SELECTION FOR DROUGHT RESISTANCE
IN COTTON UTILIZING STOMATAL
RESISTANCE MEASUREMENTS

By

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ABSTRACT

Drought is a major hazard of crop production over a great portion of the earth's surface, including Oklahoma. Some evidence exists that stomatal resistance to water-vapor diffusion is related to drought resistance in plants. The objectives of this research were to conduct two-way selection for stomatal resistance within 16 F_2 populations of cotton (*Gossypium hirsutum* L.), to determine what proportion of the selected differences for stomatal resistance were transmitted to the F_3, and to study indirect selection effects on agronomic and fiber quality characteristics. An autoporometer was used to measure stomatal resistance.

Statistical analyses of stomatal resistance revealed that direct selection was generally ineffective. Only one population displayed a significant and positive response. Subsequent analyses for indirect selection response for agronomic and fiber properties in that population revealed reductions in picked and pulled lint percent and an increase in 1/8" gauge stelometer at the 0.20 probability level. Based on these results, this method of screening for drought resistance is probably not of value to cotton breeders.

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[1] Written in *Crop Science* format.

Additional index words: _Gossypium hirsutum_ L., Correlated response, Lint yield, Lint percent, Fiber properties.

INTRODUCTION

Plant growth depends on the interaction of many factors, any of which may restrict growth. Water, one of the most important of those factors, is essential for crop production because it is a major constituent of plant tissue often comprising as much as 90 to 95% of the plant's fresh weight. Water provides plants with mechanical strength, a means for gas exchange, an internal transportation system, and other necessary functions. Water is taken up by the roots, then moves through the stem into the leaves, and transpires into the air in vapor form primarily through the stomata. Transpiration occurs because plants have not evolved a method of assimilating gases, especially CO_2, without losing water vapor (42).

Water stress affects the growth rate of plants in at least two ways, i.e., the rate of increase in leaf area is slowed by loss of turgor and the rate of photosynthesis is decreased by the closing of stomata and other means (28). Water stress also inhibits full recovery of these processes after irrigation or rainfall (2).

At this time, more than 75% of the cotton (Gossypium hirsutum L.) grown in the U.S. is produced in areas with either irrigation or relatively high rainfall (32). Much of the acreage now being put into crop production was previously thought to be marginal land. There will undoubtedly be increased dryland crop production in the future due to rising irrigation costs and reduced water availability. In many field situations moderate dehydration on a daily basis or larger water deficits between irrigations or rainfalls may occur (10). Understanding the physiological processes that affect water use would be profitable in increasing the drought resistance and productivity of cotton (1, 32).

The stomatal resistance of a plant is considered to be an important component of its drought resistance. Absorption of water by plants is initiated and controlled primarily by transpiration. Stomata are important in controlling the transpiration of water and in the exchange of gases such as carbon dioxide (39). Stomata generally close in response to water stress, tending to conserve water and prevent further dehydration (18). The greater a plant's stomatal resistance, the better its adaptation to drought (17).

Many investigators have studied stomatal resistance of cotton in both the laboratory and the field (10). Roark and Quisenberry (33) found that some drought adaptations of ancestral cottons have been lost in the development of modern cultivars. The stomata on recent cultivars are more open and numerous than on older cultivars (32). Stomatal resistance varies greatly among and within crop species (6, 17). Through selection for stomatal diffusive resistance, it may be possible to improve the drought resistance of cotton.

The objectives of this research were to:

(a) Conduct two-way selection for stomatal resistance within 16 F_2 populations of cotton,

(b) Determine what proportion of the selected differences for stomatal resistance were transmitted to the F_3, and

(c) Study indirect selection effects on agronomic and fiber quality characteristics.

LITERATURE REVIEW

Breeding for Stomatal Behavior

Stomatal behavior influences photosynthesis and transpiration (7, 24), and the suggestion has been made that selection for differences in the trait could prove useful in breeding cotton cultivars with improved water-use efficiency (32, 33). However, this possibility has not yet been fully investigated (29).

