

## Inheritance of seed physical traits in upland cotton under different temperature regimes

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### Abstract

Physical seed traits such as seed weight, volume and density are determinants of seed vigour in cotton, while seed surface area is of prime importance in lint production. Two Pak-upland cotton crosses, plus their parental, F<sub>2</sub> and back cross generations were evaluated over two years to determine the inheritance pattern of their seed physical traits under heat stress and non-stress field regimes. The heat stress regime suppressed the average expression of seed traits in all generations. The results showed there to be low genetic variability with respect to physical seed traits, particularly seed volume, seed density and seed surface area, among several generations of the two cotton crosses. The inheritance of seed physical traits was complex in both crosses due to the presence of substantial non-allelic interactions (digenic epistatic effects) and the influence of *generation × temperature regime* interaction. The two crosses expressed different patterns of inheritance for seed physical traits. Those governing seed volume and seed surface area were highly sensitive to the temperature regime in both crosses and were controlled by additive genetic effects under heat stress conditions, and by dominant genetic effects under non-stress regime. The non-stress regime favoured the expression of dominant genetic effects. From a breeding point of view, the heat stress regime could be a more favourable environment for enhancing selection efficiency.

**Additional key words:** genetic effects, *Gossypium*, heat stress, seed vigour.

### Resumen

#### La herencia de caracteres físicos de la semilla de algodón de tierras altas bajo diferentes regímenes de temperatura

Caracteres físicos tales como peso, volumen y densidad son determinantes en el vigor de la semilla y, en el caso del algodón, el área superficial de la misma es fundamental en la producción de las hilas. Con el fin de comprender el patrón de la herencia de los caracteres físicos de semillas de algodón sometidas a estrés por altas temperaturas y sin estrés, se evaluaron durante dos años dos cruces de algodón de tierras altas de Pakistán y sus parentales, así como generaciones F<sub>2</sub> y de retrocruzamiento de ambos parentales. El régimen de estrés por altas temperaturas suprimió la expresión media de los caracteres de las semillas en todas las generaciones. Los resultados revelaron una menor variabilidad genética en varias generaciones de los dos cruces para caracteres físicos de la semilla analizados, particularmente aquellos asociados con el volumen, la densidad y el área superficial de la semilla. La herencia de los caracteres físicos de la semilla fue compleja en ambos cruces debido a la presencia de interacciones no alélicas (efectos epistáticos digénicos) y a la interacción *generación × régimen de temperatura*. Los dos cruces expresaron patrones diferentes de herencia para caracteres físicos de semilla. El patrón de herencia del volumen y área superficial de la semilla en ambos cruces mostró una alta sensibilidad a la temperatura, y estuvo controlado por componentes aditivos bajo estrés por altas temperaturas y por componentes dominantes bajo condiciones no estresantes. El régimen sin estrés favoreció la expresión de efectos genéticos dominantes. Desde el punto de vista de la mejora genética, el estrés por altas temperaturas podría ser un medio más favorable para incrementar la eficiencia de la selección.

**Palabras clave adicionales:** efectos genéticos, estrés por altas temperaturas, *Gossypium*, vigor de la semilla.

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## Introduction

Physical seed traits such as the seed index, the seed volume and seed density are all determinants of seed vigour (Ferguson and Turner, 1971; Krieg and Bartee, 1975; Minton and Supak, 1980; Leffler and Williams, 1983), and in cotton all strongly influence crop stands, growth and seed cotton yield (Minton and Supak, 1980; Hofmann *et al.*, 1988). The seed index (the weight of 100 seeds) is related to seed cotton yield (Rahman *et al.*, 1991), while the number of seeds per boll is recognised as the largest contributor to lint yield after the number of bolls per unit area (Worley *et al.*, 1974, 1976). The desirability of a larger number of seeds per boll has been emphasised as a requirement for greater seed surface areas, and hence lint production within the boll (Culp and Harrell, 1975; Harrell and Culp, 1976).

The environment can strongly affect both morphological and physiological seed traits (Dalianis, 1982), but temperature is thought to be the most important environmental factor influencing seed development (Barrow, 1983; Zhang *et al.*, 1993). In cotton bolls emerging in the later part of the season, the seeds are generally smaller (Kohel and Cherry, 1983; Leffler, 1986). The literature contains information on the importance of seed physical traits as markers of seed vigour, improved germination and improved crop stands. However, these traits, especially seed volume, density and surface area, have received little attention from the breeding point of view. This study examines the impact of heat stress and non-stress environments on the inheritance pattern of physical seed traits. This is not only important for improving seed vigour, but is also helpful in assessing genotypic responses to heat stress.

