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QUANTITATIVE DESCRIPTION OF PLANT DENSITY EFFECTS ON BRANCHING AND LIGHT INTERCEPTION IN SOYBEAN

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REDDY V. R., TIMLIN D. J. and PACHEPSKY YA. *Quantitative Description of Plant Density Effects on Branching and Light Interception in Soybean.* BIOTRONICS **28**, 73–85, 1999. The objective of this study was to quantify the effects of plant population density (PPD) on branching, light interception, and vegetative stages of soybean (*Glycine max* L.). A field study was conducted in Maryland, USA on a Beltsville silt loam soil (Fine–loamy mixed mesic Typic Fragiudult). The planting dates were 20 July 1992 and 14 June 1993. There were 10 plant densities that varied from 10 to 59 plants m^{-2}. Significant differences in plant heights among the different plant population densities were found in 1993 but not in 1992. The vegetative stage progression rates and number of branches were significantly related to PPD in both years. The internodal lengths increased with increase in PPD. Fewer branches were produced in 1992 than in 1993 at the lower PPD's and the number of branches were similar at the highest PPD's. The low PPD plants in 1992 did not have time to grow large enough canopy to capture all available light. We fit a logistic equation to the change in branch number with time. The maximum number of branches per plant as a function of PPD was described by a gaussian type equation. The fitted parameters and equations described the addition of branches.

Key words: Soybean ; Glycine max Merrill. ; Branching ; Temperature ; Light ; Vegetative development.

INTRODUCTION

Plant growth and development are largely a function of environmental conditions in addition to genetic control. Since each plant competes with its neighbors for resources, the effect of the environment is altered by the presence of neighboring plants. Row spacing and PPD determine the intensity of plant competition for resources, especially light, in row crops (*10*). As PPD increases,

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the light interception per plant decreases resulting in lower carbon fixation per plant. This reduces the plant's ability to produce new branches and potentially affects the growth rates and final sizes of plant organs, and node addition rates (*10*).

Most studies that have manipulated plant density in soybean have focused on reporting the effects of plant density or planting date on seed yield (*1, 4, 6, 9*). Plant morphological characteristics were measured mainly to explain treatment effects on yield. Soybean plant morphological characteristics that have been shown to be affected by row spacing and plant density include branch number, mainstem node number, pod number and seed number per plant (*2, 3, 7*). The numbers of these components have been shown to be decreased at high plant densities.

There is still little quantitative information on the effects of plant population density (PPD) on light interception and how light interception impacts soybean plant canopy architecture throughout the growing season, especially branching. This knowledge is necessary to predict crop response to insect damage (*12*) or weed competition. Knowledge of plant response for a range of plant densities and the ability to simulate it would be an important step towards the development of a decision support tool for farmers to use to determine the optimum planting density for a given set of conditions. The purpose of this study was (I) to quantify the relationships among PPD, light interception, and soybean plant architecture and (II) develop a mathematical description of branching and light interception as a function of plant density.

MATERIALS AND METHODS

Cultural practices

Field studies were conducted during 1992 and 1993 at the Beltsville Agricultural Research Center at Beltsville, MD on a Beltsville silt loam soil (Fine-loamy mixed mesic Typic Fragiudult). Maturity group III soybeans cv. Morgan were planted with row spacing of 0.25 m on July 20 (Day of Year (DOY) 201) and June 14 (DOY 164) respectively during 1992 and 1993. Plots were seeded in excess and hand-thinned at emergence to obtain the desired row spacings of 0.25 m, 0.51 m, 0.76 m and 1.02 m and plant populations of 10, 20 and 30 plants per meter row resulting in plant population densities (PPD) ranging from 10 to 59 plants m^{-2} (Table 1). Plots were sprinkler irrigated both years when necessary to avoid water stress. Approved herbicides were used for weed control and no cultivation was used. Weeds that escaped chemical control were removed by hand.

Experimental design and data collection

The experiment was planted in a randomized complete block design and replicated 5 times in 1992 and 4 times in 1993. Plant density was modified by varying row spacing and the number of plants per meter row. Table 1 gives the row spacings, number of plants per meter row and resulting plant densities used in the analysis.

Table 1. Arrangement of row spacing and plant densities for the study.

Row spacing	Plants per meter row		
	10	20	30
—m—		Plants m^{-2}	
0.25	39	—	—
0.51	20	39	59
0.76	13	26	39
1.02	10	20	30

Data were collected on plant height, number of vegetative and reproductive stages (Vstages and Rstages), number of branches, leaf area index (LAI) and canopy light interception non-destructively at weekly intervals during both years. The data on LAI and canopy light interception were collected using a LAI-2000 plant Canopy Analyzer[1] (LI-Cor inc., P. O. Box: 4425, Lincoln, NE 68504). Date on plant height, Vstages, Rstages and number of branches were collected on 10 different randomly selected plants from each treatment at weekly intervals.

