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Genetic analysis of stomatal conductance in upland cotton (*Gossypium hirsutum* L.) under contrasting temperature regimes

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SUMMARY

Stomatal conductance plays an important role in the heat avoidance mechanism of crop plants. Stomatal conductance in cotton is genetically determined and has been shown to be associated with heat resistance and higher yields. Experiments were carried out with six generations (parental, F_1, F_2 and back crosses) of three upland cotton crosses under heat-stressed and non-stressed greenhouse and field regimes, to understand the inheritance pattern of stomatal conductance as affected by contrasting temperature regimes. The results revealed significant variation for stomatal conductance due to generations and generation × temperature regime interaction in the three crosses. In general, heat stress reduced stomatal conductance and available genetic variability. Temperature regimes exerted a significant effect on the expression of the genes responsible for stomatal conductance. High temperature or heat stress favoured the expression of genes having additive effects, while absence of heat stress favoured those having dominant effects in two of the three crosses evaluated. The third cross showed the opposite reaction. The results suggest that genes controlling stomatal conductance in the parents of the first two crosses (MNH-552, HR109-RT, CIM-448, CRIS-19) were different from those controlling stomatal conductance in FH-900 and N-Karishma, the parents of the third cross. The selection efficiency of stomatal conductance in segregating populations was likely to be affected by the complexity of its inheritance, environmental dependency, and presence of substantial non-allelic and genotype × temperature regime interactions.

INTRODUCTION

Temperature response in plants is governed by a complex interaction of genetic, developmental and environmental factors. Stomatal conductance plays an important role in the mechanism of heat avoidance in crop plants. Higher stomatal conductance causes transpirational cooling of the leaf temperature, thus enabling photosynthesis and respiration to continue unimpaired (Lu *et al*. 1994; Radin *et al*. 1994). Higher stomatal conductance combined with smaller leaf area decreases boundary layer resistance and increases energy dissipation (Nobel 1991), which further reduces leaf temperature. Several studies have shown substantial cooling of upland cotton (*Gossypium hirsutum* L.) foliage as an adaptation to high temperatures (Lu *et al*. 1994; Nijs *et al*. 1997), through higher stomatal conductance (Jarvis & Mansfield 1981; Koniger & Winter 1993; Mahan *et al*. 1995). Stomatal conductance in Pima cotton (*Gossypium barbadense* L.) is genetically determined (Pettigrew *et al*. 1993; Lu & Zeiger 1994; Pettigrew & Meredith 1994; Lu *et al*. 1996, 1997) with quantitative genes involved in its expression (Percy *et al*. 1996), and has been shown to be associated with heat resistance and higher yields (Lu *et al*. 1994).

Although the stomatal responses of plant species to environmental factors are well-established (Schulze 1986; Zeiger *et al*. 1987), there is little information on the underlying variation and genetic mechanism responsible for such responses. Thus the aim of the present paper was to understand how variation in the expression of stomatal conductance is related to changes in gene expression and how that affects the

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inheritance pattern of stomatal conductance. Such information would provide a physiological tool for the plant breeders to bring about genetic improvement for enhanced adaptation to heat stress in upland cotton.

MATERIALS AND METHODS

The experimental material comprised three bi-parental upland cotton (*G. hirsutum* L.) crosses involving diverse parents for heat resistance, and for each of the parental, F_2 and back cross generations to both parents. Evaluation of the experimental material was carried out under heat-stressed and non-stressed greenhouse and field regimes because the field experiments assure optimum vigour, growth and reproduction but heat stress is difficult to guarantee or standardize in field experiments. In contrast, heat-stressed and non-stressed temperature conditions could be assured in the greenhouse but not the optimum crop growth and reproduction. The objective was to broaden the evidence base from which to draw precise inferences.

