HERITABILITY ESTIMATES AND CORRELATIONS OF STOMATAL RESISTANCE AND LEAF AREA IN EASTERN GAMAGRASS (*TRIPSACUM DACTYLOIDES* L.)

By

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ABSTRACT

Twenty-five male parental plants and two half sib F_1 offspring of each male parental plant were used to estimate heritability for stomatal resistance, leaf area, and plant height in eastern gamagrass, Tripsacum dactyloides L. The objective of this study was to estimate the magnitude of genetic variability of stomatal resistance and its association with leaf area and plant height. These traits are thought to influence drought resistance.

Data on stomatal resistance were taken on individual plants on 15 dates during the growing season. Two plants per plot were selected for the study and separated into two series which were alternately measured over the 15 dates. Leaf area and plant height measurements were made when the plants had matured. The heritability estimates were calculated using variance components and offspring on parent regression methods.

Heritability estimates for stomatal resistance, calculated for each date of measurement by the variance components method, were mostly zero. The estimated heritabilities calculated for each of the two series were both 0.06. The estimates obtained for each date using

regression of offspring on parent ranged from 0.57 to -0.44. An estimate of 0.21 was obtained, using the variance components method for the average resistance over the 15 dates and two series.

A significant change in stomatal aperature occurred during the approximately two hour period it took to measure the 75 plants. Generally, the stomata were opening (resistance decreasing) during this time period. Linear interpolation was used to adjust the stomatal resistance data for this change to see if it would change the heritability values but the AOV showed no significant difference from the adjusted resistance.

Leaf area had a very low heritability and plant height had a heritability and plant height had a heritability of 0.21. Variance components analysis was used to estimate these heritability values.

Genetic and phenotypic correlations indicate no close relationship between leaf area and stomatal resistance. This was also true of leaf area and height of the plant. Genetic correlation was found between height and stomatal resistance, but the phenotypic correlation was zero.

The estimates of heritability for stomatal resistance were generally very low indicating that the trait is strongly influenced by environmental factors. The major problem faced in a study of this nature was the limited time that the resistance might be stable and the number of plants that can be measured, which will still allow accurate comparisons to be made.

Additional index words: Genetic correlation, Half sib, Phenotypic correlation.

INTRODUCTION

A large portion of the world's crops and forages are grown under dryland conditions subject to periodic drought stress during the growing season. Increasing the production of crops and forages grown under these conditions is, therefore, of considerable importance and understanding the mechanisms that govern them is of vital importance (8).

Stomatal behavior has been suggested as a trait that might be genetically manipulated in breeding programs aimed at developing crop cultivars with greater water use efficiency (12). Stomatal resistance, or diffusive resistance, is a measure of the resistance of the stomata to water loss and is expressed in units of sec/cm. A higher resistance value indicated that stomata are more tightly closed. Thus, the higher values show greater resistance to water loss.

From 80 to 90% of all water vapor lost from plants is through stomatal transpiration. The size of the stomatal pore varies greatly according to the species of the plant, and among individual stomata on any one plant. They are always very minute, being measured in microns. In general, there has been no correlation found between transpiration rates and either the size or distribution of the stomata, other factors being more important (10). It is thought that plants with smaller leaf area may be more drought resistant due to less area from which to lose water.

Numerous comparisons of drought resistance have been made among species using plant properties such as stomatal resistance (4, 13). Also, intraspecific differences in stomatal behavior have been shown (1, 6), but little is known about the genetic conditioning of this trait (14).

Two major approaches to drought resistance have been used by plant breeders. First, they have assumed that a high yielding genotype under optimum conditions will also perform well under stress conditions. With this approach, breeding is directed toward yield improvement under optimum conditions. In the second approach, yield and drought resistance are considered to be separate entities with individual genetic control mechanisms. Thus, breeding requires the identification of drought resistance traits and their transfer to existing high yielding cultivars (1).

The purpose of this study was to measure stomatal resistance and leaf area in eastern gamagrass (Tripsacum dactyloides L.) and to determine heritability values and associations among traits as possible aids in breeding and selection. The specific objective was to estimate the magnitude of genetic variability of stomatal resistance and its association with leaf area and plant height.

Eastern gamagrass (Tripsacum dactyloides L.) is a robust, perennial, bunchgrass native to the central and eastern United States. It is highly palatable to all classes of livestock, and is best adapted to alluvial bottomland soils with favorable moisture conditions. Its high palatability rapidly leads to overutilization and loss of stand under grazing conditions. Consequently, natural stands are presently found only on protected sites or in well managed meadows (15).

The manuscript will be presented in a form acceptible to Crop Science Society of America for publication in it's journal, Crop Science. The same format is currently being adopted by many professional journals (5).

MATERIALS AND METHODS

Plant materials used in this study consisted of 25 male parental eastern gamagrass plants and two of their respective F_1 progenies which were half sibs (had different female parents). These male parental plants and their F_1 offspring were selected from a larger population of parental and F_1 plants used in a previous genetic study (11). The parental plants used in this and the previous studies were randomly selected from a broad germplasm base population in which many eastern gamagrass ecotypes, collected throughout the Southern Great Plains, were composited. The germplasm base is considered to be broad enough to allow the drawing of inferences about the species as a whole.