Data analysis

Data were grouped by plants m^{-2} for statistical analysis and plant population density (PPD), was used as the independent variable. Regressions were calculated using the SAS statistical package (*13*). Slopes of the regression relationships were compared by using indicator variables in the regression (*11*). Thermal time was calculated using hourly temperatures and a base temperature of 8℃. We used a logistic type equation to describe the addition of branches over time. The equation used is:

$$Y = Y_{max} \times \frac{\left(\frac{t}{t_o}\right)^c}{1+\left(\frac{t}{t_o}\right)^c} \qquad [1]$$

Y is the number of branches, $Y_{\max}$ is the maximum number of branches at maturity, t is relative time, t_o is a relative half time factor and c is an exponent. The relative time, t, was calculated from the Day of Year (DOY) for emergence and DOY for the $R2$ stage (flowering):

$$t=\frac{DOY-T_{\text{emergence}}}{T_{R2}-T_{\text{emergence}}} \qquad [2]$$

Thus, t is 0 at emergence and is 1 at $R2$. After $R2$, t is greater than 1. When t

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[1] Trade name and company name are included for the benefit of the reader and does not imply any endorsement or preferential treatment of the product by USDA-ARS.

$=t_o$, the plant has produced half the final number of branches.

We used a Gaussian type equation to describe the maximum number of branches ($Y_{\max}$) as a function of plant population density (PPD). The equation is:

$$Y=Y_0+ae^{-\left(\frac{x}{x_0}\right)^2} \qquad [3]$$

Here Y_o is the number of branches for the highest plant population density, a and x_o are parameters. The parameters $Y_{\max}$, t_o, and c in EQ. [1] parameters Y_o, a and x_o in Eq. [3] were fit using a non-linear optimization in Sigmaplot (*14*).

Theoretical light interception was calculated as the proportion of the area occupied by a plant to the area occupied by a one meter long row at the current row spacing. The per plant light interception percentage was calculated by dividing per plot light interception by the number of plants per meter row.

RESULTS AND DISCUSSION

Plant Development

The relationship between thermal time and Vstage progression varied with plant density (Fig. 1). The slopes are all significantly different from zero (Table 2) and are significantly different from each other ($p<0.01$). The increase in Vstage with thermal time was greatest for the low population density and the slope decreased with increasing plant density. This trend was similar for both years.

The relationship between thermal time and progression of Vstages at a particular plant density also differed for the two years. A comparison between years shows that the slope for each 1993 plant density was significantly higher than the slope for the corresponding 1992 plant density ($p<0.01$). The 1993 plants achieved a higher maximum Vstage than the 1992 plants (Fig. 1) even though the period for Vstage addition was the same for both plantings (71 days from germination). In 1992, the plants continued to add Vstages after *R*2 (*DOY* 246) while in 1993, Vstage addition ceased after *R*2 (*DOY* 231).

The relationships between thermal time counted from the germination and calendar time for both years were close to linear. The following regression equations were found to fit the data with $R^2=0.99$:

Thermal time$=-2612+13.08*$ (day of the year) in 1992, and

Thermal time$=-2809+16.64*$ (day of the year) in 1993.

The year 1992 appeared to be slightly cooler than 1993 since the slope of thermal time vs calendar time is lower for 1992 than for 1993. The data also show that, because of the late planting in 1992, the crop did not accumulate enough thermal time over the 71 day growing period to achieve as high a Vstage as observed in 1993. It is likely that this is one of the reasons the maxmium Vstages were less in 1992.

Figure 2 shows the average internodal length (height divided by Vstage) for the time when Vstage and height were at their maximums. In both years the internodal length increased with increase in plant population density. A visual

