GENETIC STUDIES ON DROUGHT TOLERANCE IN UPLAND COTTON (*GOSSYPIUM HIRSUTUM* L.)

M.A. A-El-Dahan and M. López
Dpto del Algodón
CIFA Las Torres-Tomejil
Seville, Spain
E.O. Leidi
Dpto de Biología Vegetal
IRNAS_CSIC
Seville, Spain
J.C. Gutiérrez
Eurogenetic
Cordoba, Spain

Abstract

A diallel study was carried out during 1998 and 1999 applying the methodology of Hayman (1954) using eight cultivars of upland cotton and their 28 crosses. The objective of this work was to study the genetic components that control the inheritance of several physiological and agronomic characters under drought conditions. The field experiments were located in Seville, southern Spain under limited condition of water. The characters evaluated were: photosynthesis, transpiration, stomatal conductance, water use efficiency, leaf temperature, specific leaf weight, water content, seed cotton yield, boll number per plant, boll weight, fibre percentage and seed index. Relationships among traits were determined using Pearson`s simple correlation test. The genetic analyses showed the importance of the additive genetic variance in the inheritance of the characters such as photosynthesis, transpiration, stomatal conductance and water content and the importance of the additive and non additive genetic variance in the inheritance of yield, boll number per plant and boll weight.

The narrow sense heritability was very low for leaf temperature, specific leaf weight and water use efficiency, low for photosynthesis, transpiration, stomatal conductance and water content and medium for seed yield, bolls per plant and boll weight. The highest values for heritability were for fibre percentage.

With the exception of water use efficiency the majority of the physiological characters under consideration show significant correlations with yield and yield components, although seed index showed a low correlation with the majority of the physiological characters.

The presence of additive variance indicates the possibility of improving these characters, using selection methods which permit the accumulation of positive genes. The presence of dominance variance in the yield characters permits the opportunity to exploit the heterosis as an important tool under drought conditions. The cultivars Maria del Mar and Tashkent 9 seem to be good parentals for a breeding program under drought condition.

Introduction

The main cotton producing area in Spain is located in the Guadalquivir Valley (SW Spain, around 37º north) where it is grown under irrigation. The cyclical droughts, the fact that the availability of irrigation water is being diminished by increasing demand from urban areas, and the increment of the cost of water, makes the disposition of drought tolerant cotton varieties be a very important factor in the choice of a variety in Spain.

In previous years, *Gossypium hirstum* L. genotypes from widely different geographical origins have been studied in the search for traits related to yield under the drought condition prevailing in the SW of Spain (Gutiérrez et al., 1994; López et al., 1995; López, 1998; Gutiérrez, 1997ab; Leidi et al., 1999; Gutiérrez et al., 2000a,b). The aim of the present work was to study the heredability of physiological and yield traits in cotton genotypes under local dry land condition for their use in genetic improvement programmes.

Materials and Methods

The experiments for the present investigation were conducted for 2 years (1998 and 1999) and involved the diallel analysis applying the methodology of Hayman (1954) of 8 cultivars of upland cotton (28 crosses F1 without including reciprocals) The cultivars were selected on the basis of previous screening studies (López et al, 1995; López, 1998; Gutiérrez et al 2000 a and b). A programme developed by Christie et al (1988) was used for Hayman´s analysis. The estimate of heritability was undertaken as defined by Mather and Jinks (1982). The list of cotton genotypes studied, with reference to their origin and characteristics, are presented in Table 1.

The field experiment of 1998 was carried out under terminal drought conditions (López et al., 1995), in Carmona (Seville, SW Spain) on a clay sail (Typic Chromoxererts). There were no applications of water during the growing season. The crops grew with a reserve of water in the soil of 183 mm. The locality has an annual mean precipitation of 580 mm and an annual mean ETP of 992 mm. In 1999 the experiment was carried out under deficit irrigation conditions in Alcalá del Rio (Seville, SW Spain) on a sandy loam soil (Typic Xerofluvents). There were only two irrigations, before planting and in flowering. The annual mean precipitation is 550 mm and the annual mean ETP is 958.6 mm. The crosses among the different parents to form the F1 was carried out in Alcalá del Rio (Seville, SW Spain), under irrigation conditions in 1997 and 1998. The experimental design was a completely randomized block design with four replications. The plots were 5 m long with rows spaced 0.95 m apart.