## Material and Methods

The experimental material consisted of two bi-parental  $F_1$  upland cotton (*Gossypium hirsutum* L.) crosses, plus their parental,  $F_2$  and back cross generations (for both parents-BCP<sub>1</sub> and BCP<sub>2</sub>). These six generations of the two crosses were evaluated over two seasons for seed physical traits, including the number of seeds per boll, the seed index, seed volume, seed density, and seed surface area, when grown in the field under heat stress and non-stress conditions.

All experiments were undertaken at the Cotton Research Institute, Faisalabad, Pakistan. The experi-

mental fields had a loam soil texture (pH 8.5, organic matter 0.93%, saturation 27%, available phosphorus 29.6 ppm, potassium 139 ppm). Seeds were sown on 7<sup>th</sup> April and 29<sup>th</sup> May in 2000 and on 14<sup>th</sup> April and 4<sup>th</sup> June in 2001. Sowing in these different months automatically created different temperature regimes for the crops. The April sowing helped in synchronizing the maximum flowering period with the hottest days of the year (May and June), while the maximum flowering for the June-sown seeds occurred during the optimum temperatures of August and September. The mean minimum and maximum temperatures of the two regimes were significantly different, with temperatures in the April regime higher than those of the June regime (Rahman, 2004; Rahman *et al.*, 2004). The April and June regimes were, therefore, referred to as the heat stress and non-stress regimes respectively.

The experimental design was a randomised complete block with three replications. Plants were spaced 30 cm apart in rows separated by 75 cm. The photosynthetically active radiation (PAR) at noon during the maximum flowering period ranged between 1,800-2,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the heat-stress regime and 1,600-2,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the non-stress regime. The ambient  $\text{CO}_2$  concentration remained between 340 and 351  $\mu\text{mol mol}^{-1}$  in both years. The experiments in both regimes and in both years were terminated 180 days after sowing (DAS). The experimental plots of both regimes received identical cultivation treatments. Plants were fertilised with 150:50:00 N:P:K (kg per ha). Potash (K) was not added since pre-experiment soil tests showed the experimental field to contain 145 ppm potassium. Nitrogen was split into three equal doses and applied at sowing, at first irrigation (33-35 DAS) and at maximum flowering. All plants were sprayed to provide insect control as required. Adequate irrigation was provided when necessary to minimise the confounding effect of drought, especially during the reproductive stage.

## Sampling and measurement of seed traits

Each parental and  $F_1$  generation was represented by 15 plants, the  $F_2$  generation by 80 plants, and the back cross generations by 40 plants per replicate. Samples of 50 random bolls from the upper, middle and lower parts of the plants were carefully hand picked, one sample each from the parental and  $F_1$  generations, 50 from each  $F_2$  generation, and 25 samples of 50 bolls

from each back cross generation per replicate. Seed-cotton was separated from the burr and weighed before ginning to separate the cottonseed and lint. The linted seed was weighed and used to estimate the number of seeds per boll employing the following equation:

$$\text{Number of seeds per boll} = (100 * \text{seed weight per boll}) / \text{linted seed index}$$

where the seed weight per boll = the weight of the seed from 50 bolls/50, and the linted seed index = the weight of 100 seeds before delinting with sulphuric acid.

Two sub samples of 100 seeds each were drawn from each 50-boll sample. These sub-samples of 100 seeds were delinted with commercial sulphuric acid (95%) at the rate of 5 ml H<sub>2</sub>SO<sub>4</sub> per g of seed, washed thoroughly with tap water, surface dried with filter paper, oven dried for 48 h at 30°C, and weighed to determine the seed index. Seed volume was determined by displacement in 30 ml ethanol using the same 100-seed sample. Seed density was calculated as the ratio of seed weight to seed volume. Seed surface area was determined according to Hodson (1920).

### Statistical and biometric procedures

The data were analysed in factorial arrangement after running a test of homogeneity of variances, assuming years and temperature regimes to have a fixed effect and genotype to have a random effect. The *generations* × *years* interaction was either non-significant ( $P > 0.05$ ) or had a much smaller influence than the main effects. Analysis of generation-means (joint scaling test) was therefore performed on the data pooled over the two years for each temperature regime. Estimates of

genetic variability were obtained over the years and temperature regimes (Wricke and Weber, 1986). The results were interpreted according to Hayman (1958, 1960).