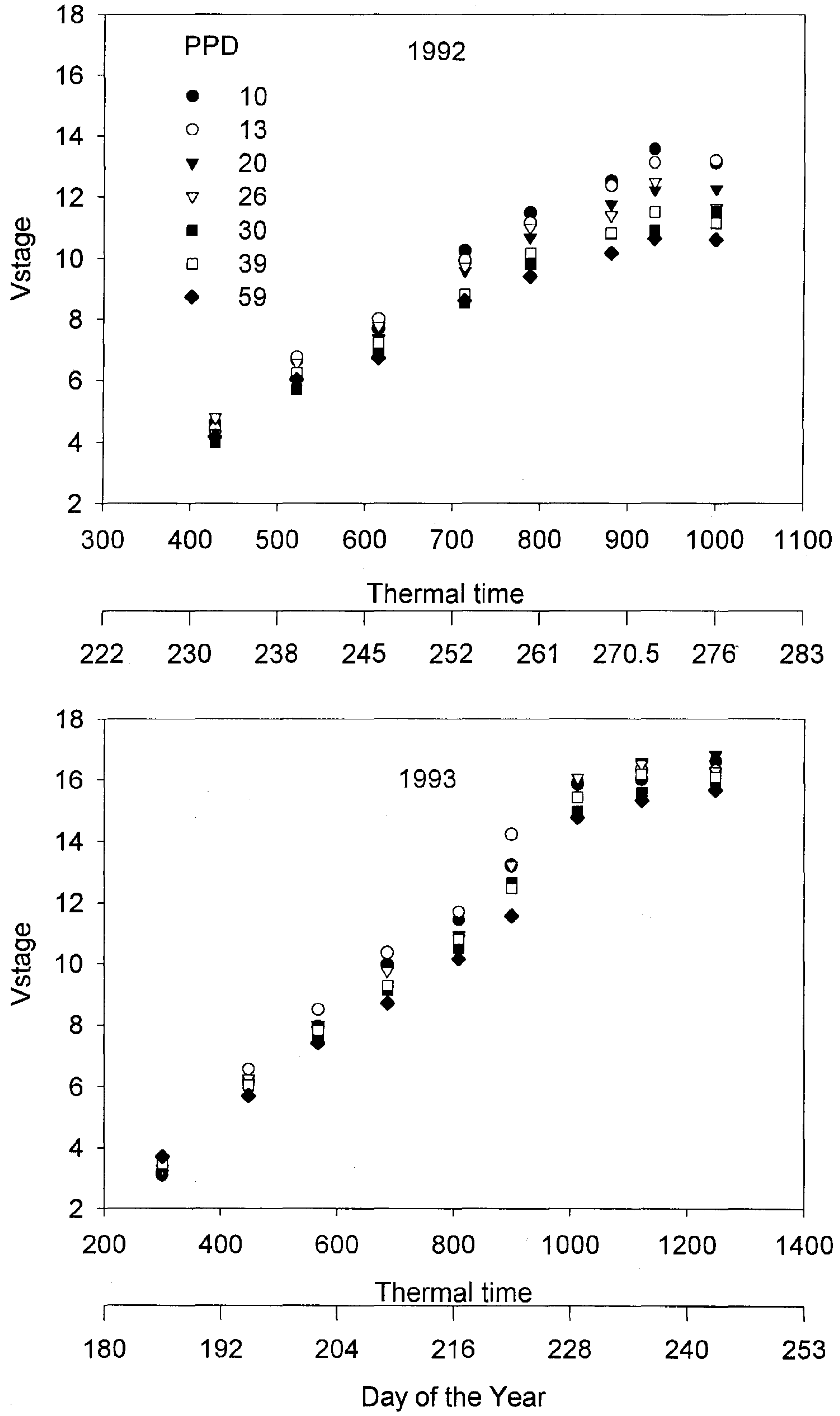

Fig. 1. The relationship between Vstage and thermal time in 1992 and 1993 for different plant population densities. Day of year (*DOY*) is given on the second X-axis for reference.

Table 2. Slopes, standard errors of slopes and error for the relationships between thermal time and Vstage for the different plant densities and planting dates.

PPD	Slope †		Error ‡	Slope		Error
	b	s_b		b	s_b	
	1992			1993		
10	0.0138**	6.03E-05	1.2	0.0146**	6.28E-05	1.1
13	0.0136**	5.27E-05	1.0	0.0152**	5.81E-05	1.0
20	0.0127**	4.16E-05	1.2	0.0145**	4.43E-05	1.1
26	0.0131**	5.95E-05	1.2	0.0144**	6.11E-05	1.1
30	0.0117**	5.42E-05	1.1	0.0138**	5.8E-05	1.0
39	0.0121**	3.27E-05	1.1	0.0140**	3.19E-05	1.0
59	0.0115**	5.06E-05	1.0	0.0133**	6.12E-05	1.0

† Units are Vstage time^{-1}
‡ Units are Vstage

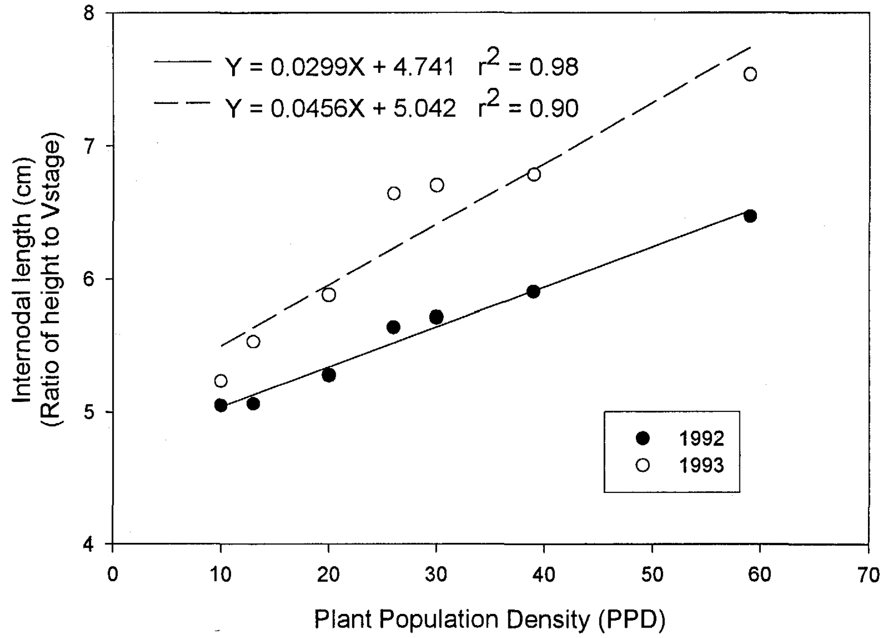

Fig. 2. Internodal length (height/Vstage) as a function of PPD for the time when Vstage and height were maximum.

inspection of Figure 2 shows that the slopes of the relationships appear different from each other. This suggests the plants did not maintain a constant relative difference in internodal lengths among PPD's for the two years. The Vstages in the late planted soybeans (1992) segregated by PPD more strongly than in 1993. This compensated for the small differences in height to result in similar relative changes in internodal length with PPD in 1992 as in 1993. The reproductive stages (Rstages) were not affected by the differences in PPD in both years (data not shown).