Evaluated Characters

Physiological Characters

Photosynthesis (Ph), Transpiration (Tr), and Stomatal Conductance (SC). The measures were made with an open system using a portable infrared gas analyser (LCA-2, Analytical Development Co. Ltd., Hoddesdon, England) equipped with a Parkinson leaf chamber and a data logger. The measurements were made from 11:00 to 12:00 at saturating photosynthetic photon flux densities (ca. 2000 µmoles m^{-2} s^{-1}) on the youngest fully expanded leaves.

Water Use Efficiency (WUE). Measured as the relation between photosynthesis rate and stomatal conductance (Morgan and LeCain, 1991; Morgan et al., 1993).

Leaf Temperature (LT). The measures were made with a hand-held infrared thermometer (model Ray R2 PAG, Raytec, Santa Cruz, California, (USA) targeting single, upper canopy, fully sunlit leaves at midday.

Water Content (WC). Measured as the relation among the difference (fresh leaf weight - dry leaf weight) and dry leaf weight. Leaves similar to those used for photosynthetic measurements were wrapped in aluminium foil, detached and introduced into plastic bags and kept in containers with ice. Dry leaf weight was determined using a temperature of 70 ºC for 48 h.

Specific Leaf Weight (SLW). Measured as the relation between dry leaf weight and leaf area. The determinations were made in the same leaves used for WC. Leaf area was measured before drying using Delta -T Image Analysis System (DIAS Delta - T, Cambridge, England).

The physiological characters were determined in two dates: early flowering (first date, D-1) and boll opening (second date, D-2).

The analysis of these characters was carried out in an individual way (date to date of every year) and in a combined way (years and dates).

Yield and Yield Components

Seed cotton Yield (Y), Boll number per plant (B), Boll Weight (BW), Fibre Percentage (PF) and Seed Index (weight of 100 seeds in grams) (SI) were determined at the end of the season. Plants were harvested by hand.

All variables were statistically analyzed using an analysis of variance procedure. Statistical differences among genotypes for traits were tested with Fischer's least significant difference test ($p>0.05$). These data are not shown in this work. Relationships between traits were determined using Pearson`s simple correlation test.

Results and Discussion

Correlations Between Physiological and Yield Characters

Tables 2 and 3 show the correlation coefficients between yield, yield components and physiological characters in two dates (D-1 and D-2), two years (1998 and 1999) and combined. With the exception of water use efficiency the majority of the physiological characters considered show significant correlations with yield and yield components, although seed index showed a low correlation with the majority of physiological characters. These results coincide with those obtained by López et al. (1995), López (1998) and Leidi et al. (1999) in drought conditions. The correlations in 1998 were higher and more significant in the second date of measurement with respect to the first date. The contrary occurred in 1999 when the second date measurements were more correlated than the first date. The physiological characters which had a more stable correlation with yield or yield components were photosynthesis, transpiration, stomatic conductance and water content. When the leaf temperature was significantly correlated with yield or yield components the value was negative.

Genetic Analysis

Preliminary analysis of variance showed that for all characters there were significant differences between genotypes ($p<0.05$) (data not shown), although for the physiological characters there was not a clear stability in the significance in every date and year considered.

Physiological Characters

Analysis of variance of the difference between Wr (the covariance of hybrids in an array with the recurrent parent)and Vr (the variance of an array) showed partial failure of the model for photosynthesis in the first and second dates of 1998 and in the first date of 1999, transpiration in the first date in 1998 and 1999, stomatic conductance, foliar temperature and specific leaf weight in the first and second dates of 1998, water content in the first date of 1998 and water use efficiency in the dates and years considered.

The component of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) for physiological characters in the first and second dates of 1998 and 1999 are presented in Tables 4 to 7.