## Results

### Cross-1: MNH-552 × HR109-RT

Analysis of variance detected significant variation for all seed traits (except seed volume) with respect to year and field temperature regime. The *generation* × *temperature regime* interaction was significant ( $P < 0.01$ ) and *generation* × *years* non-significant ( $P > 0.05$ ) for all seed traits. This suggests that the relative ranking of various generations of the cross MNH-552 × HR109-RT for seed traits was not consistent across the temperature regimes. The high magnitude of the *generation* × *temperature regime* interaction resulted in negative estimates of genetic variability for seed volume, density and surface area.

Table 1 shows the mean phenotypic expression of the seed traits in several generations of the cross MNH-552 × HR109-RT. The data show that cultivars MNH-552 and HR109-RT, the two parents of the cross, differed significantly in terms of the expression of seed volume, seed density and seed surface area under both temperature regimes ( $P < 0.05$ ). The difference in parental means for the number of seeds per boll was significant under the heat stress regime, while the seed index differed significantly under the non-stress regime. The F<sub>1</sub> means for number of seeds per boll, seed volume and surface area under the heat stress regime resembled those of the better parent, but under the non-stress

**Table 1.** Mean phenotypic expression of number of seeds per boll, seed weight (g), seed volume (ml), seed density (g ml<sup>-1</sup>) and seed surface area (cm<sup>2</sup>) of various generations of the upland cotton cross MNH-552 × HR109-RT under heat stress (April) and non-stress (June) regimes

| Generation      | Number of seeds per boll |       | 100-seed weight |      | Seed volume |      | Seed density |      | Seed surface area |      |
|-----------------|--------------------------|-------|-----------------|------|-------------|------|--------------|------|-------------------|------|
|                 | April                    | June  | April           | June | April       | June | April        | June | April             | June |
| P <sub>1</sub>  | 19.87                    | 25.94 | 7.19            | 6.93 | 5.15        | 8.04 | 0.91         | 1.41 | 0.90              | 1.00 |
| P <sub>2</sub>  | 22.57                    | 23.73 | 7.45            | 7.58 | 8.03        | 6.89 | 1.08         | 0.96 | 1.00              | 0.92 |
| F <sub>1</sub>  | 24.99                    | 29.06 | 6.62            | 6.63 | 7.78        | 6.95 | 0.96         | 0.86 | 0.98              | 0.94 |
| F <sub>2</sub>  | 21.23                    | 27.55 | 6.95            | 7.31 | 7.38        | 7.01 | 0.99         | 0.99 | 0.94              | 0.93 |
| BC <sub>1</sub> | 27.49                    | 22.56 | 6.40            | 7.13 | 7.25        | 6.54 | 0.98         | 0.99 | 0.94              | 0.91 |
| BC <sub>2</sub> | 26.85                    | 31.33 | 6.34            | 6.86 | 7.33        | 6.32 | 1.00         | 1.06 | 0.99              | 0.92 |
| CD 5%           | 4.14                     | 3.36  | 0.78            | 0.57 | 1.41        | 0.91 | 0.08         | 0.23 | 0.08              | 0.04 |

regime the means for seed index, seed volume, seed density and surface area resembled those of the lower parent. The results show that heterosis exists in the expression of these traits. The means of the F<sub>2</sub> generation resembled those of the F<sub>1</sub> in terms of number of seeds per boll, seed volume, seed density and surface area under both regimes, and for seed index under the heat stress regime. This indicates a lack of any significant depression in the F<sub>2</sub> generation compared to the F<sub>1</sub> generation (Table 1).

The joint scaling test indicated the presence of non-allelic interaction (epistasis) in the expression of all the seed traits evaluated in this cross. The fittest model of inheritance revealed both additive and dominant genetic effects for the number of seeds per boll under the heat stress and non-stress regimes (Table 2). The *additive × additive* type of digenic interaction was important under the non-stress regime and the *additive × dominant* interaction under the heat stress regime. The magnitude of the dominant genetic effect was much greater than that of the additive effect under both field regimes. Similarly, both the additive and dominant genetic effects with *dominant × dominant* digenic interaction were important for the seed index under the heat stress regime, whereas the dominant genetic effect with *additive × additive* digenic interaction was important under the non-stress regime. The size of the dominant effect was larger than that of the additive genetic effect with respect to the seed index under the heat stress regime (Table 2).