Many aspects of stomata such as length, width, sensitivity, and frequency could be considered in a breeding program. However, genetic improvements would be possible only if sufficient genetic variation existed within the population. It would also be possible, if necessary, to transfer variability from other species of the genus to the cultivated species (32). Ray et al. (32) reported that variability does exist among cotton cultivars in stomatal frequency and leaf resistance. Ciha and Brun (7) also found differences in stomatal frequencies within individual soybean [*Glycine max* (L.) Merr.] cultivars. Henzell et al. (17) indicated that stomatal sensitivity varied among sorghum [*Sorghum bicolor* (L.) Moench] genotypes. Guard-cell length, an indicator of stomatal pore size, was found by Miskin and Rasmusson (29) to differ significantly among cultivars of barley (*Hordeum vulgare* L.).

Evidence exists that selection for stomatal resistance can affect the drought resistance of a crop. Miskin and Rasmusson (29) showed relatively consistent differences among barley cultivars in stomatal frequency under field and greenhouse conditions, which suggests that genotype is prominent in determining stomatal frequency. Low stomatal-frequency lines tended to be more drought resistant than high stomatal-frequency lines, because they transpired less (7). Evidence for genotypic differences in stomatal activity due to water stress has been found for sorghum (2). Genetic aspects of leaf resistance in cotton, found by Roark and Quisenberry (33), were that high leaf resistance was completely dominant to low resistance, and that leaf resistance was associated with both additive and dominance genetic variances with an estimated narrow-sense heritability of 25%. The genetic component of leaf resistance appeared mainly in the afternoon, while the environmental component appeared throughout the day (33). If possible, selection for stomatal resistance should be made using a simple method, allowing a large sample size, and with a minimal environmental component (17).

Factors Influencing Stomatal Resistance

Investigators have shown that a complex of physiological and environmental factors can alter a number of stomatal factors (9, 10). The variability in response of stomatal resistance indicates that many interactions of factors are involved. Stomatal resistance depends largely on the frequency, size, and sensitivity of the stomata (21).

Environmental factors affect transpiration largely through the physiological processes connected with stomatal changes (42). Some environmental factors to which stomata respond are humidity gradients, light intensity, temperature, wind speed, and water stress (15, 27, 42). Environmental conditions have also been shown to influence stomatal frequency (7) and stomatal aperture (39).

Stomata react differently on leaves grown under different conditions (34). Some physiological factors which may affect stomatal resistance are carbon dioxide level, water potential, leaf age or position, and abscisic acid (ABA) concentration. Stomatal resistance depends on the interaction of these factors, although some have a larger effect than do others. It has been suggested by Dale (11) that hour-of-the-day, solar radiation, and temperature combined account for at least 60% of the variation in observed values of stomatal aperture.

Water Potential. Light and water are the environmental factors most likely to modify stomatal behavior in the field (22, 40, 41). Stomatal behavior influences a plant's water use under semiarid conditions (33). In turn, one of the many physiological processes of a plant affected by water deficits is stomatal behavior (10).

As plant-water deficits increase, the stomata close (5, 34, 38). Water stress causing the stomata to close tends to override the opening effects due to light and hour-of-the-day because the guard cells bordering the stomata lose their turgidity (11, 24, 31). Increased water stress in plants tends to lead to decreased leaf-water potential (13). As leaf-water potentials decrease, increases in leaf diffusive resistance occur; but complete stomatal closure due to water stress is not obtained according to Ackerson et al. (1). El-Sharkawy and Hesketh (12) disagree by stating that stomata tend to be closed in very wilted leaves.

Studies indicate that stomata of cotton are less sensitive to water stress than in those of sorghum and sunflower (Helianthus annuus L.) (12) and that little evidence exists for complete stomatal closure in field-grown cotton due to water stress (1). The highest percentage of open stomata are found with a sufficiency of water (31). Increasing water-use efficiency might be possible by selecting for "water savers", which Roark and Quisenberry (33) define as plants that "avoid drought by closing their stomata during the day even though soil water supplies may be adequate".