Greenhouse experiment

The greenhouse experiment was conducted under two temperature regimes maintained in two separate compartments of a greenhouse and designated as optimum (non-stressed) and supraoptimum (heat-stressed) regimes. The ideal temperature for cotton growth is 20–30 °C (Reddy *et al*. 1998); however, the ideal temperature for metabolic activity and photosynthesis is 23–33 °C (Burke *et al*. 1988). A temperature regime of 35/21 °C (day/night) was selected to compensate for relatively slower growth and reproduction under lower temperatures and complete the experiments in both optimum and supraoptimum compartments within equal days of the experimental period.

The optimum compartment was maintained at 35/21 °C ± 2 °C (day/night) and the supraoptimum compartment at 46/30 °C ± 2 °C. Photoperiod for both compartments was 14 h. Plants were grown in earthen pots (35 cm high, 30 cm diameter), each containing 9 kg of soil (3 : 1 mixture of silt and peat). Soil properties were: electrical conductivity 0·59 dS/m; pH 8·1; organic matter 0·13 g/kg; saturation 29 %; available phosphorus, 30·1 mg/kg; available potassium 130 mg/kg. During the experiment, urea (4·6 g/kg nitrogen) was applied to the pots in solution form (10 g urea/litre of water) 30, 60 and 90 days after sowing.

Seeds were soaked in tap water for 8 h before sowing. Four seeds were sown in each pot at 2 cm depth. Later, at the two true-leaf stage, two plants of similar size were retained in each pot and the others removed. Pots were arranged in a completely randomized design. Plants were allowed to grow under optimum temperatures (35/21 °C ± 2 °C) for 30 days after sowing, until squares were visible with the naked eye. Later, the temperature in the supraoptimum compartment was gradually increased at an average rate of 2 °C per day until the desired temperatures (46/30 °C ± 2 °C) were reached. Sunlight was the source of illumination in both compartments, however, during the morning and evening hours fluorescent bulbs were used to supplement the light period and intensity. Photosynthetically active radiation (PAR) in both compartments ranged from 1400–1600 μmol/m²/s at noon. Relative humidity varied from 65–80 % throughout the experimental period in both compartments. Pots were watered in the afternoon with 400 ml of water on alternate days before and after peak flowering and daily during the peak flowering period. Peak flowering was the period during which cotton plants produced maximum flowers (50–70 days after sowing in the greenhouse, and 60–90 days in the field). Care was taken to avoid drought or over-saturation.

Field experiments

Field experiments were carried out during the 2000 and 2001 cropping seasons. Experiments were sown on two dates to provide two temperature regimes, especially during the reproductive stage. Provision of different temperature regimes under field conditions through different sowing dates is a valid approach and has been used in various crops, for example, brassica (Morrison & Stewart 2002) and cotton (Steiner & Jacobsen 1992; Rahman *et al*. 2004). Experiments were sown on 7 April and 29 May 2000 and 15 April and 4 June 2001. April sowing was selected to synchronize peak flowering period with the highest temperatures of the year in June–July. The minimum and maximum temperatures in the early (April) and late (June) sown regimes were significantly different and are presented in Fig. 1. Early and late sown regimes were therefore referred to as heat-stressed and non-stressed, respectively. All field experiments were laid out in randomized complete blocks with three replications. Plot size in each replication measured 4·5 × 0·75 m, and accommodated 16 plants spaced 30 cm apart. Both experiments were sprayed to control insect pests when required. Adequate irrigation was applied by flooding when necessary to eliminate a confounding effect of drought, especially during the reproductive stage. Irrigation interval varied from 7–12 days, depending upon weather and crop condition.

