MOLECULAR GENETIC ANALYSIS IN COTTON (*Gossypium hirsutum* L.)

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ABSTRACT

MOLECULAR GENETIC ANALYSIS IN COTTON
(*Gossypium hirsutum* L.)

Cotton is a valuable fiber crop for different industries especially the textile, food and oil industries. Drought causes serious yield losses in cotton throughout the world. Association mapping reveals genomic loci controlling fiber quality and drought-related traits which will be helpful in cotton breeding because these loci can provide the genetic adaptability needed to produce good fibers and yield under water limitation. In the present study, 177 simple sequence repeat (SSR) markers were used to characterize an Upland cotton germplasm panel consisting of 99 *G. hirsutum* cultivars for their genetic diversity and to detect the ancestral structure of the population. Moreover, association analysis was conducted to reveal significant quantitative trait loci (QTLs) linked to a total of 22 traits for fiber quality, plant structure, yield and drought-related parameters in the panel using GLM and MLM analysis. The morphological characters were tested under both well-watered and water-limited irrigation in two locations. At both locations, GLM and MLM identified different sets of QTLs at significance level of $p \leq 0.005$ and $p \leq 0.001$. Of the identified QTLs, some loci were considered as stable and reliable QTLs detected in both locations. The QTLs identified herein could be useful in the development of cotton cultivars with high yield that have adaptability to drought conditions worldwide.

ÖZET

PAMUKTA (*Gossypium hirsutum* L.)
MOLEKÜLER GENETİK ANALİZLER

Pamuk; başta tekstil, gıda ve yağ olmak üzere birçok farklı endüstri için değerli bir mahsüldür. Kuraklık, dünya genelinde pamuk üretiminde ciddi verim kayıplarına neden olmaktadır. İlişki haritalaması çalışmaları, pamuk ıslahında fayda sağlayacak lif, kalite ve kuraklıkla ilgili özellikleri kontrol eden genomik lokusları belirleyebilmektedir. Bu lokuslar su stresi altında kaliteli lif ve yüksek verim üretmek için gereken genetik adaptasyonu sağlayabilir. Bu çalışmada, 99 *G. hirsutum* genotipinden oluşan bir Upland pamuk panelinin, 177 basit dizi tekrarı (SSR) markörü ile genetik çeşitlilik bakımından karakterizyonu ve popülasyonun atasal yapısının saptanması için kullanılmıştır. Ayrıca, GLM ve MLM analizi kullanılarak panelde lif kalitesi, bitki yapısı, verim ve kuraklıkla ilgili parametreler için toplam 22 karakterle bağlantılı önemli niceliksel özellik lokuslarının (QTL'ler) belirlendiği ilişki analizi yapılmıştır. Morfolojik karakterler, iki farklı lokasyonda normal ve kısıntılı sulama koşulları altında test edilmiştir. Her iki lokasyonda da GLM ve MLM modelleri farklı QTL setleri tanımlamıştır ($p \leq 0,005$ ve $p \leq 0,001$ önem düzeyinde). Tanımlanan QTL'lerden bazı lokuslar, her iki lokasyonda da tespit edilen kararlı ve güvenilir QTL'ler olarak belirlenmiştir. Burada tanımlanan QTL'ler, kuraklık koşullarına uyum sağlayabilen yüksek verimli pamuk çeşitlerinin dünya genelinde geliştirilmesinde fayda sağlayacaktır.

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CHAPTER 1

DIVERSITY ANALYSIS IN COTTON

1.1. Introduction

1.1.1. History, Origin and Early Cultivation of Cotton

Many factors in the breeding process have been instrumental in establishing the history of diploid and allotetraploid cotton species over millions of years, including the origin of existing patterns of genetic diversity, intensity of genetic bottlenecks, and the impact of ongoing geographical cultivation patterns (Wendel et al. 2009). The cotton genus, *Gossypium* L. comprises 55 accepted species in a family of flowering plants (Appendix A), Malvaceae (the mallow family), which consists of 250 accepted genera with 4,230 species (Figure 1.1; lifemap-ncbi.univ-lyon1.fr , de Vienne 2016).) (POWO 2021; Grimg and Boldrini 2011).

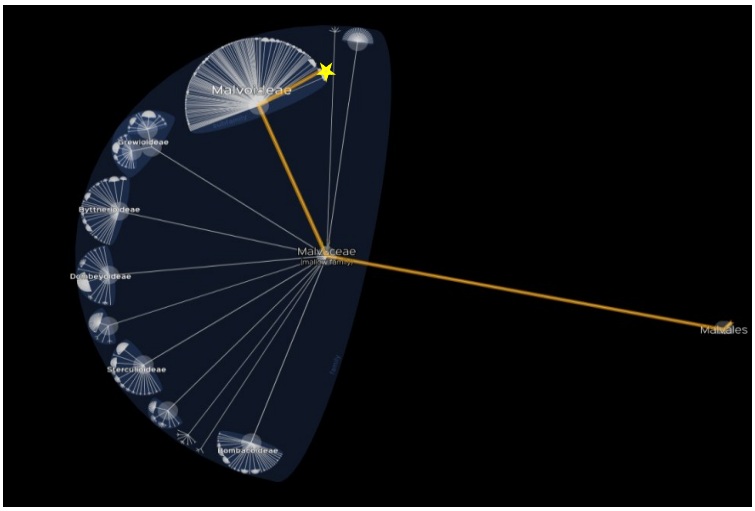

Figure 1.1. Phylogenetic tree for taxonomy of Malvales.Yellow star indicates G. *hirsutum* L.

As the genus Gossypium spread worldwide, its diploid genomes diversified more than threefold per genome. This variation between diploid genomes resulted in differences in chromosome size and meiotic behavior. Since chromosomal morphology is similar between closely related species, they have a high ability to form fertile F1 hybrids. On the other hand, even if mating between more distantly related species is successful, it results in chromosomal anomalies. Therefore, diploid cotton genomes have been characterized with single-letter symbols (A to G and K) for corresponding species clusters based on the meiotic morphology of chromosomes (Beasley 1941; (Jonathan F. Wendel, Flagel, and Adams 2012).

Presumably, 1–2 million years ago (MYA), or in the mid-Pleistocene, the first allopolyploid cotton (AD, 2n = 52) emerged through polyploidization of two progenitor genomes: A and D (Cronn et al. 2002; Seelanan, Schnabel, and Wendel 1997; Senchina 2003).

Although, many scientific studies agree that the progenitor genome for the Dt (D subgenome of tetraploid cotton shown as AtDt) subgenome of AtDt genome resembled the American cotton D_5 genome (*G. raimondii*, n = x = 13, D_5) (Endrizzi et al. 1985; (Jonathan F Wendel and Cronn 2003), there is no robust evidence about the ancestral contributor genome of the At genome (J. F. Wendel 1989). Until now, it was hypothesized that the ancestor of the At subgenome was either African cotton (*G. herbaceum* L., n = x =13, A_1) or Asian cotton (*G. arboreum* L., n = x = 13, A_2). Cytogenetic studies proposed that the A_1 genome was more closely related to the At subgenome of current tetraploid cotton (AtDt) (Gerstel 1953). This result was contrary to the assertion that the A_2 genome was the source of the At subgenome based on pheno-genetic studies (Stephens 1944). However, in 2020, Huang et al. assembled the genome of the *G. herbaceum*, A_1 variety *africanum*, and updated the whole evolutionary history of A-genomes concluding that there is a common ancestry for all existing A-genomes (A_1, A_2, At_1 and At_2). According to that study, the speciation event of A_1 and A_2 genomes from the A progenitor genome occurred after allopolyplodization (G. Huang et al. 2020). Thus, it has been suggested that the actual A-genome progenitor of the AtDt genome may not be either A_1 or A_2, but another common primitive ancestral A genome (named A_0) which was phylogenetically more related to the A_1 genome than the A_2 genome. Based on molecular genetic evidence, Huang et al. (2020) proposed that current tetraploid cotton, *G. hirsutum* $(AD)_1$ and *G. barbadense* $(AD)_2$, originated through a hybridization event between the A_0 ancestral

genome and the D_5 genome approximately 1.0-1.6 MYA. Moreover, the A_1 and A_2 genomes evolved independently without ancestry-progeny relation about 0.7 MYA from the A_0 ancestral genome. This evolutionary history is summarized in Figure 1.2 and explains how the distance between the A and D genomes is large enough to prevent fertilization. In turn this explains why the hybridization attempts between the A_1/A_2 and D_5 genomes have failed.

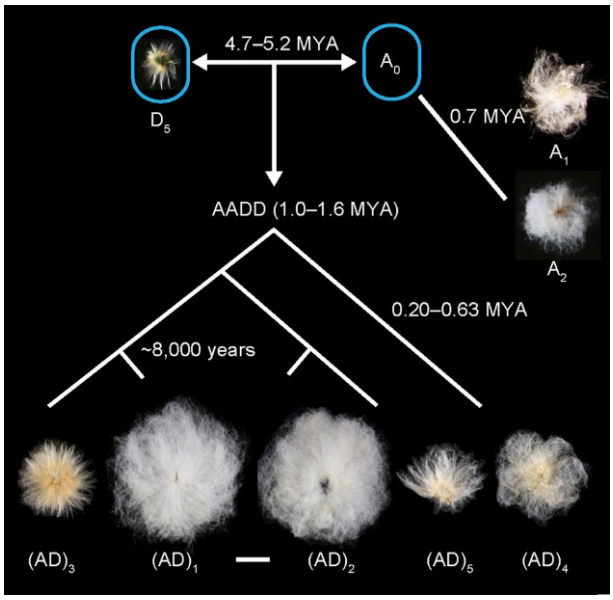

Figure 1.2. Evaluation of the evolution of the Gossypium genus based on the latest studies. Allopolyplodization preceeded speciation of the A genomes approximately 1.0-1.6 MYA (Scale bar, 10 mm; MYA, million years ago) (Source: He, Zhang, and Xiao 2020).

Gossypium species evolved into five AD- genome allopolyploids: *G. hirsutum* L. [n = 2x = 26, $(AD)_1$], *G. barbadense* L. [n = 2x = 26, $(AD)_2$], *G. tomentosum* [n = 2x = 26, $(AD)_3$], *G. mustelinum* [n = 2x = 26, $(AD)_4$] and *G. darwinii* [n = 2x = 26, $(AD)_5$] (Figure 1.2). Figure 1.3 shows the flower phenotypes of these five allopolyploids. Only four Gossypium species have been domesticated and are cultivated. These are the two diploid species: *G. herbaceum* L. (n = x =13, A_1), *G. arboreum* L. (n = x = 13, A_2) and the tetraploids *G. hirsutum* L. and *G. barbadense* L.

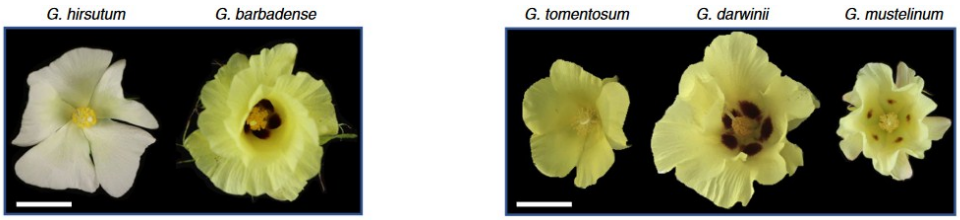

Figure 1.3. Flower morphology of five allopolyploid cotton species (Source : Chen et al. 2020). Two cultivated (*G. hirsutum* and *G. barbadense*) and three wild species (*G. tomentosum, G. mustelinum* and *G. darwinii*) are shown. Scale bars, 30 mm.

In 1753, Linnaeus named *G. hirsutum, G. barbadense, G. herbaceum* and *G. arboreum*. The modern classification of *Gossypium* was first described by Parlatore in 1866. The basic distinction of cotton species as diploid and tetraploid was reported by Zaitzev in 1928 (Glass 1949). This classification is still valid.

G. arboreum and *G. herbaceum*, also known as Old World cottons, are the only extant A- genome diploid species producing spinnable fibers in the entire *Gossypium* genus. Archaeological findings have shown cotton residues in burial remains dating back to the 6th millennium before the common era (BCE) (Moulherat et al. 2002) indicating that the Old World cottons have a long history of use by humans. Remains of cotton fiber and seeds (Figure 1.4a-b), were also found on the Indian subcontinent an important center of cotton production and trade dating back to the 3rd millennium BCE. In Africa, the first cotton remains were discovered in Nubia dating back to the 3rd millennium BCE (Chowdhury and Buth 1971). The Old World cotton species of the remains could not be identified due to their highly similar morphological features (Bouchaud, Yvanez, and Wild 2019); however, a molecular study on ancient cotton DNA performed by Palmer et al. (2012) concluded that the cotton seeds excavated in Nubia (present day Egypt) were *G. herbaceum* (Figure 1.5). Findings of cotton woven products identified in Khotan and Turfan Basin in Central Asia date to between 25 and 220 BCE; while those in Yunnan, Szechwan date to around 1st c. CE (Kuhn 1988). It is hypothesized that cotton reached the Chiang-nan region of China in 5th c. BCE, (Chao 1977) (Figure 1.6).

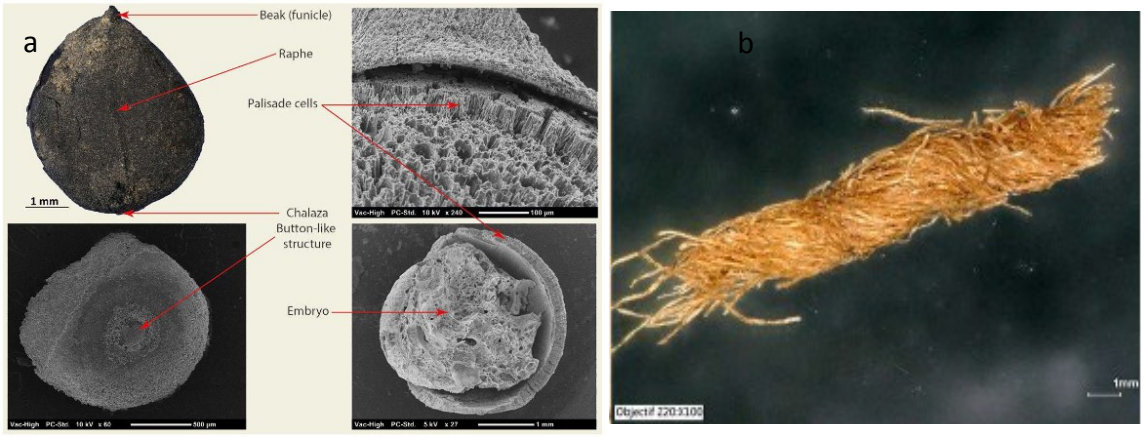

Figure 1.4.a Digital microscope image of ancient cotton seed dating back 1st – 3rd c. BCE (Source: Image by C. Bouchaud, SEM photos M. Lemoine, J. Milon). b. Ancient cotton thread from Mada'in Salih (1st – 3rd c. BCE, Image by P. Dal-Prà, Institut National du Patrimoine, LRMH ©Archaeological mission of Mada'in Salih)

Figure 1.5. Archaeological cotton remains dating back 3750 calibrated years before present (Source: Palmer et al. 2012).

Based on the archaeological evidence, Old World cotton was most probably cultivated in the North-Western Indian subcontinent in the 6-4th millennium BCE (Moulherat et al. 2002; Viot 2019). Cotton cultivation reached the south of India in the 3rd millennium BCE. In the same period, cotton spread to surrounding areas such as Jordan, the Caucasus and Nubia, (Chowdhury and Buth 1971; Betts et al. 1994; Kvavadze, Narimanishvili, and Bitadze 2010). During the 10th century, cotton slowly progressed from Iran towards the West and expanded through the Mediterranean region and Western Africa during the medieval period (Bouchaud, Tengberg, and Dal Prà 2011; Bouchaud, Yvanez, and Wild 2019) Champion and Fuller, 2019).

Table 1.1 summarizes the archaeological data about cotton cultivation (Viot 2019). Figure 1.7 shows how the cultivation of Old World cotton types spread in Asia and Africa.

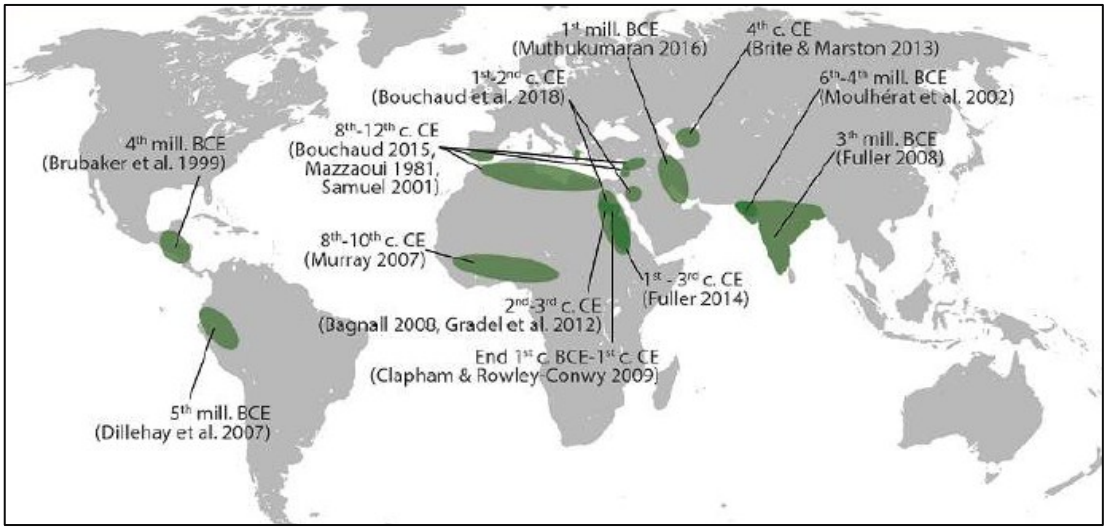

Figure 1.6. Cotton production centers based on archaeological, textile and literature findings (Source: Bouchaud, Yvanez, and Wild 2019).

Table 1.1. Archaeological evidence for cotton cultivation.

Region	Period	Material	Source
Mergarh, Kacchi Plain, Baluchistan	6400	Seeds	Costantini (1983), Fuller (2008)
Afyeh, Lower Nubia	4500	Seeds	Chowdhury and Buth (1971)
Mohenjo-Daro, Sindh	4500-3700	Seeds	Gulati and Turner (1929)
Kanmer, Kacchh	4000-3700	Seeds	Fuller (2008)
Hallur, Karnataka	2950-2900	Seeds	Fuller (2008)
Nineveh, Mesopotamia	2700	Text	Malatacca (2014), Muthukumaran (2016)
Sippar, Babylonia	2500	Text	Muthukumaran (2016)
Qal'at-Bahrain, Arabia	2500	Seeds	Bouchaud et al. (2011)
Egypt	2500	Text	Herodotus in Malatacca (2016)
Arabia	2250	Text	Theophrastus (2300 BP) in Bouchaud et al. (2011)
Mada'in Salih, Saudia Arabia	1900	Seeds	Bouchaud et al. (2011)

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Table 1.1. (cont.)

Yunnan, China	2150	Text	Chao (1977) in Zurndorfer (2011)
Sichuan, China	2050	Text	Chao (1977) in Zurndorfer (2011)
Yunnan, China	1825	Text	Kuhn (1988)
Old Jarma (Germa), Fazzan, Libyan Sahara	1800	Seeds	Pelling (2007)
Kellis, Upper Egypt	1750-1550	Seeds, Text	Bowen (2010) in Brite and Marston (2013)
Kara-tepe, Khorezm, Uzbekistan	1660-1580	Seeds	Brite (2011) in Brite and Marston (2013)
Upper Egypt	1600	Seeds	Palmer et al. (2012)
Turfan basin and Khotan basin, Xinjiang	1500 (Liang dynasty)	Text	Kuhn (1988), Zurndorfer (2011)
Merv, Turkmenistan	1400-1500	Seeds	Hermann et al. (1993) in Brite and Marston (2013)
Yingpan, Yuli County, Xinjiang	800	Fiber	Cao (2009)

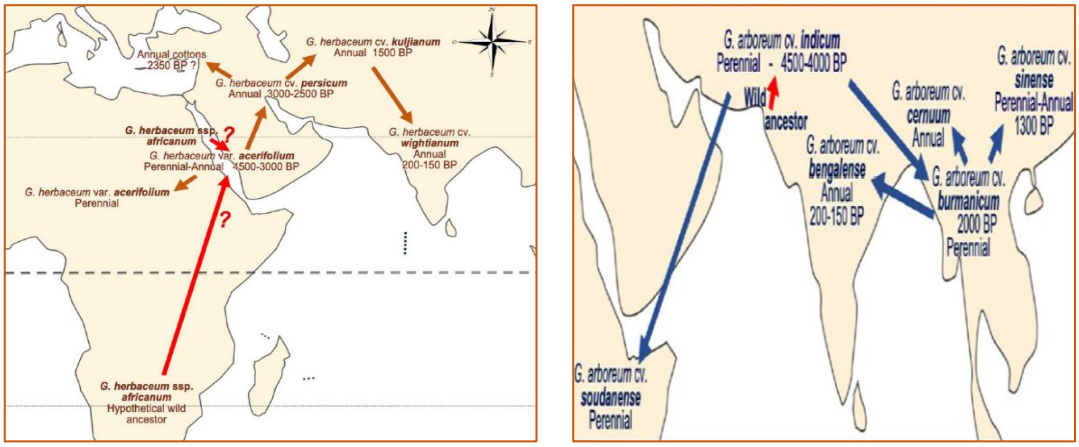

Figure 1.7. Cultivation of *G. herbaceum* and *G. arboreum* over the world. (Source: Viot 2019 references are given in Table 1.1).

In the last two centuries, the Old World cottons (*G. arboreum* and *G. herbaceum*) were gradually replaced by the New World cottons (*G. hirsutum* and *G. barbadense*). *G. hirsutum* is distributed throughout Central and Northern South America, the Caribbean, the Solomon Islands and Marquesas in the Pacific.

G. barbadense has a native range further south, centered in the northern third of South America and has a similar range as *G. hirsutum* in the Caribbean (Wendel et al. 2009).

As a commercial product, cotton was brought to the eastern coastal regions of North America from Europe through migration. All accessible fiber-producing species were tested in that period in the United States and growers found that the New World cottons yielded more than the Old World cottons. *G. hirsutum* was frequently grown in upland regions of America and for this reason it gained the common name "Upland cotton".

As Upland cotton gained agricultural importance, new cultivars adapted to regional environments developed. In this period, several cotton types were differentiated based on morphological differences: Cluster, Early, Long Limb, Rio Grande, Semicluster, Upland Long Staple (ULS), Western Big Boll and Miscellaneous types (Duggar 1907; Tyler 1910; Lubbers and Chee 2009). However, in the early 1900s, the great boll weevil infestation spread to the US from Mexico and overwhelmingly destroyed all major cotton fields. During the boll weevil invasion, many of the aforementioned cotton types were lost. Therefore, one of the results of this disaster was an immediate effort to develop cotton cultivars that could survive such attack. Most of the cultivars developed for this purpose came from the Western Big Boll type such as Lone Star, Stoneville, Coker-100 and Deltapine.

1.1.2. Domestication and Genetic Diversity

Natural introgression patterns offer clues for the flow of *G. barbadense* alleles to *G. hirsutum*, which most likely occurred in the Caribbean where their distribution overlapped. However, among modern elite varieties, the opposite situation is more common with gene flow from *G. hirsutum* to *G. barbadense*. Based on molecular marker analysis, it has been suggested that 8.9% of alleles in modern *G. barbadense* cultivars may have originated from *G. hirsutum* (G.-L. Wang, Dong, and Paterson 1995). *G. hirsutum* is possessed of a highly diverse genetic composition compared to the other commercial cotton species, a finding which is supported by many molecular studies. However, intensive cultivation and domestication clearly caused great reduction in genetic diversity such that only half of the extant genetic diversity is represented in

modern cotton cultivars (Brubaker and Wendel 1994; M. J. Iqbal et al. 2001; Rungis et al. 2005; Lacape et al. 2006).

Some characters have been selected during domestication due to the different requirements between wild and modern habitats. For example, easy seed dispersal and hard seed coat are desired in the wild; however, they are not suitable for efficient agricultural production.

At the beginning of cotton cultivation, cotton growers selected for larger bolls, higher lint percentage, longer fiber length and day-neutral flowering response. The day-neutral flowering response, most probably the first domestication trait subjected to human intervention, was a critical step in cotton production that allowed cotton to grow in regions distant from the tropics (Westengen, Huaman, and Heun 2005) (Fryxell 1979; Lee 1984). Knowledge about which features were selected by domestication and early cotton breeders and how these choices affected cotton genome composition is helpful for today's breeding efforts. Such information can guide further genome manipulation through classical and modern breeding efforts to improve cotton yield and quality characteristics.

With the industrial revolution in the 1700s many inventions such as the Flying Shuttle (McNeil 1990), Spinning Jenny (Marsden 1884), and Water Frame (McNeil 1990) reduced the workforce needed for cotton processing and increased demand for high yield and fiber qualities. These new demands arising from various needs then shaped the goals of cotton breeding programs.