The plants were planted during May of 1976 at the Agronomy Research Station at Perkins, Oklahoma. The field plot design was a randomized complete block with four replications. The soil type was Teller loam (Udic Argiustoll). Individual plots contained 10 plants spaced 122 cm apart with 3.7 m alleys separating replications. The parental plants within plots were colonal propagules.

Leaf resistance, or stomatal resistance, to water vapor loss was estimated with a diffusive resistance autoporometer (LI-COR meter and LI-20S sensor, Lambda Instruments Company, Lincoln, Nebraska) similar to that described by Kanemasu et al. (7). When the lithium chloride coated sensor is placed on a leaf, electrical conductivity through the lithium chloride increases as water vapor is absorbed as it diffuses from the leaf. Increasing conductivity causes the meter needle to move across the scale at a rate proportional to the diffusion rate (inversely proportional to the diffusive resistance). Needle movement is timed between two preselected points on the meter face and temperature is recorded. The sensor must be dehydrated with a desicator (silica gel) after each reading.

System calibration is accomplished in the laboratory by placing a known resistance between the sensor cup and water saturated filter paper. This is done at a constant temperature of 25^{o} C. The needle movement between the preselected points is timed in seconds (Δt) and plotted as Δt vs. the known resistance values and a calibration curve is established. The field Δt can be corrected by multiplying by a correction factor corrected to 25^{o} C. (9). Field Δt can be converted to resistance values based on the calibration curve with correction factors. Stomatal resistance is, therefore, estimated from the equation:

$$x = \frac{y - b}{m}$$

where x represents stomatal resistance, y is the corrected Δt, and b and m are the y-intercept and slope of the calibration curve respectively.

The existing gamagrass plots each contained 10 plants spaced 0.91 m apart in a row. Rows were spaced about 1 m apart. The plants in the plots containing a parental entry were colonal propagules of the originally selected plant. The F_1 plants were, of course, started from seed, thus, the 10 plants within an individual plot were full siblings. Each of the 25 male parents had been crossed to two different female plants, hense, for each male there were two sets of half-sib F_1 offspring. Measurements of stomatal resistance, leaf area, and plant height were made on two plants from each of 25 male parental and 50 F_1 hybrid plots. It required four hours to measure stomatal resistance on the entire 150 plants and since it was felt that this might be excessive in terms of stomatal changes that might occur during this length of time, one of the two selected plants from each plot was assigned to "series I" with the remaining plants assigned to "series II". All of these plots were in block (replication) 1 of the nursery which had been planted in a randomized complete block with four replications. The experiment was designed to estimate heritability, therefore, replication was not needed.

Beginning May 16, 1979, stomatal resistance measurements were taken approximately twice a week through July 3rd in the following manner: measurements were alternately made on the series I and series II plants on the adaxial surface of the second leaf from the inflorescence (head) except in the early growth stages before the inflorescence had appeared. All measurements were taken approximately 9:00 to 11:00 a.m. In order to estimate the amount of stomatal change occurring during these two hour periods, the first two plants measured during a period were re-measured at the end of the period. Measurements were also begun on different ends of the nursery on an alternating basis in an effort to "average out" any stomatal resistance differences resulting from the two hour interval from first to last plant measured on a given day.

Two additional measures of stomatal resistance were made on regrowth forage (plants were mowed in July to remove old growth) in September making a total of 15 measurement dates, eight on series I and seven on series II.

Leaf area measurements were taken in June and early July when the plants were mature. The leaves were collected in the field and taken to the laboratory to be measured. A LI-COR leaf area meter (Lambda Instruments Company, Lincoln, Nebraska) was used which expresses leaf area in cm^2. The leaves for which resistance was measured were collected for leaf area determinations.

Plant height was measured in cm from the ground level to a "visually assessed" average height of the uppermost leaves. This was also done in July when the plants had matured.

Narrow sense heritability was estimated for each of the 15 measurement dates, by series over dates, and the average over series and dates for stomatal resistance and leaf area. Heritability for plant height was estimated by the average over series and dates only. The estimates were derived from variance components analysis and regression of offspring on parent using the half sib method. The heritabilities were calculated from the following formulae:

$$\hat{h}^2 = \frac{4\ \hat{\sigma}^2 m}{\hat{\sigma}^2 t}$$

$$\hat{h}^2 = \text{regression coefficient} \times 2$$

where $\hat{\sigma}^2 m$ and $\hat{\sigma}^2 t$ represent the male family and total components of variance, respectively.

The relationship among all characters was determined by computing the phenotypic, genetic, and environmental correlations among all parts based on the means.

RESULTS AND DISCUSSION

Heritability estimates for stomatal resistance, calculated for each date of measurement by the variance components method, were mostly zero (Table I). The estimated heritabilities calculated for each of the two series were identically 0.06. The estimates obtained for each date using regression of offspring on parent ranged from 0.57 to -0.44 (Table I). An estimate of 0.21 was obtained, using the variance components method for the average resistance values over the 15 dates and two series. The standard error shows that this heritability value is not significantly different than zero.