With respect to the inheritance of seed volume, the additive genetic effect with *additive × additive* and

*additive × dominant* digenic interaction was evident under the heat stressed regime, while under the non-stress regime both the additive and dominant genetic effects with *additive × dominant* and *dominant × dominant* digenic interactions were apparent (Table 2). The size of the dominant effect was about four times that of the additive genetic effect. This indicates that the non-stress field regime favours the expression of a strong, dominant effect for seed volume. With respect to the inheritance of seed density, both additive and dominant genetic effects were important under both field regimes. In addition, *dominant × dominant* digenic interaction was important under the heat stress regime whereas the *additive × dominant* interaction was important under the non-stress regime (Table 2). Similarly, both the additive and dominant genetic effects, with a significant influence of *additive × dominant* and *dominant × dominant* digenic interaction, controlled the expression of surface area under the non-stress regime (Table 2). The size of the mean additive effect was much larger than that of the dominant effect. Under the heat stress regime, however, the additive genetic effect with *additive × additive* digenic interaction influenced the expression of surface area.

### Cross-2: CIM-448 × CRIS-19

Analysis of variance showed that variation due to year was significant for the number of seeds per boll, the seed index, seed volume and surface area ( $P < 0.01$ ), and that the *generation × year* interaction was not

**Table 2.** Estimates of different genetic effects associated with the expression of number of seeds per boll, seed weight (g), seed volume (ml), seed density (g ml<sup>-1</sup>) and seed surface area in the upland cotton cross MNH-552 × HR109-RT under heat stress (April) and non-stress (June) regimes

| Effect                  | Number of seeds per boll |               | Seed index   |              | Seed volume  |              | Seed density |              | Seed surface area |              |
|-------------------------|--------------------------|---------------|--------------|--------------|--------------|--------------|--------------|--------------|-------------------|--------------|
|                         | April                    | June          | April        | June         | April        | June         | April        | June         | April             | June         |
| F <sub>2</sub> mean (m) | 15.97 ± 2.05             | 24.84 ± 0.46  | 7.32 ± 0.11  | 7.90 ± 0.46  | 7.44 ± 0.18  | 7.49 ± 0.27  | 1.01 ± 0.02  | 1.16 ± 0.03  | 0.95 ± 0.01       | 0.96 ± 0.02  |
| Additive (d)            | -1.36 ± 0.49             | 1.11 ± 0.46   | -0.14 ± 0.11 |              | -1.44 ± 0.39 | 0.59 ± 0.27  | -0.07 ± 0.02 | 0.21 ± 0.04  | -0.05 ± 0.02      | 0.41 ± 0.02  |
| Dominant (h)            | 10.88 ± 3.97             | 4.38 ± 1.63   | -1.71 ± 0.68 | -1.29 ± 0.57 |              | -2.02 ± 0.88 | -0.06 ± 0.03 | -0.33 ± 0.09 |                   | -0.09 ± 0.04 |
| Add × Add (i)           | 5.38 ± 2.10              |               |              | -0.65 ± 0.40 | -0.85 ± 0.43 |              |              |              | -0.04 ± 0.01      |              |
| Add × Dom (j)           |                          | -10.07 ± 1.67 |              |              | 1.45 ± 0.86  | -1.22 ± 0.63 |              | -0.23 ± 0.09 |                   | -0.08 ± 0.03 |
| Dom × Dom (l)           |                          |               | 0.98 ± 0.48  |              |              | 1.56 ± 0.23  | 0.03 ± 0.02  |              |                   | 0.07 ± 0.03  |
| Chi square              | 1.12                     | 0.08          | 0.64         | 1.58         | 0.61         | 0.23         | 0.99         | 1.29         | 2.90              | 0.01         |
| df                      | 2                        | 2             | 2            | 3            | 2            | 1            | 2            | 2            | 3                 | 1            |

df: degrees of freedom.