Domestication and further selection pressure during cultivation have resulted in a genetic bottleneck in modern cotton cultivars. High genetic diversity is of first priority for use in the development of new cultivars with desired features. Therefore, molecular genetic studies are the prerequisite to identify genetic variation within current Upland cotton germplasm. In the absence of pedigree information, genetic diversity analysis provides a good starting point for parental selection in breeding programs by revealing the genetic relationships among cotton varieties or germplasm lines. Germplasm has gained more importance thanks to their utilization as potential gene sources to develop desired lines by cotton breeders. Thus, genetically distant cotton genotypes or cotton genotypes with a particular trait such as (a)biotic resistance or outstanding fiber quality can be selected as breeding material to give rise to increased variability and adaptability.

Population structure is another important analysis to investigate population genetics. Population structure analysis traces the genotypes of a population to a theoretical common ancestor and reveals the ancestral history of the individuals.

As a result, the best representative number of subpopulations is identified and the individuals are assigned to these subpopulations based on a threshold of probability of membership (Pritchard, Stephens, and Donnelly 2000; Seyoum et al. 2018).

The genetic diversity and structure of a population or a genotype is more accurately evaluated using molecular genetic markers rather than classical markers such as morphological or biochemical markers since molecular markers are not altered by environmental effects. There are different types of molecular markers that can be used to efficiently analyze genomic variation. The predominantly used DNA markers are single nucleotide polymorphism (SNP), simple sequence repeat (SSR), restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD) and sequence related amplified polymorphism (SRAP) markers (Nadeem et al. 2018; Powell et al. 1996). SNP markers are highly reproducible, abundant and relatively cost effective, codominant markers based on a nucleotide difference at a defined locus of DNA sequence. SSRs, also known as microsatellites, are codominant, highly polymorphic markers based on tandem repeats which are frequently distributed in the genome. These two types of markers have largely replaced other markers which are more difficult to screen. For example, RFLP was the first developed DNA marker system, but is cumbersome because it is based on hybridization in which polymorphisms are detected after restriction digestion of genomic DNA. AFLP markers are dominant and cost effective systems in which genomic DNA digestion is followed by polymerase chain reaction (PCR). AFLP markers can be difficult to score with the data provided limited somewhat by their dominant nature. The RAPD marker system is a dominant, highly polymorphic PCR-based method performed by a random single and short primer. This system, however, can be difficult to reproduce and it can give band patterns which can be difficult to score.

Many studies evaluated genetic diversity and population structure in cotton using SSR markers. Seyoum et al. (2018) assessed genetic diversity and population structure of germplasm consisting of 302 Upland cotton accessions using 198 SSR markers. In that study, SSR analysis produced 897 alleles of which 78% were polymorphic in the panel. The germplasm was divided into three sub-groups with an

average genetic diversity of 27%. Tyagi et al. (2014) performed similar characterization analysis in a panel of 378 Upland cotton genotypes using 120 SSR markers by which 546 alleles were produced. They revealed overalkl lower genetic variation in the panel (19%) which contained admixed and five-structured subpopulations.

Zhu et al. (2019) conducted diversity and structure analysis in 557 Upland cotton genotypes in which 132 SSR loci generated 662 alleles with a low genetic diversity (25%). Population structure analysis revealed five sub-groups in the germplasm. Sun et al. (2021) genotyped 204 Upland cotton accessions using 191 polymorphic SSR markers. A total of 1,198 alleles produced by the SSR markers revealed moderate genetic diversity in the panel with a polymorphic information content of 0.63, and the population was divided into two structured sub-groups. In another study, Jamil et al. (2021) characterized and clustered 25 cotton materials. A total of 1,294 polymorphic alleles generated by 244 SSR markers grouped the panel into two sub-groups and revealed a high PIC value of 0.73 within cotton genotypes.

Genetic diversity and population structure studies are important for bottleneck detection, germplasm conservation and improvement of cotton genotypes.

1.1.3. Linkage Disequilibrium

Linkage disequilibrium (LD) is non-random co-inheritance of two loci through generations. LD is generated between polymorphisms that result from a common history through recombination and mutation (Flint-Garcia, Thornsberry, and Buckler 2003). LD is utilized in genetic analyses such as determining genetic variation of admixed populations and assessing population structure, genotype-phenotype association studies, as well as in marker assisted selection programs (de Souza et al. 2018; Gupta, Rustgi, and Kulwal 2005).

LD is influenced by several factors such as recombination rate, genetic drift, migration, population mating pattern and natural selection. Outcrossing species and admixture populations produce low LD which rapidly decays due to high recombination frequency when compared to populations of self-pollinating and genetically similar individuals. On the other hand, domestication and cultivation with selection for or against a particular feature generate specific bottlenecks in the corresponding genomic regions. This results in LD between the genomic region which is responsible for the

feature of interest and the DNA region that is physically linked to it. Similarly, epistasis and different biological pathways that contribute to common mechanisms cause significantly low LD even if they are not located in physically linked genomic positions.

1.1.4. Aim of the Study

In the present chapter, the aim of the study was (I) to characterize an Upland cotton germplasm panel consisting of 99 *G. hirsutum* cultivars for their genetic diversity with 177 SSR markers, (II) to detect the ancestral structure of the population and (III) to reveal promising cotton genotypes harboring high genetic diversity that could be useful materials in future breeding programs.

1.2. Materials and Methods

1.2.1. Materials

The germplasm panel consisted of 99 elite Upland cotton genotypes (*G. hirsutum* L.) (Table 1.2) provided by Nazilli Cotton Research Center (Aydın, Turkey). The material represents cultivars bred in Turkey, those introduced into the country by seed companies and breeding/germplasm lines.

Table 1.2. The cotton genotypes used in this study and their origins.

Genotype	Origin	Genotype	Origin	Genotype	Origin
152F	Uzbekistan	DPL C 37 Prima	USA	Paymaster 404	USA
Acala 5	USA	DPL SR 383	USA	PG 2018	Turkey
Acala 1517	USA	Elsa	Australia	Rex 1	USA
Aleppo 1	Syria	Ersan 92	Turkey	S 9	Syria
Auburn M	USA	Eva	Greece	Sahel 1	Iran
Ayhan 107	Turkey	Flora	Australia	Sahin 2000	Turkey
Az 31	Israel	GC 555	USA	Samarkant Uzbek	Uzbekistan
Ba 119	Turkey	GC 262	USA	Sayar 314	Turkey
Ba 308	Turkey	Gloria	Australia	Sealand 542	USA
Ba 525	Turkey	GSA 78	USA	Semu SS/G	Australia

(Cont. on the next page)

Table 1.2. (cont.)

Barut 2005	Turkey	GSN 12	Turkey	SG 1001	USA
Blightmaster	USA	GW Teks	USA	SG 125	USA
Cabu/Cs2-1-83	USA	Julia	Australia	Sicala 3/2	Australia
Candia	Australia	Lachata	Spain	Sicala 33	Australia
Carmen	Australia	Lankart 57	USA	Sindos 80	Greece
Caroline Queen	USA	Mcnair 220	USA	Sj U 86	USA
Celia	Australia	Menderes 2005	Turkey	Sj V Visalia Elmer	not known
Claudia	Australia	Ms 30/1	Turkey	Somon	Albanian
Coker 208	USA	N 727 CC	Australıa	Stoneville 213	USA
Corona	Spain	Napa 122	Turkey	Stoneville 453	USA
DAK 66/3	Turkey	Nata	Spain	Stoneville 8751	USA
Delcerro	USA	Nazilli 143	Turkey	Taskent Uzbek	Uzbekistan
Delcerro Ms 30	USA	Nazilli 84 S	Turkey	Taskent 1	Uzbekistan
Delta Diamond	Spain	Nazilli 87	Turkey	Taskent 6	Uzbekistan
Delta Opal	USA	Nazilli M503/1	Turkey	TKY 9309	USA
DP 388	USA	Nazilli M503/2	Turkey	TKY 9409	USA
DPL 20	USA	Nazilli M39	Turkey	TKY3304 GS316	USA
DPL 5415	USA	NGF 63	Turkey	Togo	S. Africa
DPL 6	USA	Niab 111	Pakistan	Tomcot 22	USA
DPL 882	USA	Niab 999	Pakistan	Tomcot Cabcs	USA
DPL 883	USA	Nieves	Australia	Tomcot Sphinx	USA
DPL 886	USA	Np Ozbek 100	Turkey	Vulcano	Spain
DPL 90	USA	Np Ege 2009	Turkey	Zeta 2	Greece

1.2.2. Methods

1.2.2.1. DNA Marker Analysis

Genomic DNA was isolated manually from leaves as described by Doyle and Doyle (1987). The average DNA concentration and purity were measured using a Multiskan™ FC Microplate Photometer (Thermo Fisher). DNA concentration was adjusted to 50 ng/µl for further analysis and stored at -20°C.

A total of 177 pairs of SSR primers (DPL, BNL, DOW, JESPR, TMB, CIR, MUSS, GH, MGHES, NAU, STV) (Table 1.3) were used to characterize the Upland

cotton germplasm panel. The primer collection was selected to span the entire genome with at least three markers per chromosome. All primer information is available at the Cotton Database Resources (www.cottongen.org).

Polymerase chain reaction (PCR) was conducted in a total volume of 25 µl, containing 2.5 µl 10× PCR buffer (50 mM KCl, 10 mM Tris-HCl, (pH 8.3), 1.5 µl $MgCl_2$ (25 mM), 0.5 µl dNTP (0.2 mM), 0.5 µl forward and 0.5 µl reverse primers (10 pmol each), 0.3 µl Taq polymerase (0.25 U), 18.2 µl sterile ultra-distilled water, and 1 µl DNA (~ 50 ng/µl). PCR conditions were optimized as follows: 1 cycle of 5 min at 94 °C for denaturation, 35 cycles with 1 min at 94 °C, 1 min at 55–60 °C annealing temperature (depending on primer pair), 1 min at 72 °C for extension, and a final extension step of 7 min at 72 °C in Applied Biosystems™ Veriti™ 96-Well Thermal Cycler. A Fragment Analyzer™ automated CE System was used to separate DNA fragments at high resolution with the DNF-900-55-DNA-35-500 bp separation method. The data were analyzed using PROSize 3.0 analytical software. Allele sizes were determined by binning fragments into ±2 base pair bins. Genotype data matrix was constructed scoring alleles dominantly with "1" for presence, "0" for absence, and "9" for missing data.

Table 1.3. Simple sequence repeat (SSR) markers used in our study.

Number	Marker	Chromosome Location	A/D Chromosome
1	BNL0119	Chr20	D10
2	BNL0169	Chr20	D10
3	BNL0256	Chr10	A10
4	BNL0387	Chr24	D08
5	BNL0530	Chr04	A04
6	BNL0625	Chr11, Chr12	A11, A12
7	BNL0786	Chr15	D01
8	BNL0946	Chr20	D10
9	BNL1034	Chr11,Chr17, Chr21	A11, D03, D11
10	BNL1047	Chr25	D06
11	BNL1145	Chr02, Chr20	A02, D10
12	BNL1151	Chr11	A11
13	BNL1227	Chr26	D12

(Cont. on the next page)

Table 1.3. (cont.)

14	BNL1231	Chr11	A11
15	BNL1495	Chr13	A13
16	BNL1521	Chr24	D08
17	BNL1531	Chr16	D07
18	BNL1551	Chr21	D11
19	BNL1667	Chr01, Chr02, Chr14, Chr15	A01, A02, D01, D02
20	BNL1673	Chr12	A12
21	BNL1693	Chr01,Chr15	A01, D01
22	BNL1897	Chr02	A02
23	BNL2443	Chr17	D03
24	BNL2495	Chr26	D12
25	BNL2496	Chr17	D03
26	BNL2544	Chr18	D13
27	BNL2570	Chr20	D10
28	BNL2882	Chr14	D02
29	BNL2960	Chr10	A10
30	BNL3031	Chr09, Chr23	A09, D09
31	BNL3034	Chr03, Chr14	A03, D02
32	BNL3090	Chr15	D01
33	BNL3371	Chr17	D03
34	BNL3383	Chr23	D09
35	BNL3441	Chr03	A03
36	BNL3474	Chr08	A08
37	BNL3502	Chr14	D02
38	BNL3545	Chr02	A02
39	BNL3580	Chr01	A01
40	BNL3594	Chr06	A06
41	BNL3955	Chr06,Chr17,Chr22	A06, D03, D04
42	BNL3985	Chr23	D09
43	BNL3989	Chr03,Chr13	A03, A13
44	BNL4017	Chr03	A03
45	BNL4030	Chr19	D05
46	BNL4061	Chr13	A13

(Cont. on the next page)

Table 1.3. (cont.)

47	BNL4071	Chr05	A05
48	CIR009	Chr01	A01
49	CIR081	Chr12	A12
50	CIR169	Chr07	A07
51	CIR218	Chr22	D04
52	CIR307	Chr15	D01
53	CIR320	Chr07	A07
54	DOW003	-	-
55	DOW004	Chr11	A11
56	DOW006	Chr18	D13
57	DOW036	Chr25	D06
58	DOW038	Chr04	A04
59	DOW044	-	-
60	DOW051	Chr21	D11
61	DOW053	Chr19	D05
62	DOW054	-	-
63	DOW055	Chr14	D02
64	DOW056	-	-
65	DOW057	Chr08	A08
66	DOW058	Chr01	A01
67	DOW059	Chr20	D10
68	DOW062	Chr25	D06
69	DOW069	Chr04	A04
70	DOW070	Chr22	D04
71	DOW073	Chr03	A03
72	DOW074	Chr14	D02
73	DOW075	Chr17	D03
74	DOW077	Chr16	D07
75	DOW082	Chr18	D13
76	DOW083	Chr12	A12
77	DOW085	Chr26	D12
78	DOW093	Chr06	A06

(Cont. on the next page)

Table 1.3. (cont.)

79	DOW094	Chr18	D13
80	DOW100	Chr03	A03
81	DPL009	Chr07	A07
82	DPL019	Chr11	A11
83	DPL039	Chr26	D12
84	DPL045	Chr17	D03
85	DPL049	Chr18	D13
86	DPL068	Chr24	D08
87	DPL071	Chr19	D05
88	DPL075	Chr25	D06
89	DPL080	Chr06	A06
90	DPL088	Chr06	A06
91	DPL094	Chr01	A01
92	DPL100	Chr12	A12
93	DPL112	Chr07	A07
94	DPL119	Chr07	A07
95	DPL135	Chr20	D10
96	DPL136	Chr07	A07
97	DPL140	Chr19	D05
98	DPL156	Chr05	A05
99	DPL168	Chr16	D07
100	DPL176	Chr08	A08
101	DPL181	Chr21	D11
102	DPL186	Chr07	A07
103	DPL193	Chr21	D11
104	DPL196	Chr22	D04
105	DPL199	Chr11	A11
106	DPL204	Chr12	A12
107	DPL212	Chr19	D05
108	DPL216	Chr02	A02
109	DPL220	Chr08	A08
110	DPL223	Chr16	D07
111	DPL228	Chr21, Chr24	D08, D11

(Cont. on the next page)

Table 1.3. (cont.)

112	DPL241	Chr05	A05
113	DPL247	Chr19	D05
114	DPL253	Chr11	A11
115	DPL299	Chr04	A04
116	DPL307	Chr23	D09
117	DPL322	Chr15	D01
118	DPL354	Chr14	D02
119	DPL405	Chr14	D02
120	DPL490	Chr01	A01
121	DPL513	Chr01	A01
122	DPL520	Chr25	D06
123	DPL541	Chr09	A09
124	DPL570	Chr11	A11
125	DPL659	Chr09	A09
126	DPL674	Chr02	A02
127	DPL679	Chr09	A09
128	DPL684	Chr06	A06
129	DPL717	Chr21	D11
130	DPL728	Chr14	D02
131	DPL743	Chr12	A12
132	DPL847	Chr06	A06
133	DPL866	Chr12, Chr26	A12, D12
134	DPL885	Chr09	A09
135	DPL890	Chr26	D12
136	GH052	Chr22	D04
137	GH107	Chr04	A04
138	GH537	Chr25	D06
139	JESPR014	Chr26	D12
140	JESPR066	Chr08	A08
141	JESPR119	Chr06	A06
142	JESPR135	Chr11, Chr21	A11, D11

(Cont. on the next page)

Table 1.3. (cont.)

143	JESPR151	Chr23	D09
144	JESPR152	Chr15	D01
145	JESPR153	Chr13	A13
146	JESPR157	Chr08, Chr24	A08, D08
147	JESPR197	Chr05	A05
148	JESPR204	Chr13	A13
149	JESPR205	Chr15	D01
150	JESPR208	Chr09, Chr23	A09, D09
151	JESPR218	Chr19	D05
152	JESPR220	Chr22	D04
153	JESPR228	Chr07, Chr16	A07, D07
154	JESPR273	Chr06, Chr19, Chr25	A06, D05, D06
155	JESPR274	Chr23	D09
156	JESPR300	Chr12	A12
157	JESPR308	Chr24	D08
158	MGHES22	Chr24	D08
159	MUSS151	Chr23	D09
160	MUSS261	-	-
161	MUSS414	Chr20	D10
162	MUSS425	Chr03	A03
163	MUSS532	Chr21	D11
164	NAU2277	Chr02	A02
165	STV023	Chr07	A07
166	TMB0043	Chr21	D11
167	TMB0083	Chr26	D12
168	TMB0382	Chr23	D09
169	TMB0514	Chr02	A02
170	TMB0799	Chr12	A12
171	TMB0836	Chr03	A03
172	TMB1295	Chr19	D05
173	TMB1356	Chr10	A10
174	TMB1427	Chr08	A08
175	TMB1910	Chr15	D01

(Cont. on the next page)

Table 1.3. (cont.)

176	TMB2018	Chr17	D03
177	TMB2068	Chr16	D07

Chromosomal positions of molecular markers are based on Blenda et al. (2012) and Yu et al. (2012). Chromosome assignments of A and D sub-genome are based on (Wang et al. 2006).

1.2.2.2. Genetic Diversity and Population Structure Analysis

Pairwise distances between cultivars were calculated using DARwin5 (Dissimilarity Analysis and Representation for Windows) (Perrier and Jacquemoud-Collet 2006) with the Dice coefficient and the unweighted neighbor-joining algorithm. Pairwise PhiPT (Fpt) values, analogous to Fst genetic distances, were calculated among subgroups by molecular variance analysis (AMOVA) with 99 permutations using GenAlEex 6.503 software (Peakall and Smouse 2012; Peakall and Smouse 2006).

Population structure was analyzed using STRUCTURE 2.3.4 software (Pritchard, Stephens, and Donnelly 2000) with a model-based clustering method of an admixture model. For clustering, the length of the burn-in period was 50,000 and MCMC (Markov Chain Monte Carlo) replication after burn-in was 300,000 for accurate parameter estimation. Cluster numbers (called K) from 2 to 10 were tested with 20 iterations each to identify the structure of the population. The Q matrix was generated after structure analysis and demonstrates the proportion of assignment of each individual to the most correct cluster. The data were processed with the STRUCTURE HARVESTER online program (Earl and VonHoldt 2012) to visualize STRUCTURE results implementing the Evanno method (Evanno, Regnaut, and Goudet 2005) to deduced the best K. The cut-off value for assignment to subpopulations was set to 60%. Individuals with an assignment probability lower than 60% were not assigned to any group and described as “admixed”.

1.2.2.3. Linkage Disequilibrium

Pairwise linkage disequilibrium (LD) was estimated as the correlation coefficient (r^2) (Kruglyak 1999; Ardlie, Kruglyak, and Seielstad 2002; Terwilliger

2002) between all pairs of SSR marker loci using TASSEL 2.1 (Bradbury et al. 2007) with the rapid permutation test of 10,000 shuffles ($p \leq 0.01$). The LD decay pattern of marker pairs was generated for pairs with significant LD ($p \leq 0.01$ and $r^2 \geq 0.01$). Before conducting LD analysis, SSR alleles with frequencies below 0.05 were removed using the site filtration function of TASSEL because minor alleles can bias LD estimations.

1.3. Results

1.3.1. Genetic Diversity Analysis

The 177 SSR markers revealed a total of 967 fragments among the 99 genotypes with an average of 5.5 alleles per marker. Fragment lengths ranged from 76 to 434 bp. During diversity analysis four genotypes (Delta Diamond, Gloria, Nazilli 143, and Niab 111) were excluded from the distance calculation due to a low percent of valid data (< 50%) for each unit pair. The unweighted neighbor-joining tree yielded four different sub-groups for the population (Figure 1.8 and Table 1.4). This distribution was supported with principal coordinate analysis (PCoA) (Figure 1.9). These four sub-groups, described as Group 1, Group 2, Group 3, and Group 4 were composed of 46, 22, 15 and 8 individuals, respectively. Four individuals were not classified to a group: Auburn M, Delcerro, Sicala 3/2, and SJ U 86.

The pairwise dissimilarity between cotton cultivars ranged from 22%, between TKY 9309 and GC 555, to 60%, between Sealand 542 and PG 2018, with a mean dissimilarity of 38%. The pairs with the highest (> 54%) and lowest (< 25%) dissimilarities are listed in Table 1.4. A high correlation existed between the pairwise dissimilarities and distances as represented in the tree ($r = 0.92$) calculated by mantel test. Based on origins, 72% (33/46) of G1 consisted of USA-bred cultivars and 73% (11/15) of G3 was composed of Turkish cultivars. However, G2 contained mostly mixed-origin individuals.

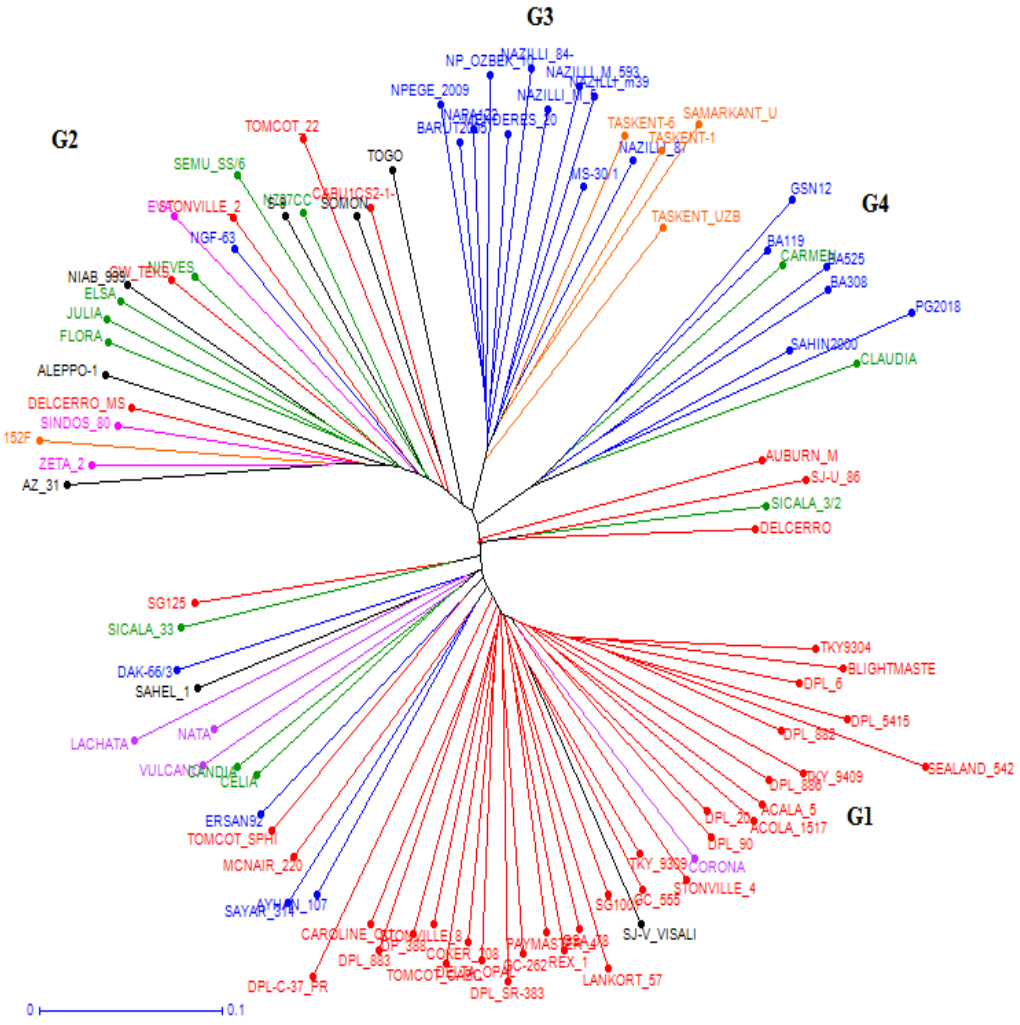

Figure 1.8. Genetic diversity of Upland cotton germplasm. Colors represent origins: red, USA; blue, Turkey; green, Australia; orange, Uzbekistan; fuchsia, Greece; light purple, Spain. Accessions from countries with fewer than three individuals remain black. For more details, see Table 1.4.