There was a significant change in the stomatal resistance of individual plants during each of the approximately two hour periods that it took to measure the 75 plants. The average difference in resistance readings taken at the beginning of a period and those taken at the end of the period for individual plants was 3.8 sec/cm with a wide range of 19.16 to -8.55 sec/cm (Table II). The magnitude of change in stomatal opening is greater when changing at low resistance as compared to changes at higher resistances, i.e. the magnitude of change is greater with a change in resistance of 4 to 6 sec/cm as compared to 12 to 14 sec/cm. Overall, the stomata were opening as the collection period progressed into the late morning. A positive difference indicated that the stomata were opening and resistance was decreasing while a negative difference indicates increasing resistance to water vapor loss and the closing of stomata. This change in resistance during the data collecting may have resulted in less accurate heritability estimates. Linear interpolation was used to adjust this change in resistance that was occurring over the data collecting periods. This was accomplished by dividing the average difference by 74 (74 of the 75 plants measured would be changing due to time) and then multiplying by the sequence of the plant being measured, i.e., 10th plant, and adding this value to the measured resistance. The AOV was not significantly different for the adjusted resistance when compared to the measured resistance.

Heritability estimates for leaf area, using the variance components method, were near zero to negative for each measurement date, series, and average over dates and series (Table III). Two leaves per plant were measured to obtain the estimate (second leaf from the inflorescence), but the leaves on each individual plant had a wide range of leaf area. Heritability estimates of leaf width in eastern gamagrass ranging from 0.32 to 0.38 have been reported (11). The heritability estimate for plant height was 0.21.

The correlations between leaf area and resistance were not significant. This was true also for the leaf area and height correlations. There was a significant genetic correlation between height and resistance which indicate that shorter plants would have higher stomatal resistance, but the phenotypic correlation was zero (Table IV).

An appendix contains the stomatal resistance data for each date and series over dates (Table V) and the leaf area data for each date, series, and the average over date and series (Table VI). Table VII contains the plant height data for each series and the average over each series.

CONCLUSIONS

The data indicate the heritability of stomatal resistance, leaf area, and plant height in eastern gamagrass to be very low. Resistance of stomata to water loss is apparently controlled by environmental factors much more than by genetic factors. A genetic correlation of intermediate magnitude and negative sign was found for stomatal resistance and plant height.

One of the problems faced in this study was the change in stomatal resistance that occurred during the two hour data collection period. The stomata tended to open as the morning progressed. The desirable number of plants to study, and the limited time in which the resistance values might be stable, demand a method in which measurements can be taken more rapidly. This might be overcome by using fewer plants or conducting the study under controlled environmental conditions or both. More accurate estimates of heritability might be obtained in this way. Heritable differences in stomatal behavior have been reported in cotton (12). The International Maize and Wheat Improvement Center (CIMMYT), El Batan, Mexico, has made some progress in selecting wheat based on leaf permeability from which stomatal resistance can be estimated. Leaf permeability can be measured more rapidly than diffusion (2, 3).

TABLE I

ESTIMATES OF HERITABILITY AND THEIR STANDARD ERRORS
FOR STOMATAL RESISTANCE BY SERIES AND DATE

Series	Date	Variance Components Method		Regression Method	
		Heritability	Standard Error	Heritability	Standard Error
I	5/24	0.28	0.93	-0.11	0.41
	6/05	0.00	0.49	-0.06	0.44
	6/08	0.00	0.79	0.10	0.26
	6/13	0.00	0.44	0.38	0.34
	6/20	0.00	0.90	0.37	0.37
	6/27	0.00	0.78	-0.21	0.46
	7/03	0.00	0.46	0.07	0.36
	9/27	0.00	0.71	0.06	0.17
II	5/16	0.00	0.73	0.00	0.31
	5/29	0.99	0.88	-0.36	0.46
	6/12	0.00	0.74	0.10	0.26
	6/19	0.00	0.57	0.57	0.28
	6/21	0.17	0.93	-0.44	0.41
	7/02	0.00	0.61	-0.05	0.30
	9/20	0.00	0.78	0.00	0.27

TABLE II

STOMATAL RESISTANCE VALUES OF INDIVIDUAL PLANTS
AT THE BEGINNING AND ENDING OF A TWO
HOUR PERIOD OF MEASUREMENT

Date	Pedigree	Series	1st Reading	2nd Reading	Change in Res.
6/08	5-1 x 5	I	16.43	4.46	11.97
	18-2 x 18		7.29	9.66	-2.37
6/12	8	II	6.09	8.94	-2.85
	5-2 x 5		8.56	4.69	3.87
6/13	8	I	14.39	14.43	-0.04
	5-2 x 5		14.69	7.94	6.75
6/19	5-1 x 5	II	7.89	7.05	0.84
	18-2 x 18		4.97	7.02	-2.05
6/20	5-1 x 5	I	26.04	6.88	19.16
	18-2 x 18		18.20	7.98	10.22
6/21	8	II	15.51	9.55	5.95
	5-2 x 5		16.34	6.05	10.29
6/27	8	I	12.24	10.82	1.42
	5-2 x 5		9.66	2.35	7.31
7/02	5-1 x 5	II	10.93	8.26	2.67
	18-2 x 18		7.63	10.60	-2.97

TABLE II (Continued)