**Table 3.** Mean phenotypic expression number of seeds per boll, seed weight (g), seed volume (ml), seed density (g ml<sup>-1</sup>), and seed surface area (cm<sup>2</sup>) for various generations of the upland cotton cross CIM-448 × CRIS-19 under heat stress (April) and non-stress (June) regimes

| Generation      | Number of seeds per boll |       | 100-seed weight |      | Seed volume |      | Seed density |      | Seed surface area |      |
|-----------------|--------------------------|-------|-----------------|------|-------------|------|--------------|------|-------------------|------|
|                 | April                    | June  | April           | June | April       | June | April        | June | April             | June |
| P <sub>1</sub>  | 25.41                    | 24.43 | 6.42            | 6.97 | 5.66        | 7.29 | 1.13         | 0.96 | 0.90              | 0.95 |
| P <sub>2</sub>  | 23.08                    | 20.69 | 8.37            | 7.65 | 8.33        | 6.90 | 1.00         | 1.11 | 1.00              | 0.93 |
| F <sub>1</sub>  | 27.51                    | 30.56 | 6.87            | 7.96 | 7.14        | 10.3 | 0.97         | 0.79 | 0.94              | 1.14 |
| F <sub>2</sub>  | 27.35                    | 23.17 | 6.81            | 7.13 | 6.94        | 7.67 | 0.98         | 1.00 | 0.91              | 1.01 |
| BC <sub>1</sub> | 22.89                    | 26.09 | 7.13            | 7.74 | 7.28        | 7.80 | 0.97         | 1.00 | 0.96              | 0.97 |
| BC <sub>2</sub> | 26.34                    | 24.77 | 7.87            | 7.48 | 7.76        | 7.58 | 1.02         | 0.99 | 0.97              | 0.94 |
| CD 5%           | 2.49                     | 4.92  | 0.72            | 0.41 | 0.62        | 1.37 | 0.07         | 0.16 | 0.04              | 0.08 |

significant for any seed trait except seed density ( $P < 0.05$ ). The *generation × temperature regime* interaction was, however, significant for the seed index, seed volume, seed density, seed surface area ( $P < 0.01$ ) and the number of seeds per boll ( $P < 0.05$ ). Consequently, only the number of seeds per boll and the seed index showed significant genetic variability.

Table 3 shows the means for the seed traits of several generations of this cross. The two parental cultivars, CIM-448 and CRIS-19, differed significantly ( $P < 0.05$ ) for all physical seed traits under both regimes, except for seed volume and surface area, for which they showed no significant differences under the non-stress regime ( $P > 0.05$ ). The F<sub>1</sub> mean for the number of seeds per boll under the heat stress regime, and that for the seed index under the non-stress regime, resembled the mean of the better parent. Similarly, the F<sub>1</sub> means for

seed index, seed density and surface area under the heat stress regime resembled those of the lower parent. With respect to seed volume and seed surface area under the non-stress regime, as well as the number of seeds per boll under the heat stress regime, the means of both parents were exceeded. The joint scaling test showed the presence of non-allelic interaction (epistatic effects) of various types in the expression of all the seed traits under both the heat stress and non-stress regimes (Table 4).

The fittest model of inheritance for the number of seeds per boll under the non-stress regime (Table 4) comprised both additive and dominant mean components with *additive × additive* digenic interaction. Under the non-stress regime, however, the additive mean effect with *additive × dominant* and *dominant × dominant* interaction was important. The magnitude of

**Table 4.** Estimates of various genetic effects associated with the expression of number of seeds per boll, seed index (g), seed volume (ml) and seed density (g ml<sup>-1</sup>) in the upland cotton cross CIM-448 × CRIS-19 under heat stress (April) and non-stress (June) regimes.

| Effect                  | Number of seeds per boll |              | Seed index   |              | Seed volume  |             | Seed density |              | Seed surface area |             |
|-------------------------|--------------------------|--------------|--------------|--------------|--------------|-------------|--------------|--------------|-------------------|-------------|
|                         | April                    | June         | April        | June         | April        | June        | April        | June         | April             | June        |
| F <sub>2</sub> mean (m) | 24.55 ± 0.28             | 15.64 ± 3.25 | 6.88 ± 0.13  | 7.71 ± 0.16  | 7.04 ± 0.11  | 3.31 ± 1.39 | 0.97 ± 0.01  | 1.03 ± 0.01  | 0.94 ± 0.01       | 0.93 ± 0.01 |
| Additive (d)            | 1.10 ± 0.39              | 1.86 ± 0.44  | -1.02 ± 0.15 | -0.34 ± 0.28 | -1.37 ± 0.12 |             | 0.06 ± 0.01  | -0.07 ± 0.01 | -0.05 ± 0.02      |             |
| Dominant (h)            |                          | 15.16 ± 5.63 |              |              |              | 6.77 ± 2.03 |              |              |                   | 0.07 ± 0.02 |
| Add × Add (i)           |                          | 6.93 ± 3.27  | 0.56 ± 0.21  | -0.40 ± 0.18 |              | 3.70 ± 1.45 | 0.10 ± 0.02  |              | 0.01 ± .005       |             |
| Add × Dom (j)           | -6.85 ± 1.25             |              |              | 0.60 ± 0.40  | 0.56 ± 0.26  |             | -0.12 ± 0.03 | 0.26 ± 0.05  | 0.04 ± 0.02       |             |
| Dom × Dom (l)           | 4.56 ± 1.65              |              |              |              |              |             |              | -0.24 ± 0.06 |                   | 0.11 ± 0.03 |
| Chi square              | 4.84                     | 0.08         | 2.23         | 2.43         | 2.41         | 1.92        | 0.19         | 1.73         | 2.82              | 2.16        |
| df                      | 2                        | 2            | 3            | 2            | 3            | 3           | 2            | 2            | 2                 | 3           |