Stomatal response to water stress may be altered by past and present growing conditions of the plant (20). Stomata of field-grown plants tend to be less sensitive than greenhouse- or growth chamber-grown plants (10, 28). The decrease in stomatal sensitivity of field-grown plants may be due to a prolonged exposure to drought conditions implying increased adaptation to soil-moisture stress or a "hardening" effect (1, 4, 20). Thus, stomatal resistance comparisons among plants should be made only if they are grown under the same conditions.

The effect of water stress on photosynthesis and plant growth is partly due to its effect on stomatal behavior (28). Water stress causes the stomata to close thereby reducing plant carbon dioxide uptake and photosynthesis rate. On the other hand, further stomatal closure may result from the reduced photosynthesis rate. A reduction in the growth of new roots can occur because of the lack of photosynthate to the root system. With fewer roots, less water is taken up, causing increased stomatal closure (1, 13, 31, 36). Reductions in photosynthesis and increases in stomatal resistance with increased leaf-water deficits have been reported in cotton (1).

Stomatal behavior does not depend directly on soil-moisture supply (11). As the soil-water potential decreases, the water potential of leaves also decreases (31). Stomatal behavior is regulated primarily by the water content of the epidermal and guard cells bordering the opening (13). A water deficit develops in the leaves, and the guard cells lose turgor, which causes the stomata to close (22, 28).

One of the many discrepancies in stomatal behavior is the reaction of stomata to water stress. Slatyer, as cited by Kanemasu and Tanner (22), suggests that stomatal resistance may not be greatly affected by water deficits until a critical leaf-water potential is reached. Transpiration below that critical point may be controlled by nonstomatal means (4). Sanchez-Diaz and Kramer (34) showed a small decrease followed by a rapid increase in the stomatal resistance of water-stressed plants. Other researchers have found that stomata remain open over a wide range of water potentials, but close sharply over a narrow range of water potential (3, 25). However, Blum and Sullivan (4) suggest that "stomatal response to soil moisture tension was linear".

Stomata are thought to regain original activity levels upon irrigation following water stress-induced stomatal closure (11, 31, 34). However, the rate of recovery depends on the intensity and duration of the water stress. Plants also tend to recover more quickly and completely if they have been prestressed (10, 13).

Photosynthesis. The relation between photosynthesis and water deficits has been studied extensively (20). In general, water stress causes a reduction in the rate of photosynthesis. Growing plants take up carbon dioxide and lose water through stomata (35). Resistance to carbon dioxide uptake by the leaf is a critical factor limiting photosynthesis (42). Water stress causes stomatal closure, thereby limiting carbon dioxide uptake by the plant. The extent of the limitation depends largely on stomatal frequency, size, and degree of opening (7, 12). El-Sharkawy and Hesketh (12) and Troughton (38) demonstrated that under a favorable environment, leaf-diffusive resistance is the limiting factor for photosynthetic rates.

Ackerson et al. (1) showed that water stress reduced photosynthesis in the leaves of cotton. However, a change in stomatal resistance had a greater effect on transpiration than on photosynthesis because stomatal closure reduced the escape of water vapor from the leaf more than it restricted assimilation of carbon dioxide (7). The recovery of photosynthesis was related to the decrease in stomatal-diffusion resistance, but photosynthesis never regained prestress levels (13).

Increasing the efficiency of water use by plants may be possible through selection for higher stomatal resistance. However, this type of selection may simultaneously reduce the photosynthetic rate and growth of the plant. With irrigation or in environments where water is not a limiting factor, better results may be obtained by selecting for lower leaf-diffusive resistance (10, 16, 38).