Determination of stomatal conductance

Stomatal conductance in the greenhouse and field experiments was measured with a portable steady-state

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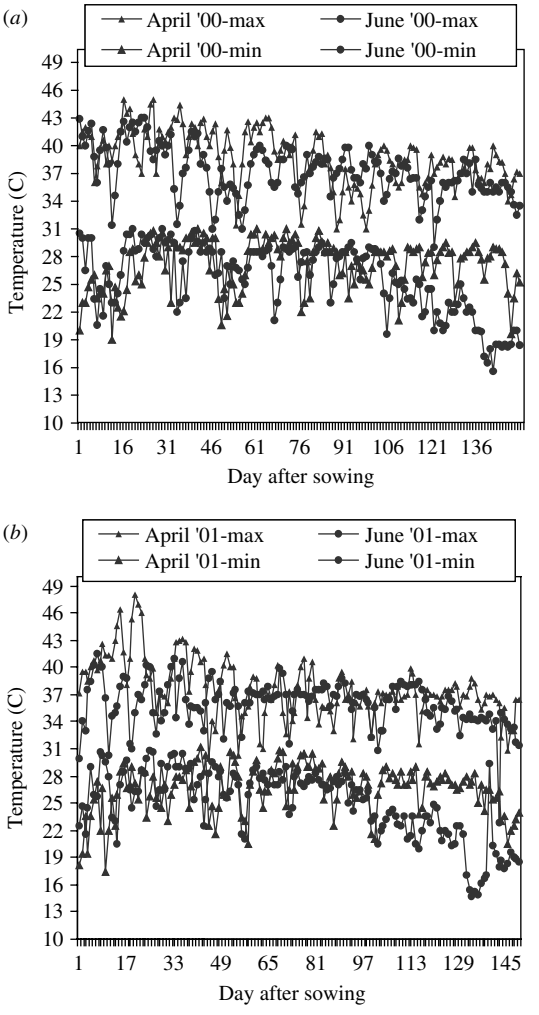

Fig. 1. (*a*) Minimum (min) and maximum (max) temperatures from sowing to 150 days after sowing in April (heat-stressed) and June (non-stressed) regimes during 2000 crop season. (*b*) Minimum (min) and maximum (max) temperatures from sowing to 150 days after sowing in April (heat-stressed) and June (non-stressed) regimes during 2001 crop season. In both seasons, maximum and minimum temperatures of the two regimes were compared through two-tailed *t*-statistics.

porometer (PMR-2, PP Systems, UK) during the peak flowering and fruiting period of crop growth.

Environmental conditions during data recording

Measurements were recorded between 12.00 and 14.00 h in the greenhouse and between 13.00 and 15.00 h in the field on clear sunny days. During the data recording, PAR varied from 1300–1400 and 1600–1700 μmol/m²/s, and relative humidity from 60–65 and 45–50% in the greenhouse and field, respectively. The time of data recording was chosen because at this period plants suffer maximum heat stress and maximum phenotypic differences among genotypes are apparent (Roark & Quisenberry 1977; Lu *et al*. 1994). Ambient CO_2 concentration remained at 340–351 μmol/mol in the field and 320–324 μmol/mol in the greenhouse. Air temperature in the field ranged from 42–44 °C in both years. The temperature of the porometer ranged from 28·3–35·8 °C during data recording in all experiments. The inlet flow rate was kept between 45 and 50 cm^3/min, and adjusted to give at least 10% RH difference between inlet and outlet. Care was taken to provide adequate water to the experimental materials to eliminate the confounding effect of drought on stomatal conductance. Stomatal conductance was recorded between the 4th and 10th day after irrigation in a 7–12 days irrigation schedule. All measurements were recorded from the youngest fully expanded leaves on the main stem (20–23 days old). Leaves were tagged on the day they unfolded and this was counted as day 1. Due to the small time window of maximum heat stress during the day at which maximum phenotypic differences could be available, data was recorded in a cyclical manner and sample sizes were necessarily limited. Leaves on the plants were tagged on different days so that leaves of the required age were available during the cyclic measurements of the data. Data were recorded from a maximum of two plants from each generation in a cycle. After completing the required number of plants from each genotype and generation, the next replication was started. The sample size for each parental and F_1 entry was 3 plants per replication in the greenhouse and 5 plants per replication in the field experiments. Sample size for each F_2 generation was 12 and 32 plants, and for each back cross generation 6 and 16 plants per replication in the greenhouse and field, respectively.