Date	Pedigree	Series	1st Reading	2nd Reading	Change in Res.
7/03	5-1 x 5	I	19.80	12.50	7.30
	18-2 x 18		10.65	6.66	3.99
9/20	5-1 x 5	II	6.01	4.70	1.31
	18-2 x 18		17.38	6.38	11.00
9/27	5-1 x 5	I	4.43	5.48	-1.05
	18-2 x 18		5.08	13.64	-8.56

Average Change = 3.825

TABLE III

HERITABILITY ESTIMATES FOR LEAF AREA USING VARIANCE COMPONENTS ANALYSIS

Series	Date	Heritability	Standard Error
-	6-18	0.05	0.93
-	7-04	0.00	0.71
-	7-10	0.00	0.75
I	-	-0.19	-
II	-	-0.56	-

Grand Average 0.00

TABLE IV

PHENOTYPIC, GENETIC, AND ENVIRONMENTAL CORRELATIONS OF THE CHARACTERS STUDIED

Character	Leaf Area	Plant Height
Stomatal Resistance	a) 0.1483 b) undefined* c) 0.079	0.00 -0.504 -0.0189
Plant Height	0.3982 undefined* 0.3303	

a) phenotypic correlation
b) genetic correlation
c) environmental correlation

* Genetic correlation cannot be calculated because the square root of the negative variance component of leaf area used in the calculation is undefined.

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APPENDIX

TABLE V

STOMATAL RESISTANCE MEASUREMENTS FOR PARENTS AND THEIR F_1 OFFSPRING BY AND OVER PLANT SERIES AND DATES OF MEASUREMENT

Parents & Offspring	Series I								
	5/24	6/05	6/08	6/13	6/20	6/27	7/03	9/27	Average
1*	13.40	59.00	18.42	8.56	7.29	6.22	10.27	10.57	16.71
1-1 x 1**	10.25	44.12	25.33	11.61	7.52	16.18	6.70	13.91	16.95
1-2 x 1	11.38	16.89	8.85	10.78	10.49	8.72	8.26	8.53	10.53
2	16.86	11.78	13.73	11.54	7.73	6.00	4.65	3.28	9.44
2-1 x 2	15.13	8.35	9.16	16.31	7.43	9.29	9.95	8.57	10.52
2-2 x 2	16.47	17.48	22.99	16.36	15.04	7.97	19.10	8.68	15.51
3	13.42	11.22	9.83	6.31	5.09	6.88	5.35	7.08	8.14
3-1 x 3	9.40	18.11	18.44	4.43	9.29	9.20	4.25	7.98	10.13
3-2 x 3	11.02	21.99	14.63	13.31	8.94	8.59	5.00	8.09	11.44
4	26.84	12.24	22.69	12.24	7.63	9.51	2.74	9.16	10.02
4-1 x 4	11.41	18.35	8.46	16.38	8.11	9.44	11.89	12.37	12.05
4-2 x 4	10.12	30.92	14.70	10.23	9.68	9.33	6.99	10.92	12.86
5	5.65	15.20	11.41	7.62	9.27	10.23	4.58	7.52	8.92
5-1 x 5	18.93	14.39	16.43	8.54	26.04	9.66	19.80	4.43	14.77
5-2 x 5	15.63	20.34	8.96	14.69	11.34	9.66	0.16	8.15	10.09
6	22.88	13.31	11.32	13.19	9.20	4.78	6.77	7.88	11.16
6-1 x 6	6.58	86.74	13.49	14.17	14.93	9.72	6.03	11.13	20.34
6-2 x 6	26.24	17.80	8.11	9.20	8.17	7.17	6.35	5.27	11.03
7	35.62	13.10	8.59	9.92	8.43	8.43	7.29	7.50	12.36
7-1 x 7	9.53	52.68	10.82	12.31	8.43	10.10	8.91	8.31	15.13
7-2 x 7	22.87	24.37	11.08	9.94	11.65	11.32	4.21	8.30	12.96
8	21.12	8.63	7.43	14.39	9.29	12.24	7.21	11.28	11.44

TABLE V (Continued)