The additive genetic variance (D) was significant for the physiological characters in the first date in the two years, except for: leaf temperature, specific leaf weight and water use efficiency in 1998; and for leaf temperature and specific leaf weight in 1999. In the second date of determination, D variance was significant for: leaf temperature, specific leaf weight, water content in 1998; and for photosynthesis, transpiration and stomatal conductance in 1999.

The dominant genetic variations (H_1 and H_2) were significant in the first date of determination in 1999 for: stomatal conductance and water use efficiency; in this date H_2 component was significant for specific leaf weight and water content. In the second determination in 1998, the H_1 and H_2 components were significant for specific leaf weight, and water content. H_1 and H_2 components were significant in the second determination of 1999 for most of the physiological characters, except for: leaf temperature, specific leaf weight and water use efficiency.

The proportion $(H_1/D)^{0.5}$ (average degree of dominance) showed the three degrees of dominance (partial, complete and over) for all the physiologic characters in the two considered dates and years, without presenting clear stability from year to year.

The ratio of dominant to recessive allels (Kd/Kr) in the parents, did not show stability from year to year for the physiological characters, except for: transpiration and stomatal conductance in the first date, and for water content in the second date. In these cases they showed values of this proportion more than the unity, indicating the existence of more dominant genes than recessive ones in the parents in both years.

The narrow sense heritability was very low for leaf temperature, specific leaf weight and water use efficiency and low for photosynthesis, transpiration, stomatal conductance and water content.

In the graphical analyses the highest values of the standard deviation of the parents mean were detected by Maria del Mar for most of the studies physiological character, as well as the lowest value for leaf temperature. The genes that increased the characters were recessive in Maria del Mar for photosynthesis, transpiration, stomatal conductance, leaf temperature and water content. This cultivar can be consider a good parental in a breeding program for drought tolerance in the environmental conditions found in this study.

Yield and Yield Components

Analysis of variance of the difference between Wr (the covariance of hybrids in an array with the recurrent parent) and Vr (the variance of an array) showed no partial failure of the model for all the characters considered, with the exception of seed index.

The component of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) for production characters in the two years are presented in Tables 8 and 9.

The additive genetic variance was significant for the yield characters in the two considered years, except for: seed index and fibre index in 1998, and seed index in 1999.

The dominant genetic variations (H_1 and H_2) were significant in both years, except for seed yield and boll number per plant in 1999, and H_2 component for seed index in 1998.

The average degree of dominance $(H_1/D)^{0.5}$ presented the three degrees of dominance (partial, complete and over) without presenting clear stability from year to year, except for fibre percentage and boll weight that presented partial dominance and complete dominance respectively in the two considered years.

The ratio of dominant to recessive allels Kd/Kr of the parents showed values near or similar to the unit, indicating the existence of the same number of dominant and recessive genes in the parents for: seed yield, boll number per plant, boll weight and fibre percentage in 1998, and fibre percentage in 1999. This proportion presented a value higher than the unity for boll weight in 1999, indicating the existence of more dominant genes than recessive ones in the parents for this character. The characters seed yield, boll number per plant and seed index in 1999 presented values of this proportion smaller than the unity, indicating the existence of more recessive genes than dominant ones in the parents. Taking into account this data, only fibre percentage was stable in both years.

The value of the narrow sense heredability was medium for seed yield, bolls per plant and boll weight. The highest values of the heritability were for fibre percentage.

In the graphical analysis the highest values of the standard deviation of the parents mean were detected by Maria del Mar and Tashkent 9. The genes that increased the characters in these cultivars were dominant and / or recesive, according to the character and the environmental conditions of the years considered.

Conclusions

The importance of additive genetic variance in the inheritance of characters such as photosynthesis, transpiration, stomatal conductance, water content and the importance of the additive and non additive genetic variance in the inheritance of seed yield, boll number per plant and boll weight and the significant correlation between yield characters and physiological characters indicate that breeding for drought tolerance in cotton is possible. In this sense the presence of additive variance indicates the possibility of improving these characters, using selection methods which permit the accumulation of positive genes. The presence of dominant variance in the yield characters permits the opportunity to exploit the heterosis as an important tool under drought conditions. The cultivars Maria del Mar and Tashkent 9 seem to be good parentals for a breeding program under drought condition.