Branching

The number of branches per plant decreased with increased PPD. The maximum number of branches in 1992 ranged from 6 at a PPD of 10 to 3 at a PPD of 59 (Fig. 3). The average of the maximum number of branches for the growing season in 1993 ranged from 8.1 at a PPD of 10 to 2.5 at a PPD of 59, a three- fold decrease (Fig. 3). The total number of branches was generally larger in 1993 than in 1992 for a particular PPD although the differences in numbers of branches was larger for the lowest PPD's. Higher branch numbers at lower plant densities was also observed in post-optimal planting dates (*8*).

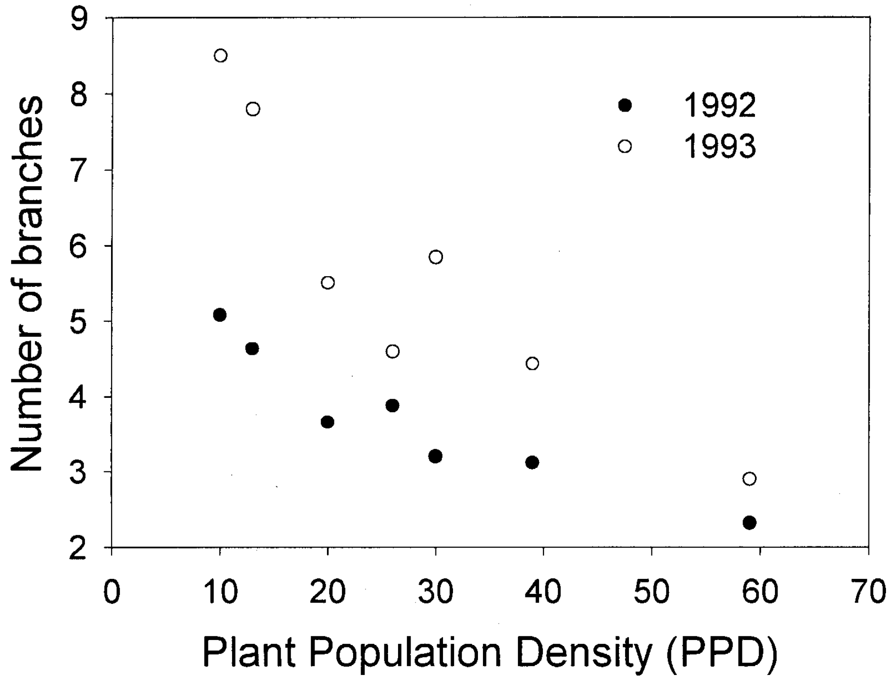

Fig. 3. The maximum number of branches as a function of plant population density for 1992 and 1993.

The timing of branch initiation varied by planting date and plant population density. In 1992, the first branches appeared rapidly over a period of 20 days for all plant densities. Few branches were added after this period except for the lowest plant densities. In 1993 the initial branches were added more slowly than in 1992 but branches continued to be added over a longer period of time (60 days in 1993 vs. 20 days in 1992). The plants were able to produce more branches in 1993 than in 1992 because there was more time available before flowering. Branch additions in 1993 appeared to be delayed until DOY 218-221 for higher PPD's. These results suggest that it took longer to accumulate enough carbon to produce a branch for the plants at higher densities.

Light Interception

Total light interception was higher during early stages of growth in the higher plant population density plots than in the low density plots (Fig. 4). The