Statistical and biometrical procedures

In the analyses of variance, years and temperature regimes were assumed to have fixed effects and generations to have a random effect. In the field experiments, the generation × year interaction was non-significant ($P > 0{\cdot}05$), therefore, generation mean analyses were run on the data averaged over years for each temperature regime. Estimates of various genetic effects and digenic interactions were computed by employing a joint scaling test and interpreted following Hayman (1958, 1960). For computations, computer software developed by Dr Pooni, University of Birmingham, was utilized. This program uses means and weights of various generations and by solving simultaneous equations, allows testing of different models one by one. All possible models were tested and the fittest model was reported. The ideal model

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Table 1. *Mean phenotypic expression of stomatal conductance (mol/m²/s) in various generations of the three upland crosses under heat-stressed (HS) and non-stressed (NS) greenhouse and field regimes*

	MNH-552 × HR109-RT				CIM-448 × CRIS-19				FH-900 × N-Karishma			
	Greenhouse		Field		Greenhouse		Field		Greenhouse		Field	
	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS
P_1	0·49	0·56	0·86	1·25	0·42	0·56	0·82	1·21	0·38	0·59	0·83	1·25
P_2	0·37	0·62	0·72	1·05	0·54	0·58	0·77	1·08	0·40	0·46	0·87	0·90
F_1	0·41	0·65	0·78	1·12	0·46	0·60	0·63	0·80	0·48	0·48	1·10	1·10
F_2	0·37	0·58	0·61	0·86	0·39	0·59	0·70	0·84	0·39	0·47	1·14	1·21
BC_1	0·38	0·61	0·80	0·96	0·37	0·71	0·80	0·94	0·34	0·63	0·70	0·90
BC_2	0·39	0·65	0·62	0·84	0·56	0·63	0·65	0·91	0·34	0·68	0·78	0·96
S.E.	0·026	0·031	0·051	0·066	0·020	0·036	0·020	0·041	0·020	0·031	0·046	0·077

should have all components significant (approximately twice their standard error) and a χ^2 value less than 1·96 (or the appropriate value). The model closest to this ideal situation was considered as the fittest model.

RESULTS

Analyses of variance on greenhouse data revealed significant generation × temperature regime interaction for stomatal conductance in all the three crosses. The generation × temperature regime interaction was also significant for stomatal conductance in the field, revealing environmental sensitivity of stomatal conductance. The generation × year interaction was non-significant ($P > 0{\cdot}05$) in all of the three crosses, and the magnitude of the generation × year × temperature regime interaction was much smaller than that of the main effects, indicating that temperature regime interaction was the more important cause of variation in stomatal conductance. In the field, variation due to generations was, nevertheless, much higher in magnitude than the interaction variation; in contrast the interaction variance was of higher magnitude in the greenhouse experiment. This could be due to the comparatively longer duration of heat stress and higher difference in the intensities of the two temperature regimes in the greenhouse than could be achieved in the field. Heat stress, in general, reduced stomatal conductance and available genetic variability among generations (Table 1).

Cross-1: MNH-552 × HR109-RT

The two parents of the cross differed significantly for stomatal conductance under both heat-stressed and non-stressed regimes. Cultivar MNH-552, the female parent, was relatively more heat tolerant because it expressed higher stomatal conductance in all environments except the non-stressed greenhouse regime (Table 1). Under the heat-stressed greenhouse regime, the F_1, F_2, BC_1 and BC_2 generations resembled the parent with lower stomatal conductance, while under the non-stressed greenhouse and both field regimes, the F_1 mean resembled the higher parent and the backcross generations tended towards the recurrent parents. A significant reduction in stomatal conductance was also evident in the F_2 generation. Suppression of stomatal conductance caused by continuous heat stress might have been the cause of the relatively lower variation among generations under the heat-stressed greenhouse regime.