References

Christie B.R.,V.I.Shatuck and J.A.Dick.1988.The Diallel Cross: Its Analysis and Interpretation.University of Guelph, Ontario, Canada.134 pp.

Hayman, B.I. 1954. The theory and analysis of diallel crosses. Genetics, New Jersey, 39:789-809.

Gutiérrez, J.C., M. López and E.O. Leidi. 1994. Genotypic behaviour of Upland cotton under dry land conditions in Southern Spain. World Cotton Research Conference-1. Vol. Abs. Brisbane, Australia. p.103.

Gutiérrez, J.C. 1997a. Registration of "María del Mar " Cotton. Crop Sci. 37:1389.

Gutiérrez, J.C. 1997b. Registration of "Victoria " Cotton. Crop Sci. 37:1389.

Gutiérrez J.C., M. López, E.O. Leidi. 2000a. The Crop Water Stress Index (CWSI) as an Indicator of water stress and yield performance among cotton cultivars. In: New Frontiers in Cotton Research: Proc. World Cotton Res. Conf.-2 (2nd 1998; Athens, Greece); F. Gillham (Ed); Publishers: WCRC-2 Organizing and Scientific Committees, Thessalonica, Greece. pp: 125-129.

Gutiérrez J.C., M. López and E. O. Leidi. 2000b. Drought Susceptibility Index as an Indicator of Genotypic Drought Tolerance in Upland Cotton. In: New Frontiers in Cotton Research: Proc. World Cotton Res. Conf.-2 (2nd 1998; Athens, Greece); F. Gillham (Ed); Publishers: WCRC-2 Organizing and Scientific Committees, Thessalonica, Greece. pp: 130-134.

Leidi E.O., M. López, J. Gorham and J.C. Gutiérrez. 1999. Variation in carbon isotope discrimination and other traits related to drought tolerance in upland cotton cultivars under dry land conditions. Field Crop. Res. 61 :109-123.

López, M., J.C. Gutiérrez and E.O. Leidi. 1995. Selection and Characterization of cotton cultivars for dry land production in the South-West of Spain. Eur. J. Agron. 4(1):119-126.

López, M. 1998. Estudio de variabilidad genotípica de cultivares de algodón en respuesta a condiciones de sequía. Doctoral Thesis. University of Córdoba (Spain). 242 pp.

Mather, K. and J.L. Jinks. 1982. Biometrical Genetics. 3rd edition, Chapman and Hall. London. 396 pp.

Morgan, J.A. and D.R. LeCain. 1991. Leaf gas exchange and related leaf traits among 15 winter wheat genotypes. Crop Sci. 31:443-448.

Morgan, J.A.; D.R. LeCain; T.N. McCaig and J.S. Quick. 1993. Gas exchange, carbon isotope discrimination, and productivity in winter wheat. Crop Sci. 33:178-186.

Table 1. List of cotton genotypes studied in 1998 and 1999 with reference to their origin and characteristics.

Genotypes	**Origin**	**Characteristics**	
Maria del Mar	Spain *	Highly drought tolerant	Mid season
Victoria	Spain **	Medium drought tolerant	Long season
Zaire 407/1157	Zaire	Low drought tolerant	Long season
Precoce 1	Brazil	Medium drought tolerant	Early season
CNPA 3H	Brazil	Medium drought tolerant	Mid season
Acala 151777/BR	USA	Medium drought tolerant	Long season
Paymaster 792	USA	Low drought tolerant	Early season
Tashkent 9	Uzbekistan	Highly drought tolerant	Early season

* Gutierrez J.C.1997 a.** Gutierrez J.C.1997 b.

Table 2. Coefficients of the correlation of physiological characters (photosynthesis, transpiration, stomatal conductance, leaf temperature, specific leaf weight, water content, water use efficiency) and yield characters (seed yield, bolls per plant and boll weight).