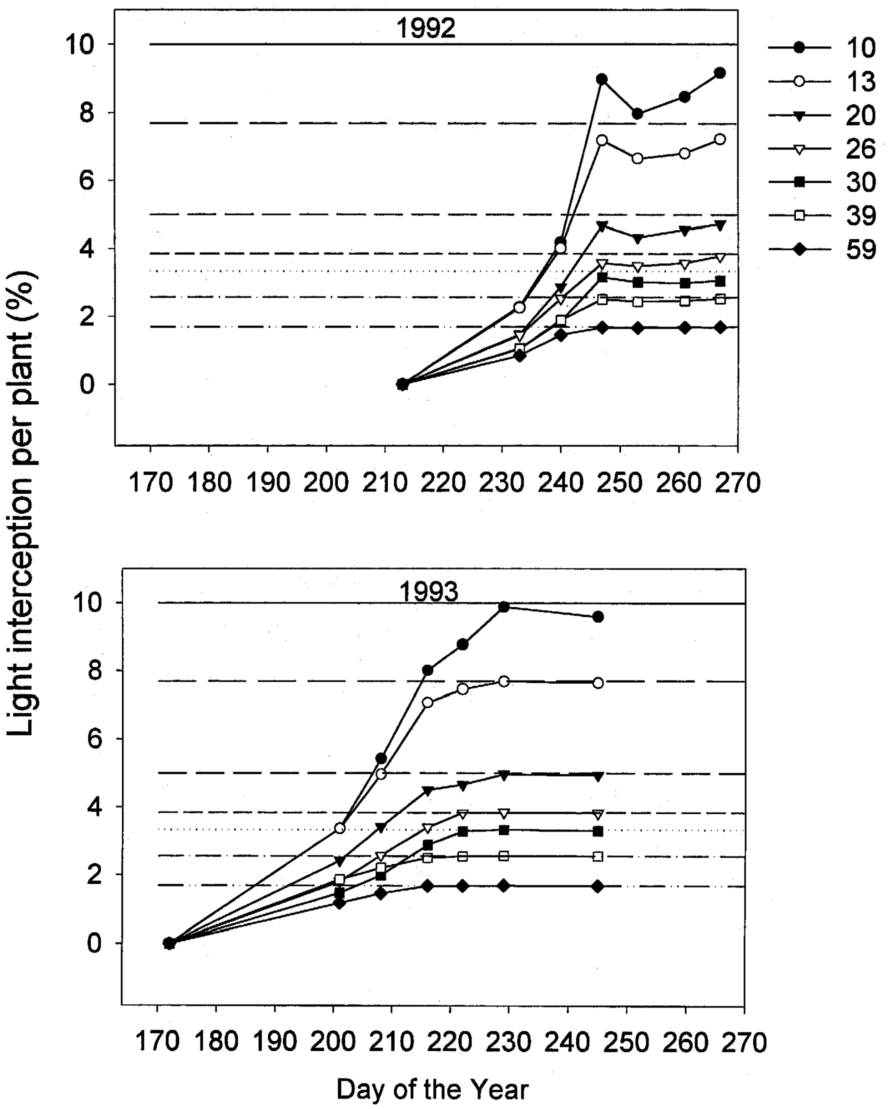

Fig. 4. Light interception (%) per plant and time for the different plant densities in 1992 and 1993. The horizontal lines indicate the maximum theoretical value of percent light interception.

maximum light interception was reached at about the same time for all the plant densities in 1992. In 1993 the two highest plant densities reached their maximum light interception about 20 days before the two lowest densities reached their maximum light interceptions. This reflects the differences in plant heights and number of branches as a function of plant density for the two years.

At the ends of the growing seasons, the 1993 plants (*DOY* 229 and 245) had significantly higher light interception than did the 1992 (*DOY* 261 and 267) plants over all planting densities except the 59 plants m^{-2} treatment ($p<0.01$). The plants reached the theoretical maximum light interception per plant at all plant densities in 1993 (Fig. 4). In 1992 the plants at plant population densities below 39 plants m^{-2} did not reach the maximum value of per plant light interception. The differences between the theoretical and measured per plant light interceptions were larger in 1992 for the more widely spaced plants.

The addition of branches for various plant densities appear to be correlated to light available to each plant (Fig. 5). The relationship was strongest in 1993. The per plant light interception (PPLI) in 1993 increased to a maximum of 9.8 % (Fig. 4 & 5) at a PPD of 10 which resulted in the production of 8.25 branches. As plant density increased to 59 the PPLI decreased to 1.57 % resulting in a decreased number of branches (Fig. 4 and 5). In 1992 the plants reached their maximum light interception with the addition of the first one or two branches. Later branch additions did not add to PPLI. The increase in PPLI with branch