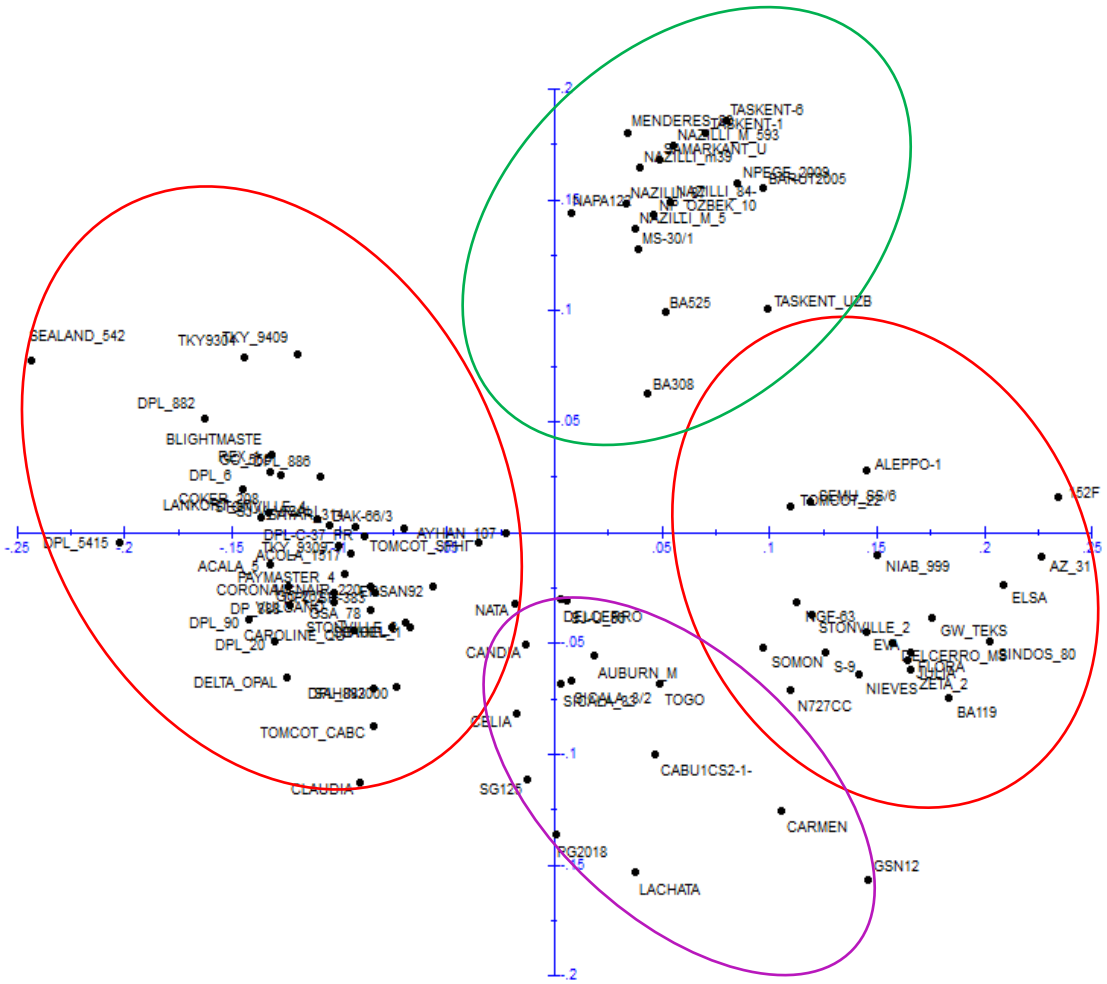

Figure 1.9. Principle coordinate analysis of the population. Population was separated into four groups (showed with circles).

Table 1.4. Assignments of genotypes to related groups based on population structure and unweighted neighbor joining tree.

	Inferred ancestry [a]			
	Subpop	Subpop		Group [b]
Genotype	A	B		
152F	0.99	0.01	A	G4
Acala 5	0.01	0.99	B	G1
Acala 1517	0.06	0.94	B	G1
Aleppo 1	0.83	0.17	A	G4
Auburn M	0.4	0.61	B	none
Ayhan 107	0.33	0.67	B	G1
Az 31	0.98	0.02	A	G4

(Cont. on the next page)

Table 1.4. (cont.)

Ba 119	1	0	A	G2
Ba 308	0.78	0.23	A	G2
Ba 525	0.8	0.2	A	G2
Barut 2005	0.69	0.31	A	G3
Blightmaster	0.02	0.98	B	G1
Cabu/Cs2-1-83	0.54	0.46	Admixed	G4
Candia	0.35	0.65	B	G1
Carmen	0.92	0.08	A	G2
Caroline Queen	0.03	0.97	B	G1
Celia	0.3	0.7	B	G1
Claudia	0.42	0.58	Admixed	G2
Coker 208	0.01	0.99	B	G1
Corona	0.02	0.98	B	G1
DAK 66/3	0.11	0.89	B	G1
Delcerro	0.37	0.63	B	none
Delcerro Ms 30	0.88	0.12	A	G4
Delta Diamond	0.92	0.08	A	excluded
Delta Opal	0.02	0.98	B	G1
DP 388	0.03	0.97	B	G1
DPL 20	0.01	0.99	B	G1
DPL 5415	0.01	0.99	B	G1
DPL 6	0.01	0.99	B	G1
DPL 882	0.01	0.99	B	G1
DPL 883	0.03	0.97	B	G1
DPL 886	0.04	0.96	B	G1
DPL 90	0.01	0.99	B	G1
DPL C 37 Prima	0.08	0.92	B	G1
DPL SR 383	0.09	0.92	B	G1
Elsa	0.99	0.01	A	G4
Ersan 92	0.1	0.9	B	G1
Eva	0.86	0.14	A	G4
Flora	0.97	0.04	A	G4
GC 555	0.01	0.99	B	G1
GC 262	0.01	0.99	B	G1
Gloria	0.98	0.02	A	excluded
GSA 78	0.02	0.98	B	G1
GSN 12	0.98	0.02	A	G2
GW Teks	0.97	0.04	A	G4
Julia	0.91	0.09	A	G4
Lachata	0.55	0.45	Admixed	G1
Lankart 57	0.02	0.98	B	G1
Mcnair 220	0.07	0.93	B	G1

(Cont. on the next page)

Table 1.4. (cont.)

Menderes 2005	0.5	0.5	Admixed	G3
Ms 30/1	0.46	0.55	Admixed	G3
N 727 CC	0.71	0.29	A	G4
Napa 122	0.42	0.58	Admixed	G3
Nata	0.28	0.72	B	G1
Nazilli 143	0.63	0.37	A	excluded
Nazilli 84 S	0.61	0.4	A	G3
Nazilli 87	0.47	0.53	Admixed	G3
Nazilli M503/1	0.5	0.5	Admixed	G3
Nazilli M503/2	0.55	0.45	Admixed	G3
Nazilli M39	0.51	0.49	Admixed	G3
NGF 63	0.79	0.21	A	G4
Niab 111	0.99	0.01	A	excluded
Niab 999	0.91	0.09	A	G4
Nieves	0.85	0.15	A	G4
Np Ozbek 100	0.55	0.45	Admixed	G3
Np Ege 2009	0.62	0.38	A	G3
Paymaster 404	0.02	0.98	B	G1
PG 2018	0.75	0.25	A	G2
Rex 1	0.01	0.99	B	G1
S 9	0.82	0.18	A	G4
Sahel 1	0.15	0.85	B	G1
Sahin 2000	0.42	0.58	Admixed	G2
Samarkant Uzbek	0.56	0.44	Admixed	G3
Sayar 314	0.16	0.84	B	G1
Sealand 542	0.02	0.98	B	G1
Semu SS/G	0.81	0.19	A	G4
SG 1001	0.03	0.97	B	G1
SG 125	0.35	0.65	B	G1
Sicala 3/2	0.43	0.57	Admixed	none
Sicala 33	0.43	0.57	Admixed	G1
Sindos 80	0.99	0.01	A	G4
Sj U 86	0.46	0.54	Admixed	none
Sj V Visalia Elmer	0.02	0.99	B	G1
Somon	0.66	0.34	A	G4
Stoneville 213	0.77	0.23	A	G4
Stoneville 453	0.01	0.99	B	G1
Stoneville 8751	0.13	0.87	B	G1
Taskent Uzbek	0.73	0.27	A	G3
Taskent 1	0.62	0.38	A	G3
Taskent 6	0.59	0.41	Admixed	G3

(Cont. on the next page)

Table 1.4. (cont.)

TKY 9309	0.01	0.99	B	G1
TKY 9409	0.02	0.98	B	G1
TKY3304 GS316	0.02	0.98	B	G1
Togo	0.57	0.43	Admixed	G4
Tomcot 22	0.7	0.3	A	G4
Tomcot Cabcs	0.07	0.93	B	G1
Tomcot Sphinx	0.22	0.78	B	G1
Vulcano	0.05	0.96	B	G1
Zeta 2	0.94	0.06	A	G4

a Assignment to one of two subpopulations (K = 2) according to population structure analysis based on a membership threshold ≥ 0.6.
b Group (G) assignment to one of four groups according to unweighted neighbor-joining dendrogram results.

Table 1.5. Pairs of genotypes with the highest and the lowest genetic dissimilarities

Pair of Genotypes	**Genetic Dissimilarity (%)**	**Pair of Genotypes**	**Genetic Dissimilarity (%)**
PG2018 – Sealand 542	60	TKY 9309 - GC 555	22
Az 31 – Sealand 542	60	Napa 122 – Barut 2005	23
Delcerro Ms – Sealand 542	57	Np Ege 2009 – Barut 2005	24
Sindos 80 – Sealand 542	56	DPL 882 – DPL 6	24
152F – Sealand 542	56	DPL 20 – DPL 90	24
Zeta 2 – Sealand 542	55	Menderes 20 – Barut 2005	24
PG2018 – Niab 999	55	DPL 882 – Acala 5	24
GW Teks – Sealand 542	55	Napa 122 – Menderes 20	24
GSN12 – Sealand 542	55	DPL 886 – DPL 882	24
		Flora – Celia	24
		TKY 9304 – DPL 882	24

1.3.2. Population Structure Analysis

According to the population structure analysis, the ΔK value peaked at K = 2 with a smaller peak at K = 4 (Figure 1.10). For K = 2, the population was divided into two sub-populations (sub-populations A and B) with 35 and 46 individuals, respectively. Eighteen individuals were not assigned to any subgroup due to a membership probability less than 60% and designated as "Admixed". Hence, the optimum cluster number to avoid excluding loci in the association analysis (See Chapter 2 and Chapter 3) was determined to be two (K = 2, Table 1.4). Pairwise ϕpt values between sub-populations of A and B were calculated. Genetic variation between groups was 11% and within groups was 89% (Figure 1.11).

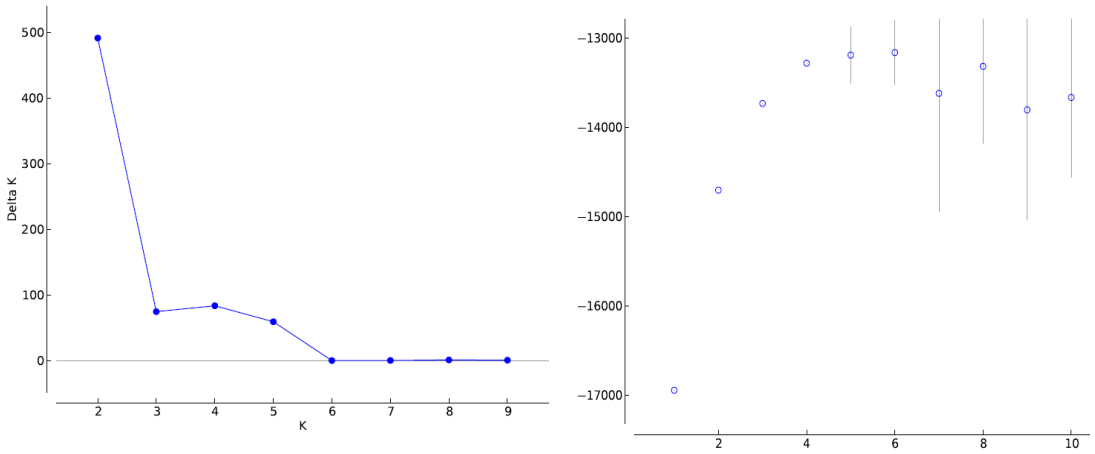

Figure 1.10. a. ΔK was used to determine the group number (K) representing the best population structure. b. The log-likelihood for different group numbers.

The secondary peak of ΔK at K = 4 was examined and could support dividing the population into four subgroups. According to this, the population was assigned to four subgroups (SG1 to SG4) with 41 (41%), 23 (23%), 16 (16%) and 3 (3%) individuals, respectively. Sixteen individuals failed to be assigned to a subgroup (16%). There was a high degree of correspondence between the two sets of results: population structure at K = 4 and population diversity results for four groups as shown in the diversity dendrogram (Figure 1.12). All individuals (100%) of sub-groups SG1 and SG4 were assigned to group 1 and group 4 of the dendrogram, respectively. In addition, 87% and 94% of sub-groups

SG2 and SG3 individuals were assigned to group 2 and group 3 of the dendrogram, respectively. Four of the 16 “admixed” individuals could not be assigned to diversity groups (Auburn M, Delcerro, Sicala 3/2 and SJ U 86); the rest being distributed among group 1 (5), group 2 (5), and group 4 (2).

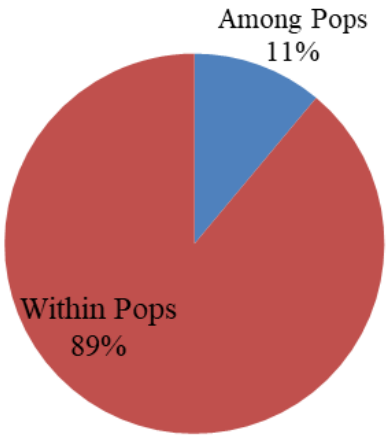

Figure 1.11. Analysis of molecular variance (AMOVA) for subgroups

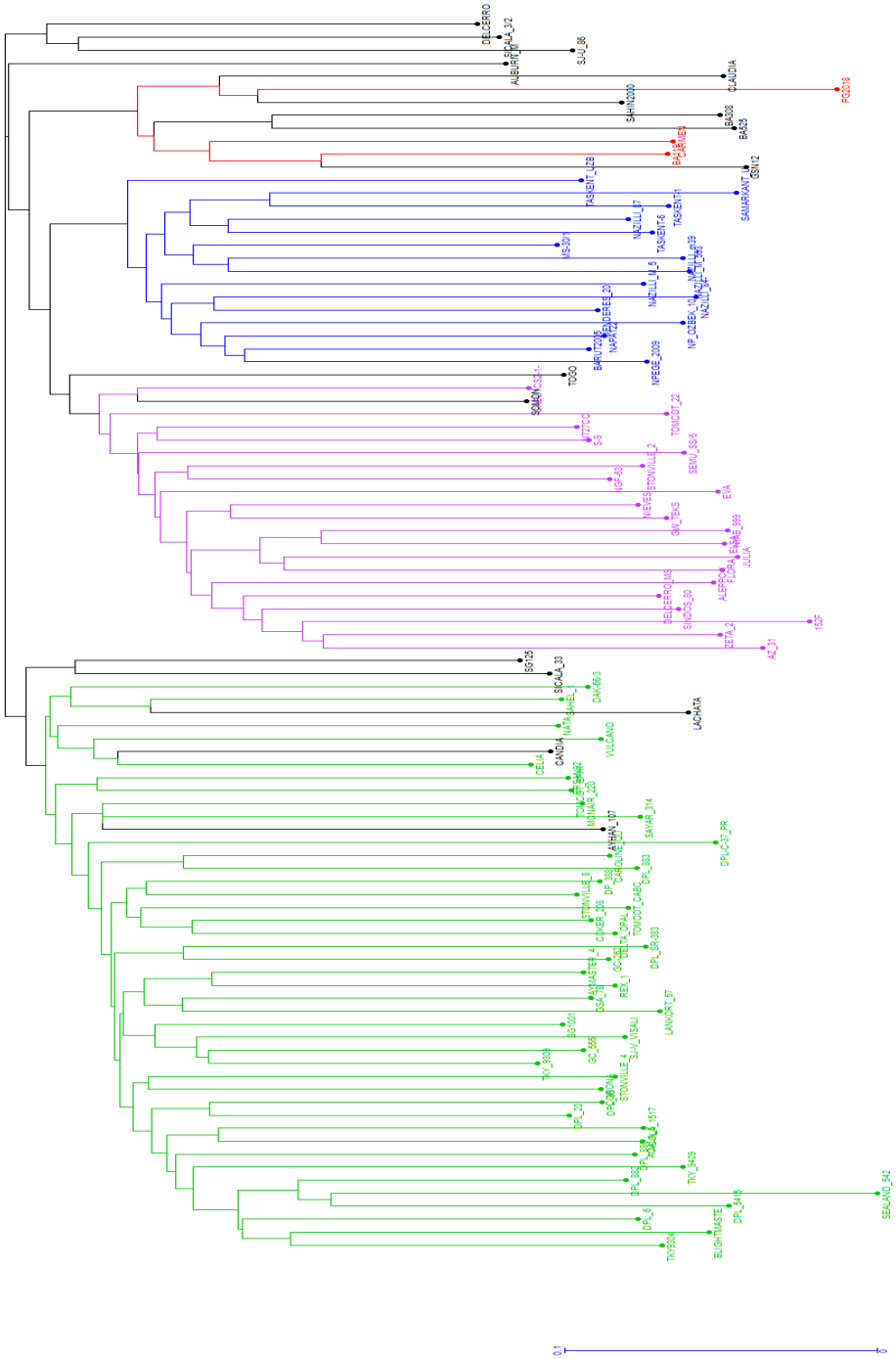

Figure 1.12. Genetic relationships between Upland cotton genotypes estimated by unweighted neighbor-joining algorithm. Colors; green (SG1), pink (SG2), blue (SG3) and red (SG4) represent the individuals of the clusters based on K = 4 obtained by STRUCTURE analysis. “Admixed” individuals are in black.

1.3.3. Linkage Disequilibrium

Site filtration of minor alleles brought the allelic data from 967 to 625 loci. A total of 9,185 (4.3%) marker pairs of the 625 SSR loci across 99 *G. hirsutum* L. cultivars were in linkage disequilibrium (LD) at a significance level of $p \leq 0.01$ and $r^2 \geq 0.01$. LD analysis of pairwise estimates for r^2 ranged from 0.06 to 1 for markers located within 0–170 cM. The average r^2 values of global, linked and unlinked SSR marker pairs were 0.16, 0.25 and 0.15, respectively with most of the r^2 values ranging from 0.06 to 0.3. The LD decay plot shows how r^2 (LD) declined with genetic distance (cM) between marker pairs (Figure 1.13).

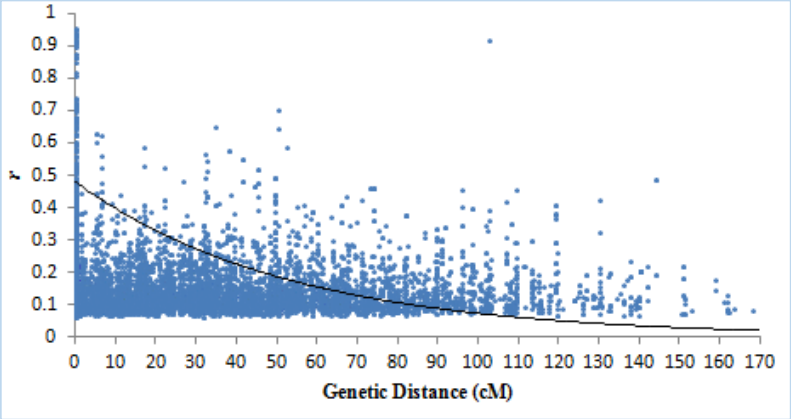

Figure 1.13. Linkage disequilibrium decay plotted as r^2 against genetic distance (cM) at significance level $p \leq 0.01$, ($r^2 \geq 0.01$).

1.4. Discussion

In the present chapter, genetic diversity, ancestral background and linkage disequilibrium were investigated in a panel of 99 *G. hirsutum* cotton genotypes. A total of 177 SSRs produced 967 loci in the cotton germplasm with an average of 5.5 alleles per marker. Previous genetic analyses performed with SSR markers have revealed similar levels of polymorphism, with averages ranging from 2.2 to 5.1 alleles per marker (Qin et al. 2015; Nie et al. 2016; Cai et al. 2014; Du et al. 2016; Y. Zhang et al. 2011). Genetic diversity analysis identified moderate genetic dissimilarity (38%) within cotton germplasm which is consistent with genetic studies generated with SSRs (36%,

Du et al. 2016; 38%, Nie et al. 2016). The cotton cultivars derived from the same breeding program closely clustered in the same diversity groups. For instance: DPL 6 and 882; Np Ege and Np Ozbek; TKY 9304 and TKY 9309 were clustered closely with dissimilarities of 24, 29 and 24%, respectively. Moreover, cultivars from the same origins tend to form their own groups such as the cultivars from USA, Turkey and Uzbekistan.

Linkage disequilibrium is non-random co-segregation of two loci through generations. In the present study, LD analysis indicated that 4.3% of SSR locus pairs were in LD ($p \leq 0.01$) which is comparable with previous studies which found values of 3% and 4%, $r^2 > 0.05$ (Saeed, Wangzhen, and Tianzhen 2014; Abdurakhmonov et al. 2009, respectively) and is considerably lower than in other studies that reported values of 9.4%, 17.3%, and 21% (Qin et al. 2015; Nie et al. 2016; Mei, Zhu, and Zhang 2013, respectively). As the LD level (coefficient of determination, r^2) approaches 1 for two loci, coexistence of those loci is more frequent in the population. Analysis of pairwise LD based on average r^2 revealed that linked marker pairs (on the same chromosome) were higher (an average $r^2 = 0.25$) than global (an average $r^2 = 0.16$) and unlinked marker pairs (on the different chromosome) (an average $r^2 = 0.15$). This is similar to the results reported by previous studies that clearly demonstrated that physical linkage affects the detection of LD (H. Mei, Zhu, and Zhang 2013; Zhao et al. 2014). High LD was observed in our cotton germplasm panel (60 - 70 cM, $r^2 \geq 0.1$) which is much higher than previous studies 25 cM ($r^2 \geq 0.1$), 12 – 13 cM ($r^2 = 0.1$) and 8.6 cM ($r^2 > 0.1$) as reported by Abdurakhmonov et al. (2009); Mei et al. (2013); Qin et al. (2015), respectively. LD is affected by many components such as genetic drift, natural selection, and especially recombination rate. It tends to be high (slow decay) in self-pollinated crops because of their low effective recombination rate. While cotton is naturally cross-pollinating, it has been bred to be self-pollinating as a means of maintaining genomic purity in the crop (Simpson 1954) Therefore, it is expected for the LD to be relatively high in Upland cotton, as demonstrated in this study. The effects of cultivation and breeding on the germplasm are clearly seen in the high level of LD decay in this study.

Genetic analysis in this study clearly emphasized that domestication and intensive breeding of limited genetic material have caused a genetic bottleneck in modern cotton lines indicating that genetic diversity must be urgently broadened. This

narrow genetic basis is the main obstacle to achieving further advances in desired quality and productivity in cotton cultivars.

Genetic characterization of cotton germplasm is important for its use in breeding because this analysis allows breeders to select the most appropriate combinations of parental genotypes and effective use of genetic materials especially when pedigree information is not available. The findings of the present genetic study could be useful information to enhance genetic diversity in breeding programs by allowing selection of elite cotton genotypes based on their dissimilarity.

CHAPTER 2

IDENTIFICATION OF STABLE QTLS FOR FIBER QUALITY AND PLANT STRUCTURE IN UPLAND COTTON (*G. hirsutum* L.) UNDER DROUGHT STRESS

2.1. Introduction

2.1.1. Cotton Quality Features

Cotton is a fiber crop that has great economic and social importance with its various uses. It was primarily domesticated and cultivated for its fiber, however, its seed is also processed as vegetable oil and animal feed in the food and feed industry. The short fibers that remain on the seed after ginning, called linters (seed hair) are also economically important and used in many fields such as automotive, furniture and paper applications (Wakelyn 2006) (Figure 2.1).