Estimates of various genetic effects revealed the presence of epistasis (non-allelic interaction) for stomatal conductance in all environments, which was predominantly of the additive × additive type (Table 2). The inheritance of stomatal conductance appeared to be controlled by the additive mean component in the presence of heat stress in the greenhouse and the dominant mean component in its absence. In the field environments, however, both additive and dominant genetic effects were important. The dominant mean component was larger in magnitude than the additive mean component under both field regimes. Additive × additive gene interaction was expressed in the presence of heat stress, and additive × additive and dominant × dominant types in non-stressed conditions. Since the estimates of dominant and dominant × dominant mean components carried the same sign, complementary epistatic effects appeared to be operative in the inheritance of stomatal conductance in this cross under the non-stressed field regime.

Cross-2: CIM-448 × CRIS-19

Cultivars CIM-448 and CRIS-19, the parents of this cross, expressed significantly different stomatal conductance in all regimes except the non-stressed greenhouse regime. Cultivar CRIS-19, the male parent, showed higher stomatal conductance under

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Table 2. *Estimates of various genetic effects associated with the expression of stomatal conductance (mol/m²/s) in various generations of the cross MNH-552 × HR109-RT as revealed by the fittest model of inheritance under heat stressed and non-stressed greenhouse and field regimes*

	Greenhouse		Field	
Effect	Heat-stressed	Non-stressed	Heat-stressed	Non-stressed
m	0·36 ± 0·041	0·94 ± 0·092	1·04 ± 0·092	0·99 ± 0·093
d	0·07 ± 0·031		0·13 ± 0·013	0·11 ± 0·024
h		−0·28 ± 0·124	0·35 ± 0·173	0·25 ± 0·133
i	0·06 ± 0·031	−0·33 ± 0·102	0·41 ± 0·101	0·49 ± 0·092
j				
l				0·17 ± 0·060
χ^2	1·71	1·55	0·51	0·54
D.F.	3	3	2	1

Note: m = F_2 mean; d = additive mean component; h = dominant mean component; and i, j, l, respectively are additive × additive, additive × dominant and dominant × dominant digenic interactions.

Table 3. *Estimates of various genetic effects associated with the expression of stomatal conductance (mol/m²/s) in various generations of the cross CIM-448 × CRIS-19 as revealed by the fittest model of inheritance under heat stressed and non-stressed greenhouse and field regimes*

	Greenhouse		Field	
Effect	Heat-stressed	Non-stressed	Heat-stressed	Non-stressed
m	0·46 ± 0·022	0·83 ± 0·121	1·37 ± 0·062	1·13 ± 0·032
d	−0·06 ± 0·021		0·06 ± 0·023	0·07 ± 0·021
h		−0·22 ± 0·102	−0·14 ± 0·069	
i		−0·26 ± 0·122	0·07 ± 0·041	0·26 ± 0·041
j	−0·13 ± 0·078	0·08 ± 0·051	0·09 ± 0·043	
l				
χ^2	1·42	0·36	0·03	1·30
D.F.	3	2	1	3

Note: m = F_2 mean; d = additive mean component; h = dominant mean component; and i, j, l, respectively are additive × additive, additive × dominant and dominant × dominant digenic interactions.

the heat-stressed greenhouse regime. Cultivar CIM-448 had higher stomatal conductance in both field regimes. In the greenhouse, the BC_1 of this cross combination had significantly higher stomatal conductance compared with all other generations in the absence of heat stress (Table 1). The F_1 mean for stomatal conductance resembled the lower parent under the heat-stressed greenhouse regime and remained significantly lower than both parents in the field regimes. Back cross generations tended towards the recurrent parent in the presence of heat stress.