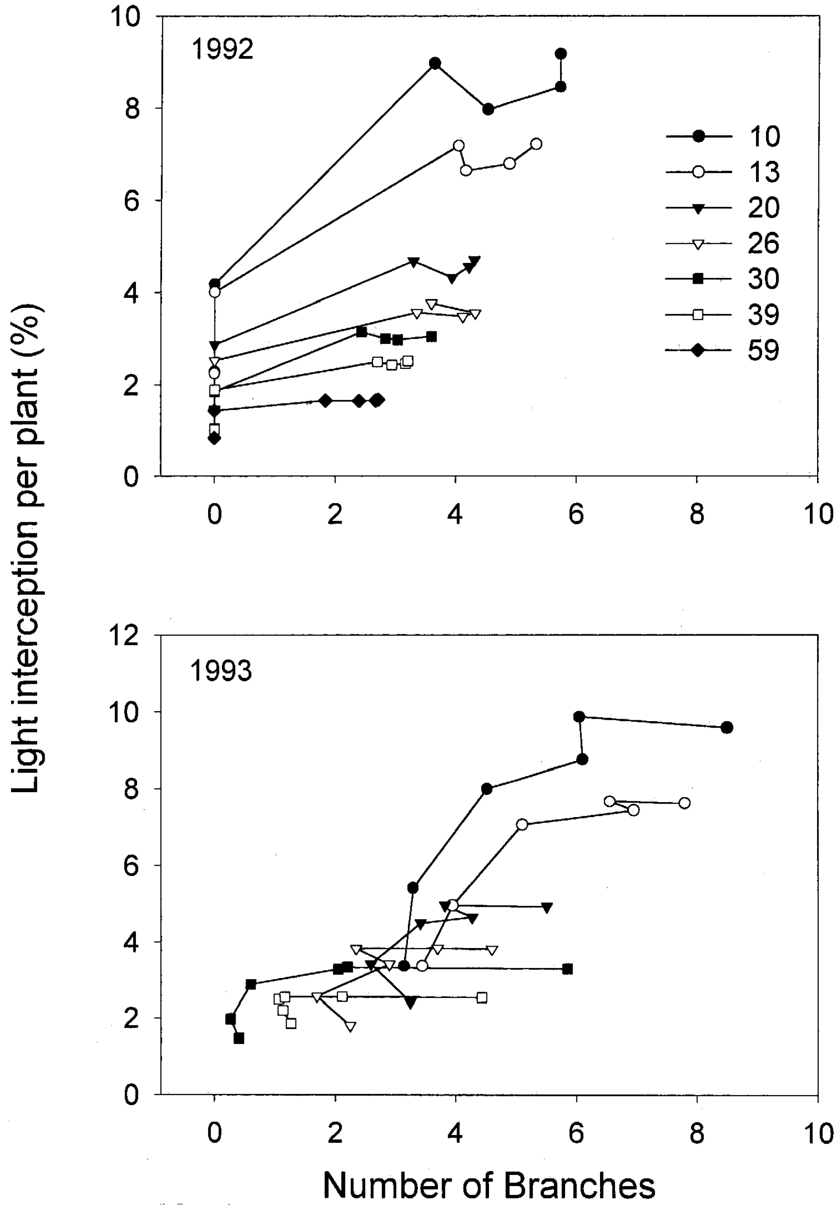

Fig. 5. Light interception per plant as a function of number of branches for the different plant population densities in 1992 and 1993.

addition was largest for the lower plant densities for both years. For the most dense plantings, addition of branches did not add substantially to the PPLI. The more widely spaced plants in 1992 did not have enough time to accumulate sufficient vegetative growth to take advantage of the increased available light.

Mathematical Description of Branch Addition

Equation [1] was used to describe the rate of addition of branches over time for the different plant population densities. Separate parameters were fit for

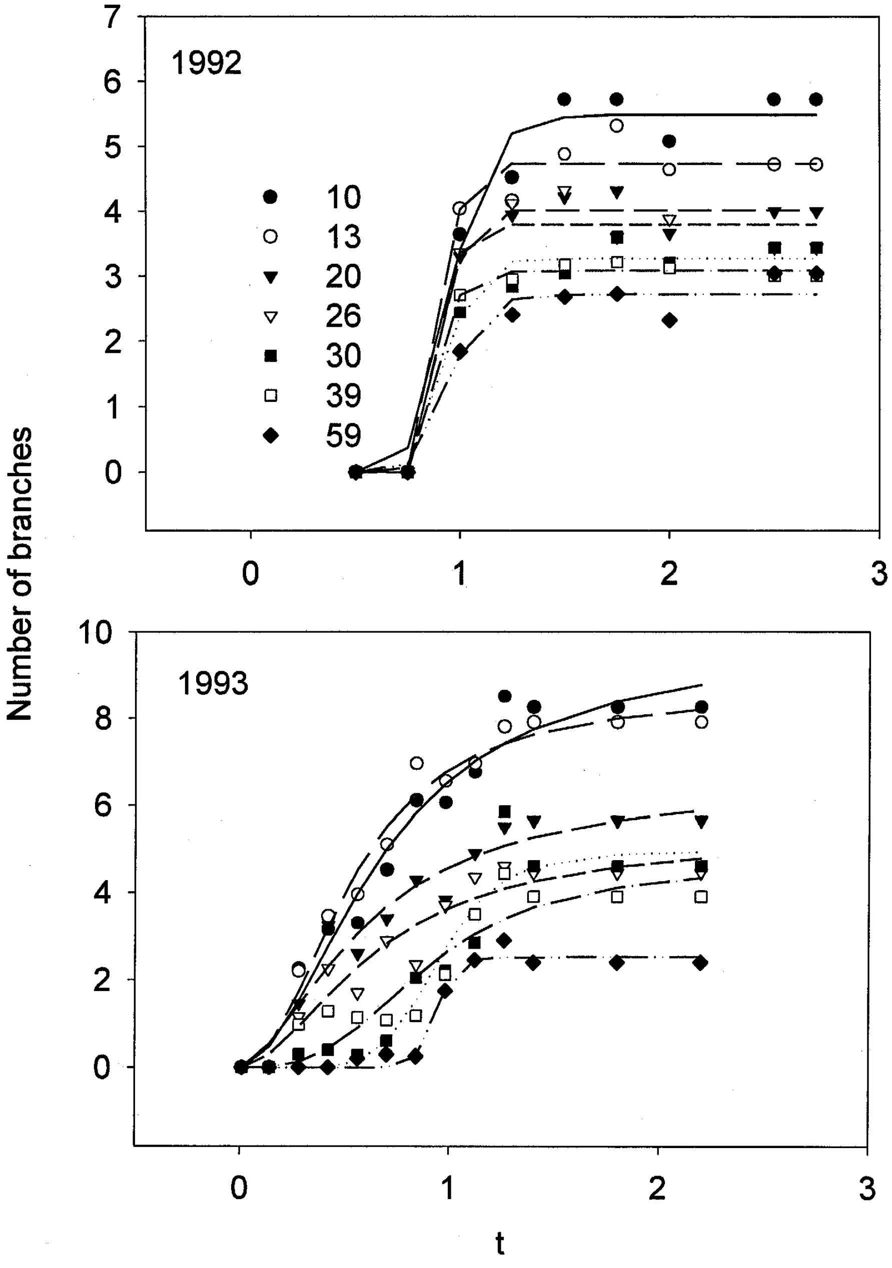

Fig. 6. The number of branches as a function of relative time with respect to $R2$ and the number of branches predicted by Eq. [1].