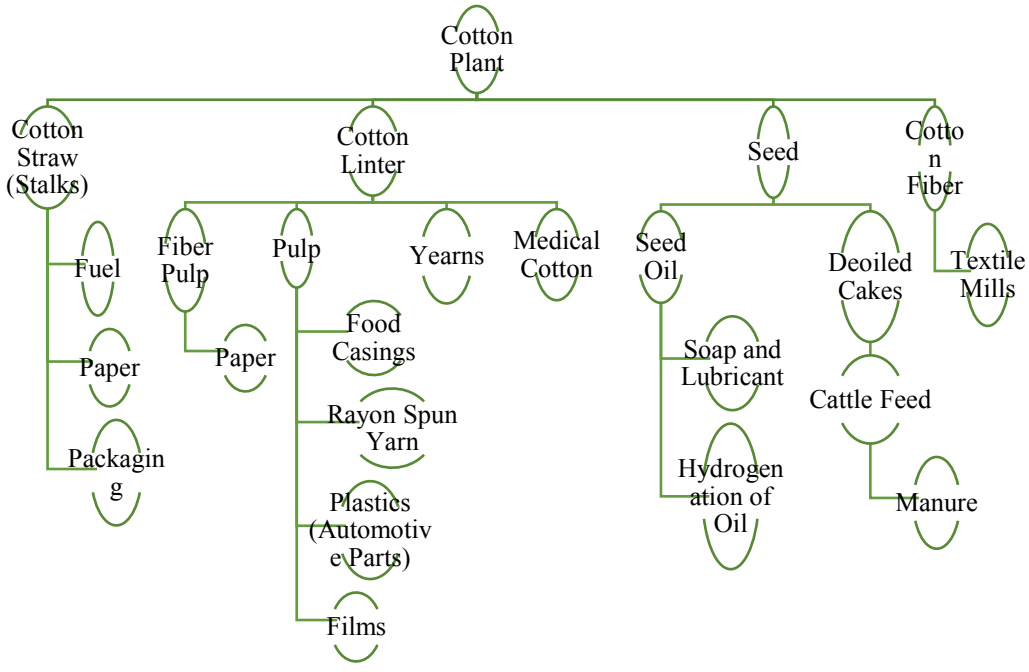

Figure 2.1. Cotton uses in different industries

The quality of cotton is very important for cotton producers and users as it directly affects harvesting and ginning efficiency, thus yield and market price. Quality parameters of cotton are highly related to production efficiency, durability of yarns and fabrics, and directly impact the processing of cotton yarn, such as dyeing and finishing. There are various parameters that define and classify cotton quality (Figure 2.2.): color and reflectance degree, short fiber index, the amount of the foreign matter (trash), fiber uniformity, fiber length, fiber fineness, fiber elongation, fiber strength, ginning efficiency and spinning consistency (Johnson et al. 1996;Wakelyn 2006; James et al. 2010; Baytar et al. 2014).

Each of the aforementioned factors have different importance for cotton quality. Color grade and brightness of fibers are affected by many factors such as moisture, rainfall, microorganism-related effects (insect, fungi), growth and storage conditions, and are important for the downstream processing of cotton fabrics such as dyeing. The short fiber index considers fibers with a length of less than 12.7 mm, and a low short fiber index is desirable for high quality fiber because short fibers cannot wrap around each other as much as long fibers, resulting in trash and increased processing cost. Length uniformity is estimated as percentage of the mean length divided by the upper half mean length. Uniformity directly affects spinning process, evenness and strength of yarn. A uniformity value below 77% is considered as low quality and most probably includes a high amount of short fiber content. Therefore, higher fiber uniformity (> 80%) is desired for improved quality of cotton fabrics (Peng et al. 2009; James et al. 2010). Abiotic stresses as well as physical factors such as excessive cleaning or drying in the gin have direct impact on fiber length. Fiber length affects strength and evenness of the yarn and efficiency of the spinning process.

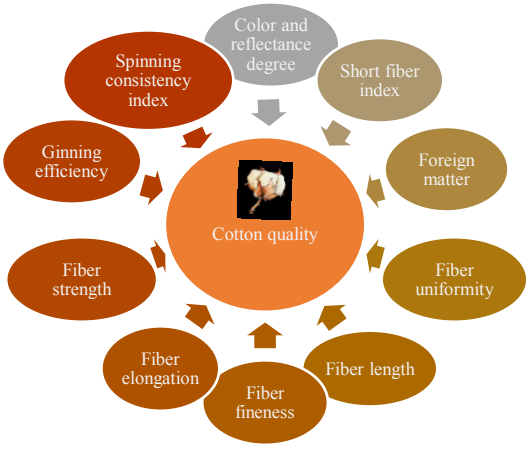

Figure 2.2. Cotton quality factors

Table 2.1. Quality grades of cotton fiber

Fiber length		**Fiber elongation**	
Short	2.51	Very low	< 5.0
Medium	2.51 – 2.79	Low	5.0 – 5.8
Long	2.79 – 3.20	Average	5.9 – 6.7
Extra long	> 3.20	High	6.8 – 7.6
Fiber fineness		Very high	> 7.6
Very fine	< 3.0	**Fiber uniformity**	
Fine	3.0 – 3.9	Very low	< 77
Average	4.0 – 4.9	Low	77 – 79
Coarse	5.0 – 5.9	Average	80 – 82
Very coarse	> 6.0	High	83 – 85
		Very high	> 85
Fiber strength		**White Color**	
Weak	< 23	Good middling	11
Intermediate	24 – 25	Middling	31
Average	26 – 28	Low middling	51
Strong	29 – 30	Strict good ordinary	61
Very strong	> 31	Good ordinary	71

The degree of fiber elongation, along with fiber strength, is important in reducing breakage during downstream fiber processing. Higher fiber elongation is a desired feature in textile manufacturing processes otherwise fibers with a low degree of elongation are broken down due to ginning and mechanical processing (Peng et al. 2009; Mathangadeera et al. 2020). Fiber fineness is another important fiber quality property. It is significantly affected by environmental factors such as cultivation conditions, sowing time, fertilization, soil moisture, temperature changes and nutrient composition (Peng et al. 2009; James et al. 2010; Baytar et al. 2014). The finer the fibers, the more durable, shiny and softer they are. Therefore, a low level of fiber fineness is a desirable trait in the cotton industry. Fiber strength is the force to break the fibers in grams per denier which is related to the diameter of the cotton fibers. Fiber strength is highly affected by extreme weather conditions and mechanical processes causing yield and quality losses. Higher fiber strength produces strong cotton yarns because stronger fiber is not easily broken down and, thus, processed more efficiently which is a very important and desirable trait for cotton manufacturing. Spinning consistency index is an overall estimation value of the spinning ability of cotton fibers in yarn-spinning that is measured by the high volume instrument. Easily spinnable fiber is strongly demanded in the textile manufacturing industry.

2.1.2. Drought Stress and Its Breeding in Cotton

Abiotic stress is any kind of adverse effects that result from complex environmental conditions on living organisms such as ultraviolet light, freezing, high temperature, drought, waterlogging, salinity, heavy metals, insufficient oxygen and insufficient minerals (Hirayama and Shinozaki 2010; Ullah et al. 2017; Abdelraheem et al. 2019). Although cotton is native to arid and semi-arid regions, its intrinsic response to water stress is highly dependent on the developmental stage of the plant and the degree of dry periods. Drought stress can cause flower bud shedding, low fiber elongation, altered fiber wall thickness, and smaller boll size, decreased plant height, leaf area and number of nodes, and result in poor fiber quality and reduced fiber yield (Loka, Oosterhuis, and Ritchie 2011; Ullah et al. 2017) (Figure 2.3).

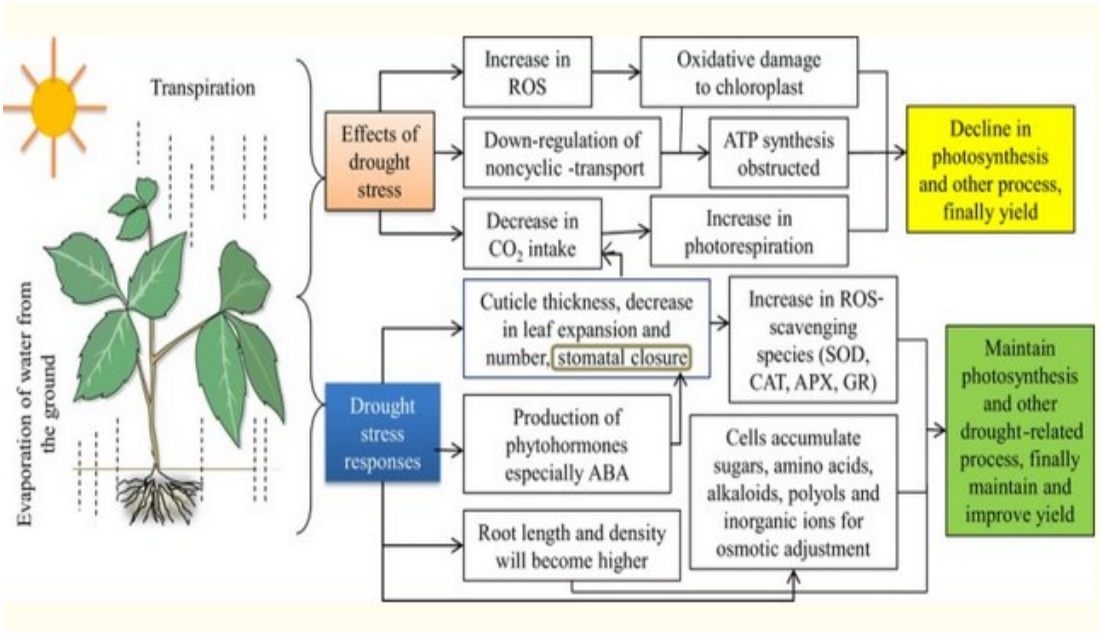

Figure 2.3. Effects of drought stress and plant responses in cotton
(Source: Ullah et al., 2017)

Drought stress is one of the major threats resulting in global yield losses up to 80% in cotton. It is predicted that increasing water stress and sudden climate changes will continue exponentially in the future (USDA 2015; Ullah et al. 2017). Therefore, drought tolerant cotton lines are of vital importance to maintain yield demand in the future. Although plant survival is very critical in drought conditions, development of a

stress-tolerant cotton line alone is not enough. Instead, it is desirable to have both good yield and high quality characteristics under drought-stress conditions.

Breeding for drought tolerance is a challenge in cotton. The success of traditional breeding efforts for development of drought-tolerant cultivars is restricted due to the complex genetic background of the drought tolerance mechanism, inadequate genetic diversity for the trait and the quantitative nature of drought-related traits under the influence of environmental conditions (Levi et al. 2009). Nonetheless, many traditional attempts have been applied to improve drought tolerance in cotton. For this purpose, three main approaches have been exerted. The first is the cultivation of cotton cultivars with high yield under optimum environmental conditions with the expectation that the cultivar will produce a reasonable yield under water deficiency. The second strategy is the direct selection for high yield parameters under drought conditions. The third breeding strategy is to start with a drought resistant line and work on it to increase yield characteristics (Quisenberry et al. 1980; Rosielle and Hamblin 1981; Y Saranga et al. 2004). However, development of new varieties with classical plant breeding requires a long time, high cost and intensive labor. Moreover, the main problems encountered in cotton breeding studies include the difficulties of generating the desired traits due to genetic linkage of unwanted characters during breeding, the complex structure of agronomic characters, difficulties in precise measurement of these traits, and the very narrow genetic polymorphism between cultivated cotton varieties.

The addition of molecular technologies to classical plant breeding can help shorten the breeding period and enable efficient development of (a)biotic stress-tolerant, high quality cotton lines. In recent years, molecular techniques such as plant biotechnology, genetic engineering and molecular DNA markers, have been widely integrated with classical plant breeding programs, and have resulted in significant advantages and innovations.

Thus, molecular and classical breeding methods can be combined to minimize cotton production losses and maximize yield and quality in extreme conditions. Drought stress-tolerant varieties are a sustainable approach to maintain cotton yield in case of extreme water deficiency. Therefore, selection of suitable parents as breeding material and identification of target genes or trait-marker associations are of importance for successful molecular breeding of drought tolerant cotton.

2.1.3. Association Mapping

Association mapping is a method used to identify genomic loci which contribute to the control of complex traits. Association mapping is based on LD principles, in other words, it utilizes non-random associations between traits and genomic loci (Kumar Singh Kushwaha et al. 2017; Kaler et al. 2020). There are three main steps to conduct association mapping studies: (I) characterization of a panel segregating for the trait of interest, (II) polymorphic genotypic data and (II) suitable software. The success of association mapping studies depends on many factors and details such as population size, amount of segregation of the trait in the population, phenotyping accuracy, marker density, genotyping accuracy, genome coverage, choice of the most appropriate model(s) to detect significant loci, control of Type I and II errors, and correction of p values.

There are two main categories of association mapping studies: association mapping for candidate gene (CGA) or genome-wide association mapping (GWA). In CGA, the target genes within a population are examined for the relationship of their polymorphism to traits of interest. On the other hand, in GWA, whole genome variation is investigated with high resolution to detect all possible significant loci associated with the tested traits.

Association mapping is conducted through three main steps. First, s suitable population is selected and this population is phenotyped under multiple environmental conditions for the traits of interest. Secondly, genotypes are surveyed with molecular markers (SSR, SNP, AFLP, RFLP etc.) to reveal polymorphic regions, to identify population structure and LD. Lastly, appropriate association models (GLM, MLM, etc.) are applied to determine marker trait associations (MTAs). In the end, raw data is processed and only significant associations are detected (Pasam and Sharma 2014).

2.1.4. Molecular Breeding of Fiber Features in Cotton

Drought-tolerant cotton lines with improved fiber quality will certainly be a desirable benchmark in the near future. Therefore, cotton lines with superior features should be selected under drought stress. However, simultaneous breeding of drought parameters and fiber traits in classical breeding may cause inaccuracies in selection

because this approach is based on phenotypic observations. Molecular genetic advances promise alternative strategies that can be leveraged along with traditional breeding methods. One such method is the MAS (Marker Assisted Selection) approach using molecular markers in crop breeding.

2.1.4.1. Marker Assisted Selection in Cotton

Quantitative traits are complex phenotypic characters controlled by more than one gene and under effects of both genetic and environmental factors (Heino 2014; Benton and Stearne 1993) such as plant height, weight, yield and size. Molecular marker assisted selection (MAS) is a process developed to overcome the problems encountered by classical breeding through integrating molecular marker technology into genotype selection in breeding (Figure 2.4). Molecular DNA markers are absolutely not affected by any external effects such as environmental factors and growth conditions, and are independent of plant developmental stages (Francia et al. 2005). A DNA marker which is significantly associated with a desired characteristic, such as high quality, high yield and (a)biotic stress tolerance, can be utilized in MAS to improve or develop cultivars. This approach saves time and workload and helps achieve success in breeding.

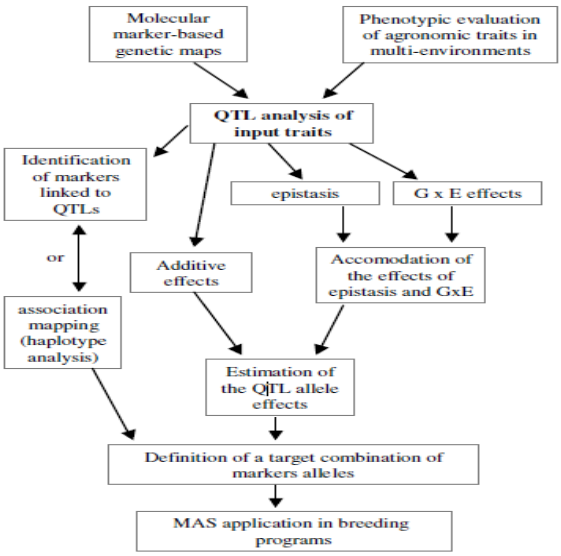

Figure 2.4. Marker assisted selection in breeding
(Source: Francia et al. 2005).

Due to their importance, fiber features have been targeted by many association mapping studies utilizing SSRs in Upland cotton. These include work that investigated fiber traits (Tan et al. 2015; Tang et al. 2015; H. Wang et al. 2015; Nie et al. 2016; C. Huang et al. 2018; Deng et al. 2019; Li et al. 2021), yield parameters (Mei, Zhu, and Zhang 2013; Jia et al. 2014; Li et al. 2017; Ali et al. 2020; Guo et al. 2021), yield and fiber characteristics (Abdurakhmonov et al. 2009; Qin et al. 2015; H. Wang et al. 2015; T. Zhang et al. 2020; Kumar et al. 2021) and fiber quality traits (Abdurakhmonov et al. 2008; Cai et al. 2014; Tang et al. 2015; Nie et al. 2016; Ademe et al. 2017; Iqbal and Rahman 2017; Dong et al. 2019; Saeed et al. 2021). For instance, Guo et al. (2021) identified 140 markers for ten yield-related traits in 503 Upland cotton cultivars using 179 SSR markers. In another study, Zhang et al. (2020) detected 82 marker-trait associations for 15 fiber and yield quality-related traits using 19 microsatellite markers in 285 Upland cotton accessions. Huang et al. (2018) screened Upland cotton cross populations using 284 SSR markers. They revealed that 54 SSR loci were significantly associated with fiber quality and, that 14 of them matched previously reported quantitative trait loci (QTL). In another association study, 57 significant associations were determined for fiber quality in 305 Upland cotton accessions using 198 SSR markers. Of the significant loci, 34 were identified for more than one fiber trait (Ademe et al. 2017). Cai et al. (2014) identified 107 significant fiber trait-associations in 99 *G. hirsutum* accessions using 97 polymorphic SSR markers. They reported that 70 SSR loci of 107 associations were significant in more than one environment and, that 36 SSR loci had been identified in previous studies which indicated the stability of the loci. These and similar association analysis studies will be helpful for fiber quality trait breeding of modern cotton cultivars.

2.1.5. Aim of the Study

Upland cotton is one of the leading fiber crops accounting for over 90% of global cotton production in the world (Jenkins 2003; Rai et al. 2013). Fiber quality is a primary goal of breeders because fiber traits directly affect the yield and economic value of cotton production. In addition, improvements in spinning technology have increased demand for high quality cotton fiber (Wendel and Cronn 2003). Drought, which causes yield losses up to 70%, is a serious problem throughout the world.

Therefore, the development of drought tolerant individuals with high quality fiber traits is crucial to both agronomy and industry. For this purpose, in the present study, it was aimed to identify stable QTLs for fiber quality and plant structure in Upland cotton (*G. hirsutum* L.) under drought stress. Association mapping allows identification and localization of the genomic regions controlling the traits. The identified markers can be used in marker-assisted breeding approaches for development of drought tolerant cotton cultivars using molecular marker technologies.

2.2. Materials and Methods

2.2.1. Materials

The germplasm panel of 99 Upland cotton (*G. hirsutum* L.) genotypes was supplied by NCRC (Nazilli Cotton Research Center), Aydın, Turkey. The panel consisted of genotypes grown for commercial production in Turkey and known to differ in fiber quality traits (Table 1.2).

2.2.2. Methods

2.2.2.1. Morphological Characterization

Morphological characterization of seven fiber and four plant structure traits was performed during growing seasons in 2011 and 2012 at two locations under well-watered and water-limited conditions: Agricultural Research Station of Adnan Menderes University (ADU) and Özaltın Agricultural Enterprises Industry and Commerce Inc. (OAE), both in Koçarlı, Aydın, Turkey. Water content of the field soil ranged from 20% to 28% at ADU and from 13% to 14% at OAE, respectively. Wilting point ranged from 7% to 10% at ADU and from 4% to 6% at OAE.

A complete randomized block design was established with four replicates of each of the 99 genotypes with 12 m single row, 0.7 m space between rows and 0.20 m between individual plants. Soil moisture was measured by the gravimetric method. The irrigation treatments were based on replenishment of soil water depletion. The control

treatment was designated to receive 100% replenishment. Plants were irrigated when available soil moisture decreased to 50% in the 1.20 m root zone. In the water-limited treatment, plants were irrigated with 50% of the full irrigation amount. In each location approximately 626 mm and 313 mm of water were applied for the well-watered and water-limited treatments, respectively. Harvest was performed by hand on 29 September 2011 and 14 September 2012 (Sezener et al. 2015). Morphological characterization was carried out at both sites (ADU and OAE) for two years.

Seeds were separated from seedcotton (cotton with seeds) using a roller gin. The fibers were incubated at 21 °C and 65% relative humidity for 48 h until 7–8% humidity. After that, fiber quality features were measured using fifty bolls for each individual. Fiber length (FL) (mm), fiber fineness (FF) (mic), fiber strength (FS) (g teks^{-1}), fiber elasticity (FE) (%), fiber uniformity (FU) (%) and spinning conversion index (SCI) were measured using a USTER-HVI machine according to HVI cotton standards. Earliness (EAR) (%) was estimated as weight (kg ha^{-1}) of seedcotton at first harvest divided by weight (kg ha^{-1}) of total seedcotton (first and second harvest).

Total boll number (TBN) per plant was total number of bolls at first and second position. First position boll retention was calculated with following formula: [100*(total of 1st position boll number−1st position fallen boll number)/total of 1st position boll number]. Second position boll retention was calculated with following formula: [100*(total of 2nd position boll number−2nd position fallen boll number)/total of 2nd position boll number]. Plant height (PH) (cm) was the length between the cotyledonary node and terminal bud.

All data were evaluated with JMP 5.0 statistical software (JMP®, Version 5.0, SAS Institute Inc., Cary, NC, 1989–2007). Bivariate correlation coefficients between traits were calculated by PAWS statistics software (SPSS Inc. Released 2009, PASW Statistics for Windows, Version 18.0, Chicago: SPSS Inc.) with Pearson Correlation, two-tailed method. The mean data from the two locations were used to establish phenotype histograms for each water treatment using Microsoft Excel (2007).

2.2.2.2. Association Analysis for Fiber Traits and Plant Structure

Association analysis was performed with 177 SSR markers (Table 1.3) for seven fiber and four plant structure traits. QTL identification was performed with TASSEL

software ver. 2.1. The general linear model was corrected with Q matrix (GLM + Q) and the mixed linear model corrected with Q matrix and kinship (K) (MLM + K + Q) (Bradbury et al. 2007). Q matrix was calculated with STRUCTURE 2.3.4. Relative kinship matrix (K matrix) was calculated with TASSEL 2.1. software and Q matrix at K = 2 was used in the association analysis because it was the best representation for the population structure. Minor alleles (< 0.05) were removed from data before conducting association analysis using the site filtration function in TASSEL. The significance level to detect SSR marker loci associated with fiber traits was set at $p \leq 0.005$. False discovery rate (FDR) for p values was calculated with QVALUE software (Storey 2002) ($q < 0.2$) (Weller et al. 1998; Benjamini and Yekutieli 2005) Only markers with p-values ≤ 0.005 and q values ≤ 0.2 were considered to be significant. The phenotypic variance explained (PVE) by individual markers (r^2) was used to estimate the QTL effect. We classified QTLs as major and minor based on a threshold PVE value of 10% (Collard et al. 2005; Nabukalu et al. 2021).

2.3. Results

2.3.1. Morphological Characterization

Seven fiber traits and four plant structure traits were characterized under both well-watered and water-limited treatments in two locations (ADU and OAE) (Table 2.2 and Table 2.3). There was a significant location effect on fiber elasticity, fiber uniformity, spinning consistency index, earliness, first and second position boll retention, and total boll number under well-watered conditions. Under water-limited conditions, location effect was significant for fiber elasticity, earliness, second position boll retention, total boll number and plant height (Table 2.4). All phenotypic traits were normally distributed under both treatments (Figure 2.5 and Figure 2.6).

Table 2.2. Morphological results for fiber quality and plant structure features under well-watered conditions.

Well-watered conditions	Fiber length (mm)	Fiber fineness (mic)	Fiber strength (g/teks)	Fiber elasticity (%)	Fiber uniformity (%)	Spinning conversion index	Earliness (%)	1st PBR (%)	2nd PBR (%)	Total boll number per plant (n)	Plant height (cm)
152F	28.8	4.3	34.3	6.4	86.6	111.0	77.6	61.2	38.3	8.2	122.3
Acala 5	31.2	3.8	38.9	5.3	84.3	122.3	71.5	61.3	58.2	11.4	112.2
Acala 1517	29.6	3.9	34.3	5.9	84.5	105.8	68.4	61.8	47.6	9.6	97.2
Aleppo 1	28.5	4.2	33.1	6.2	84.9	99.5	88.4	58.7	29.8	8.2	108.3
Auburn M	28.6	4.0	29.7	6.9	83.9	86.8	76.9	61.2	45.9	11.5	101.2
Ayhan 107	28.8	4.3	33.9	5.7	85.1	102.5	90.2	68.5	41.7	8.1	86.3
Az 31	31.5	4.2	37.7	5.8	85.5	121.6	61.2	52.9	37.1	8.7	110.1
Ba 119	28.8	4.2	33.8	6.7	85.6	106.1	82.6	68.8	49.7	10.6	94.0
Ba 308	28.6	4.6	32.2	6.2	85.4	95.6	83.4	63.6	38.0	7.8	86.3
Ba 525	28.7	5.0	34.5	6.7	85.3	99.1	73.9	70.0	49.3	9.8	95.1
Barut 2005	29.1	3.9	32.7	5.6	83.8	97.5	75.2	73.3	55.2	11.9	104.8
Blightmaster	26.5	4.8	29.9	6.9	84.7	79.8	72.3	62.8	46.3	10.2	100.0

(Cont. on the next page)

Table 2.2. (cont.)

