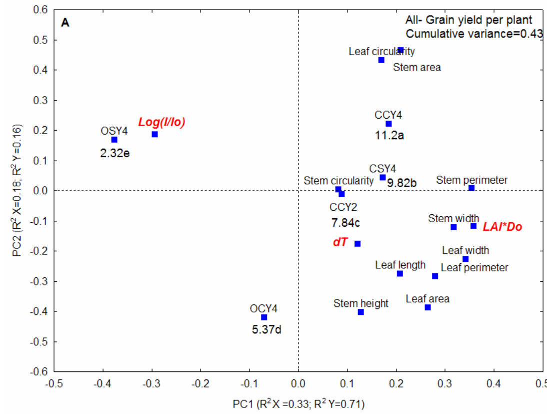

Fig. 3. Mean separation and variance in grain yield per plant accounted for by differences among management strategies and soybean characteristics as predicted by the first two components in principal components regression. Means followed by the same letter do not differ significantly at the 5% level of probability.

Neural network analyses

Calibration and validation regression models were developed to predict *Do* as a function of *dT* are presented in Table 1. Correlation coefficients (R values) between measured and predicted grain yield using *Do* as a predictor was non-significant during the first two growth stages; however, R values increased steadily from 0.74 (RGS3) to 0.96 as the plants approached maturity (RGS6); the respective r-values for the validation models were smaller (0.65 to 0.94) albeit significant ($p<0.05$); however, the validation models performed very poorly during the first two reproductive growth stages. The intercept and slope the regression models increased steadily as plants approached maturity, the intercept approaching zero and the slope approaching unity.

The MLPR neural network identified four independent variables with significant contribution in predicting both *Do* and grain yield m^2 (Table 2). Plant dry weight was an important variable in predicting *Do* and grain yield m^{-2}. A much simpler multi-layer perception neural network, with 13 hidden layers, was capable of predicting *Do* as compared to the more complex general regression neural network, with 43 hidden layers, needed to predict grain yield gm^{-2}. However, almost equal variation in *Do* (0.76) and grain yield gm^{-2} (0.79) was explained by the predictor variables (Table 2). Plant weight was the most important variable in predicting *Do*, followed by plant volume, plant circularity and plant perimeter; whereas *Do* was the most important variable, followed by plant dry weight, plant volume and plant circularity, in predicting grain yield gm^{-2}. The SD-ratios for *Do* (0.646) and for grain yield m^{-2} (0.632) were relatively similar.

Table 1. Calibration (C) and validation (V) partial least squares (PLS) regression models predicting soybean plant fractal dimension (*Do*) as a function of midday differential canopy temperature (*dT*) at six reproductive growth stages (RGS1 – RGS6, a and b are intercept and slope of regression models, respectively; *, p<0.05).

Growth stage		PLS regression model C	r	V	r
RGS1	a	1.34	0.21	1.52	-0.26
	b	0.04		-0.07	
RGS2	a	1.37	0.20	1.52	-0.26
	b	0.04		-0.06	
RGS3	a	0.68	0.74*	0.78	0.65*
	b	0.52		0.46	
RGS4	a	0.53	0.79*	0.58	0.74*
	b	0.63		0.60	
RGS5	a	0.29	0.89*	0.34	0.86*
	b	0.79		0.76	
RGS6	a	0.11	0.96*	0.14	0.94*
	b	0.92		0.89	

Sensitivity analyses

The relationship between four predictors (Table 2) and *Do* was quantified and a regression equation was developed to predict *Do* as a function of each predictor while holding each of the remaining predictors at its mean value. Plant dry weight, stem volume, stem circularity and stem perimeter (Fig. 4) displayed different, albeit large and significant, effects on *Do*. The quadratic effect of stem volume was not significant. A plant dry weight of 6-7 g is capable of producing a maximum *Do* of 1.45-1.46; however, *Do* did not respond positively to any further increases in the plant dry weight beyond this level.