Parents & Offspring	Series I								
	5/24	6/05	6/08	6013	6/20	6/27	7/03	9/27	Average
8-1 x 8	48.03	19.45	9.29	6.44	11.46	13.82	6.81	10.91	15.77
8-2 x 8	8.48	16.88	11.83	24.83	11.37	7.51	4.32	13.55	12.34
9	32.72	8.02	13.10	12.51	10.23	8.54	7.54	6.36	12.37
9-1 x 9	5.89	9.46	25.68	9.42	10.56	8.57	12.55	4.24	10.79
9-2 x 9	11.33	43.42	15.61	26.49	8.87	9.31	3.60	23.64	17.78
10	20.55	29.32	12.31	7.43	7.54	8.43	7.41	7.86	12.60
10-1 x 10	10.29	9.77	17.47	9.66	4.87	8.21	10.60	12.34	10.40
10-2 x 10	4.28	16.38	20.71	14.17	10.27	13.14	7.41	9.96	12.04
11	28.93	11.10	15.11	13.67	11.91	7.71	6.16	6.68	12.65
11-1 x 11	15.82	15.94	12.46	13.25	9.59	6.13	7.34	1.60	10.26
11-2 x 11	9.69	17.04	11.78	7.62	11.35	7.16	6.13	7.50	9.78
12	13.02	18.86	20.12	9.90	8.46	9.03	6.24	4.09	11.21
12-1 x 12	7.32	12.96	14.37	6.86	7.17	9.44	3.71	9.74	8.94
12-2 x 12	12.08	13.12	10.78	20.83	7.03	15.75	7.97	4.05	11.45
13	8.96	12.55	9.99	8.02	12.50	9.27	8.02	27.44	12.09
13-1 x 13	7.80	15.59	8.59	9.24	13.31	11.56	15.26	8.09	11.18
13-2 x 13	6.57	11.19	12.86	5.74	9.02	7.60	7.43	13.55	9.24
14	17.76	9.33	11.30	7.21	12.66	7.98	11.54	30.26	13.50
14-1 x 14	10.87	16.43	12.24	8.83	16.88	6.70	9.73	11.04	11.59
14-2 x 14	41.95	23.32	8.65	11.35	11.13	7.08	6.88	7.57	14.74
15	18.47	26.14	19.62	11.24	5.74	11.80	12.48	7.88	14.17
15-1 x 15	75.29	8.11	18.15	8.57	15.57	7.54	9.53	9.87	19.07
15-2 x 15	17.79	92.89	14.04	5.92	10.89	8.54	5.68	19.50	21.90
16	11.97	15.22	14.12	16.03	7.86	5.28	2.94	9.98	10.42
16-1 x 16	19.45	11.11	12.59	10.93	8.74	13.01	5.28	5.90	10.87
16-2 x 16	14.70	75.95	13.71	7.76	9.24	8.81	7.82	11.28	18.65

TABLE V (Continued)

Parents & Offspring	Series I								
	5/24	6/05	6/08	6/13	6/20	6/27	7/03	9/27	Average
17	9.52	12.42	9.37	17.13	10.21	8.17	4.63	4.89	9.50
17-1 x 17	13.53	9.03	13.62	12.27	8.87	9.42	6.42	5.03	9.77
17-2 x 17	12.99	18.88	15.22	14.52	9.49	8.68	6.46	11.44	12.21
18	17.95	15.50	8.24	12.86	8.68	12.38	9.81	22.35	13.47
18-1 x 18	16.38	45.60	12.31	8.24	8.30	9.02	6.42	10.45	14.59
18-2 x 18	23.84	16.40	7.29	16.78	18.20	11.74	10.65	5.08	13.74
19	37.52	13.36	9.99	10.08	6.09	8.11	10.27	8.72	13.01
19-1 x 19	13.79	8.35	12.42	9.49	9.77	8.26	5.65	18.47	10.77
19-2 x 19	12.65	15.50	13.89	11.34	11.50	16.55	6.42	7.50	11.91
20	5.88	54.19	23.43	8.32	7.56	7.34	6.38	4.78	14.73
20-1 x 20	21.28	17.19	12.81	11.50	12.09	10.58	7.03	4.39	12.10
20-2 x 20	5.74	12.70	12.81	8.89	8.08	7.25	10.38	6.07	8.99
21	9.77	18.15	9.75	9.35	10.86	8.63	6.38	9.04	10.24
21-1 x 21	41.81	11.78	13.23	20.43	10.23	10.84	8.24	9.14	15.71
21-2 x 21	35.01	54.16	9.84	7.43	8.78	11.80	4.25	11.32	17.82
22	19.84	18.13	5.50	8.70	8.04	6.84	3.40	8.78	9.90
22-1 x 22	39.26	17.54	9.99	18.59	13.49	23.26	3.05	12.24	17.17
22-2 x 22	16.37	23.36	22.44	10.62	8.32	9.97	9.81	9.27	13.77
23	27.38	41.55	11.37	24.11	18.42	7.97	13.69	3.78	18.53
23-1 x 23	9.14	28.57	11.11	8.72	11.02	9.20	4.58	7.40	11.21
23-2 x 23	20.24	10.12	13.58	17.21	12.92	8.50	10.89	13.64	13.38
24	6.21	11.56	11.50	9.31	9.44	10.34	9.62	7.19	9.39
24-1 x 24	13.69	64.13	11.94	8.11	10.03	6.73	8.57	6.86	16.25
24-2 x 24	13.50	11.30	7.62	9.60	4.60	9.77	6.22	9.78	9.04
25	10.58	11.92	6.18	9.66	8.94	7.45	8.02	7.74	8.81
25-1 x 25	14.78	63.18	12.90	11.92	9.31	7.67	6.38	14.33	17.55
25-2 x 25	17.37	8.19	19.14	11.61	7.38	14.63	8.46	14.06	12.60

TABLE V (Continued)