Several researchers have suggested that photosynthesis in water-stressed plants is not controlled by stomata (38). Ackerson et al. (1) indicated that photosynthetic reduction could not be attributed to stomatal closure. In research by Pallas et al. (31), cotton leaves maintained relatively high photosynthetic rates even though they were visibly wilted. In a study of the stomata of two bean (*Phaseolus vulgaris* L.) cultivars, Izhar and Wallace, as cited by Miskin and Rasmusson (29), found that the cultivar with the fewer stomata had the higher photosynthetic rate.

Light. Ackerson et al. (1) obtained evidence indicating that the major factor controlling stomatal activity in field-grown cotton was light rather than leaf-water potential. Kanemasu and Tanner's (21) research supported this idea by implying that differences in stomatal resistance at low water potentials (below -8 bars) could be attributed to light.

Stomata open with light and close with darkness when ample soil water is available. Also, a higher percentage of stomata open at high radiation levels than under low radiation (24, 31). In a study by Whiteman and Koller, as cited by Kanemasu and Tanner (21), stomatal resistance of sunflower leaves decreased as light increased until a threshold light level was reached at which point stomatal resistance began to increase. The increase in stomatal resistance at higher light levels may be due to a water deficit caused by a promotion of water loss associated with high light conditions (5).

Light also indirectly affects the leaf-diffusive resistance of a plant by increasing stomatal frequency as light intensity increases. Plants grown in the shade have fewer stomata per unit area than those grown in the sun (7, 8). It has been suggested that light may also change stomatal widths (39).

Hour-of-the-Day. Stomatal aperture is correlated with hour-of-the-day (11). Kanemasu and Tanner (21) found that plants exposed to constant light levels daily for 24 hours still had stomatal resistance values higher at night than during the day. This response may be due to an endogenous diurnal rhythm. The leaf-diffusive resistance of a plant usually decreases throughout the morning, reaches its lowest level in the afternoon, and then increases in late afternoon and overnight (1, 17, 20, 26, 31, 33, 40). After sunset, increased stomatal resistance permits cell hydration (20).

Stomatal Size and Frequency. A large variation exists between species for stomatal size and frequency. These two traits help regulate diffusion of water from the plant (12, 39). However, a negative correlation appears to exist between stomatal size and frequency. This relationship tends to result in approximately equal total pore areas among cultivars (6, 29).

Stomatal frequency in mature leaves may depend upon light intensity, temperature, and water stress. The mean frequency of stomata is higher for plants grown at high light intensity than for those grown at low intensities. Variation in temperature has little effect on stomata frequency. Water stress causes an increase in the frequency of stomata. Although an increase in stomatal frequency due to water stress and higher light intensity has been measured, a decrease in total stomatal number is common for water-stressed plants; and no changes in total stomata number are noted for plants grown under higher light intensities. This suggests that the change in stomatal frequency may be due to leaf expansion as expansion is also linked to water stress and light intensity (6, 7, 29). Miskin and Rasmusson (29) found that drought-tolerant plants had a lower stomatal frequency than drought-susceptible ones.

Most reports conclude that stomatal frequency on the upper leaf surface is generally lower than stomatal frequency on the lower surface (7, 31, 39). In contrast, Cooper and Qualls (8) reported that alfalfa (*Medicago sativa* L.) and birdsfoot trefoil (*Lotus corniculatus* L.) had a higher stomatal frequency on the upper leaf surface. Despite their relative frequencies, most of the time a greater percentage of stomata are open on the upper leaf surface than on the lower. However, the lower surface tends to exhibit lower stomatal resistance, probably because of its larger stomatal numbers (19, 22, 31). The stomata of the upper leaf surface are more sensitive to water stress and light intensity than are those of the lower surface (17, 21, 34). Sanchez-Diaz and Kramer (34) reported that the upper stomata of sorghum closed first, but that the stomata of cotton closed simultaneously on both leaf surfaces.