	Seed yield			**Bolls plant^{-1}**			**Boll weight**		
	Year		**Comb.**	**Year**		**Comb.**	**Year**		**Comb.**
Character	**1998**	**1999**		**1998**	**1999**		**1998**	**1999**	
Ph 1-D	0.305	0.530**	0.549**	0.257	0.465**	0.401*	0.518**	0.475**	0.582**
Ph 2-D	0.425**	0.381**	0.468**	0.310	0.485**	0.495**	0.469**	0.274	0.398*
Tr 1-D	0.347*	0.347*	0.376*	0.389*	0.314	0.339*	0.496**	0.266	0.351*
Tr 2-D	0.513**	0.341*	0.522**	0.350*	0.397*	0.429**	0.660**	0.293	0.358**
SC 1-D	0.290	0.431**	0.417*	0.304	0.411*	0.372*	0.474**	0.371*	0.350*
SC 2-D	0.561**	0.273	0.416*	0.426**	0.371*	0.395*	0.648**	0.262	0.422**
LT 1-D	-0.347*	-0.415**	-0.468**	-0.45**	-0.369*	-0.477**	-0.396*	-0.361*	-0.258
LT 2-D	0.036	-0.154	-0.136	-0.402*	-0.298	-0.328*	-0.226	-0.059	0.027
SLW 1-D	0.119	0.379*	0.551**	0.240	0.199	0.443**	-0.042	0.417*	0.508**
SLW 2-D	-0.013	-0.052	0.008	0.066	-0.109	-0.082	-0.094	0.102	0.228
WC 1-D	0.301	0.389*	0.419**	0.102	0.362*	0.359*	0.258	0.315	0.304*
WC 2-D	0.438**	0.406*	0.477**	0.273	0.455**	0.426**	0.444**	0.317	0.367*
WUE 1-D	-0.100	-0.188	-0.103	-0.184	-0.105	-0.166	-0.067	-0.170	0.017
WUE 2-D	-0.099	0.288	0.121	-0.064	0.281	0.209	-0.192	0.165	-0.030

*, ** Significant at 0.05 and 0.01 probability levels, respectively.
Ph = Photosynthesis; Tr = Transpiration; SC = Stomatal Conductance; LT = Leaf Temperature;
SLW = Specific Leaf Weight; WC = Water Content; WUE = Water Use Efficiency; 1-D = First Date; 2-D = Second Date.

Table 3. Coefficients of the correlation of physiological characters (photosynthesis, transpiration, stomatal conductance, leaf temperature, specific leaf weight, water content, water use efficiency) and fibre percentage and seed index.

	Fibre %			Seed index		
	Year			Year		
Character	1998	1999	Comb.	1998	1999	Comb.
Ph 1-D	0.469**	0.207	0.470**	0.264	0.118	0.253
Ph 2-D	0.434**	0.220	0.408*	0.377*	-0.065	0.260
Tr 1-D	0.311	0.161	0.286	0.137	0.060	0.076
Tr 2-D	0.588**	0.300	0.585**	0.537**	0.066	0.484**
SC 1-D	0.300	0.164	0.273	0.183	0.029	0.083
SC 2-D	0.526**	0.241	0.464**	0.515**	-0.049	0.258
LT 1-D	-0.102	-0.101	-0.024	-0.347*	-0.062	-0.150
LT 2-D	-0.037	0.104	0.081	0.036	0.062	0.079
SLW 1-D	-0.208	0.257	0.171	-0.057	0.448**	0.395**
SLW 2-D	-0.237	0.335*	0.177	-0.047	0.178	0.264
WC 1-D	0.315	0.159	0.271	0.252	0.321	0.269
WC 2-D	0.332*	0.229	0.355*	0.325	0.311	0.310
WUE 1-D	0.049	-0.064	0.029	0.139	0.033	0.166
WUE 2-D	-0.219	0.093	-0.118	-0.135	-0.054	-0.074

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Ph = Photosynthesis; Tr = Transpiration; SC = Stomatal Conductance; LT = Leaf Temperature; SLW = Specific Leaf Weight; WC = Water Content; WUE = Water Use Efficiency; 1-D = First Date; 2-D = Second Date.