Estimates of various genetic effects for this cross combination suggested the presence of non-allelic (epistatic) interaction for stomatal conductance (Table 3). The fittest model of inheritance in the greenhouse revealed a predominance of additive genetic effects with additive × dominant digenic interaction in the presence of heat stress and dominant genetic effects with additive × additive and additive × dominant interactions in non-stressed conditions. Under the heat-stressed field regime, both additive and dominant genetic effects with additive × additive and additive × dominant interactions were evident. The magnitude of the dominant mean effect was larger than that of the additive effect. In non-stressed conditions in the field, however, additive genetic effect and additive × additive type of digenic interaction were involved in the inheritance of stomatal conductance.

Cross-3: FH-900 × N-Karishma

The two parent cultivars, FH-900 and N-Karishma, showed significantly different stomatal conductance

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Table 4. *Estimates of various genetic effects associated with the expression of stomatal conductance (mol/m²/s) in various generations of the cross FH-900 × N-Karishma as revealed by the fittest model of inheritance under heat stressed and non-stressed greenhouse and field regime*

	Greenhouse		Field	
Effect	Heat-stressed	Non-stressed	Heat-stressed	Non-stressed
m	0·39 ± 0·029	0·76 ± 0·031	1·98 ± 0·042	1·73 ± 0·203
d		0·06 ± 0·021		−1·15 ± 0·303
h	−0·09 ± 0·112		−1·63 ± 0·091	
i		−0·24 ± 0·051	−0·54 ± 0·052	−0·50 ± 0·201
j	−0·08 ± 0·111		−0·61 ± 0·032	−0·37 ± 0·071
l	0·18 ± 0·103	−0·31 ± 0·059	1·06 ± 0·039	0·62 ± 0·121
χ^2	0·08	0·95	1·55	0·95
D.F.	2	2	1	1

Note: m = F_2 mean; d = additive mean component; h = dominant mean component; and i, j, l, respectively are additive × additive, additive × dominant and dominant × dominant digenic interactions.

under non-stressed conditions both in the greenhouse and the field. Cultivar FH-900 had higher stomatal conductance under non-stressed conditions (Table 1). Under heat stress, however, both parents had similar stomatal conductance. The F_1 mean significantly exceeded both parents, showing heterotic effects under heat stress, but resembled the lower parent in non-stressed conditions in the greenhouse and the better parent in the field. Back cross generations tended towards recurrent parents, especially under heat stress.

Estimates of various genetic effects for this cross (Table 4) indicated the presence of non-allelic interaction for stomatal conductance in both heat-stressed and non-stressed regimes. The inheritance of stomatal conductance for this cross appeared to be controlled by dominant genetic effects with additive × dominant and dominant × dominant types of digenic interactions under heat stress and additive genetic effect with additive × additive and dominant × dominant types of digenic interaction under non-stressed conditions in the greenhouse. Likewise, in the field, the dominant mean component with additive × additive, additive × dominant and dominant × dominant types of digenic interactions were important under heat stress, and the additive mean component with all the three types of digenic interactions in non-stressed conditions (Table 4). This suggested that dominant and dominant × dominant mean components would have major influence in the segregating behaviour of this cross under heat-stressed conditions. Under heat-stressed field and greenhouse regimes, estimates of dominant (*h*) and dominant × dominant (*l*) mean components carried different signs, indicating the involvement of duplicate epistasis in the inheritance of stomatal conductance.