Leaf Position and Age. Leaf position and age signficantly affect stomatal closure (1, 6, 13, 19, 37, 41). Two investigations demonstrated that stomatal resistance of cotton leaves increased with age (1, 19). As leaf-water potentials decrease, stomatal closure of the older leaves occurs first, followed by the stomata of increasingly younger leaves. The leaves at the top of the plant show lower stomatal resistance than those at the bottom. The higher stomatal resistance of the older leaves in the lower portion of the plant may be attributed to microclimatic differences such as decreased light intensity due to shading from the canopy. Also involved may be a physiological adaptation which allows the young, upper portions of the plant to continue to photosynthesize at the expense of the older, lower leaves (6, 22, 37).

Several investigators have shown that the younger the leaf, the higher the stomatal frequency because leaf expansion is not yet complete. They also found that younger leaves have more stomata than older leaves (13, 29). Mean stomatal length increases progressively with leaf age (6). Increases in stomatal resistance with age may be partially attributed to these occurrences as well.

Temperature. Changes in leaf-diffusive resistance due to temperature may occur in two ways. Decreased leaf-water content is induced by low root temperatures, thus causing reduced photosynthesis and increased leaf-diffusive resistance (2, 13, 38). High temperatures may also cause increases in carbon dioxide which result in stomatal closure (24). Stomatal response to temperature is important in that high evaporative cooling and photosynthesis are dependent on low stomatal resistance. The optimum temperature for photosynthesis is higher in humid than in dry air (15).

MATERIALS AND METHODS

"Stomatal resistance" is defined as the amount of transpiration occurring at a given time. It is regulated by the degree to which the stomata are open. A LI-COR model LI-65 autoporometer was used to measure stomatal resistance. The instrument has a digital readout which records time to the nearest one hundredth of a second. The instrument is set to start and stop at specific chamber relative humidities. The time (Δt) required for the chamber humidity sensor to pass from a lower to a higher set-point is a function of stomatal resistance. The autoporometer has a battery-powered pump which dries the humidity sensor to the same point before each reading is taken. The sensor is clamped on the leaf to be measured, and the chamber dried by pumping air through a tube of silicon crystals. The autoporometer requires only a brief sensor contact with leaves, and this should help in avoiding stomatal reaction effects during data collection.

Each reading was taken on a mature leaf near the center of the plant. The plants were in bloom when the measurements were taken. Measurements were taken on the abaxial leaf surface, because cotton has more stomata on the abaxial than on the adaxial surface. Midrib and secondary ribs of the leaf were avoided in these measurements. Measurements were not taken on plants bordering alleys or skips within the row to only use competitive plants. Measurements were made throughout the day starting at 0900, if the dew was gone from the plants, until 1500. No measurements were made on cloudy days.

Temperature and Δt were recorded for each reading, and used to calculate stomatal resistance (sec cm^{-1}) using Δt and temperature along with a calibration curve (23, 30).

Sixteen F_2 populations of cotton (Table 1) were each planted separately at Perkins, Okla., under irrigation in 1979. The soil type was a Teller loam (a fine-loamy, mixed, thermic Udic Argiustolls). The plants were grown in one to three row plots depending upon seed supply. Rows were 15.2 m long and 1.0 m apart, and plants within rows were thinned to 30 cm apart. Each row was divided into four groups of 10 plants each, excluding plants bordering the alleys and skips. One measurement of stomatal resistance per plant was made. After the plants of all 16 populations had been measured, a second measurement was made on each plant. The measurements were taken approximately 3 weeks apart. The two measurements per plant were averaged together. Then within each group of 10 plants, the two plants with the highest average stomatal resistance were selected and the two plants with the lowest average stomatal resistance were selected. The subdivision of an entire population for evaluation and selection purposes is Gardner's Grid system of selection (14). The grid method reduces environmental variation by making selections based on measurements taken within a short period of time in a small area. It has been demonstrated that the use of grids increases the effectiveness of plant selection in cotton (43). The selected plants were then selfed heavily, and the seed was harvested after maturity.

All selfed seed were delinted and bulked over groups within a population from the selections for high stomatal resistance and likewise for the selfed seed from the selections for low stomatal resistance.