Cabu/Cs2-1-83	29.2	4.5	31.7	6.5	84.1	90.3	84.3	60.6	50.2	12.4	88.5
Candia	30.2	4.3	37.2	6.1	86.8	122.6	67.3	73.9	59.4	10.4	84.8
Carmen	30.3	4.3	37.2	5.7	85.9	119.1	65.8	64.8	47.2	10.5	98.3
Caroline											105.7
Queen	27.9	5.1	30.2	6.2	84.3	79.8	67.0	64.0	54.0	12.5	
Celia	31.3	4.7	40.8	5.6	87.2	133.6	68.0	60.4	59.0	11.6	87.8
Claudia	30.8	4.3	37.2	5.7	85.7	118.8	62.9	66.2	48.5	12.1	96.8
Coker 208	28.6	4.7	32.3	5.9	85.5	95.3	67.4	64.8	40.7	9.4	96.7
Corona	28.0	4.1	30.2	7.0	83.9	86.3	89.3	62.3	42.3	12.9	85.9
DAK 66/3	27.7	5.1	34.4	6.0	83.9	88.5	76.4	68.1	42.5	11.0	99.8
Delcerro	31.1	4.0	41.4	6.3	86.2	137.1	81.6	57.5	55.1	11.4	99.3
Delcerro Ms 30	33.2	3.9	41.3	5.3	86.1	141.1	64.7	53.8	54.0	10.8	103.3
Delta											102.6
Diamond	30.5	4.5	38.0	6.1	85.9	120.1	63.5	70.2	48.1	12.2	
Delta Opal	30.0	4.7	34.4	6.2	85.6	104.8	64.2	70.0	58.9	11.4	101.5
DP 388	29.6	4.5	34.4	6.6	84.9	102.3	78.7	63.3	58.0	11.3	91.7
DPL 6	31.4	4.4	37.1	5.7	86.2	121.3	64.6	64.3	43.4	10.8	105.2
DPL 20	28.9	4.5	34.5	7.1	86.0	107.3	75.3	65.7	35.1	8.3	88.5
DPL 5415	29.6	4.6	32.4	6.6	85.0	96.3	74.1	64.1	36.7	11.0	101.2

(Cont. on the next page)

Table 2.2. (cont.)

DPL 882	30.6	4.2	38.4	6.2	85.7	123.3	67.5	57.9	41.4	9.8	114.0
DPL 883	31.8	3.9	37.7	5.9	86.0	127.8	65.3	59.3	40.6	9.6	107.5
DPL 886	30.5	4.6	33.2	5.7	84.4	97.3	67.2	60.0	46.8	13.2	108.2
DPL 90	29.4	4.3	34.0	6.2	84.3	99.8	80.3	68.9	49.1	10.5	93.0
DPL C 37 Prima	27.4	5.1	29.9	7.0	84.8	79.3	75.9	63.1	42.7	9.7	103.0
DPL SR 383	28.3	5.0	34.8	6.0	85.3	98.8	70.6	55.2	49.2	10.8	87.2
Elsa	30.8	4.6	37.5	6.1	86.5	120.6	70.7	74.4	46.9	12.5	98.6
Ersan 92	28.5	5.0	36.0	6.2	86.5	108.0	75.9	58.3	40.4	10.2	107.1
Eva	30.3	4.6	36.6	6.7	86.1	115.1	59.1	58.8	51.6	11.6	118.1
Flora	29.2	4.7	34.0	5.6	85.1	100.1	77.3	63.8	40.8	10.0	86.6
GC 262	29.9	4.6	34.0	6.1	85.0	101.3	69.8	62.8	47.2	10.8	103.7
GC 555	31.3	4.4	37.1	6.1	86.9	124.3	69.6	61.8	46.7	11.8	103.7
Gloria	30.2	4.7	36.9	6.4	85.8	114.1	81.2	69.8	43.9	12.1	97.6
GSA 78	29.2	4.5	31.9	6.6	83.7	89.3	71.2	62.4	42.9	10.0	86.5
GSN 12	29.7	4.3	35.2	6.1	85.7	111.5	70.4	65.1	47.7	11.9	98.9
GW Teks	30.4	4.7	37.0	6.1	85.8	114.1	63.2	59.5	48.7	11.5	102.3
Julia	29.6	4.5	36.0	5.4	84.7	106.6	72.3	63.2	60.7	12.1	88.1
Lachata	28.6	4.4	33.2	5.9	84.7	97.3	86.3	60.3	35.8	10.4	95.9

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Table 2.2. (cont.)

Lankart 57	29.5	4.7	34.1	6.5	86.1	106.3	74.2	65.4	56.1	11.4	88.2
Mcnair 220	29.5	4.4	34.6	5.9	85.2	105.3	70.9	62.7	58.3	11.2	95.5
Menderes 2005	30.9	4.4	38.2	5.9	84.7	116.5	77.3	65.7	38.5	8.3	104.8
Ms 30/1	30.0	4.4	32.7	6.9	83.4	92.0	62.6	65.6	47.9	14.3	109.6
N 727 CC	26.8	4.5	32.2	6.3	83.4	84.3	89.5	72.1	49.3	12.9	88.9
Napa 122	30.5	4.6	33.7	6.4	87.3	113.0	79.2	70.1	46.7	10.1	96.1
Nata	28.9	4.4	37.7	5.4	83.7	105.8	80.8	57.4	39.1	13.4	109.4
Nazilli M503/2	30.0	3.9	30.1	7.4	84.6	96.0	71.4	79.1	60.8	21.3	117.6
Nazill 143	28.4	4.7	33.2	6.3	84.3	92.5	70.8	73.0	42.4	10.3	114.6
Nazilli 84 S	29.0	4.6	33.2	6.6	84.9	97.5	81.2	67.2	50.7	11.3	104.6
Nazilli 87	28.9	4.3	35.3	6.5	86.1	111.5	72.5	65.3	42.1	6.9	105.3
Nazilli M39	29.4	4.6	33.7	6.2	85.5	102.0	66.8	65.6	49.7	11.6	115.3
Nazilli M503/1	31.2	3.5	35.5	6.8	85.8	122.5	69.8	75.8	63.2	14.9	118.6
NGF 63	29.4	4.6	33.5	6.3	85.7	102.5	73.4	68.4	57.1	12.3	112.3
Niab 111	31.9	3.8	32.6	6.9	84.9	107.6	79.5	71.7	58.5	11.3	92.3
Niab 999	30.3	4.4	39.2	5.4	84.7	118.1	69.4	63.7	48.6	8.7	87.8
Nieves	30.0	4.0	34.6	5.4	84.9	108.3	83.9	71.0	54.6	13.8	96.1
Np Ege 2009	30.0	4.8	35.9	6.8	87.7	118.0	76.9	76.5	55.7	12.3	116.1

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Table 2.2. (cont.)

Np Ozbek 100	26.8	4.7	33.6	6.6	86.6	101.0	86.1	77.5	52.8	13.3	100.8
Paymaster 404	27.9	4.4	34.4	6.1	85.0	100.8	78.5	62.1	49.1	11.5	94.0
Pg 2018	29.2	4.6	34.6	7.1	85.3	103.6	78.0	67.5	48.8	9.7	93.1
Rex 1	28.7	4.4	33.1	5.8	85.7	101.8	81.3	55.1	48.9	8.2	95.1
Sj V Visalia											89.6
Elmer	31.2	4.3	38.4	5.7	85.7	123.3	71.9	68.2	40.0	11.9	
S 9	30.7	4.0	34.0	6.0	84.6	107.1	85.0	59.9	42.5	7.4	84.6
Sahel 1	27.7	4.5	31.3	6.3	84.5	88.3	79.5	52.1	31.5	8.4	97.4
Samarkant Uzbek	27.1	5.1	32.1	6.7	85.0	86.0	78.7	59.6	52.5	11.3	104.6
Somon	29.2	4.5	34.9	6.1	85.6	106.3	67.0	52.0	29.4	9.4	101.1
Sayar 314	28.9	4.6	33.8	6.2	84.3	96.5	70.1	65.2	40.5	9.9	107.6
Sealand 542	32.4	3.9	33.8	5.7	83.7	105.8	69.0	59.2	54.8	9.8	109.0
Semu SS/G	27.4	4.2	31.5	6.6	84.2	89.3	74.6	50.7	41.2	10.6	109.9
SG 1001	29.3	4.1	36.3	6.0	84.0	107.3	87.2	60.7	47.7	10.2	93.6
SG 125	29.1	4.8	33.8	6.7	87.3	108.8	88.2	70.9	50.9	13.7	87.6
Sicala 3/2	30.0	4.3	35.8	6.6	87.1	120.3	72.1	57.7	55.8	13.4	112.1
Sicala 33	30.7	4.1	34.2	5.6	86.0	113.3	81.7	62.9	49.5	13.1	103.1
Sindos 80	29.6	4.4	32.4	6.3	83.6	91.6	74.7	62.7	47.8	11.1	100.1

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Table 2.2. (cont.)

Sj U 86	29.9	4.2	36.3	6.3	85.6	114.6	57.0	67.9	42.6	11.5	105.6
Stoneville 213	28.8	4.2	33.7	6.2	86.0	106.3	80.7	61.8	52.1	10.5	91.6
Stoneville 453	28.8	4.5	33.0	5.5	84.9	96.8	84.4	63.7	46.5	13.8	100.6
Stoneville 8751	28.8	4.7	36.6	6.4	86.0	110.8	84.9	60.3	30.0	8.7	84.1
Sahin 2000	29.6	3.8	30.5	7.2	83.9	93.3	80.1	70.5	59.3	12.8	111.6
Tomcot 22	30.7	4.7	37.9	5.7	85.0	114.1	56.0	62.5	49.4	12.8	103.3
Tomcot Cabcs	29.2	4.3	32.4	5.9	83.2	89.8	84.7	57.6	38.6	10.0	90.9
Tomcot Sphinx	30.7	4.5	36.1	6.4	86.2	116.1	69.3	65.4	49.5	9.8	87.3
Taskent 1	27.7	4.3	33.9	6.2	85.4	102.0	83.2	68.4	52.6	9.9	96.3
Taskent Uzbek	29.3	3.8	35.2	5.7	84.8	111.5	84.0	62.5	40.8	10.1	112.6
Taskent 6	29.4	4.4	34.0	6.4	85.3	104.5	90.1	65.2	58.3	12.4	101.3
TKY3304 GS316	30.0	4.1	39.8	6.1	87.0	132.8	78.1	50.2	26.5	8.2	93.6
TKY 9309	30.4	4.3	37.9	5.5	86.1	122.3	69.2	59.5	41.6	11.7	104.6
TKY 9409	31.7	4.2	38.8	5.5	86.4	129.3	69.9	49.7	38.0	9.8	99.9
Togo	30.7	4.7	36.4	5.6	84.5	106.8	61.0	56.4	48.6	10.9	112.9
Vulcano	29.0	4.5	33.7	5.9	83.8	94.3	89.9	59.5	33.6	10.0	83.6

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Table 2.2. (cont.)

Zeta 2	30.1	4.2	38.1	5.7	86.4	124.6	74.8	60.4	30.7	9.7	110.8
Average	29.6	4.4	34.8	6.2	85.3	106.4	74.8	63.7	46.8	11.0	100.0
SD	1.3	0.3	2.6	0.5	1.0	13.2	8.2	6.1	8.0	1.9	9.4
LSD	1.56	0.72	4.22	0.67	2.37	23	21.91	8.96	18.53	4.63	24.48
CV	2.56	8.12	5.91	5.41	1.36	10.46	14.39	6.81	19.1	19.28	11.91

Table 2.3. Morphological results for fiber quality and plant structure features under water-limited conditions

Water-limited conditions	Fiber length (mm)	Fiber fineness (mic)	Fiber strength (g/teks)	Fiber elasticity (%)	Fiber uniformity (%)	Spinning conversion index	Earliness (%)	1st PBR (%)	2nd PBR (%)	Total boll number per plant (n)	Plant height (cm)
152F	27.0	4.8	31.8	6.6	85.0	87.9	85.1	54.9	34.5	8.0	92.6
Acala 5	29.5	4.2	39.2	5.6	86.4	126.0	85.2	59.4	51.4	7.9	86.8
Acala 1517	28.1	4.5	35.0	5.8	84.9	101.5	81.0	55.4	50.6	5.9	73.8
Aleppo 1	27.9	4.1	32.0	6.2	81.8	81.4	87.0	57.9	41.2	7.7	85.4

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Table 2.3. (cont.)

Auburn M	26.3	4.3	30.1	6.5	83.4	79.0	82.0	58.6	48.6	8.0	64.8
Ayhan 107	29.1	4.0	33.8	5.8	85.7	108.9	96.5	70.7	52.9	10.7	75.4
Az 31	30.2	4.5	36.5	5.4	83.0	100.8	80.6	57.3	29.4	7.1	90.9
Ba 119	27.5	5.0	34.1	6.7	84.4	90.5	86.9	64.7	46.3	8.3	70.7
Ba 308	27.9	5.1	31.1	5.9	84.4	82.3	93.0	67.2	43.4	6.4	77.1
Ba 525	27.9	5.3	32.6	6.5	84.1	83.3	89.8	60.4	45.6	9.4	81.1
Barut 2005	29.1	4.3	32.8	5.8	86.0	104.4	89.6	69.6	44.7	10.0	82.9
Blightmaster	26.4	4.9	29.8	6.3	83.3	72.5	89.2	56.8	48.5	6.9	76.1
Cabu/Cs2-1-83	27.4	4.6	31.6	6.3	83.5	83.0	87.5	51.5	42.0	6.2	72.8
Candia	28.3	5.1	36.1	5.8	84.6	98.3	85.4	73.7	45.9	6.9	73.6
Carmen	29.2	4.9	37.6	5.6	85.8	111.9	82.0	60.4	40.5	8.6	78.7
Caroline Queen	26.2	5.1	29.6	5.8	83.6	70.5	92.0	58.3	48.1	6.2	81.8
Celia	28.6	5.0	36.5	5.1	86.2	107.8	89.0	62.4	47.3	6.9	68.4
Claudia	28.8	5.1	37.5	5.8	85.3	106.8	84.7	66.9	45.6	8.3	71.2
Coker 208	26.0	4.9	29.7	6.0	82.5	68.0	87.5	62.0	51.6	7.6	74.1
Corona	27.4	5.3	31.8	6.6	83.7	77.8	80.5	58.1	33.4	6.8	64.0
DAK 66/3	28.2	5.4	34.2	5.6	85.0	91.9	85.1	65.4	45.7	10.4	84.1

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Table 2.3. (cont.)

Delcerro	29.6	4.9	38.2	5.8	83.6	104.8	92.6	63.0	27.1	6.1	86.4
Delcerro Ms 30	32.4	4.5	43.0	4.9	85.7	137.8	84.9	60.8	41.3	7.7	89.9
Delta Diamond	28.6	5.2	34.4	6.0	84.4	91.3	86.2	64.1	49.4	9.4	77.6
Delta Opal	27.8	5.3	34.6	5.6	84.3	89.5	80.9	61.0	56.9	9.1	70.1
DP 388	27.2	5.5	34.9	6.4	85.8	94.5	91.3	63.7	52.3	6.9	62.8
DPL 6	28.8	4.9	32.6	5.8	84.9	93.0	82.5	64.4	47.2	6.0	72.1
DPL 20	28.2	4.7	30.4	6.7	83.7	81.0	94.0	63.7	51.1	6.5	61.8
DPL 5415	27.9	4.9	31.6	6.0	84.7	87.0	91.1	63.3	42.5	7.8	62.3
DPL 882	29.5	4.5	37.6	5.7	84.9	112.0	83.4	59.9	49.7	5.9	74.8
DPL 883	30.2	4.5	37.2	5.6	84.6	110.5	79.7	50.5	42.8	5.7	73.1
DPL 886	29.6	4.5	36.0	5.5	84.1	104.0	89.4	62.9	48.9	8.6	73.6
DPL 90	28.0	5.2	31.8	6.2	84.0	81.5	92.1	58.1	51.6	7.5	63.6
DPL C 37 Prima	25.8	4.9	29.6	6.9	82.6	68.0	99.2	65.5	49.0	6.5	72.6
DPL SR 383	27.1	5.0	29.0	5.6	83.2	73.0	95.3	57.2	39.5	7.0	65.6
Elsa	28.7	5.2	35.4	5.8	84.9	96.8	95.6	61.6	37.2	7.8	81.4
Ersan 92	28.0	5.2	32.7	6.2	85.0	88.4	88.5	65.3	39.8	10.2	86.1
Eva	28.7	4.7	34.7	6.4	82.6	88.8	84.9	57.6	38.9	7.3	86.9

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Table 2.3. (cont.)

Flora	28.4	5.2	37.1	5.4	84.4	99.8	93.3	56.2	39.6	6.7	77.9
GC 262	27.7	4.6	34.7	6.3	85.1	99.5	95.5	64.9	37.9	7.1	68.6
GC 555	28.6	4.4	34.0	6.0	85.7	104.5	86.0	62.9	53.1	7.5	71.1
Gloria	27.8	5.2	36.2	6.3	86.2	103.8	95.7	68.9	36.4	7.2	77.6
GSA 78	28.2	4.4	32.9	5.9	82.6	86.0	90.4	55.9	41.7	6.8	68.6
GSN 12	28.4	5.1	35.4	5.8	85.0	98.0	84.7	62.5	43.0	8.6	77.2
GW Teks	29.7	4.4	39.4	6.1	85.4	120.8	89.5	62.7	43.7	6.3	73.1
Julia	27.9	5.1	34.3	5.2	84.8	92.8	94.7	61.0	47.6	7.3	71.1
Lachata	27.1	5.4	30.7	6.1	83.6	72.8	81.7	65.7	45.2	8.9	75.8
Lankart 57	28.1	4.7	35.0	5.7	84.7	99.0	88.6	61.1	42.6	6.9	76.6
Mcnair 220	27.9	5.0	32.9	5.7	84.4	88.0	94.4	57.7	47.0	7.9	72.1
Menderes 2005	31.1	4.3	38.0	5.8	84.0	113.4	93.5	58.1	40.1	8.0	84.4
Ms 30/1	29.1	4.8	31.0	6.9	85.1	90.9	74.5	60.9	44.6	12.1	86.4
N 727 CC	26.2	4.9	30.8	6.4	82.6	71.8	91.9	64.4	48.6	8.9	71.0
Napa 122	30.1	5.2	34.8	6.5	85.9	103.9	96.8	71.8	56.2	10.3	79.1
Nata	28.6	5.3	36.9	5.2	84.4	98.3	88.4	64.3	38.1	9.6	73.5
Nazilli M503/2	28.8	3.7	31.8	6.7	83.7	95.9	90.1	71.8	44.2	9.9	88.6
Nazill 143	27.5	5.1	31.5	6.1	84.2	81.4	89.9	63.8	46.7	9.1	81.4

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Table 2.3. (cont.)

Nazilli 84 S	27.6	5.2	35.1	5.8	84.8	93.9	94.7	67.4	37.2	9.3	79.6
Nazilli 87	27.9	5.1	32.9	5.8	84.9	89.4	81.3	62.0	41.0	8.2	85.4
Nazilli M39	27.0	5.1	29.5	6.8	83.9	72.9	81.6	66.2	38.2	9.2	93.9
Nazilli M503/1	28.4	3.8	30.0	7.1	84.2	90.9	89.4	66.6	38.7	10.5	87.1
NGF 63	30.3	4.9	35.4	5.7	86.3	110.9	88.3	64.0	45.3	9.9	82.9
Niab 111	29.4	4.5	33.8	7.5	84.2	97.3	94.0	73.5	46.9	8.6	73.6
Niab 999	27.8	5.1	32.8	5.7	83.2	81.3	89.2	67.2	44.4	6.0	70.6
Nieves	29.6	4.6	39.6	5.2	83.9	112.3	89.0	56.7	36.7	7.9	80.5
Np Ege 2009	28.1	5.4	34.1	6.5	84.5	89.9	89.5	68.5	45.3	10.4	93.9
Np Ozbek 100	25.5	4.9	28.2	6.6	82.8	63.4	76.5	63.0	38.9	8.7	80.6
Paymaster 404	26.6	4.7	29.9	6.3	84.2	78.0	95.6	59.8	41.2	6.6	66.8
Pg 2018	26.1	5.4	32.1	6.5	83.7	75.3	92.6	60.1	39.4	7.7	81.1
Rex 1	26.5	4.9	30.2	5.8	83.8	75.8	87.6	60.0	32.5	7.2	81.8
Sj V V. Elmer	29.2	4.9	39.2	6.0	84.6	110.8	84.8	69.5	40.7	7.7	79.8
S 9	28.2	4.7	31.0	6.1	81.4	71.8	89.7	67.2	36.8	8.1	78.6
Sahel 1	27.6	5.0	33.9	6.4	84.2	89.8	83.3	62.6	33.4	7.9	82.8
Samarkant Uzbek	27.5	5.3	33.9	6.7	84.7	89.4	83.2	64.2	38.6	9.2	88.4

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Table 2.3. (cont.)

Somon	28.1	5.0	34.4	5.9	84.6	93.8	83.5	49.7	41.3	7.3	89.0
Sayar 314	29.0	4.9	33.4	5.5	83.8	90.4	81.8	64.3	46.1	10.1	91.9
Sealand 542	29.5	4.5	35.1	6.3	84.3	101.5	85.2	57.2	59.5	7.8	78.1
Semu SS/G	26.7	5.1	30.9	6.3	84.5	79.8	90.4	54.2	44.5	9.2	77.0
SG 1001	26.8	5.2	32.6	5.9	83.7	79.8	89.3	65.9	36.3	7.5	81.8
SG 125	28.0	5.4	32.4	6.9	86.0	90.3	90.1	65.0	36.2	8.4	83.5
Sicala 3/2	29.3	4.5	39.7	7.2	85.9	122.8	83.7	60.8	47.7	9.8	86.0
Sicala 33	30.1	4.8	35.5	5.7	87.4	115.3	88.8	61.2	43.3	8.1	79.3
Sindos 80	28.2	4.6	31.3	5.6	84.0	86.3	91.9	57.9	32.9	9.7	86.4
Sj U 86	29.2	4.7	35.8	6.2	83.6	97.3	84.7	64.2	38.7	7.6	87.4
Stoneville 213	27.1	4.7	31.9	6.3	84.1	85.3	87.4	62.9	54.7	6.7	73.0
Stoneville 453	27.7	4.6	30.3	6.0	83.5	79.8	89.8	69.9	43.3	10.1	87.8
Stoneville 8751	28.8	4.5	34.8	5.8	84.6	101.3	91.2	59.9	38.0	7.0	72.0
Sahin 2000	28.0	4.0	28.9	6.9	82.9	79.4	88.9	67.4	51.1	10.3	87.0
Tomcot 22	28.6	5.1	36.3	5.5	84.5	98.8	89.1	60.5	44.2	8.8	81.6
Tomcot Cabcs	28.1	4.8	33.2	6.3	84.6	92.3	90.6	61.0	39.4	7.6	75.0
Tomcot Sphinx	27.5	4.6	30.4	5.8	82.6	74.8	92.3	61.6	35.3	6.0	80.9

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Table 2.3. (cont.)

Taskent Uzbek	26.5	4.6	29.5	6.2	82.8	71.9	86.6	59.5	31.4	7.7	78.6
Taskent 1	28.6	4.3	32.2	5.6	84.2	92.9	76.5	58.1	35.5	7.9	90.4
Taskent 6	27.6	4.5	30.7	6.0	85.2	89.4	86.5	57.8	35.1	9.5	82.1
TKY3304 GS316	28.8	4.7	38.9	6.3	86.8	122.3	86.5	63.3	30.3	6.8	74.5
TKY 9309	29.0	5.1	39.8	5.5	86.3	117.8	82.4	54.4	34.3	6.6	85.5
TKY 9409	29.3	4.7	37.8	5.9	85.6	113.8	80.5	58.8	41.6	5.8	76.3
Togo	28.8	5.3	37.0	5.5	84.5	99.8	83.5	55.9	44.2	8.1	86.5
Vulcano	28.3	5.3	35.0	6.1	83.7	89.3	75.4	62.1	41.5	7.1	65.5
Zeta 2	29.2	4.8	37.0	5.6	85.1	107.3	76.1	62.4	41.6	8.1	90.4
Average	28.2	4.8	33.8	6.0	84.4	93.2	87.6	62.1	42.8	8.0	78.5
SD	1.2	0.4	3.1	0.5	1.1	14.7	5.2	4.8	6.4	1.4	7.8
LSD	1.91	0.57	3.95	0.51	2.46	22.53	16.46	12.38	16.72	4.18	11.21
CV	3.29	5.93	5.67	4.3	1.42	11.65	9.21	9.67	18.91	25.09	6.99

Table 2.4. Variance analysis of the data at ADU and OAE under well-watered and water-limited conditions

	FL (mm)	FF (mic)	FS (g/teks)	FE (elg)	FU (uni)	SCI (sci)	EAR (%)	1. p.b.r. (%)	2.p.b.r. (%)	TBN (n)	PH (cm)
Well-watered											
Location	2.4	0.1	7.4	0.7*	11.0*	888.9*	1014.6*	208.1*	9304.6*	453.1*	44.0
Replicate	7.1*	0.0	11.2	0.5	2.7	303.3	351.9	341.4*	567.4	16.3	151.0
Genotype	285.0*	19.9	1137.6*	41.8*	192.0	30688.5*	11641.8	6079.7*	12350.3	6207.0*	14836.9
Location x Genotype	114.7*	6.9	404.8	13.1	164.2	13624.0	11315.6	2932.0	6839.3	6184.2*	15673.9
Error	15.7	3.4	115.0	3.03	36.1	3401.2	3086.5	517.7	2210.3	138.3	3850.1
Water-limited											
Location	1.2	0.0	15.3	0.4*	2.6	467.4	1562.6*	9.4	7991.3*	33.6*	558.2*
Replicate	0.7	0.2	8.7	0.3	4.4	249.4	757.58*	215.0	42.7	29.8	59.9
Genotype	280.7*	27.2*	1658.0*	45.0*	239.3	43121.1*	5292.3	4127.3	6969.2	271.8	7944.0*
Location x Genotype	84.3	6.8	386.3	9.7	152.6	14415.4	9222.2	2200.0	11952.7*	357.6	4724.9
Error	23.5	2.2	100.6	1.8	39.0	3266.1	1744.7	986.8	1801.2	113.0	809.5

***** *significant at 0.05 level*

Fiber length (FL) ranged from 26.5 mm to 33.2 mm with a mean value of 29.6 mm under the well-watered treatment and from 25.5 mm to 32.4 mm with a mean value of 28.2 mm under the water stress treatment. FL had a statistically significant ($p \leq 0.05$) decrease ($\bar{x}$= -5%) in the majority of the panel (91%) under water stress. In contrast, fiber fineness (FF) significantly increased ($\bar{x}$= +10%) in 86% of the panel and decreased in 12% of the panel under water-limited conditions. FF ranged from 3.5 mic to 5.1 mic with a mean value of 4.4 mic under the well-watered regime and from 3.7 mic to 5.5 mic with a mean value of 4.8 mic under the water-limited regime. Fiber strength (FS) ranged from 29.7 g teks^{-1} to 41.4 g teks^{-1} (with a mean of 34.8 g teks^{-1}) under well-watered conditions and from 28.2 g teks $^{-1}$ to 43 g teks^{-1} (with a mean value of 33.8 g teks^{-1}) under water-limited conditions. Under water stress, FS decreased significantly ($\bar{x}$= -3%) in 63% of the panel however this trait increased or remained constant in 37% of the panel. Fiber elasticity (FE) of the genotypes ranged from 5.3% to 7.4% under the well-watered regime and from 4.9% to 7.5% under the water-limited regime with mean values of 6.2% and 6.0%, respectively. FE decreased significantly ($\bar{x}$= -3%) in 62% of the genotypes and increased or remained constant in the rest of the genotypes under limited irrigation. Fiber uniformity (FU) ranged from 83.2% to 87.7% under well-watered conditions and from 81.4% to 87.4% under water-limited conditions with mean values of 85.3% and 84.4%, respectively. While FU decreased significantly ($\bar{x}$= -1%) in 65% of the panel under water stress, it increased significantly or remained constant in 13% and 22% of the panel, respectively. Spinning conversion index (SCI) ranged from 79.3 to 141.1 with a mean value of 106.4 under the well-watered regime and from 63.4 to 137.8 with a mean value of 93.2 under the water-stress regime. SCI decreased significantly ($\bar{x}$= -13%) in 85% of the genotypes and increased significantly in 13% of the panel under limited irrigation.