DISCUSSION

Previous reports on the inheritance of stomatal conductance have shown both additive and dominant mean components of variation (Roark & Quisenberry 1977). Later experiments on Pima cotton (*Gossypium barbadense* L.) in single environments determined a simple additive dominant model as well as one with complex digenic interactions for stomatal conductance (Percy *et al*. 1996). The present study revealed variation in the inheritance pattern of stomatal conductance, from additive with additive × additive mean components to more complex one involving both additive and dominant mean components with all three types of digenic interactions. Variation in the inheritance pattern of stomatal conductance could be due to genotype per se as well as to differential expression of genes across a range of environments. The results of the present investigation provided evidence of this effect. Temperature regimes exerted a significant effect on the expression of genes responsible for stomatal conductance. High temperature or heat stress favoured the expression of genes having dominant effects, while non-stressed conditions favoured those having additive effect in two of the three crosses evaluated (MNH-552 × HR109-RT and CIM-448 × CRIS-19). The third cross (FH-900 × N-Karishma) showed the opposite reaction. In this cross, genes having additive effects were expressed under heat stress, and those having dominant effects were expressed under non-stressed conditions. The results suggest that the genes controlling stomatal conductance in the parents of the first two crosses (MNH-552, HR109-RT, CIM-448 and CRIS-19) were different from those controlling stomatal conductance in FH-900 and N-Karishma. A modification

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of the inheritance pattern of stomatal conductance in response to temperature regimes would influence the breeding strategy to be adopted in the segregating generations. Heat-stressed conditions, inducing additive and additive × additive interaction effects in the first two crosses, could be helpful in fixing desirable additive alleles in the segregating populations, while in the third cross such a benefit could be obtained in non-stressed conditions. Since the performance of backcross generations tended towards the recurrent parent in the presence of heat stress, modified backcrossing procedures performed in the presence of heat stress could also be useful in improving stomatal conductance.

The present paper and previous reports (Radin *et al*. 1994; Percy *et al*. 1996) have shown the existence of substantial variation for stomatal conductance within cultivated cotton species and cultivars. However, including stomatal conductance as a heat avoidance mechanism in applied breeding programmes would need to be considered in relation to biomass (yield) production, because genotypes having higher stomatal conductance do not necessarily have higher yields, especially under non-stressed conditions (Rahman 2004). Moreover, reduced selection efficiency could be encountered because of the presence of complex non-allelic and genotype × temperature regime interactions. Inter-mating and recurrent selection for general combining ability under heat stress could be a useful breeding strategy. Molecular markers linked to higher stomatal conductance for marker-assisted selection could be explored for dissecting genotype × environment interaction and selecting superior genotypes. Genetic improvement through a correlated response (indirect selection) could also be a rational and pragmatic approach under such circumstances, as has been reported to have occurred incidentally in the advanced Pima cotton cultivars (Cornish *et al*. 1991; Lu & Zeiger 1994). The conclusion of the present work is that substantial genetic variability for stomatal conductance is available within the upland cotton germplasm, providing the potential for genetic improvement in this trait. However, the environmental sensitivity and variation in the pattern of inheritance across environments would complicate the process.

REFERENCES

Burke, J. J., Mahan, J. R. & Hatfield, J. L. (1988). Crop specific thermal kinetic windows in relation to wheat and cotton biomass production. *Agronomy Journal* **80**, 553–556.

Cornish, K., Radin, J. W., Turcotte, E. L., Lu, Z. & Zeiger, E. (1991). Enhanced photosynthesis and stomatal conductance of Pima cotton bred for increased yield. *Plant Physiology* **97**, 484–489.

Hayman, B. I. (1958). The separation of epistatic from additive and dominance variation in generation means. *Heredity* **12**, 371–390.

Hayman, B. I. (1960). Maximum likelihood estimation of genetic components of variation. *Biometrics* **16**, 369–381.

Jarvis, P. G. & Mansfield, T. A. (1981). *Stomatal Physiology*. Cambridge, UK: Cambridge University Press.

Koniger, M. & Winter, K. (1993). Reduction of photosynthesis in sun leaves of *Gossypium hirsutum* L. under conditions of high light intensities and suboptimal leaf temperatures. *Agronomie* **13**, 659–668.

Lu, Z. M. & Zeiger, E. (1994). Selection for higher yields and heat resistance in pima cotton has caused genetically determined changes in stomatal conductance. *Physioogial Plantarum* **92**, 273–278.