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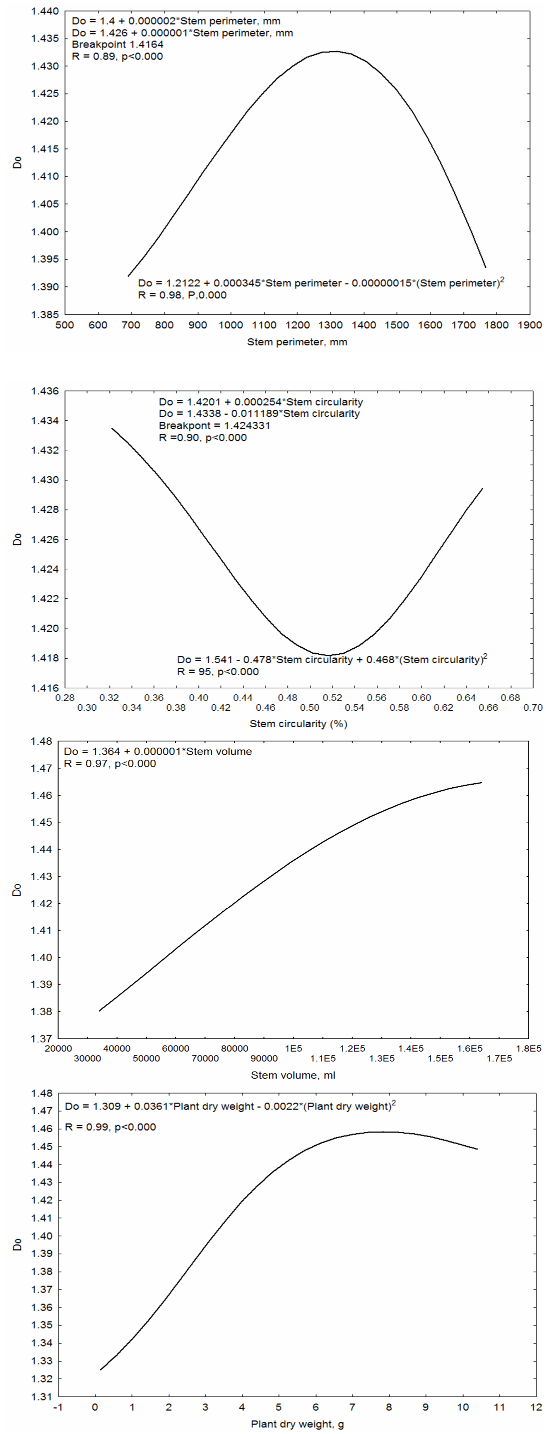

Fig. 4. Sensitivity analyses of plant dry weight, stem volume, stem circularity and stem perimeter as predictors of fractal dimension (*Do*) of soybean plants.

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Table 2. Statistics of the Multi-Layer Perception Neural Network (MLPR-NN) with 9:9-13-7-1:1 layers predicting soybean fractal dimension (*Do*), and of the General Regression Neural Network (GR-NN) with 13:13-43-2-1:1 neurons predicting soybean grain yield gm^{-2} as a function of three plant traits and the fractal dimension (*Do*).

Variable	Ratio and (rank)		Test statistics	
	Do	Grain yield, gm^{-2}	*Do*	Grain yield, gm^{-2}
Plant dry weight, g	1.572 (1)	1.599 (2)		
Plants volume	1.488 (2)	1.352 (3)		
Plant circularity	1.347 (3)	1.351 (4)		
Plant perimeter	1.141 (4)			
Do		1.732 (1)		
Mean			1.425	172.1
S.D.			0.059	56.0
S.D. Ratio			0.646	0.632
R^2			0.76	0.79

On the other hand, *Do* responded linearly to plant volume and, in a piecewise fashion, to stem circularity (i.e., ratio of minor to major axes, with a breakpoint at *Do*=1.424331) and stem perimeter (with a breakpoint at *Do*=1.4164. Similarly, a nonlinear regression equation was developed to predict grain yield (gm^{-2}) as a function of each predictor (i.e., *Do*, plant dry weight, plant volume, and stem circularity, Table 2) while holding each of the remaining predictors at its mean value (Fig. 5). Positive and significant relationships were found among grain yield and each predictor, and the nonlinear portion of the regression equations was significant except for *Do*.