Parents & Offspring	Series II							
	5/16	5/29	6/12	6/19	6/21	7/02	9/20	Average
1	8.48	12.05	9.46	10.03	9.09	11.19	4.59	9.27
1-1 x 1	10.96	17.70	9.77	10.65	8.56	7.21	6.90	10.25
1-2 x 2	20.89	6.32	6.70	15.70	9.83	3.25	7.72	10.05
2	8.29	11.75	9.84	10.07	9.64	5.50	9.22	9.18
2-1 x 2	9.24	7.94	11.11	13.56	11.89	12.77	6.29	10.40
2-2 x 2	6.48	8.37	6.35	23.49	5.00	13.02	12.67	10.76
3	6.06	36.46	14.48	12.26	9.25	5.24	4.97	12.67
3-1 x 3	10.29	8.24	7.86	9.75	7.05	6.07	5.85	7.87
3-2 x 3	6.31	4.88	10.69	9.90	7.47	7.84	6.13	7.60
4	16.26	12.68	6.35	12.20	5.98	10.73	9.38	10.51
4-1 x 4	10.35	11.87	9.38	9.90	9.03	7.29	4.10	8.84
4-2 x 4	7.43	11.24	7.92	18.85	12.90	12.18	2.89	10.48
5	11.46	16.83	15.90	14.50	5.11	8.79	2.70	10.75
5-1 x 5	20.10	99.99	8.89	7.89	7.84	10.93	6.01	23.09
5-2 x 5	6.13	7.73	8.56	9.24	16.34	6.64	4.26	8.41
6	4.01	12.62	6.86	10.88	11.83	2.94	8.15	8.18
6-1 x 6	10.03	15.52	10.30	16.43	11.41	8.00	7.21	11.27
6-2 x 6	21.06	20.79	21.31	9.59	9.68	5.52	9.35	13.90
7	13.49	15.16	6.44	14.08	8.63	11.13	8.10	11.00
7-1 x 7	12.01	15.44	10.07	12.88	8.79	9.25	4.44	10.41
7-2 x 7	6.22	13.15	6.97	16.18	12.74	10.01	11.75	10.98
8	19.23	12.40	6.09	10.43	15.51	11.41	3.56	11.23
8-1 x 8	15.88	9.21	10.95	8.30	14.35	4.87	4.70	9.75
8-2 x 8	10.55	31.52	10.21	13.54	16.07	14.93	10.21	15.29
9	16.44	5.87	6.44	9.22	17.70	5.92	5.06	9.52
9-1 x 9	14.28	7.03	11.69	10.43	5.63	9.03	5.90	9.14
9-2 x 9	9.43	9.66	9.75	8.68	9.48	7.38	4.44	8.40

TABLE V (Continued)

Parents & Offspring	Series II							
	5/16	5/29	6/12	6/19	6/21	7/02	9/20	Average
10	8.78	8.67	8.81	10.16	11.43	9.29	3.98	8.73
10-1 x 10	9.49	8.80	11.83	18.66	6.09	7.78	5.33	9.71
10-2 x 10	9.03	7.79	5.79	9.49	6.60	5.92	8.43	7.57
11	8.02	8.11	11.80	13.05	9.53	9.48	9.44	9.91
11-1 x 11	8.33	49.32	9.11	9.88	11.24	3.95	5.68	13.93
11-2 x 11	9.78	54.03	11.59	10.01	10.69	9.40	8.83	16.33
12	10.55	8.08	5.72	13.80	8.63	8.78	5.59	8.73
12-1 x 12	10.99	6.36	7.54	9.75	16.53	7.38	3.63	8.88
12-2 x 12	16.06	3.78	6.68	10.40	9.97	4.65	3.82	7.90
13	11.22	9.00	14.52	18.66	10.97	6.94	12.35	11.95
13-1 x 13	6.13	8.77	11.35	8.56	7.38	9.18	4.11	7.92
13-2 x 13	10.93	4.66	14.48	10.64	8.54	6.94	6.90	9.01
14	16.95	4.92	9.64	23.49	8.32	2.72	3.97	10.00
14-1 x 14	6.06	31.13	7.56	14.25	13.05	10.84	7.87	12.96
14-2 x 14	9.20	47.53	7.67	14.74	15.59	9.31	3.89	15.41
15	9.55	52.63	3.92	14.65	9.14	7.58	4.75	14.60
15-1 x 15	8.69	11.93	9.77	14.35	8.72	8.43	4.89	9.54
15-2 x 15	16.27	5.38	12.70	21.26	8.83	10.80	4.13	11.33
16	15.34	21.26	7.21	8.17	7.56	10.88	6.75	11.02
16-1 x 16	12.66	14.27	8.68	11.67	4.52	5.96	3.20	8.70
16-2 x 16	8.78	9.69	17.72	11.76	8.24	10.23	7.52	10.56
17	8.56	11.36	7.93	11.50	7.43	8.78	6.37	8.84
17-1 x 17	10.07	7.41	5.59	21.59	12.22	12.72	3.83	10.49
17-2 x 17	5.64	8.61	12.00	9.95	15.00	6.97	4.90	9.01
18	10.90	9.30	10.49	11.85	14.61	6.48	8.40	10.29
18-1 x 18	6.76	7.38	16.60	12.88	6.81	9.83	5.44	9.30
18-2 x 18	5.43	19.83	9.09	4.97	15.02	7.63	17.38	11.33

TABLE V (Continued)