Table 4. Components of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) (broad sense H_a, narrow sense H_e) for photosynthesis and transpiration in the two dates and years.

	Photosynthesis				Transpiration			
Year	1998		1999		1998		1999	
Component	Date 1	Date 2	Date 1	Date 2	Date 1	Date 2	Date 1	Date 2
D	5.877** ± 1.974	0.769 ± 1.593	10.511** ± 3.343	7.489** ± 1.200	2.127** ± 0.405	0.270 ± 0.187	1.040* ± 0.405	1.394** ± 0.267
F	-8.195 ± 4.665	-1.273 ± 3.764	8.802 ± 7.898	5.049 ± 2.836	2.007* ± 0.956	-0.369 ± 0.442	0.233 ± 0.958	1.728 ± 0.631
H_1	-3.585 ± 4.538	6.310 ± 3.662	11.343 ± 7.684	9.213** ± 2.759	1.502 ± 0.930	-0.358 ± 0.430	1.162 ± 0.932	1.930** ± 0.613
H_2	1.188 ± 3.948	5.608 ± 3.186	9.825 ± 6.685	7.759** ± 2.401	1.012 ± 0.810	-0.223 ± 0.375	1.411 ± 0.811	1.34* ± 0.534
h^2	4.240 ± 2.648	-0.884 ± 2.137	-0.317 ± 4.483	8.338** ± 1.610	-0.003 ± 0.543	-0.043 ± 0.251	0.620 ± 0.544	0.503 ± 0.358
E	8.668** ± 0.658	2.220** ± 0.531	7.400** ± 1.114	2.748** ± 0.400	0.677** ± 0.135	0.760** ± 0.062	1.633** ± 0.135	0.908** ± 0.089
t^2	0.822	1.031	0.464	0.059	2.160	0.801	0.299	2.075
$(H_1/D)^{0.5}$	-	2.870	1.040	1.110	0.840	-	1.060	1.180
$H_2/4H_1$	-	0.220	0.220	0.210	0.170	-	0.300	0.170
K_d/K_r	-	0.550	2.350	1.870	3.560	-	1.240	3.230
Ha	0.363	0.556	0.355	0.586	0.452	-	0.279	0.338
He	0.342	0.275	0.141	0.293	0.247	-	0.123	0.093

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 5. Components of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) (broad sense H_a, narrow sense H_e) for stomatal conductance and leaf temperature in the two dates and years.

	Stomatal Conductance				**Leaf Temperature**			
Year	**1998**		**1999**		**1998**		**1999**	
Component	**Date 1**	**Date 2**	**Date 1**	**Date 2**	**Date 1**	**Date 2**	**Date 1**	**Date 2**
D	0.0083** ± 0.0019	0.0005 ± 0.0003	0.0359** ± 0.0067	0.0043** ± 0.0004	-1.4796 ± 0.2098	1.1069* ± 0.5321	0.1496 ± 0.2776	-0.6115 ± 0.4781
F	0.0044 ± 0.0045	-0.0001 ± 0.0007	0.0398* ± 0.0159	0.0048** ± 0.0011	-2.6801 ± 0.4958	2.5642* ± 1.2573	-1.2885 ± 0.6558	-1.8330 ± 1.1300
H_1	0.0027 ± 0.0044	0.0002 ± 0.0007	0.0388* ± 0.0155	0.0051** ± 0.0011	-2.7000 ± 0.4823	1.8631 ± 1.2233	-2.3759 ± 0.6381	-4.7034 ± 1.1000
H_2	0.0026 ± 0.0038	0.0001 ± 0.0006	0.0288* ± 0.0135	0.0039** ± 0.0009	-1.9142 ± 0.4196	0.3797 ± 1.0643	-1.1286 ± 0.5512	-3.1577 ± 0.9560
h^2	-0.0017 ± 0.0026	-0.0000 ± 0.0004	0.0198* ± 0.0090	0.0064** ± 0.0006	-0.2539 ± 0.2842	-0.1304 ± 0.7134	0.0323 ± 0.3723	5.4490** ± 0.6412
E	0.0046** ± 0.0006	0.0008** ± 0.0001	0.0153** ± 0.0022	0.0016** ± 0.0002	1.9952** ± 0.0699	1.2041** ± 0.1774	2.5985** ± 0.0925	4.6500** ± 0.1590
t^2	1.430	0.240	0.501	0.042	2.25	0.176	0.041	0.077
$(H_1/D)^{0.5}$	0.57	0.69	1.04	1.09	-	1.30	-	-
$H_2/4H_1$	0.25	0.10	0.19	0.19	-	0.05	-	-
K_d/K_r	2.78	0.66	3.29	3.08	-	17.66	-	-
Ha	0.361	0.325	0.400	0.449	-	0.082	-	-
He	0.269	0.305	0.118	0.120	-	0.010	-	-