Discussion

Short growing seasons in the upper Midwestern USA present serious time limitations on crop growth, in which soybean crop needs to establish and maximize canopy coverage rapidly to exploit available light [3]. Crop plants have been shown to adjust their architectural traits (Table 2) in response to management practices [2] and plant architecture, as characterized by *Do*, has been shown to impact grain yield in many crops [1].

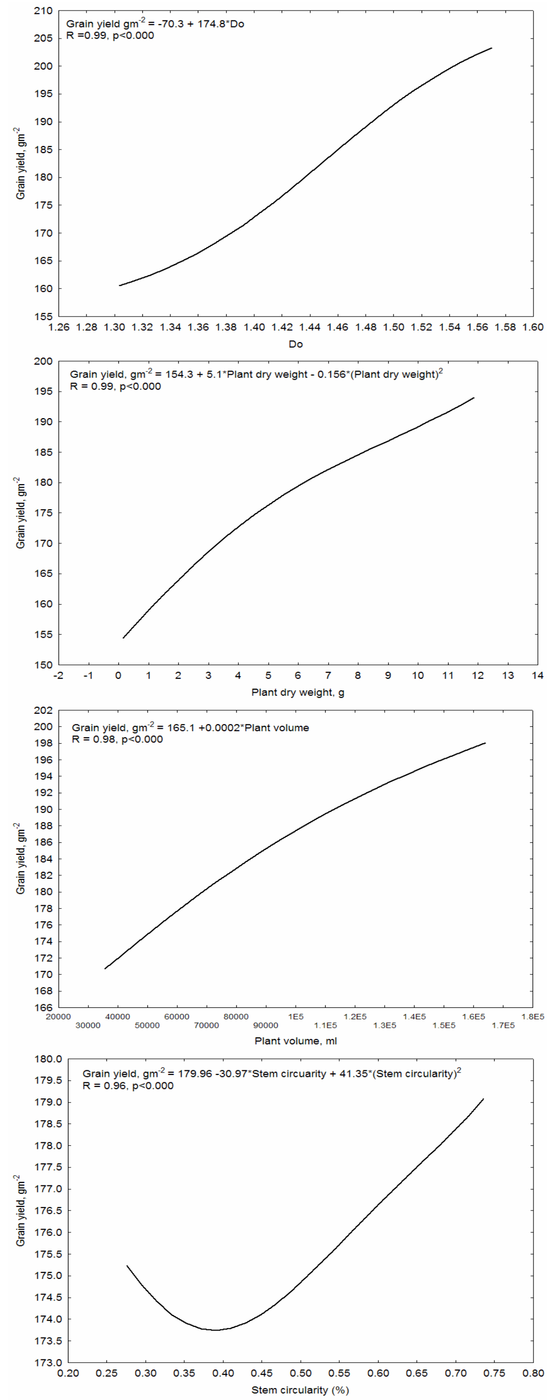

Fig. 5. Sensitivity analyses of fractal dimension (*Do*), plant dry weight, plant volume, and stem circularity as predictors of grain yield gm^{-2} of soybean.

Different management practices created a range of microenvironments in which soybean plants developed different architectures, as reflected by their *Do*, *dT* and log(*I/Io*) values and on the large percentage of correct classification (75.0-100.0%). 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 Fig. 1. The largest grain yield per plant (11.2 g) was positively associated with *Do,* conventional system, and conventional tillage, and was a result of maximum plant growth and development under the favorable conditions created by the CCY4 management strategy (Fig. 3).

The PLS regression models, especially during RGS3 to RGS6 (Table 1), succeeded in predicting *Do* as a function of midday differential canopy temperature (*dT*), the value of which depends on air temperature, but will differ from it due to canopy characteristics, thermal characteristics and thermal conditions near the soil surface [10]. Reliability of the predictive equations (expressed as r-values) increased as the plants grew and changed the microenvironment within the canopy, and with time.

The response curves generated by the ANN models provided valuable information about the relationships among grain yield m^{-2} and a set of predictors beyond the information provided by simple correlation and regression models [9]. We identified important *Do* and seed yield predictors using ANN models in an attempt to develop timely management practices that may help create optimum plant geometric structures (expressed as *Do*) capable of maximizing light interception and midday differential canopy temperature, and thus producing the largest grain yield.

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