each plant density and each planting date. The predicted and measured branch numbers as functions of time are given in Figure 6. The fitted parameters are given in Table 3. Figure 6 shows that Eq. [1] describes the changes in branch numbers with time and plant density fairly well over both years.

Table 3. Values of parameters fit to Eq. [1]

PPD	t_o		c		$Y_{\max}$		Error	
	1992	1993	1992	1993	1992	1993	1992	1993
10	0.96±0.03	0.68±0.10	10.9±3.9	1.9±0.4	5.5±0.2	9.7±1.1	0.42	0.60
13	0.92±0.07	0.53±0.04	21.4±22.5	2.2±0.3	4.7±0.1	8.6±0.5	0.34	0.44
20	0.94±0.12	0.61±0.13	24.9±54.5	1.7±0.4	4.0±0.1	6.6±0.9	0.21	0.49
26	0.97±39.4	0.65±0.15	68.3±100	1.9±0.6	3.8±0.1	5.3±0.8	0.34	0.49
30	0.94±0.04	0.95±0.06	14.9±7.8	6.6±2.3	3.3±0.1	5.0±0.5	0.25	0.65
39	0.93±0.08	0.90±0.17	26.9±36.3	3.0±1.3	3.1±0.0	4.6±0.9	0.10	0.65
59	0.95±0.04	0.94±0.02	12.8±7.4	19.7±5.5	2.7±0.1	2.5±0.1	0.27	0.18

The parameter t_o is close to 1.0 for all plant densities in 1992 and close to 1.0 only for plant densities greater than 26 in 1993 (Table 3). The 1993 t_o is close to ~0.5 for the lower plant densities (PPD <26). When t_o is close to one, half the branches have been put on near the time for $R2$. For t_o less than one, half the branches have been put on earlier than $R2$. Our interpretation of this result is that when the crop is planted early and has more room for light interception, the plant begins to put on branches earlier and continues to put on branches for a longer time.

The parameter c was much higher for all plant densities in 1992 than in 1993 and tended to be larger for the higher plant densities in 1993. The parameter, c, is a measure of the curvature of the relationship. When the value of c is large, the number of branches increases rapidly with time as can be seen in Figure 6 for the low population densities. There was no clear relationship between the parameters c and t_o. Higher values of c, however, corresponded to values of t_o near one. This reflects the fact that when the plant is putting on branches late, the branches are added quickly.

Figure 7 shows the fit of Eq. [3] to the final branch numbers ($Y_{\max}$) fit to Eq. [1]. The fitted parameters for Eq. [3] were $Y_o=2.7\pm0.2$ and $Y_o=3.0\pm0.8$, $a=3.0\pm0.3$ and $a=7.4\pm0.6$, $X_o=23.8\pm3.0$ and $X_o=25.1\pm3.4$ for 1992 and 1993 data respectively. In both 1992 and 1993 the predicted maximum number of branches decreased with increasing plant density. Parameters Y_o and X_o were similar for both years. Only parameter a was different for the two years of data. This suggests that the effects of planting date and plant density are separable. The parameter X_o with a value of ~25 indicates that the slope of maximum branch number vs. PPD changes at a PPD of about 25 for both years of data.