Parents & Offspring	Series II							
	5/16	5/29	6/12	6/19	6/21	7/02	9/20	Average
19	7.98	9.95	6.82	19.40	9.02	7.82	4.18	9.31
19-1 x 19	7.81	7.70	7.29	9.02	2.31	8.63	3.71	6.63
19-2 x 19	11.20	10.52	6.13	16.08	11.57	9.07	9.36	10.56
20	2.51	9.88	7.34	26.03	13.04	8.37	7.52	10.67
20-1 x 20	8.30	11.97	20.76	6.82	7.87	5.98	4.13	9.40
20-2 x 20	8.12	24.27	5.68	34.77	9.62	8.46	6.90	13.97
21	8.46	9.43	17.10	9.75	7.43	7.21	2.07	8.77
21-1 x 21	8.79	7.59	11.06	9.03	2.31	4.34	10.18	7.61
21-2 x 21	18.49	12.03	8.11	11.76	11.10	10.80	6.98	11.32
22	9.49	9.11	17.70	13.86	6.86	6.48	1.37	9.26
22-1 x 22	7.94	18.02	11.19	11.15	16.25	4.56	6.55	10.80
22-2 x 22	11.76	10.66	14.48	10.43	5.63	9.37	5.41	9.67
23	10.16	8.80	5.37	10.32	6.13	6.75	4.45	7.42
23-1 x 23	17.78	5.85	9.99	9.22	10.16	8.68	10.24	10.27
23-2 x 23	13.95	19.87	11.26	15.62	29.47	6.75	5.90	14.68
24	7.09	15.14	9.92	8.41	13.75	11.89	5.43	10.23
24-1 x 24	7.42	7.41	6.82	9.46	6.77	5.78	5.94	7.08
24-2 x 24	8.76	11.50	10.49	10.84	8.35	13.16	6.29	9.91
25	9.17	5.22	7.73	27.89	7.56	8.48	12.35	11.20
25-1 x 25	5.41	7.05	6.66	26.12	8.00	8.65	8.52	10.05
25-2 x 25	20.21	14.27	7.80	9.40	8.39	7.49	7.29	10.69

* Single number represent male parent.
** Crosses represent F_1 offspring (female parent x male parent).

TABLE VI

LEAF AREA (cm^2) MEASUREMENTS BY DATE, SERIES, AND INDIVIDUAL PLANT

Parents & Offspring	Series I			Series II		
	6/18	7/10	Average	7/04	7/10	Average
1	33.56	56.49	45.03	50.03	55.94	52.99
1-1 x 1	59.16	40.54	49.85	49.93	43.85	46.89
1-2 x 1	31.35	39.80	39.58	38.79	43.83	41.31
2	66.24	39.41	52.83	40.09	52.58	46.34
2-1 x 2	40.32	55.48	47.90	58.17	57.71	57.94
2-2 x 2	50.35	31.37	40.86	50.62	43.19	46.91
3	33.60	38.32	35.96	39.02	35.59	37.31
3-1 x 3	37.02	35.74	36.38	41.80	36.66	39.23
3-2 x 3	39.67	46.55	43.11	38.48	43.64	41.06
4	42.36	37.80	40.08	37.81	42.88	40.35
4-1 x 4	44.14	31.81	37.98	43.62	36.69	40.16
4-2 x 4	47.47	45.41	46.44	49.17	64.31	56.74
5	36.87	35.24	36.06	30.27	44.30	37.29
5-1 x 5	25.34	37.32	31.33	41.13	48.88	45.01
5-2 x 5	62.01	55.54	58.78	55.16	49.88	52.52
6	37.79	32.32	35.06	33.18	30.94	32.06
6-1 x 6	31.85	39.10	35.46	35.05	36.76	35.91
6-2 x 6	31.64	36.49	34.07	47.51	51.07	49.29
7	63.56	47.69	55.63	39.56	50.60	45.08
7-1 x 7	39.21	39.32	39.27	39.52	40.20	39.86
7-2 x 7	49.03	66.51	54.77	46.44	42.11	44.28
8	29.12	40.84	34.98	43.34	40.67	42.01
8-1 x 8	63.29	67.21	65.25	43.53	60.87	52.20

TABLE VI (Continued)

Parents & Offspring	Series I			Series II		
	6/18	7/10	Average	7/14	7/10	Average
8-2 x 8	66.49	33.20	49.85	50.96	35.82	43.39
9	29.01	49.01	39.01	45.45	58.61	52.03
9-1 x 9	49.19	46.70	47.95	49.37	49.39	49.38
9-2 x 9	43.20	47.44	45.32	38.56	43.38	40.97
10	54.99	51.95	53.47	46.21	40.01	43.11
10-1 x 10	50.85	35.91	43.38	44.73	35.77	40.25
10-2 x 10	39.65	61.63	50.52	78.62	60.02	69.32
11	39.40	51.75	45.58	50.58	53.01	51.80
11-1 x 11	55.34	45.32	50.33	28.18	36.93	32.56
11-2 x 11	40.83	46.62	43.73	59.61	28.05	43.83
12	43.89	43.38	43.64	42.21	38.64	40.43
12-1 x 12	61.70	48.72	55.21	44.91	30.78	37.85
12-2 x 12	55.33	58.55	56.94	51.69	34.60	43.15
13	51.74	54.79	53.27	41.15	42.88	42.02
13-1 x 13	54.13	37.86	45.99	37.01	40.30	38.66
13-2 x 13	36.00	45.62	40.81	56.97	36.46	46.72
14	53.63	48.57	51.10	52.43	54.16	53.30
14-1 x 14	54.23	62.34	59.79	59.86	56.73	58.30
14-2 x 14	50.38	48.24	49.31	28.04	33.20	30.62
15	37.88	37.81	37.85	27.76	35.18	31.47
15-1 x 15	48.17	57.92	53.05	50.39	52.18	51.29
15-2 x 15	49.93	44.55	46.86	30.35	39.59	34.97
16	50.10	53.26	51.68	66.99	35.24	51.12
16-1 x 16	26.96	38.06	32.51	45.78	37.63	41.71
16-2 x 16	57.73	60.27	59.00	42.51	58.75	50.63
17	47.91	38.18	43.05	45.52	40.17	42.85