For agronomic traits, earliness (EAR) of the genotypes increased significantly ($\bar{x}$= +17%) in the majority of the panel (93%) under water-limited conditions and ranged from 56.0% to 90.2% with a mean value of 74.8% under well-watered conditions and from 74.5% to 99.2% with a mean value of 87.6% under water-limited conditions. First position boll retention (1st PBR) ranged from 49.7% to 79.1% (with a mean value of 63.7%) under well-watered conditions and from 49.7% to 73.7% (with a mean value of 62.1%) under water-limited conditions. Water stress decreased this trait significantly ($\bar{x}$= -3%) in 60% of the panel.

Second position boll retention (2nd PBR) ranged from 26.5% to 63.2% under the well-watered regime and from 27.1% to 59.5% under water-limited conditions with mean values of 46.8% and 42.8%, respectively. Like 1st PBR, this trait decreased significantly ($\bar{x}$= -9%) in the majority (65%) of the genotypes under water stress. Total boll number (TBN) per plant ranged from 6.9 to 21.3 (with a mean of 11.0) under well-watered conditions and from 5.7 to 12.1 (with a mean of 8.0) under the water-limited regimes. This trait significantly decreased ($\bar{x}$= -27%) in 94% of the panel under water stress. Plant height (PH) ranged from 83.6 to 122.3 cm (with a mean value of 100.0 cm) under well-watered conditions and from 61.8 to 93.9 cm (with a mean value of 78.5 cm) under water-limited conditions. As expected, water stress led to significantly decreased PH ($\bar{x}$= -21%) in all genotypes.

Significant correlations were detected between fiber traits under both watering regimes ($p < 0.05$ and $p < 0.01$) (Table 2.5 and Table 2.6). FS was positively correlated with FU, FL, SCI under both treatments. In contrast, FS was negatively correlated with EAR, FE and 1st PBR under well-watered conditions but only with FE under water-limited conditions. FE showed negative correlation with FL and SCI under both watering treatments. FE was positively correlated with 1st PBR and TBN under water-limited conditions and with only 1st PBR under well-watered conditions. While FU was positively correlated with both FL and SCI, FF was negatively correlated with both FL and SCI under both watering treatments. For boll traits, TBN, 1st PBR and 2nd PBR were positively correlated with each other under well-watered conditions. Under well-watered conditions, PH correlated positively with TBN and negatively with EAR. However, under water-limited conditions, PH correlated positively with FL and TBN; and negatively with EAR and 2nd PBR.

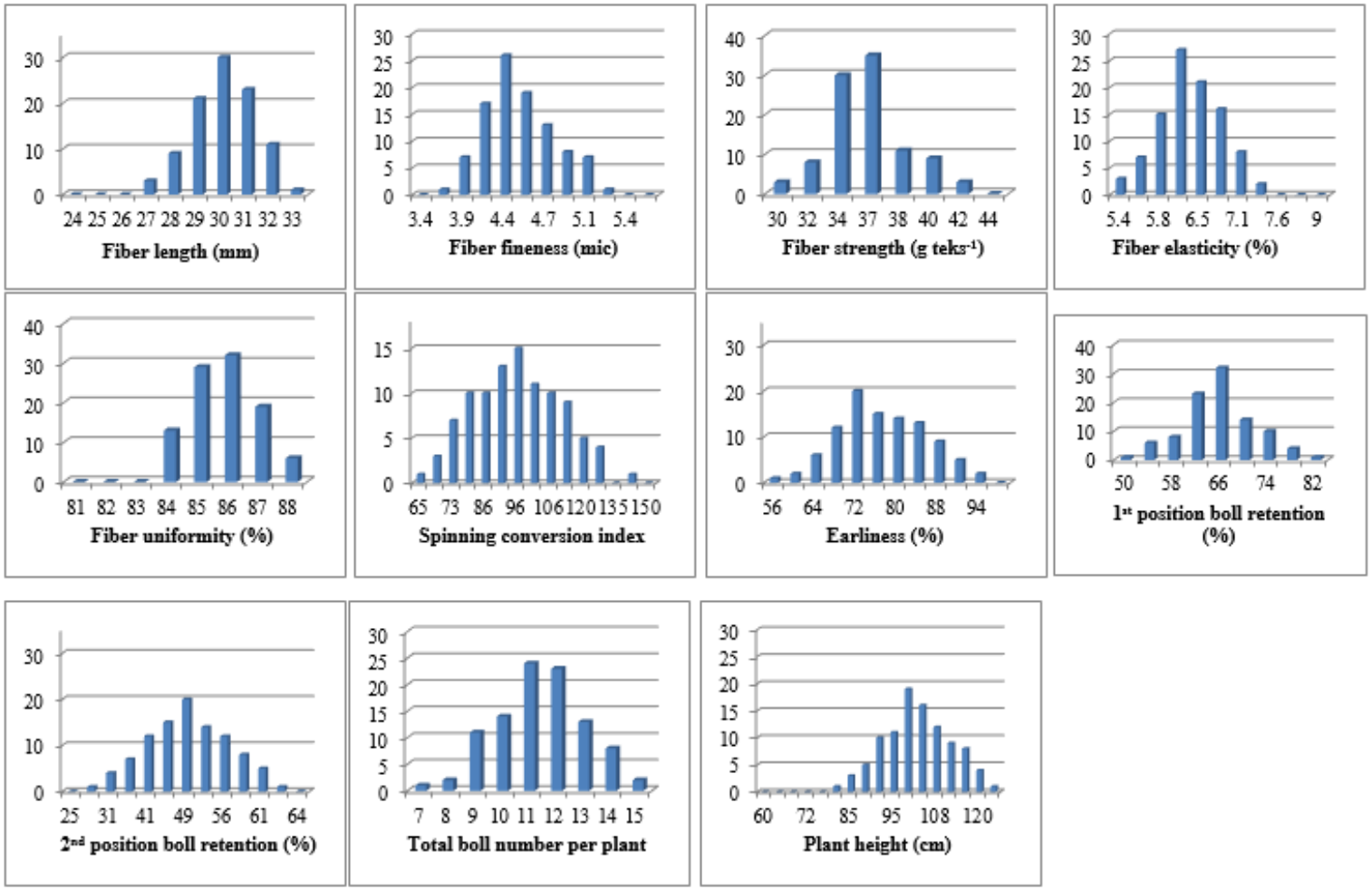

Figure 2.5 Phenotype distribution for eleven traits under well-watered conditions.

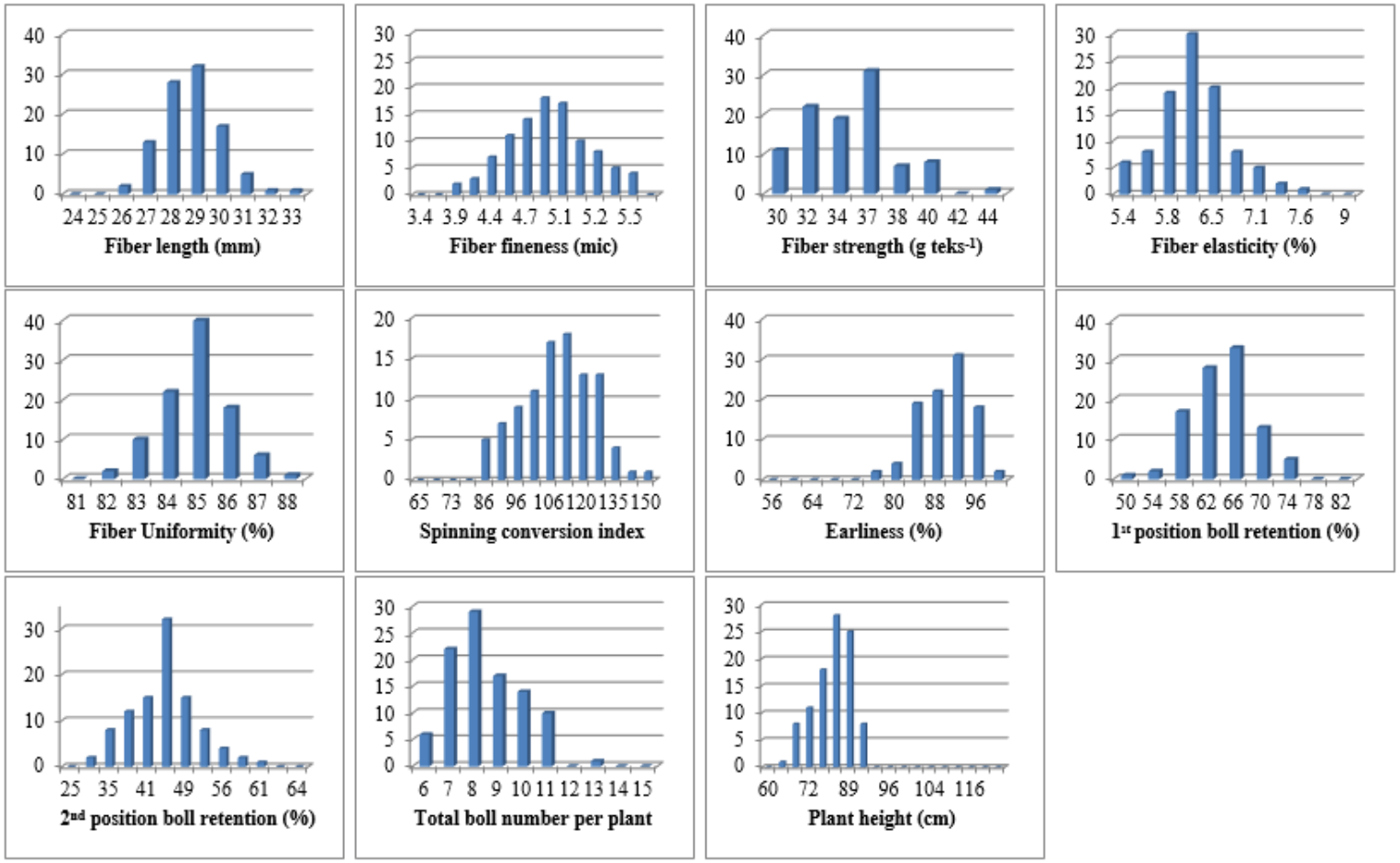

Figure 2.6 Phenotype distribution for eleven traits under water-limited conditions.

Table 2.5. Correlation coefficients between the traits under well-watered conditions

Trait	FL (mm)	FF (mic)	FS (g/teks)	FE (%)	FU (%)	SCI	EAR (%)	1st PBR (%)	2nd PBR (%)	TBN	PH (cm)
FL (mm)	1	-0.46**	0.66**	-0.37**	0.31**	0.78**	-0.47**	-0.08	0.19	0.09	0.16
FF (mic)		1	-0.16	0.14	0.12	-0.36**	-0.07	0.05	-0.1	-0.06	-0.16
FS (g/teks)			1	-0.53**	0.52**	0.92**	-0.37**	-0.21*	-0.04	-0.12	0.05
FE (%)				1	0	-0.40**	0.17	0.34**	0.14	0.17	0.07
FU (%)					1	0.69**	-0.18	0.05	0.04	-0.06	0.04
SCI						1	-0.34**	-0.12	0.05	-0.06	0.12
EAR (%)							1	0.1	-0.14	-0.1	-0.39**
1st PBR (%)								1	0.68**	0.42**	0
2nd PBR (%)									1	0.55**	0.08
TBN										1	0.26**
PH (cm)											1

** Significant correlation with the p value of 0.01.

* Significant correlation with the p value of 0.05.

Table 2.6. Correlation coefficients between the traits under water-limited conditions

Trait	FL (mm)	FF (mic)	FS (g/teks)	FE (%)	FU (%)	SCI	EAR (%)	1st PBR (%)	2nd PBR (%)	TBN	PH (cm)
FL (mm)	1	-0.31**	0.76**	-0.36**	0.46**	0.85**	-0.14	0.03	0.02	0.08	0.29*
FF (mic)		1	0.01	-0.1	0.12	-0.24*	0	0.05	-0.06	-0.02	-0.13
FS(g/teks)			1	-0.45**	0.56**	0.94**	-0.16	-0.07	-0.06	-0.16	0.12
FE (%)				1	-0.17	-0.36**	0.06	0.28**	0.08	0.23*	0.01
FU (%)					1	0.73**	-0.06	0.09	0.1	0.13	0.04
SCI						1	-0.14	-0.02	0.01	-0.03	0.15
EAR (%)							1	0.26*	0.08	-0.05	-0.27**
1st PBR (%)								1	0.16	0.39**	0.02
2nd PBR (%)									1	0.13	-0.34**
TBN										1	0.44**
PH (cm)											1

** Significant correlation with the p value of 0.01.

* Significant correlation with the p value of 0.05.

2.3.2 Association Analysis for Fiber Traits and Plant Structure

We identified different sets of QTLs for each treatment in the two locations at a significance level of $p \leq 0.005$. At both locations, GLM detected a total of 57 and 58 marker-trait associations under well-watered and water limited conditions, respectively. MLM detected two and 23 associations under well-water and water-limited regimes, respectively (Table 2.7 and Table 2.8).

2.3.2.1. Well-Watered Conditions

Under well-watered conditions, association analysis detected significant marker loci linked to seven of eleven traits; FL, FE, SCI, EAR,1st PBR, TBN and PH. No significant association was identified for four traits; FF, FS, FU and 2nd PBR. GLM and MLM analyses identified 34 and two marker-trait associations, respectively, at ADU. However, GLM detected 23 marker-trait associations at OAE. MLM did not identified any association at OAE ($p \leq 0.005$). Of identified marker loci, 40 were highly significant ($p < 0.001$) and the rest were suggestive ($0.001 < p < 0.005$) marker loci.

The total phenotypic variation explained (PVE, r^2) by the individual marker loci ranged from 9% to 27% at ADU and; from 9% to 15% at OAE, of which 47 were considered as major-effect loci (PVE > 10%). The most significant marker locus, BNL1151-198 was identified for PH ($p = 3 \times 10^{-8}$, $q \leq 0.05$) with the highest major-effect (27%).

Of the detected markers at ADU, two for EAR were supported by both GLM and MLM methods: DPL080 and DPL223. Moreover, three markers were detected in both locations (ADU and OAE) and considered as stable QTLs which were BNL3502 linked to FE and both of DPL088 and JESPR274 linked to1st PBR.

Moreover, some markers associated to more than one traits. For example, BNL1151 was linked to 1st PBR, TBN and PH. Similarly, BNL3502 associated to FE, TBN and PH.

Table 2.7. Trait-associated marker loci identified by GLM and MLM models under well-watered conditions at two locations (ADU and OAE).

	ADU				OAE			
	GLM				GLM			
Trait	Marker Locus	r^2 (%)	p		Trait	Marker Locus	r^2 (%)	p
FL	$DOW070_{84}$	14	0.0007		FL	$BNL2882_{206}$	11	0.001
	$JESPR153_{145}$	12	0.0008			$BNL2882_{210}$	11	0.001
FE	$BNL3502_{200}$	14	0.0001			$DPL156_{285}$	12	0.001
SCI	$DPL156_{283}$	16	0.0001			$DPL659_{202}$	12	0.001
	$DPL156_{285}$	13	0.0005		FF	$BNL1231_{190}$	13	0.0006
EAR	$DPL080_{232}$	12	0.0002			$MUSS425_{287}$	11	0.0009
	$DPL223_{228}$	16	0.0001		FS	$DPL405_{281}$	11	0.001
1^{st} PBR	$BNL1151_{207}$	10	0.001			$DPL520_{281}$	11	0.001
	$BNL3594_{173}$	12	0.001			$DPL717_{289}$	15	0.0001
					FE	$BNL3502_{150}$	10	0.002
	$DPL088_{129}$	11	0.0007			$BNL3502_{200}$	11	0.001
		11	0.001			$DOW056_{245}$	12	0.001
	$JESPR157_{233}$	14	0.0001			$DPL112_{158}$	15	0.0001
	$JESPR157_{238}$	12	0.0004		SCI	$NAU2277_{170}$	9	0.002
	$JESPR274_{137}$	15	0.0001			$BNL1034_{240}$	11	0.002
TBN	$BNL1151_{207}$	9	0.003			$BNL2882_{210}$	12	0.0008
	$BNL3502_{200}$	10	0.002			$DPL405_{281}$	14	0.0002
	$DOW056_{245}$	10	0.002			$DPL659_{202}$	12	0.001
	$DPL136_{174}$	14	0.0003		1^{st} PBR	$DOW038_{325}$	14	0.0003
	$DPL520_{197}$	11	0.0009			$DPL088_{129}$	9	0.003
	$JESPR274_{137}$	11	0.002			$DPL176_{274}$	14	0.0003
	$MGHES22_{252}$	15	0.0003			$DPL247_{167}$	10	0.002
	$TMB1910_{212}$	12	0.0008			$JESPR274_{117}$	11	0.002
PH	$BNL1151_{198}$	27	3×10^{-8}					
	$BNL1151_{207}$	25	6×10^{-8}					
	$BNL2496_{121}$	10	0.0007					
	$BNL3502_{200}$	12	0.0001					
	$DPL100_{160}$	12	0.0003					
	$DPL100_{175}$	17	0.0001					
	$DPL181_{160}$	15	0.00002					
	$DPL193_{128}$	10	0.0007					
	$DPL247_{167}$	15	0.00001					
	$DPL307_{207}$	18	0.000002					

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Table 2.7. (cont.)

$JESPR274_{137}$	11	0.0006
$MGHES22_{252}$	12	0.0006
	MLM	
Trait	Marker Locus	p
EAR	$DPL080_{232}$	0.0002
	$DPL223_{228}$	0.0002

2.3.2.2. Water-Limited Conditions

Under water-limited conditions, GLM and MLM analysis separately identified 36 and 17 marker-trait associations, respectively, at ADU; and 22 and five associations, respectively, at OAE ($p \leq 0.005$). Of the identified marker loci, 32 were highly significant ($p < 0.001$) and 44 were major-effect loci (PVE > 10%). Of these loci, 15 and four marker loci at ADU and OAE, respectively, were supported by both GLM and MLM analysis. DPL405 associated with FS was detected at both locations. Moreover, BNL3502 with two alleles remained to be linked to FE by two methods at both locations. Therefore, these marker loci were considered stable QTLs (Table 2.8). No QTL was detected for FF, SCI and 2nd PBR under water-limited conditions. The most significant marker loci, BNL3502-200 ($p = 5 \times 10\text{-}9$, $q = 2.1 \times 10\text{-}6$), was detected linked to FE with the highest PVE value (31%) under water-limited conditions.

Table 2.8. Trait-associated marker loci identified by GLM and MLM models under water-limited regime at two locations (ADU and OAE).

	ADU					
	GLM				MLM	
Trait	Marker Locus	r^2 (%)	p	Trait	Marker Locus	p
FS	$BNL1521_{158}$	13	0.002	FL	$DOW070_{84}$	0.0004
	$DPL112_{159}$	10	0.002	FE	$BNL3502_{150}$	0.0008
	$DPL199_{244}$	11	0.002		$BNL3502_{200}$	0.00007

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Table 2.8. (cont.)

	$DPL247_{167}$	10	0.002	FU	$BNL0946_{273}$	0.001
	$DPL405_{281}$	10	0.002		$DPL199_{247}$	0.002
	$JESPR157_{238}$	10	0.002		$DPL354_{166}$	0.002
	$MUSS414_{295}$	10	0.002		$TMB0799_{358}$	0.001
FE	$BNL3502_{150}$	14	0.0001	EAR 1st	$DPL080_{232}$	0.0002
	$BNL3502_{200}$	24	5×10^{-7}	PBR	$BNL1673_{202}$	0.002
	$MGHES22_{240}$	13	0.001		$DPL156_{231}$	0.001
FU	$BNL0946_{273}$	12	0.001		$DPL168_{241}$	0.002
	$DPL199_{247}$	12	0.002		$GH537_{154}$	0.0001
	$DPL354_{166}$	12	0.002		$TMB1356_{183}$	0.002
	$TMB0799_{358}$	11	0.001	TBN	$DPL080_{238}$	0.0001
EAR 1st	$DPL080_{232}$	12	0.0003	PH	$BNL2496_{121}$	0.001
PBR	$BNL1667_{156}$	15	0.0004		$DPL674_{236}$	0.0007
	$BNL1673_{202}$	11	0.0008		$MGHES22_{185}$	0.0009
	$DPL088_{129}$	10	0.002			
	$DPL156_{231}$	13	0.0005			
	$DPL168_{241}$	11	0.001			
	$GH537_{154}$	16	0.0004			
	$TMB1356_{183}$	10	0.002			
	$BNL3594_{173}$	15	0.0003			
TBN	$BNL3989_{325}$	18	0.0001			
	$DPL080_{238}$	15	0.00009			
	$DPL354_{166}$	13	0.001			
	$DPL890_{166}$	15	0.0002			
	$GH107_{232}$	13	0.001			
	$TMB0083_{197}$	14	0.0007			
	$TMB0836_{190}$	12	0.0007			
	$BNL2496_{121}$	10	0.001			
PH	$DOW083_{227}$	10	0.0009			
	$DPL674_{236}$	21	0.00003			
	$DPL717_{400}$	9	0.002			
	$JESPR208_{127}$	9	0.003			
	$MGHES22_{185}$	20	0.00002			

OAE

	GLM				MLM	
Trait	Marker Locus	r^2 (%)	p	Trait	Marker Locus	p
FL	$DPL075_{203}$	16	0.00006	FL	$DPL75_{203}$	0.00009
FS	$BNL3502_{200}$	12	0.0006	FS	$TMB1427_{176}$	0.0004

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Table 2.8. (cont.)

	$DPL405_{281}$	12	0.0009	FE	$BNL3502_{150}$	6×10^{-6}
	$TMB1427_{176}$	16	0.00006		$BNL3502_{200}$	1.8×10^{-7}
FE	$BNL3502_{150}$	23	1×10^{-6}	EAR	$MUSS425_{287}$	0.0009
	$BNL3502_{200}$	31	5×10^{-9}			
TBN	$BNL1151_{207}$	14	0.0003			
	$BNL3502_{200}$	9	0.002			
	$DPL100_{175}$	12	0.0008			
	$DPL112_{159}$	14	0.0002			
	$JESPR014_{170}$	16	0.0002			
	$JESPR157_{238}$	13	0.0002			
	$JESPR274_{127}$	10	0.002			
	$MGHES22_{185}$	13	0.0008			
	$TMB2068_{146}$	11	0.002			
PH	$BNL0530_{192}$	9	0.001			
	$BNL1034_{315}$	11	0.0006			
	$BNL1151_{207}$	13	0.0003			
	$BNL1667_{156}$	14	0.0002			
	$DPL100_{175}$	11	0.0009			
	$DPL307_{207}$	11	0.0008			
	$TMB1295_{226}$	15	0.00009			

2.4. Discussion

In the present chapter, an Upland cotton panel was genotyped with 177 SSR markers to conduct genome-wide association analysis of eleven fiber traits under two water treatments in two different locations. Our study revealed which genotypes were the most stable, i.e., showed the least change in fiber quality under drought stress.