In 1980, the bulked seed from the original selections were planted in three split-plot (16 X 2) experiments with main plots, i.e., populations, in randomized complete blocks with four replications. The first experiment was at Perkins under dryland conditions. The second and third experiments were at Chickasha under irrigation and on dryland, respectively. The soil type at Chickasha is a Reinach silt loam (a coarse-silty, mixed, thermic Pachic Haplustolls). Rows were 9.1 m long in the Perkins dryland and Chickasha irrigated experiments and 7.1 m long in the Chickasha dryland test. At all three locations, the rows were 1.0 m apart; and plants within rows were thinned to 30 cm apart. Because the two dryland experiments were under such severe drought stress, the irrigated test at Chickasha was chosen in which to measure direct selection response for stomatal resistance in the F_3 generation. Three randomly selected plants were measured per plot; and they were measured in the same manner as in the previous year, but without grids. If selection was effective, a significant difference in stomatal resistance should have existed in the expected direction between plants grown from the selfed seed of plants originally selected for high stomatal resistance vs. those selected for low. Unfortunately, because of limited seed supplies, two of the populations were not included in the Chickasha irrigated test, i.e., populations 4 ('Tamcot SP21' X 'Paymaster 303') and 12 ('Paymaster Dwarf' X 'Westburn M'). Therefore, direct selection response could only be evaluated in 14 of the 16 original populations.

The experiments at all three locations were also used to estimate indirect selection responses in lint yield, lint percent, and fiber quality differences between the high vs. low selection groups within each parental combination showing significant and positive direct selection responses. Plot weights of snapped cotton were converted into lint yield expressed in kg ha^{-1}. Fifteen-boll samples from the plots were ginned on an eight-saw laboratory-type cotton gin, and data used to calculate picked lint percent (the ratio of lint to seedcotton weights expressed as a percentage) and pulled lint percent (the ratio of lint weight to the combined weights of seedcotton plus bur expressed as a percentage) were recorded. The lint was evaluated in the Oklahoma State University Cotton Quality Research Laboratory. Lint properties analyzed were 2.5% span length, uniformity index, micronaire, 0" gauge stelometer, and 1/8" gauge stelometer. The 2.5% span length was measured on the digital fibrograph and is expressed in mm. The ratio of 50% (also measured on the fibrograph) to 2.5% span length is uniformity index reported as a percentage. Measurement of fiber fineness was with the micronaire instrument in standard units of µg $inch^{-1}$. Fiber strength was estimated on the stelometer, using the 0" (0.00 cm) gauge and 1/8" (0.32 cm) gauge settings which are reported here in mN tex^{-1}. Analyses of variance were calculated for each of the agronomic and fiber properties in those populations of the 14 which displayed a significant and positive response to direct selection for stomatal resistance.

RESULTS AND DISCUSSION

Sixteen F_2 populations of cotton were measured in 1979 for stomatal resistance (Table 1). The upper and lower 20% of the plants in each population were selected, selfed, and seed bulked separately. The high vs. low bulks from the selected plants were compared in three replicated experiments the following year for evaluation of their direct and indirect selection responses.

Direct Selection Response

The direct selection response, i.e., the trait stomatal resistance, was measured within the high and low selections for each of the populations grown at Chickasha in 1980 under irrigation. This trait was not evaluated in the dryland experiments because of the severity of the drought in 1980. Mean selection and response values for stomatal-resistance measurements are given in Table 2. Analyses of variance were used to detect significant differences between the high vs. low means. For population no. 8, i.e., 'Paymaster Dwarf' X M73-130, the high selection was significantly higher in 1980 than the low selection at the 0.10 probability level. This was the only population in which the direct selection response was positive and significant. It could represent a case of a Type I error. Several significant, but negative, responses were noted. No differences could be determined between the high vs. low selections in the other F_2 populations. In general, direct selection for stomatal resistance was ineffective.