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 6. Components of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) (broad sense H_a, narrow sense H_e)for specific leaf weight and water content in the two dates and years.

Year	Specific leaf weight				Water content			
	1998		1999		1998		1999	
Component	Date 1	Date 2	Date 1	Date 2	Date 1	Date 2	Date 1	Date 2
D	-0.0015 ± 0.0013	0.0027* ± 0.0014	-0.0013 ± 0.0007	0.0007 ± 0.0018	0.0060** ± 0.0012	0.0522** ± 0.0043	0.0043** ± 0.0016	0.0050 ± 0.0038
F	-0.0028 ± 0.0031	0.0034 ± 0.0033	-0.0054 ± 0.0016	-0.0070 ± 0.0043	-0.0102 ± 0.0029	0.0288** ± 0.0104	-0.0052 ± 0.0039	0.0061 ± 0.0090
H_1	0.0041 ± 0.0031	0.0068* ± 0.0032	0.0014 ± 0.0015	0.0037 ± 0.0041	-0.0094 ± 0.0029	0.0430** ± 0.0100	0.0070 ± 0.0038	0.0317** ± 0.0088
H_2	0.0051 ± 0.0027	0.0057* ± 0.0028	0.0027** ± 0.0013	0.0064 ± 0.0036	-0.0068 ± 0.0026	0.0294** ± 0.0088	0.0095** ± 0.0033	0.0245** ± 0.0076
h^2	0.0032 ± 0.0018	-0.0009 ± 0.0019	0.0217** ± 0.0009	-0.0022 ± 0.0024	-0.0015 ± 0.0017	0.0090 ± 0.0059	0.0036 ± 0.0022	-0.0037 ± 0.0051
E	0.0025** ± 0.0004	0.0044** ± 0.0005	0.0043** ± 0.0002	0.0051** ± 0.0006	0.0085** ± 0.0017	0.0097** ± 0.0015	0.0044** ± 0.0055	0.0086** ± 0.0012
t^2	4.17**	0.829	5.00**	4.23**	0.871	2.17	1.692	1.065
$(H_1/D)^{0.5}$	-	1.58	-	7.73	-	0.91	1.28	2.53
$H_2/4H_1$	3.31	0.21	0.35	0.46	-	0.17	0.34	0.19
K_d/K_r	-	2.33	-	-0.79	-	1.87	0.36	1.64
Ha	0.371	0.274	0.353	0.440	-	0.727	0.571	0.515
He	0.049	0.037	0.166	0.269	-	0.520	0.339	0.171

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 7. Components of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) (broad sense H_a, narrow sense H_e) for water use efficiency in the two dates and years.