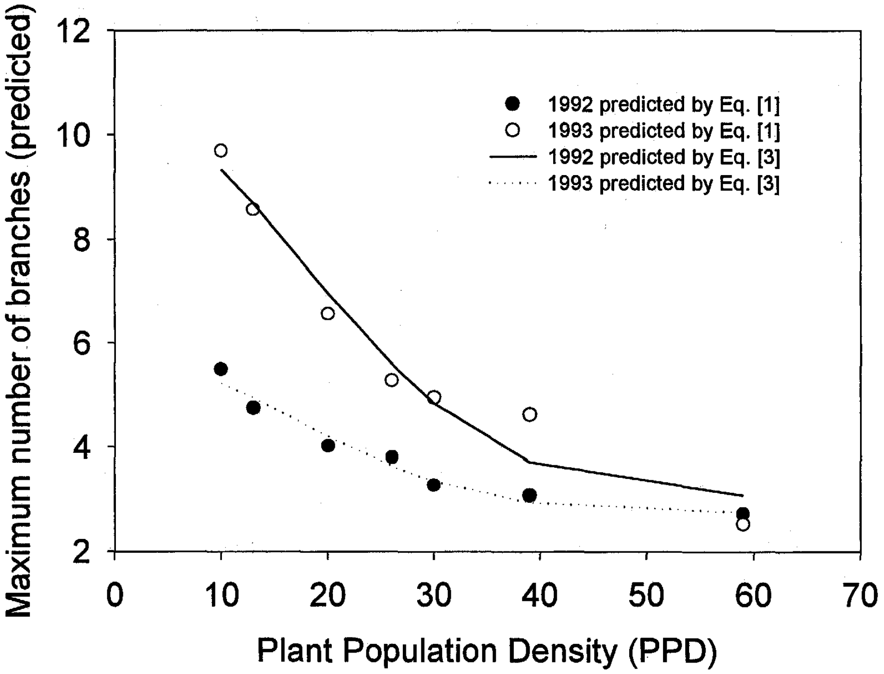

Fig. 7. The maximum number of branches ($Y_{\max}$) predicted by Eq. [1] and the fit of Eq. [3] to $Y_{\max}$ as a function of plant population density.

This is similar to the location of the change in slope for the relationship between light interception and plant density (data not shown).

We can conclude that the relative changes in maximum number of branches as a function of plant density is affected by light interception. A larger number of branches provides for more light interception at lower plant densities and allows plants to maintain yield per unit area with decrease in PPD (*4*). At the later planting date, the rate at which the maximum number of branches change with plant density decreases compared to the earlier planting date. The plants in the lower PPD's when planted late cannot take advantage of the increased available light. At the highest plant density, planting date appears to have little effect on the maximum number of branches because the early planted plants cannot intercept enough light to take advantage of the longer time available for carbon accumulation. It has been shown that shade imposed at optimal planting dates affected pod number and yield the same as defoliation (*5*).

The differences in growth and development for the two years can be attributed to the amount and quality of radiation available. Plants grown later in summer experience shorter days and less direct sunlight than plants sown earlier. This results in potentially less photosynthesis. From earlier studies, measurements of light interception and time were reported for two growing seasons (*15*), where one growing season was characterized by less radiation due to cloudy conditions. In that study plants grown during the cloudy year had lower canopy photosynthesis and the differences in photosynthesis among the row spacing treatments were greater in the cloudy year (*15*). The plants in the wider row spacing did not reach maximum levels of light interception in the cloudy year.

These observations suggest that when plants are very close to one another and there is intense competition for light, the plants are not as sensitive to changes in light quality. Because the densely sown plants are less sensitive to light quality there is less of an effect of planting date on plant characteristics. This hypothesis is supported by the similarities in branch numbers and light interception for the 59 PPD treatment over the two years.

Results of this work are applicable to modeling branching rate as a function of PPD and planting date. The maximum number of branches for a particular planting date can be modeled as a function of light interception. Parameters derived from field studies and mechanistic modeling can be used to calculate maximum branch number as a function of planting date.

REFERENCES

1. Beatty, K. D., Eldridge, I. L. and Simpson, Jr., A. M. (1982) Soybean response to different planting patterns and dates. *Agron. J.* **74**, 859–862.
2. Board, J. E. and Settimi, J. R. (1986) Photo period effect before and after flowering on branch development in determinate soybean. *Agron. J.* **78**, 995–1002.
3. Board, J. E. (1985) Yield components associated with soybean yield reductions at nonoptimal planting dates. *Agron. J.* **77**, 135–140.
4. Board, J. E., Harville, B. G. and Saxton, A. M. (1990) Narrowrow seed yield enhancement in determinate soybean. *Agron. J.* **82**, 64–68.
5. Board, J. E., Wier, A. T. and Boethel, D. J. (1995) Source strength influence on soybean yield formation during early and late reproductive development. *Crop Sci.* **35**, 1104–1110
6. Boerma, J. R. and Ashley, D. A. (1982) Irrigation, row spacing, and genotype effects on late and ultra-late planted soybeans. *Agron. J.* **74**, 995–999.
7. Boquet, D. J., Koonce, K. L. and Walker, D. M. (1982) Selected determinate soybean cultivar yield responses to row spacings and planting dates. *Agron. J.* **74**, 136–138.
8. Boquet, D. J. (1990) Plant population density and row spacing effects on soybean at post-optimal planting dates. *Agron. J.* **82**, 59–64.
9. Cooper, R. L. (1997) Response of soybean cultivars to narrow rows and planting rates under weed-free conditions. *Agron. J.* **69**, 89–92.
10. Harper, J. L. (1977) *Population biology of plants.* Academic Press, New York.
11. Neter, J. and Wasserman, W. (1974) *Applied linear statistical models.* Richard D. Irwin Inc., Homewood, IL.
12. Higley, L. G. and Pedigo, L. P. (1990) Soybean growth responses and intraspecific competition from simulated seed corn maggot injury. *Agron. J.* **82**, 1057–1063.
13. SAS Institute. (1987) *SAS/STAT Guide for personal computers.* 6th ed. SAS Inst., Cary, NC.
14. SPSS, Inc. (1997) *Sigmaplot for Windows: Transform and curve fitting.* version 4.0., Chicago, IL.
15. Wells, R. (1991) Soybean growth response to plant density: Relationships among canopy photosynthesis, leaf area and light interception. *Crop Sci.* **31**, 755–761.