The original selections for stomatal resistance may not have been successful for several reasons. One reason may have been low selection pressure. Selection for stomatal resistance was conducted at only the 20% level in 1979. The low selection pressure was in part due to the considerable time required to take the measurements. A more efficient method of obtaining readings would be required to substantially increase the number of plants which could be measured and thus increase selection pressure.

The heritability of stomatal resistance is likely low (33). Only small responses to selection are possible with traits having low heritabilities, and such small responses are difficult to detect and evaluate. Some of the populations may not have possessed genetic variation for the trait making selection response in those populations impossible. Only three stomatal resistance measurements per entry in each of the four replications were made in the test sampled in 1980. This number of measurements may have been insufficient to obtain an accurate value for stomatal resistance in an F_3 population. Considerable sampling variation could have resulted making detection of differences more difficult, particularly if those differences were small. It should be noted that the climatic conditions at Chickasha and Perkins were unusually hot and dry for the 1980 growing season. Lint yield in the two dryland experiments was especially poor due to the severe lack of soil moisture and high temperatures. Yields in the irrigated test were also considerably below average. Conditions were so severe that perhaps even in the irrigated test, differences between selection groups were obscured. Measurements were also made throughout the day beginning in the morning at approximately 0900. Roark and Quisenberry

(33) reported that they were able to detect genetic differences primarily in the afternoon and not in the morning.

Indirect Selection Response

The hypothesis that the physiological character, stomatal resistance, would interact with environmental conditions thereby allowing better plant performance could not be supported by these experiments. Only in population no. 8 could direct and positive selection response be tentatively substantiated. Without direct selection response, indirect selection response is meaningless. Analyses of variance were used to test for indirect selection responses of agronomic and fiber traits in population no. 8. Selection response means for each of the eight variables investigated are shown in Table 3. Those data indicated that picked lint percent, pulled lint percent, and 1/8" gauge stelometer were significant at only the 0.20 probability level. The lint percents responded in the negative direction while 1/8" gauge fiber strength increased. Again, these differences could be due to Type I errors. Lack of response in these traits could be due to the absence of genetic variation for such traits in this population or in the lack of genetic correlations between them and stomatal resistance.

Based on these results, one must conclude that this method of screening for drought resistance is probably not practical. Differences in stomatal resistance are very small and difficult to measure, and the time required to make those measurements precludes large numbers of evaluations.

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LIST OF TABLES

Table 1. Identification of the 16 F_2 populations of cotton selected for stomatal resistance.

Code no.	Pedigree of F_2 population
1	'Tamcot SP21' X 'Westburn M'
2	'Tamcot SP37' X 'Westburn M'
3	'Paymaster 303' X 'Westburn M'
4	'Tamcot SP21' X 'Paymaster 303'
5	'HyBee 200A' X 'DES 24'
6	'Stoneville 213' X 'Deltapine 16'
7	'HyBee 200A' X 'Deltapine 16'
8	'Paymaster Dwarf' X M73-130†
9	'Westburn M' X M73-130†
10	'Earlycot 31' X 'Westburn M'
11	'Paymaster Dwarf' X 'Westburn M'
12	'Lankart LX 571' X 'Westburn 70'
13	'Lockett 4789-A' X 'Westburn 70'
14	'Deltapine 16' X 'Lockett 4789-A'
15	'Stoneville 7A' X 'Lankart LX 571'
16	'Deltapine 16' X 'Lankart LX 571'

†Strain "M73-130" has the pedigree: 'Stripper 61-28' X CA 1012 F_5 where "CA 1012" is a line developed by L. L. Ray (formerly with the Texas Agriculture Experiment Station at Lubbock).

Table 2. Direct selection response for stomatal resistance in 16 populations of cotton.