2.4.1. Phenotypic Evaluation

Nine of the traits decreased significantly ($p \leq 0.05$) in response to water-stress: fiber length (-5%), fiber strength (-3%), fiber elasticity (-3%), fiber uniformity (-1%), spinning conversion index (-13%), 1st (-3%) and 2nd (-9%) position boll retention, total boll number per plant (-27%) and plant height (-21%). However, fiber fineness and earliness significantly increased by +10% and +17%, respectively, under water-limited

conditions. A strong positive correlation was observed between fiber strength and spinning conversion index under both well-watered and water-stress conditions (r = 0.92 and r = 0.94, respectively). Thus, and not surprisingly, a high degree of fiber strength results in high spinning performance.

Although most of the traits decreased significantly under water stress, certain genotypes showed significantly increased or stable performance under drought conditions. The genotypes showing a slight increase in fiber length under water stress conditions were Samarkant Uzbek (+2%), DAK 66/3 (+2%) and NGF 63 (+3%). Changes in fiber fineness under water stress conditions were highest in Delcerro (+21%), Nata (+21%), Semu SS/G (+21%), Lachata (+23%), SG 1001 (+26%) and Corona (+30%). Fiber strength showed the greatest increase in Flora (+9%), Sicala 3/2 (+11%) and Nieves (+14%). Fiber elasticity showed the highest increase in Nazilli M39 (+9%), Sealand 542 (+9%), Sicala 3/2 (+10%) and Stoneville 453 (+10%). Fiber uniformity in the germplasm panel as a whole was not changed much by the watering regimes (-1%). However, several genotypes showed an increase (+2%) in FU under water-stress: MS-30/1, Acala 1517 and Barut 2005. The largest increases in spinning conversion index were seen in GW Teks (+6%), Ayhan 107 (+6%), DPL 886 (+7%), Barut 2005 (+7%) and NGF 63 (+8%). Earliness was most improved under water-stress in GW Teks (+42%), Eva (+44%), SJ U 86 (+49%) and Tomcot 22 (+59%). First and second position boll retention increased the most in TKY 9409 (+18%), Sahel 1 (+20%) and TKY 3304 GS316 (+26%) and; Zeta (+34%), Aleppo (+38%), Somon (+41%) and DPL 20 (+45%), respectively. The genotypes showing the highest increase in total boll number were S 9 (+9%), Nazilli 87 (+20%) and Ayhan 107 (+32%). In contrast, plant height was significantly decreased in all genotypes by water-stress. The genotypes with the least decrease were Flora (-10%), Tomcot Sphinx (-7%), S 9 (-7%) and SG 125 (-5%). Overall, Ayhan 107, Barut 2005, Gw Teks and S 9 were identified as promising genotypes based on morphological results. Since drought tends to be a limiting factor in cotton production, the identification of genotypes showing the least change under water-limited conditions may be useful for breeders hoping to improve fiber quality.

2.4.2. Association Analysis

Different sets of QTLs were associated with the eleven traits under each watering regime in each location (ADU and OAE) by GLM and MLM analyses. By comparing these sets, we determined which of the fiber trait associated-QTLs were stable in the two locations. Three of the QTLs identified under the well-watered regime and two of the water-limited QTLs were stable in both locations (ADU and OAE). The three stable QTL under well-watered conditions were BNL3502 (on D02) for FE; DPL088 (A06) and JESPR274 (on D09) for 1st PBR. The two stable QTL under water-limited conditions were DPL405 (on D02) for FS and BNL3502 (on D02) for FE (Table 2.9). The aforementioned QTLs showing notable stability in different locations may be useful in marker-assisted approaches toward cotton improvement.

Table 2.9 Traits and linked markers that were stable under both watering-regimes

Trait	**Marker**
1st PBR	DPL088
EAR	DPL080
FE	BNL3502
FL	DOW070
FS	DPL405
PH	BNL2496
	MGHES22
TBN	BNL3502
	BNL1151

Markers linked to these traits may be particularly useful for improving fiber quality under drought conditions since they could possess genetic adaptability against changing water availability conditions.

Genomic regions impacting more than one trait were revealed in this study. For example, BNL3502 was associated with FS, FE, TBN and PH. Similarly, BNL1151 was linked to 1st PBR, TBN and PH. The most impactful chromosome was D02 (carrying 15/130 QTLs. Jamshed et al. (2016) also reported D02 as rich in QTL clusters

associated with fiber quality traits. Taken together, the aforementioned results could indicate which regions of the genome control agricultural traits related to drought response in cotton. Those genomic regions could be potential targets in studies aimed to elucidate the mechanisms underlying drought tolerance/stress.

Individual markers with high PVE values on the traits could be useful for marker-assisted selection of the best genotypes in breeding programs. For instance, two alleles ($BNL3502_{150}$ and $BNL3502_{200}$) of the marker BNL3502 on D02 had strong effects (PVE values of 23% and 31%, respectively) on FE under water stress at OAE. Similarly, on A11, the alleles $BNL1151_{198}$ and $BNL1151_{207}$ were associated with PH at ADU under well-watered conditions with PVE values of 27% and 25%, respectively. Thus it should be possible to combine alleles that support high fiber quality and also provide adaptation against adverse effects of changing water availability.

Comparing our results with those of previous QTL analyses provides an efficient way to distinguish highly stable and reliable QTLs underlying fiber traits. Several loci identified in the present study were also reported in previous studies. BNL1034 was identified for fiber length by B. Wang et al. (2017) and by H. Wang et al. (2015); however, this locus was associated with seed cotton yield and plant height in our study. BNL1231 was linked to fiber strength, fiber elongation, short fiber content (C. Huang et al. 2018), lint percent (Wang et al. 2007), lint index and lint yield (He et al. 2007) but was associated with fiber fineness in the present study. JESPR208 was identified for seed index by Wang et al. (2007) and for boll weight by Mei et al. (2013) however this locus was associated with plant height in our study. JESPR274 was associated with seed cotton weight (Nazeer et al. 2022), boll weight (Ademe et al. 2017) and lint index (Wang et al. 2007) previously; however, we found it linked to three plant structure related traits: 1st PBR, TBN and PH. BNL1521 was reported for fiber strength (Cai et al. 2014), seed cotton yield, elongation and upper half mean length (Abdelraheem et al. 2020); however, we detected it for fiber strength. JESPR153 were reported for both fiber strength and fiber length (Cai et al. 2014), similarly we detected it for fiber length.

BNL1667, previously identified with boll weight, lint percentage (Ali et al. 2020) and fiber fineness (Zeng et al. 2009), was reported for two structure traits in our study: 1st position boll retention and plant height. BNL3502 was associated with plant height, boll weight (Kumar et al. 2021), monopodia, staple length, staple strength

(Gawande et al. 2019) and fiber strength (Rakshit et al. 2010); similarly, it was identified for four traits here: fiber strength, fiber elongation, total boll number and plant height. BNL3594 was reported being linked to lint yield, seed yield and boll number (Mei, Zhu, and Zhang 2013) and to fiber strength (Jamshed et al. 2016) however the marker was detected for 1st position boll retention in our study.

Differences in the QTLs identified in different studies, even those using similar markers and population systems, could result from weak but important differences in the effects which environmental conditions have on phenotypes. One of the main concerns of breeders trying to implement marker-assisted selection is a lack of repeatability of QTL results under different environmental conditions. Therefore, it is necessary to confirm markers and QTL reliability under a wide range of environmental factors. Only in this way can associated markers be used to increase the efficiency of breeding programs.

G. hirsutum L. (AADD) is an allopolyploid cotton. Many studies have reported that the D-subgenome contributes more diversity than the A-subgenome (Jiang et al, 1998; Wright et al. 1998; Jiang et al., 2000; Paterson et al. 2000; Saranga et al. 2001). Moreover, many previous QTL studies detected major QTLs for fiber traits on D rather than A-chromosomes (Kohel et al. 2001; Paterson et al. 2003; Ulloa et al. 2005). In our study, the majority of associations (58%) for the related traits were identified on D chromosomes and the remainder (42%) were on A-chromosomes.

Cotton, a species native to semi-arid and subtropical regions, is known to have a degree of drought tolerance originating from its wild ancestors. However, domestication and long-term selection have resulted in reduced genetic variation for drought mechanisms (Saeed et al. 2011). Our association analysis of fiber-related traits is unique because it was conducted under both well-watered and water stress conditions in two locations. The QTLs we have identified could provide a means of improving key agricultural traits in cotton at a time when climate change threatens to exacerbate drought conditions worldwide.

CHAPTER 3

ASSOCIATION MAPPING OF YIELD COMPONENTS AND DROUGHT TOLERANCE RELATED TRAITS IN *G. hirsutum L.*

3.1. Introduction

3.1.1. Cotton Production and Drought Stress

Cotton is an economically important commodity grown for fiber, food and cattle feed in general. However, the plant's most valuable commodity is its seed fibers which are the main raw material of the world's textile industry. Demand for cotton is on the rise as industrial development increases standards of living worldwide. The top five cotton-producing countries are India, China, USA, Brazil and Pakistan; together they produce 76% of the world's cotton (Figure 3.1 and Figure 3.2). While Turkey is seventh in cotton production, contributing only 3%, it ranks in the top four in terms of yield (approximately 1742 kg ha^{-1} in 2021) (Figure 3.3) (USDA-FAS 2021).

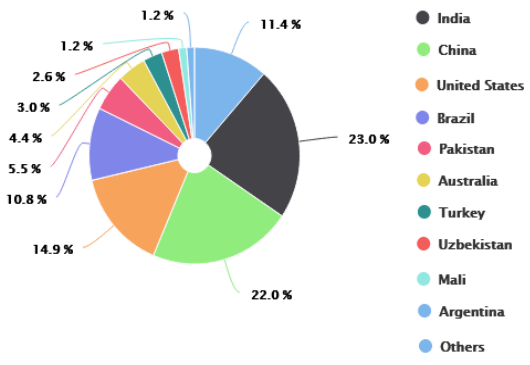

Figure 3.1 Top ten countries worldwide for cotton production

(Source: UDSA-FAS 2021)

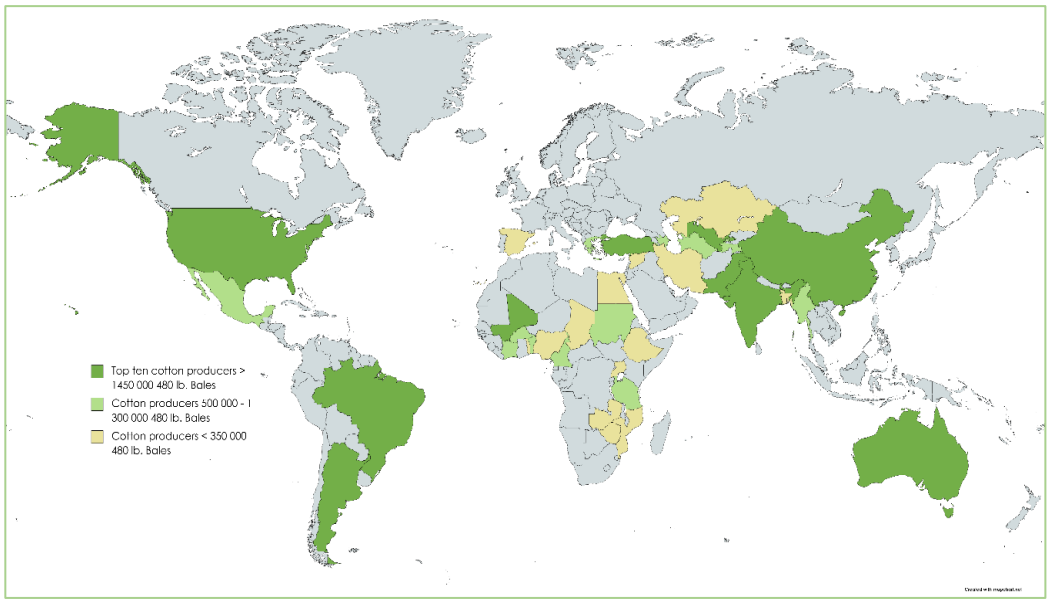

Figure 3.2. Cotton producers in the world (Source: Data from USDA-FAS 2021; Mapchart was generated on https://mapchart.net/world.html). The top ten cotton producers with more than 1450,000 480 lb. bales are highlighted with darker green, the cotton producers with range of 500,000 – 1,300,000 480 lb. bales are highlighted with light green, the cotton producers with less than 350,000 480 lb. bales are highlighted with yellow on the map.

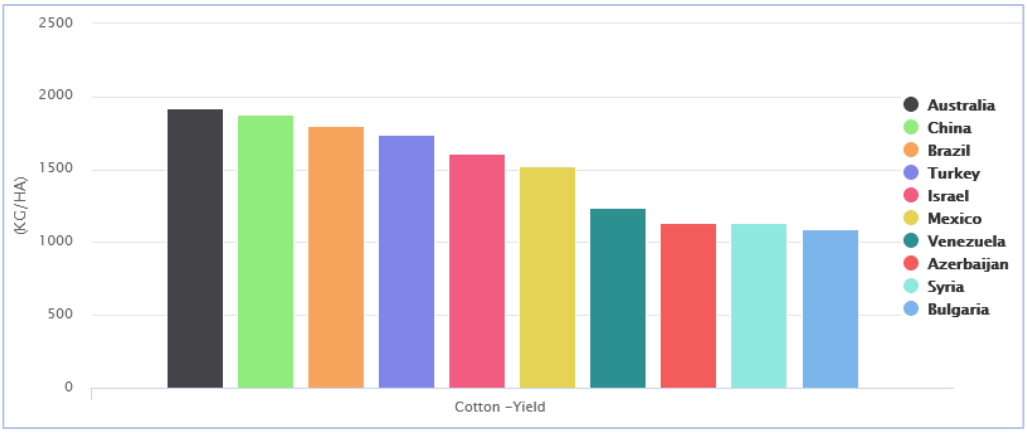

Figure 3.3. Top ten countries worldwide for cotton yield (Source: USDA-FAS 2021).

A wide range of biotic and abiotic stresses cause serious yield losses in cotton including diseases such as *Verticillium* and *Fusarium* wilts; insect pests such as aphids,

armyworms and cutworms; and adverse soil conditions such as drought, salinity and mineral toxicity (Saeed et al. 2011). Drought is one of the most important risk factors for agricultural production in the world with Turkey in the medium to high risk group (Figure 3.4).

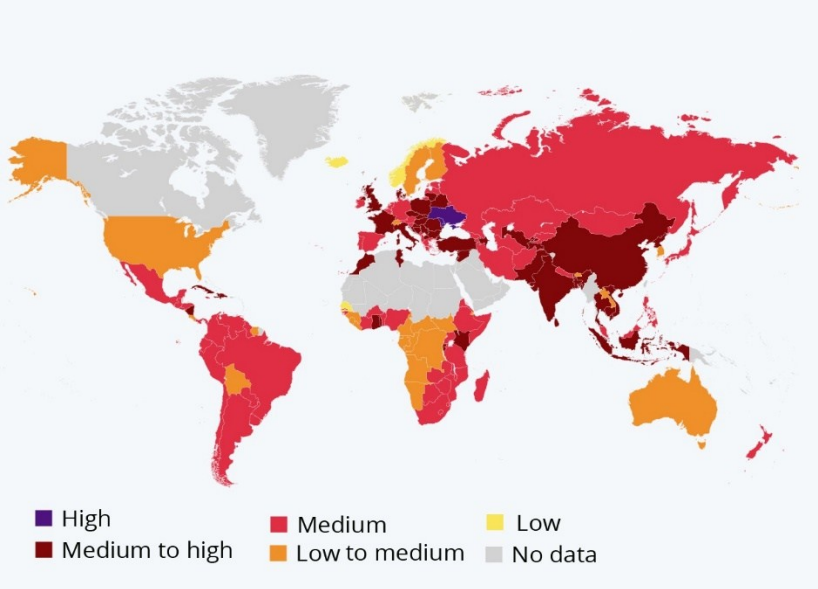

Figure 3.4. Drought risk in the world
(Source: www.statista.com/chart/25101/countries-by-drought-risk/)

Drought limits the movement of water from the soil into the plant, thereby resulting in decreased osmotic potential of the plant. Plants have various adaptations (drought tolerance mechanisms) to overcome this abiotic stress. The three main mechanisms are: stomatal closure to reduce transpiration and thereby sustain internal water potential (drought avoidance), early blooming and early maturity to shorten the life cycle (drought escape), and coping with water stress without altering physiological or developmental features (drought tolerance) (M. Iqbal et al. 2013).

Although cotton is known to have relatively good drought tolerance, water stress can cause adverse effects on cotton quality and yield. These effects depend on the developmental stage of the plant, as well as the duration and extent of water stress. It is clearly seen that the main cotton producing lands are under the risk of drought stress as shown in Figure 3.2 and Figure 3.4.

3.1.2. Breeding for Yield and Drought Tolerance

Breeding for drought tolerance presents challenges due to the complicated nature of drought tolerance components. Conventional breeding of drought tolerant cotton cultivars has been restricted by the complex genetic background of drought tolerance mechanisms, inadequate genetic variation for the trait in the crop and the low heritability of drought-related traits (Levi et al. 2009). Nevertheless, many breeders have applied classical breeding approaches to achieve water stress adaptation in cotton (Quisenberry et al. 1981; Levi et al. 2009; Sezener et al. 2015; Paloti et al. 2017; Singh et al. 2018).

The development of molecular markers has provided new avenues for improvement of quantitative traits using a combination of molecular and traditional breeding methods. The genetic factors or QTL underlying traits of interest can be identified with DNA markers and an appropriate plant population. Markers linked with drought tolerance or yield can then serve as rapid and efficient tools in MAS in cotton (Shen et al. 2006).

Many QTL studies have examined morphological characters, fiber quality and productivity traits in cotton (for example, Mei et al. 2004; Wu et al. 2009; Sun et al. 2012; Liang et al. 2014; C. Zhang et al. 2019; W. Liu et al. 2020). Moreover, there are some QTL studies performed for drought tolerance-related traits (Abdelraheem, Fang, and Zhang 2018; Abdelraheem, Kuraparthy, et al. 2021; Abdelraheem, Thyssen, et al. 2021; Shukla et al. 2021). For example, Shukla et al. (2021) identified 19 QTLs for drought tolerance traits in a RIL population derived from a cross between drought tolerant (AS2) and susceptible (MCU13) Upland cotton parents. In another study, Abdelraheem, Kuraparthy, et al. (2021) conducted a drought test of an Upland cotton association panel and identified 53 QTLs for drought-related traits. Similarly, Abdelraheem, Thyssen et al. (2021) applied a drought test to a MAGIC-RIL Upland cotton population and detected a total of 19 QTLs of which seven and 13 were for dry shoot weight and plant height, respectively.

However, fewer QTL analyses have looked at yield and physiological parameters under both water-limited and irrigated conditions (Saranga et al. 2001; Levi et al. 2009; Saeed et al. 2011; Saleem et al. 2015; Pauli et al. 2016). The most notable studies were performed using an interspecific population generated from a cross

between inbred lines *G. hirsutum* cv. Siv'on and *G. barbadense* cv. F-177 (Saranga et al. 2001; Levi et al. 2009). Saranga et al. (2001) examined F_2 individuals from the population and found that distinct subsets of the 161 identified QTLs were specific to the degree of water availability. Thus 33 (20%) of the QTLs were detected only under water-limited conditions whereas 13 (8%) QTLs influenced the traits only under well-watered conditions. Levi et al. (2009) used a marker-assisted backcross strategy to generate near isogenic lines (NILs) in which target QTLs for yield and physiological traits were introgressed from *G. hirsutum* cv. Siv'on into *G. barbadense* cv. F-177. The NILs and parents were tested under well-watered and water-limited treatments to assess the efficiency of marker-assisted selection (MAS) in improving cotton drought tolerance. The NILs displayed the expected phenotypes in many instances, illustrating the success of the marker-based QTL selection strategy. In other work, Saeed et al. (2011) mapped physiological and morphological traits in an F_2 intraspecific population derived from *G. hirsutum* cv. FH-901 (drought sensitive) and *G. hirsutum* cv. RH-510 (drought tolerant) under both well-irrigated and water-limited conditions. A total of seven QTLs were detected: three under the water-stress regime only and two under the well-watered regime only. In another study, Pauli et al. (2016) used a mapping population consisting of 95 RILs derived from TM-1 × NM24016 for QTL analysis and identified a total of 59 QTLs for agronomic, physiological and fiber related-traits under both well-watered and water-limited regimes.

In general, the results of these QTL studies suggest that distinct sets of genetic loci control cotton productivity and physiological quality under different conditions of water availability. Combining alleles from these independent loci into a single genotype could possibly produce a line adapted to both conditions. However, given the number of QTLs influencing key cotton traits under water-limited conditions, breeding for drought tolerance remains a daunting task.

3.1.3 Aim of the Study

In the present study, we performed association mapping to identify QTLs controlling yield and drought tolerance traits under both water-limited and irrigated conditions. A panel of 99 upland cotton accessions (mostly cultivars used in commercial production) was screened with 177 simple sequence repeat (SSR) markers.

Our findings should be useful for developing drought resistant cotton cultivars by marker-assisted selection.

3.2. Materials and Methods

3.2.1. Materials

A germplasm panel composed of 99 elite cotton lines (*G. hirsutum* L.) (Table 3.1) was provided by Nazilli Cotton Research Center (Aydın, Turkey). The genotypes of the panel were selected based on their high geometric mean productivity and low drought sensitivity index as assessed by a previous agro-morphological analysis under drought stress (Sezener et al. 2015).

3.2.2. Methods

3.2.2.1. Field Evaluation

A total of 99 cotton genotypes including five controls: BA 119, Carmen, Claudia, GSN 12 and Sahin 2000 were planted at 0.70 m row width and 0.20 m spacing between individuals on 19 May 2011 and 3 May 2012 seasons at the Agricultural Research Station of Adnan Menderes University (ADU) and at Özaltın Agricultural Enterprises Industry and Commerce Inc. (OAE), both of which are in Kocarli, Aydin, Turkey. Each genotype was planted occupied a single 12 m row with four replications in an augmented experiment design. Two watering regimes were applied using drip irrigation: well-watered (100%, full irrigation) and water-limited (50%, deficit irrigation). Hand harvesting was conducted on 29 September 2011 and 14 September 2012.

Yield traits and drought-related parameters were measured under control and water stress field conditions. The yield traits were seed cotton yield (SCY) (kg ha^{-1}), lint yield (LY) (kg ha^{-1}), lint percentage (LP) (%) and water-use efficiency (WUE). In addition, seven parameters were calculated for each genotype to assess drought tolerance: yield potential (YP), yield reduction (YR) (%), yield index (YI), drought

sensitivity index (DSI), stress tolerance index (STI), harmonic mean (HM) and geometric mean productivity (GMP).

Seed cotton yield was calculated as total weight of seed cotton (kg) ha^{-1}. Lint yield was calculated as total weight of lint (kg) ha^{-1}. After ginning the cotton, lint percentage was determined with the following formula: [g lint / (g lint + g seed) x 100%]. Water-use efficiency was calculated using the formula: yield (Y) in kg ha^{-1} / total applied water (mm) (Howell and Hiler 1975). Yield potential was calculated as $(\hat{Y}s + \hat{Y}p) / 2$, where $\hat{Y}s$ and $\hat{Y}p$ are the means of all genotypes under well-watered and water-limited conditions, respectively (Rosielle and Hamblin 1981). Percentage yield reduction was calculated as 100 – (Ys/Yp *100). Yield index was calculated as $Ys / \hat{Y}s$ (Gavuzzi et al. 1997). Drought sensitivity index was calculated as of (1 - Ys/Yp) / D, where D is 1 - (mean yield of all cotton cultivars under water-limited condition / mean yield of all cotton cultivars under well-watered condition) (Fischer and Maurer 1978). Stress tolerance index was calculated as $(Yp * Ys) / (\hat{Y}p)^2$ (Fernandez, 1992; (Schneider et al. 1997). Harmonic mean was calculated as 2 (Yp * Ys) / (Yp + Ys) (Schneider et al. 1997) where Yp and Ys are mean yields of a given cultivar under well-watered and water-limited conditions, respectively. Geometric mean productivity was calculated as $(Yp * Ys)^{1/2}$ (Fernandez 1992; Schneider et al. 1997). PAWS statistics software (SPSS Inc. Released 2009, PASW Statistics for Windows, Version 18.0, Chicago: SPSS Inc) with Pearson Correlation, two-tailed method was employed to evaluate bivariate correlation coefficients between traits.