Lu, Z. M., Radin, J. W., Turcotte, E. L., Percy, R. & Zeiger, E. (1994). High yields in advanced lines of pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature. *Physiologia Plantarum* **92**, 266–272.

Lu, Z. M., Chen, J., Percy, R., Sharifi, M. R., Rundel, P. W. & Zeiger, E. (1996). Genetic variation in carbon isotope discrimination and its relation to stomatal conductance in Pima cotton (*Gossypium barbadense* L). *Australian Journal of Plant Physiology* **23**, 127–132.

Lu, Z. M., Chen, J., Percy, R. G. & Zeiger, E. (1997). Photosynthetic rate, stomatal conductance and leaf area in two cotton species (*Gossypium barbadense* and *Gossypium hirsutum*) and their relation with heat resistance and yield. *Australian Journal of Plant Physiology* **24**, 693–700.

Mahan, J. R., McMichael, B. L. & Wanjura, D. F. (1995). Methods for reducing the adverse effects of temperature stress on plants – a review. *Environmental and Experimental Botany* **35**, 251–258.

Morrison, M. J. & Stewart, D. W. (2002). Heat stress during flowering in summer brassica. *Crop Science* **42**, 797–803.

Nijs, I., Ferris, R., Blum, H., Hendrey, G. & Impens, I. (1997). Stomatal regulation in a changing climate – a field study using free air temperature increase (FATI) and free air CO_2 enrichment (FACE). *Plant, Cell and Environment* **20**, 1041–1050.

Nobel, P. S. (1991). *Physiochemical and Environmental Plant Physiology*. London: Academic Press.

Percy, R. G., Lu, Z. M., Radin, J. W., Turcotte, E. L. & Zeiger, E. (1996). Inheritance of stomatal conductance in cotton (*Gossypium barbadense*). *Physiologia Plantarum* **96**, 389–394.

Pettigrew, W. T. & Meredith, W. R. (1994). Leaf gas exchange parameters vary among cotton genotypes. *Crop Science* **34**, 700–705.

Pettigrew, W. T., Heitholt, J. J. & Vaughn, K. C. (1993). Gas exchange differences and comparative anatomy among cotton leaf-type isolines. *Crop Science* **33**, 1295–1299.

Radin, J. W., Lu, Z., Percy, R. G. & Zeiger, E. (1994). Genetic variability for stomatal conductance in Pima cotton and its relation to improvements of heat

https://doi.org/10.1017/S0021859605005186 Published online by Cambridge University Press

adaptation. *Proceedings of National Academy of Sciences USA* **91**, 7217–7221.

Rahman, H. (2004). *Genetic basis of heat resistance in upland cotton* (Gossypium hirsutum *L.*). Ph.D. thesis, Bahauddin Zakariya University, Multan, Pakistan.

Rahman, H., Malik, S. A. & Saleem, M. (2004). Heat tolerance of upland cotton during the fruiting stage evaluated using cellular membrane thermostability. *Field Crops Research* **85**, 149–158.

Reddy, K. R., Robana, R. R., Hodges, H. F., Liu, X. J. & McKinion, J. M. (1998). Interactions of CO_2 enrichment and temperature on cotton growth and leaf characteristics. *Environmental and Experimental Botany* **39**, 117–129.

Roark, B. & Quisenberry, J. E. (1977). Environmental and genetic components of stomatal behaviour in two genotypes of Upland cotton. *Plant Physiology* **59**, 354–356.

Schulze, E. (1986). Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology* **37**, 247–274.

Steiner, J. J. & Jacobsen, T. A. (1992). Time of planting and diurnal temperature effects on cotton seedling field emergence and rate of development. *Crop Science* **32**, 238–244.

Zeiger, E., Farquhar, G. D. & Cowan, I. R. (1987). *Stomatal Function*. Stanford, CA: Stanford University Press.

https://doi.org/10.1017/S0021859605005186 Published online by Cambridge University Press