Selection response	Stomatal resistance of population							
	1	2	3	4	5	6	7	8
	sec cm^{-1}							
Selection 1979								
High	5.25**	5.26**	4.76**	4.76**	5.24**	5.69**	5.63**	4.91**
Low	3.95	4.06	3.60	3.63	3.89	4.25	4.14	3.94
Response 1980								
High	3.61†	4.53	5.56	--§	4.75	3.92	5.29	4.57‡
Low	5.68	4.64	5.66	--	4.54	4.69	6.29	3.11

Selection response	Stomatal resistance of population							
	9	10	11	12	13	14	15	16
	sec cm^{-1}							
Selection 1979								
High	5.08**	6.10**	5.67**	5.55**	5.80	5.36**	5.25**	5.44**
Low	3.65	4.41	4.44	4.43	3.94	3.77	3.78	3.96
Response 1980								
High	3.86‡	4.60	4.07	--§	4.92†	5.92	3.65*	4.45
Low	5.60	3.49	4.78	--	6.28	5.58	5.06	3.39

†,‡,*,** Paired comparisons were significantly different at the 0.20, 0.10, 0.05, and 0.01 levels of probability, respectively.

§ Due to limited seed supplies, these populations were not included in the experiment where direct selection responses were ultimately evaluated.

Table 3. Indirect selection response over three locations for eight agronomic and fiber traits of cotton in F_3 population no. 8.

	Agronomic traits			Fiber traits				
Selection response	Lint yield	Lint Percent		2.5% Span length	Uniformity index	Micro-naire	Gauge stelometer	
		Picked	Pulled				0-inch	1/8-inch
	kg ha^{-1}	%		mm	%	µg in^{-1}	mN tex^{-1}	
High	230	34.3†	22.6†	25.37	49.1	4.7	516.3	219.1†
Low	252	35.8	24.0	25.23	49.1	4.7	515.7	207.9

†,‡,*,** Paired comparisons were significantly different at the 0.20, 0.10, 0.05, and 0.01 levels of probability, respectively.

APPENDIX

Table 4. Analyses of variance for direct selection response for stomatal resistance in 16 populations of cotton (Table 2).

		Mean squares for population							
Source	df	1	2	3	4	5	6	7	8
Rep	3	5.02	16.11	111.53**	--§	27.22*	18.28	42.43 *	26.43**
Selection	1	25.77†	0.07	0.06	--	0.27	3.52	5.90	12.85‡
Error	3	4.88	6.42	8.15	--	38.75	1.94	13.16	6.70

		Mean squares for population							
Source	df	9	10	11	12	13	14	15	16
Rep	3	3.15	15.63	15.89*	--§	45.81**	34.33	22.54**	7.06
Selection	1	18.22‡	7.37	3.07	--	11.08†	0.70	11.87*	7.12
Error	3	10.90	7.54	10.61	--	2.34	4.19	12.18	3.19

†,‡,*,** Paired comparisons were significantly different at the 0.20, 0.10, 0.05 and 0.01 levels of probability, respectively.

§ Due to limited seed supplies, these populations were not included in the experiment where direct selection responses were ultimately evaluated.

Table 5. Analyses of variance for indirect selection response over three locations for eight agronomic and fiber traits of cotton in F_3 population no. 8 (Table 3).

		Mean squares for population no. 8							
		Agronomic traits			Fiber traits				
		Lint	Lint percent		2.5% Span	Uniformity	Micro-	Gauge stelometer	
Source	df	yield	Picked	Pulled	length	index	naire	0-inch	1/8-inch
Location (L)	2	41731**	5.93	53.44**	0.0032*	5.62†	1.09**	20.48**	28.81*
Rep (within L)	9	7288‡	2.12	3.38	0.0072	0.90	0.10‡	4.47‡	9.97‡
Selection (S)	1	2321	13.80†	12.33†	0.0002	0.00	0.01	0.03	7.82†
L X S	2	3532	0.40	2.78	0.0012	0.41	0.02	4.46†	5.13
Error	9	2514	5.56	5.27	0.0007	2.17	0.04	1.63	3.71

†,‡,*,** Paired comparisons were significantly different at the 0.20, 0.10, 0.05 and 0.01 levels of probability, respectively.

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