TABLE VI (Continued)

Parents & Offspring	Series I			Series II		
	6/18	7/10	Average	7/04	7/10	Average
17-1 x 17	26.22	55.65	40.94	38.82	37.36	38.09
17-2 x 17	50.37	59.78	55.08	42.62	47.77	45.20
18	66.86	59.36	63.11	53.86	48.70	51.28
18-1 x 18	74.68	73.87	74.28	53.51	67.12	60.32
18-2 x 18	46.25	58.85	52.55	37.28	31.43	34.36
19	31.91	69.33	50.62	46.86	43.90	45.38
19-1 x 19	46.96	40.23	43.60	54.39	49.50	51.95
19-2 x 19	35.23	47.89	41.56	50.00	48.38	49.19
20	29.72	51.06	40.39	34.96	43.02	38.99
20-1 x 20	43.24	40.75	41.99	39.02	57.91	48.47
20-2 x 20	61.61	43.18	52.39	51.42	45.66	48.54
21	43.81	58.68	51.25	50.97	61.68	56.33
21-1 x 21	36.67	52.50	44.59	49.35	54.36	53.36
21-2 x 21	40.01	52.24	46.13	34.14	45.62	39.88
22	55.45	45.56	50.51	49.49	52.18	50.84
22-1 x 22	49.24	68.51	58.88	43.72	48.92	46.32
22-2 x 22	39.76	41.35	40.56	65.66	48.81	57.24
23	50.07	29.25	39.66	67.46	50.17	58.82
23-1 x 23	58.97	39.27	49.12	39.67	47.92	43.80
23-2 x 23	61.29	50.52	55.91	42.74	49.53	46.14
24	34.29	42.42	38.36	51.22	36.66	43.94
24-1 x 24	42.69	35.73	39.21	58.64	59.33	58.99
24-2 x 24	86.62	61.18	73.90	51.02	43.08	47.05
25	41.22	67.85	54.54	35.71	59.75	47.73
25-1 x 25	56.77	49.58	53.18	55.81	59.94	57.88
25-2 x 25	74.68	54.43	64.56	85.01	48.31	66.66

TABLE VII

PLANT HEIGHT (cm) DATA MEASURED
JULY 3RD AND 8TH

Parents & Offspring	Series I	Series II	Average
1	130	134	132
1-1 x 1	140	130	135
1-2 x 1	120	130	125
2	110	116	113
2-1 x 2	130	140	135
2-2 x 2	120	124	122
3	110	112	111
3-1 x 3	126	122	124
3-2 x 3	122	120	121
4	120	100	110
4-1 x 4	120	124	122
4-2 x 4	130	130	130
5	120	120	120
5-1 x 5	110	110	110
5-2 x 5	120	110	115
6	114	110	112
6-1 x 6	120	110	115
6-2 x 6	122	120	121
7	120	125	122.5
7-1 x 7	120	124	122
7-2 x 7	134	134	134
8	120	120	120
8-1 x 8	130	110	120
8-2 x 8	126	128	127
9	140	136	138
9-1 x 9	120	130	125
9-2 x 9	100	124	112
10	126	120	123
10-1 x 10	128	124	126
10-2 x 10	130	130	130
11	140	150	145
11-1 x 11	128	120	124
11-2 x 11	124	130	127
12	130	126	128
12-1 x 12	120	130	125
12-2 x 12	116	120	118
13	132	135	133.5
13-1 x 13	130	124	127
13-2 x 13	124	110	117
14	120	120	120

TABLE VII (Continued)

Parents & Offspring	Series I	Series II	Average
14-1 x 14	140	134	137
14-2 x 14	120	126	123
15	110	120	115
15-1 x 15	150	130	140
15-2 x 15	120	116	118
16	114	120	117
16-1 x 16	126	132	129
16-2 x 16	140	134	137
17	126	120	123
17-1 x 17	130	140	135
17-2 x 17	114	120	117
18	130	120	125
18-1 x 18	140	134	137
18-2 x 18	120	110	115
19	130	130	130
19-1 x 19	130	140	135
19-2 x 19	140	150	145
20	150	136	143
20-1 x 20	106	130	118
20-2 x 20	140	130	135
21	130	120	125
21-1 x 21	120	130	125
21-2 x 21	150	138	144
22	130	136	133
22-1 x 22	140	144	142
22-2 x 22	120	140	130
23	120	114	117
23-1 x 23	124	120	122
23-2 x 23	116	115	115.5
24	122	130	126
24-1 x 24	130	144	137
24-2 x 24	135	130	132.5
25	136	134	135
25-1 x 25	120	120	120
25-2 x 25	120	118	119

VITA [2]

Paul Edward Thomas

Candidate for the Degree of

Master of Science

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