Year	Water use efficiency			
	1998		**1999**	
Component	**Date 1**	**Date 2**	**Date 1**	**Date 2**
D	-7.68 ± 18.97	-16.78 ± 24.96	18.96** ± 5.16	-2.25 ± 16.22
F	-19.90 ± 44.84	-78.00 ± 58.98	27.48** ± 12.19	-4.56 ± 38.33
H_1	-28.35 ± 43.62	32.20 ± 57.38	48.97** ± 11.86	65.94 ± 37.29
H_2	-13.69 ± 37.95	70.02 ± 49.92	37.59** ± 10.32	51.59 ± 32.44
h^2	-13.99 ± 25.45	1.005 ± 33.48	10.80 ± 6.92	-10.98 ± 21.76
E	60.41** ± 6.32	80.91** ± 8.32	9.1583** ± 1.72	25.12** ± 5.40
t^2	0.339	0.248	0.927	1.167
$(H_1/D)^{0.5}$	-	-	1.61	-
$H_2/4H_1$	-	0.54	0.19	0.19
K_d/K_r	-	-	2.64	-
Ha	-	0.265	0.542	0.458
He	-	0.106	0.072	0.180

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 8. Components of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) (broad sense H_a, narrow sense H_e) for seed yield, boll number per plant, boll weight and fibre percentage in the two years.

Year	**Seed yield**		**Bolls plant^{-1}**		**Boll weight**		**Fibre %**	
Component	**1998**	**1999**	**1998**	**1999**	**1998**	**1999**	**1998**	**1999**
D	34353** ± 4196	108407** ± 17208	0.209** ± 0.034	0.326** ± 0.065	0.290** ± 0.042	0.632** ± 0.075	4.659** ± 0.058	3.250** ± 0.087
F	873 ± 9915	-117846 ± 40663	0.008 ± 0.080	-0.319 ± 0.154	-0.23 ± 0.1	0.315 ± 0.178	-0.132 ± 0.136	-0.027 ± 0.205
H_1	54570** ± 9646	2967 ± 39560	0.308** ± 0.078	0.128 ± 0.149	0.287** ± 0.098	0.651** ± 0.173	1.565** ± 0.132	0.521** ± 0.199
H_2	45387** ± 8392	37196 ± 34417	0.247** ± 0.067	0.219 ± 0.130	0.286** ± 0.085	0.525** ± 0.151	1.040** ± 0.115	0.619** ± 0.173
h^2	116061** ± 5628	332402** ± 23082	0.525** ± 0.045	0.387** ± 0.087	0.965** ± 0.057	1.100** ± 0.101	1.235** ± 0.077	2.206** ± 0.116
E	5746** ± 1398	62912** ± 5736	0.066** ± 0.011	0.229** ± 0.022	0.063** ± 0.014	0.056** ± 0.025	0.340** ± 0.019	0.258** ± 0.029
t^2	0.966	0.587	0.239	0.120	0.496	0.974	0.877	0.095
$(H_1/D)^{0.5}$	1.26	0.17	1.21	0.63	1.00	1.02	0.58	0.40
$H_2/4H_1$	0.21	3.13	0.20	0.43	0.25	0.20	0.17	0.30
K_d/K_r	1.02	-0.53	1.03	0.12	0.93	1.65	0.95	0.98
Ha	0.851	0.626	0.746	0.592	0.784	0.862	0.896	0.871
He	0.555	0.571	0.507	0.494	0.539	0.542	0.816	0.794

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 9. Components of genetic variation and their portions as defined by Hayman (1954) and the estimate of heritability as defined by Mather and Jinks (1982) (broad sense H_a, narrow sense H_e) for seed index and fibre index in the two years.

Year Component	Seed index	
	1998	**1999**
D	-0.238 ± 0.219	0.163 ± 0.141
F	-0.914 ± 0.517	-0.136 ± 0.334
H_1	1.031* ± 0.503	0.681* ± 0.325
H_2	1.216 ± 0.438	0.603* ± 0.283
h^2	2.177** ± 0.294	0.501** ± 0.190
E	0.585** ± 0.073	0.087 ± 0.047
t^2	1.806	1.216
$(H_1/D)^{0.5}$	-	2.04
$H_2/4H_1$	0.30	0.22
K_d/K_r	-	0.66
Ha	0.484	0.796
He	0.216	0.443

*, ** Significant at 0.05 and 0.01 probability levels, respectively.