df: degrees of freedom.

the dominant effect for number of seeds per boll under the heat stress regime was much greater than that of the additive component, indicating that the heat stress regime favours the expression of the dominant mean component for the number of seeds per boll.

The expression of seed index under both regimes was predominantly influenced by the additive genetic effect with significant *additive*  $\times$  *additive* digenic interaction under the heat stress regime, and *additive*  $\times$  *additive* and *additive*  $\times$  *dominant* interaction under the non-stress regime (Table 4). Similarly, the additive genetic effect with *additive*  $\times$  *dominant* digenic interaction was important for seed volume under the heat stress regime. Under the non-stress regime, however, the dominant genetic effect with *additive*  $\times$  *additive* digenic interaction was important. The additive genetic effect also controlled the expression of seed density under both regimes. The *additive*  $\times$  *additive* and *additive*  $\times$  *dominant* digenic interactions were also important under the heat stress regime, whereas the *additive*  $\times$  *dominant* and *dominant*  $\times$  *dominant* interactions were important under the non-stress regime (Table 4). The fittest model of inheritance for surface area showed the predominant influence of the additive genetic effect with *additive*  $\times$  *additive* and *additive*  $\times$  *dominant* interactions under the heat stress regime. However, under the non-stress regime, the dominant genetic effect with *dominant*  $\times$  *dominant* interaction exerted significant effects. The magnitude of the *dominant*  $\times$  *dominant* digenic interaction was larger than that of the dominant genetic effect (Table 4).

## Discussion

Like other quantitative traits of upland cotton, seed traits are liable to modification under different environmental conditions (Rahman *et al.*, 1993b). The results of the present study reveal low genetic variability among several generations of the two crosses with respect to physical seed traits, particularly seed volume, density and seed surface area. Rahman *et al.* (1993a), however, reported substantial genetic variability for seed index, seed volume, and density in the F<sub>3</sub> generation of upland cotton evaluated in a single environment. The substantial *genotype*  $\times$  *temperature regime* interaction associated with the expression of the seed traits is an important reason for this low level of genetic variation. Moreover, breeding and agronomic practices can also affect the physical and chemical properties of

cottonseed (Cherry and Leffler, 1984). The *genotype*  $\times$  *environment* interaction results from changes in the size of the differences among genotypes in different environments, or from changes in the relative ranking of the genotypes (Allard and Bradshaw, 1964; Fernandez, 1991). Crop modelling and understanding the physiology of cotton in different environments might be helpful in explaining why a trait is expressed better in one environment than in another (Boote *et al.*, 2003).

The two crosses evaluated in the present study showed different patterns of inheritance for seed physical traits under the heat stress and non-stress field regimes. Temperature had a relatively stronger effect on the inheritance pattern of seed volume and seed surface area in both crosses; the non-stress regime was favourable to the expression of dominant genetic effects. From a plant breeding point of view, the heat stress regime appears as a more favourable environment for the selection of seed volume and surface area in these two crosses. The relatively high sensitivity of seed volume and surface area to these conditions might also be useful in assessing heat tolerance. The results of a combining ability analysis (Coyle and Smith, 1997) have also shown the importance of variation in general combining ability (additive genetic variation) with respect to the expression of seed surface area. The lower mean performance of some generations for seed traits under the heat stress regime indicates a repressing effect of high temperature. Under such circumstances, as in the case of cross CIM-448  $\times$  CRIS-19 in which the additive mean component was high for various seed traits under the heat stress conditions, the fixation of favourable genes would be more effective. For traits such as the number of seeds per boll, in which both the additive and dominant mean component with epistatic effects were involved, recurrent selection might be a useful breeding strategy.

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