3.2.2.2. Association Analysis for Yield Traits and Drought Parameters

Association analysis was performed with TASSEL 2.1 software using the general linear model (GLM) (Q) and mixed linear model (MLM) (Q and K) methods to identify QTLs for the yield and drought related traits at two locations (ADU and OAE) (Bradbury et al. 2007). Significance levels were determined at $p \leq 0.001$. Association analysis of the phenotypes (morphological data) and genotypes (SSR allelic data) was performed using the Q matrix calculated by STRUCTURE 2.3.4 and the relative kinship among individuals (K matrix) determined by TASSEL 2.1.

3.3. Results

3.3.1. Phenotypic Evaluation

Yield traits and drought tolerance-related parameters were evaluated under both water-limited and well-watered conditions to determine the response of cotton genotypes to water-stress (Table 3.1, Table 3.2 and Table 3.3). Phenotypic distributions showed that all eleven traits segregated in a quantitative fashion and therefore were suitable for QTL analysis (Figure 3.5 and Figure 3.6).

Seed cotton yield ranged from 2440 kg ha^{-1} to 6520 kg ha^{-1} with a mean of 4080 kg ha^{-1} under well-watered conditions. In contrast, it ranged from 1790 kg ha^{-1} to 3990 kg ha^{-1} with a mean of 2980 kg ha^{-1} under water-limited conditions. Lint yield ranged from 920 kg h^{-1} to 2370 kg h^{-1} under the well-watered regime and from 650 kg ha^{-1} to 1530 kg ha^{-1} under the water-limited regime with mean values of 1490 kg ha^{-1} and 1100 kg ha^{-1}, respectively. Mean values of both traits decreased under drought conditions (SCY, 27%; LY, 26%). Lint percentage showed no significant variation between both watering regimes. It ranged from 31% to 40% with a mean of 36%; and from 32% to 42% with a mean of 37% for well-watered and water-limited conditions, respectively. Water-use efficiency varied between 4 kg ha^{-1} mm^{-1} and 10.7 kg ha^{-1} mm^{-1} with a mean of 6.4 kg ha^{-1} mm^{-1} under the well-watered regime. In contrast, it ranged from 6 kg ha^{-1} to 13.3 kg ha^{-1} with an increased (53%) mean of 9.8 kg ha^{-1} mm^{-1} under water-stress conditions (Table 3.1., Table 3.2 and Figure 3.5). There was a significant location effect on LP and WU under well-watered conditions and on SCY, LY, LP and WUE under water-limited conditions (Table 3.4).

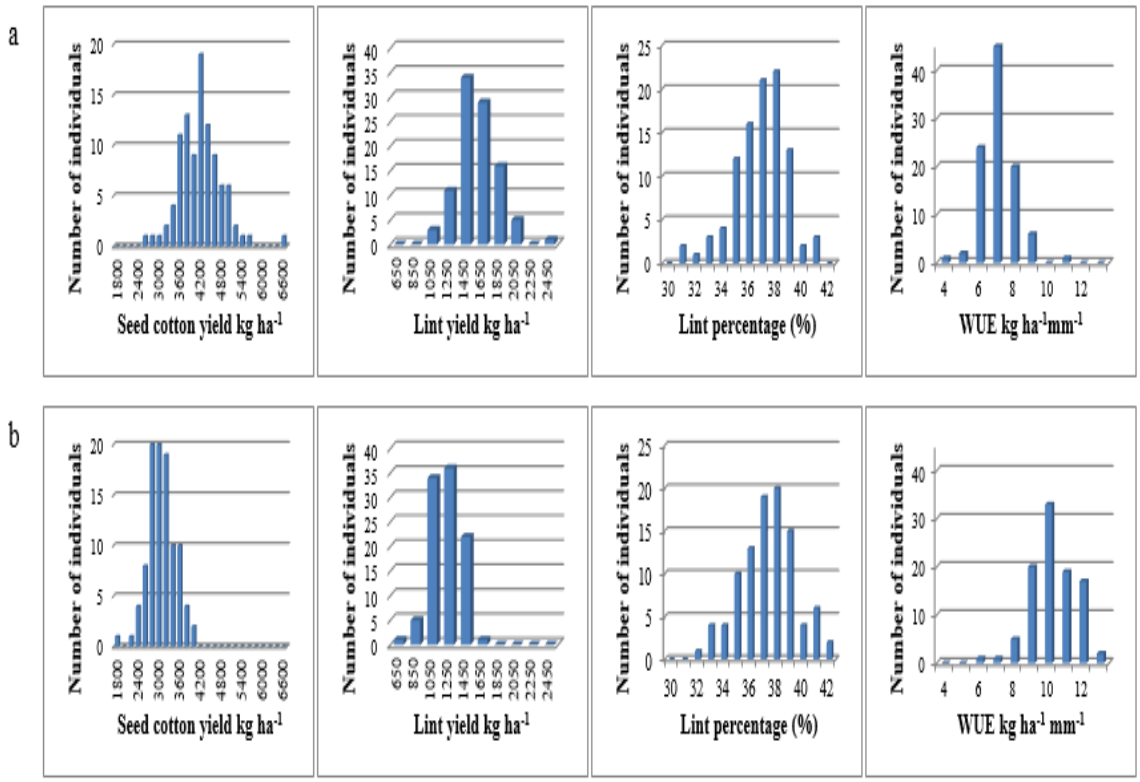

Figure 3.5 The distribution of yield and drought traits within the germplasm panel under well-watered (a) and water-limited regimes (b).

Drought parameters were calculated under water stress (50% deficit irrigation) conditions. Yield potential ranged from 212 to 526 with a mean of 353. Yield reduction ranged from 3 to 52 with a mean of 26. Yield index ranged from 0.7 to 1.3 with a mean of 1. Drought sensitivity index ranged from 0.1 to 1.9 with a mean of 0.95. Stress tolerance index varied between 0.3 and 1.6 with a mean of 0.7. Harmonic mean ranged from 207 to 495 with a mean of 343. Geometric mean productivity varied between 209 and 510 with a mean of 348 (Table 3.3, Figure 3.6).

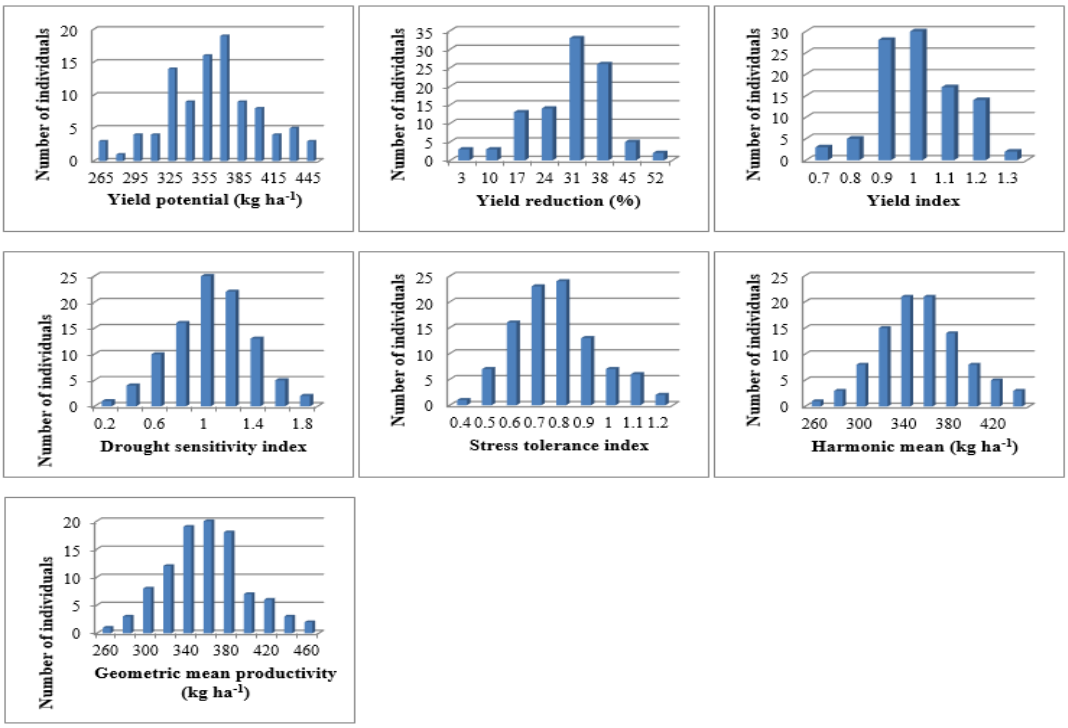

Figure 3.6. The distribution of drought parameters within the germplasm panel

Table 3.1. Morphological results of yield traits for cotton genotypes under well-watered conditions.

Well-watered condition	Seed cotton yield (SCY) (kg ha^{-1})	Lint yield (LY) (kg ha^{-1})	Lint percentage (LP) (%)	Water use efficiency (WUE) (kg ha^{-1} mm^{-1})
152F	3483	1187	34.0	5.7
Acala 5	3403	1247	36.5	5.5
Acala 1517	3271	1149	34.9	5.3
Aleppo 1	4594	1424	30.7	7.6
Auburn M	3224	1060	32.6	5.2
Ayhan 107	3345	1234	37.0	5.5
Az 31	5112	1812	35.4	8.1
Ba 119	4102	1597	38.9	6.6
Ba 308	4349	1592	36.6	7.2
Ba 525	4583	1786	39.0	7.4

(Cont. on the next page)

Table 3.1. (cont.)

Barut 2005	4911	1833	37.2	8
Blightmaster	4228	1564	36.9	6.9
Cabu/Cs2-1-83	2441	916	37.0	4
Candia	4427	1782	40.2	7
Carmen	3699	1407	38.0	6.1
Caroline Queen	4341	1670	38.5	7.1
Celia	3931	1424	36.4	6.5
Claudia	3765	1518	40.4	6.1
Coker 208	4223	1583	37.4	6.9
Corona	3128	1169	37.5	5.1
DAK 66/3	3986	1500	37.4	6.7
Delcerro	2675	924	34.8	4.3
Delcerro Ms 30	3061	933	30.7	5.1
Delta Diamond	4913	1833	37.3	7.9
Delta Opal	4146	1579	38.0	6.8
DP 388	3583	1391	38.9	5.7
DPL 6	3556	1291	36.2	5.8
DPL 20	3653	1420	38.9	5.9
DPL 5415	3753	1421	37.9	6
DPL 882	3449	1271	36.6	5.6
DPL 883	3925	1371	35.0	6.2
DPL 886	4744	1768	37.4	7.7
DPL 90	3250	1244	38.2	5.2
DPL C 37 Prima	3818	1394	36.4	6.1
DPL SR 383	3524	1269	35.9	5.7
Elsa	5062	1969	38.9	8.3
Ersan 92	3649	1365	37.4	6
Eva	4441	1587	35.7	7
Flora	4277	1585	37.0	7
GC 262	4241	1583	37.6	6.7
GC 555	4634	1683	36.6	7.3
Gloria	4775	1897	39.7	7.8
GSA 78	4100	1505	36.7	6.7
GSN 12	4261	1608	37.7	7
GW Teks	4508	1712	38.0	7.3
Julia	4230	1646	38.9	7
Lachata	3916	1407	36.0	6.5
Lankart 57	4232	1646	38.7	6.9
Mcnair 220	4075	1511	37.0	6.7
Menderes 2005	4048	1492	36.8	6.7

(Cont. on the next page)

Table 3.1. (cont.)

Ms 30/1	4061	1445	35.3	6.8
N 727 CC	4422	1721	38.9	7.3
Napa 122	3975	1510	37.9	6.6
Nata	4020	1425	35.4	6.7
Nazilli M503/2	4420	1509	34.0	7.3
Nazill 143	4988	1881	37.6	8.1
Nazilli 84 S	3911	1555	39.8	6.4
Nazilli 87	3546	1249	35.2	5.8
Nazilli M39	5332	1823	34.1	8.5
Nazilli M503/1	4817	1584	32.7	7.9
NGF 63	4157	1577	37.9	6.8
Niab 111	4037	1518	37.6	6.5
Niab 999	3947	1478	37.4	6.3
Nieves	4022	1438	35.8	6.6
Np Ege 2009	6517	2374	36.3	10.7
Np Ozbek 100	4921	1840	37.3	8.1
Paymaster 404	4012	1469	36.5	6.6
Pg 2018	4757	1834	38.6	7.8
Rex 1	4178	1420	34.2	6.8
Sj V Visalia Elmer	3603	1291	36.0	5.8
S 9	4158	1418	34.1	6.8
Sahel 1	3480	1286	37.0	5.7
Samarkant Uzbek	4044	1406	34.7	6.7
Somon	3549	1207	34.2	5.8
Sayar 314	4016	1476	36.7	6.5
Sealand 542	4162	1373	33.2	6.6
Semu SS/G	3953	1283	32.9	6.4
SG 1001	4373	1654	37.9	7.1
SG 125	4856	1962	40.3	7.9
Sicala 3/2	3791	1258	33.5	6.3
Sicala 33	4064	1432	35.4	6.7
Sindos 80	3580	1304	36.4	5.9
Sj U 86	5549	1996	35.9	8.9
Stoneville 213	3792	1343	35.6	6.2
Stoneville 453	4042	1347	33.6	6.6
Stoneville 8751	4254	1574	37.0	6.8
Sahin 2000	4536	1579	34.6	7.5
Tomcot 22	4670	1663	35.6	7.5
Tomcot Cabcs	3621	1305	36.1	6
Tomcot Sphinx	4214	1466	34.8	6.8

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Table 3.1. (cont.)

Taskent 1	4135	1486	36.0	6.7
Taskent Uzbek	4493	1413	31.3	7.4
Taskent 6	3795	1349	35.5	6.2
TKY3304 GS316	2846	1053	37.1	4.6
TKY 9309	4705	1674	35.8	7.6
TKY 9409	3681	1420	38.5	6.1
Togo	3663	1262	34.6	6
Vulcano	3425	1188	34.8	5.7
Zeta 2	3677	1312	35.9	5.9
Average	4079	1487	36.4	6.64
LSD	123	48.09	2.42	0.2
CV	14.84	15.61	3.22	14.49

Table 3.2. Morphological results of fiber traits for cotton genotypes under water-limited conditions.

Water-limited condition	**Seed cotton yield (SCY) (kg ha^{-1})**	**Lint yield (LY) (kg ha^{-1})**	**Lint percentage (LP) (%)**	**Water use efficiency (WUE) (kg ha^{-1} mm^{-1})**
152F	2727	952	34.4	9
Acala 5	2520	890	35.5	8.3
Acala 1517	2574	920	35.9	8.5
Aleppo 1	2927	989	32.8	9.9
Auburn M	2209	703	32.4	7.2
Ayhan 107	2876	1049	36.4	9.3
Az 31	3387	1177	34.7	11.1
Ba 119	3045	1260	41.3	10
Ba 308	3009	1113	37.3	10.2
Ba 525	3131	1263	40.4	10.4
Barut 2005	3683	1385	37.6	12
Blightmaster	2764	1013	36.7	9.1
Cabu/Cs2-1-83	1791	649	36.3	6
Candia	3039	1258	41.5	10.2
Carmen	2932	1115	38.0	9.6
Caroline Queen	3034	1168	38.3	10
Celia	2616	1015	38.9	9

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Table 3.2. (cont.)

Claudia	2732	1104	40.5	9
Coker 208	2582	968	37.5	8.4
Corona	2681	1040	38.6	8.8
DAK 66/3	3825	1448	37.9	12.6
Delcerro	2611	915	35.1	8.6
Delcerro Ms 30	2692	856	31.8	8.9
Delta Diamond	3349	1279	38.3	11.5
Delta Opal	3287	1277	38.7	10.8
DP 388	2640	1022	38.6	8.7
DPL 6	3012	1081	35.9	9.9
DPL 20	2774	1044	37.6	9.1
DPL 5415	2804	1062	37.8	9.1
DPL 882	2864	1028	36.0	9.5
DPL 883	2939	1024	35.1	9.5
DPL 886	2967	1076	36.3	9.8
DPL 90	2584	1023	39.4	8.5
DPL C 37 Prima	2588	888	34.6	8.4
DPL SR 383	2447	789	33.2	7.9
Elsa	3436	1396	40.6	11.7
Ersan 92	3313	1250	37.8	10.7
Eva	3467	1262	36.5	11.2
Flora	2824	1054	36.9	9.7
GC 262	2865	1070	37.3	9.3
GC 555	3492	1269	36.4	11.3
Gloria	3154	1204	38.9	10.8
GSA 78	2769	963	35.0	9.1
GSN 12	3192	1277	39.7	10.6
GW Teks	3106	1157	37.3	10.1
Julia	3093	1230	39.8	10.5
Lachata	3252	1203	36.9	10.7
Lankart 57	3131	1145	36.6	10.2
Mcnair 220	2981	1167	39.0	9.9
Menderes 2005	2805	1016	36.3	9.4
Ms 30/1	3688	1320	35.8	12.2
N 727 CC	2792	1119	40.0	9.3
Napa 122	3129	1213	38.9	10.3
Nata	2778	1037	37.2	9.1
Nazilli M503/2	3496	1168	33.1	11.3
Nazill 143	3592	1318	36.6	11.7
Nazilli 84 S	2901	1178	40.7	9.6

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Table 3.2. (cont.)

Nazilli 87	3456	1177	33.9	11.1
Nazilli M39	3700	1337	36.1	12
Nazilli M503/1	3351	1090	32.2	11
NGF 63	3231	1214	37.7	10.6
Niab 111	3156	1194	37.9	10.3
Niab 999	3468	1307	37.7	11.3
Nieves	3442	1314	38.2	11.3
Np Ege 2009	3993	1533	38.5	13.3
Np Ozbek 100	3599	1347	37.5	12
Paymaster 404	2818	1042	37.1	9.4
Pg 2018	3347	1373	40.9	11.4
Rex 1	3034	1106	36.5	9.9
Sj V Visalia Elmer	2709	1032	38.0	8.8
S 9	2847	1005	35.3	9.4
Sahel 1	2693	1029	38.0	8.9
Samarkant Uzbek	2709	942	34.4	8.9
Somon	2661	921	34.4	9
Sayar 314	3469	1311	37.8	11.1
Sealand 542	2724	946	34.9	8.7
Semu SS/G	2447	837	34.1	8.1
SG 1001	2773	1072	38.5	9.1
SG 125	3011	1286	42.5	9.9
Sicala 3/2	3332	1145	34.6	11.1
Sicala 33	3043	1111	36.5	10
Sindos 80	2825	1013	35.8	9.4
Sj U 86	3135	1181	37.7	10.4
Stoneville 213	2867	1120	39.0	9.4
Stoneville 453	3209	1125	35.0	10.7
Stoneville 8751	2731	1050	38.3	9
Sahin 2000	2840	939	33.0	9.4
Tomcot 22	2292	825	35.8	7.6
Tomcot Cabcs	2781	1029	36.8	9.3
Tomcot Sphinx	2986	1053	35.0	10
Taskent 1	2117	777	36.4	7
Taskent Uzbek	2594	880	33.5	8.5
Taskent 6	2881	1048	36.2	9.6
TKY3304 GS316	2395	859	35.6	7.9
TKY 9309	2983	1097	36.4	9.9
TKY 9409	2390	980	40.6	8
Togo	3049	1072	35.1	10.1

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Table 3.2. (cont.)

Vulcano	3041	1154	37.8	10.2
Zeta 2	3697	1333	36.0	11.9
Average	2977	1102	36.9	9.82
LSD	90.16	35.49	2.76	0.27
CV	14.77	15.61	3.66	13.64

Table 3.3. Drought parameters of fiber traits for cotton.

Genotype	**Yield potential (YP)**	**Yield reduction (YR) (%)**	**Yield index (YI)**	**Drought sensitivity index (DSI)**	**Stress tolerance index (STI)**	**Harmonic mean (HM)**	**Geometric mean productivity (GMP)**
152F	310.5	21.7	0.91	0.83	0.56	305.9	308.2
Acala 5	296.1	26	0.85	0.89	0.51	289.6	292.8
Acala 1517	292.2	21.3	0.86	0.61	0.5	288.1	290.2
Aleppo 1	376	36.3	0.98	1.4	0.8	357.6	366.7
Auburn M	271.6	31.5	0.74	1.12	0.42	262.1	266.8
Ayhan 107	311.1	14	0.96	0.62	0.57	309.3	310.2
Az 31	424.9	33.7	1.14	1.02	1.03	407.4	416.1
Ba 119	357.3	25.8	0.98	0.83	0.74	349.3	353.4
Ba 308	367.9	30.8	1.01	1.04	0.78	355.7	361.7
Ba 525	385.7	31.7	1.05	1.04	0.85	372	378.8
Barut 2005	429.7	25	1.24	0.98	1.07	420.9	425.3
Blightmaster	349.6	34.6	0.93	1.32	0.69	334.3	341.8
Cabu/Cs2-1-83	211.6	26.6	0.6	0.73	0.26	206.6	209.1
Candia	373.3	31.3	1.02	0.76	0.8	360.4	366.8
Carmen	372.7	20.7	1.07	0.79	0.81	365	368.8
Caroline Queen	368.8	30.1	1.02	1.16	0.78	357.2	362.9
Celia	327.4	33.5	0.88	1.18	0.61	314.2	320.7
Claudia	324.8	27.4	0.92	0.96	0.61	316.6	320.7
Coker 208	340.3	38.9	0.87	1.52	0.65	320.5	330.2
Corona	290.5	14.3	0.9	0.53	0.5	288.7	289.6
DAK 66/3	390.5	4	1.28	0.26	0.91	390.4	390.5
Delcerro	264.3	2.4	0.88	0.33	0.41	264.2	264.3
Delcerro Ms 30	287.6	12.1	0.9	0.41	0.49	286.4	287
Delta Diamond	413.1	31.8	1.12	0.87	0.98	398.3	405.6

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Table 3.3. (cont.)

Delta Opal	371.6	20.7	1.1	0.77	0.81	366.7	369.2
DP 388	311.2	26.3	0.89	0.81	0.56	304	307.6
DPL 6	328.4	15.3	1.01	0.45	0.64	326.1	327.2
DPL 20	321.3	24.1	0.93	0.84	0.6	315.3	318.3
DPL 5415	327.8	25.3	0.94	0.87	0.63	320.9	324.4
DPL 882	315.7	17	0.96	0.53	0.59	312.9	314.3
DPL 883	343.2	25.1	0.99	0.86	0.69	336.2	339.7
DPL 886	385.5	37.5	1	1.42	0.84	365.1	375.2
DPL 90	291.7	20.5	0.87	0.58	0.5	287.9	289.8
DPL C 37 Prima	320.3	32.2	0.87	1.12	0.59	308.5	314.3
DPL SR 383	298.6	30.5	0.82	1.19	0.51	288.9	293.7
Elsa	424.9	32.1	1.15	1.05	1.03	409.4	417.1
Ersan 92	348.1	9.2	1.11	0.44	0.72	347.3	347.7
Eva	395.4	21.9	1.16	0.64	0.91	389.4	392.4
Flora	355	34	0.95	1.14	0.72	340.2	347.5
GC 262	355.3	32.4	0.96	1.04	0.72	342	348.6
GC 555	406.3	24.7	1.17	0.79	0.96	398.3	402.2
Gloria	396.4	34	1.06	1.09	0.89	379.8	388.1
GSA 78	343.5	32.5	0.93	1.19	0.67	330.6	336.9
GSN 12	331.6	25.1	0.95	0.84	0.64	327.1	329.4
GW Teks	380.7	31.1	1.04	1.1	0.83	367.7	374.1
Julia	366.1	26.9	1.04	0.91	0.78	357.3	361.7
Lachata	358.4	16.9	1.09	0.71	0.76	355.3	356.8
Lankart 57	368.2	26	1.05	1.03	0.79	359.9	364
Mcnair 220	352.8	26.8	1	0.99	0.72	344.3	348.5
Menderes 2005	342.6	30.7	0.94	1.19	0.67	331.4	337
Ms 30/1	387.4	9.2	1.24	0.47	0.89	386.5	387
N 727 CC	360.7	36.9	0.94	1.38	0.73	342.3	351.3
Napa 122	355.2	21.3	1.05	0.89	0.74	350.2	352.7
Nata	339.9	30.9	0.93	1.26	0.66	328.5	334.1
Nazilli M503/2	395.8	20.9	1.17	0.9	0.92	390.4	393.1
Nazill 143	429	28	1.2	1.05	1.06	417.7	423.3
Nazilli 84 S	340.6	25.8	0.97	0.94	0.67	333.1	336.8
Nazilli 87	350.1	2.5	1.16	0.23	0.73	350	350.1
Nazilli M39	451.6	30.6	1.24	1.07	1.17	436.9	444.2
Nazilli M503/1	408.4	30.4	1.12	1.23	0.96	395.3	401.8
NGF 63	369.4	22.3	1.08	0.83	0.8	363.6	366.5
Niab 111	359.6	21.8	1.06	0.72	0.76	354.2	356.9
Niab 999	370.7	12.1	1.16	0.26	0.81	369.2	370
Nieves	373.2	14.4	1.15	0.56	0.82	370.9	372

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Table 3.3. (cont.)

Np Ege 2009	525.5	38.7	1.34	1.43	1.55	495.2	510.1
Np Ozbek 100	426	26.9	1.21	0.96	1.05	415.8	420.9
Paymaster 404	341.5	29.7	0.95	1.07	0.67	331.1	336.2
Pg 2018	405.2	29.7	1.12	0.94	0.95	392.9	399
Rex 1	360.6	27.4	1.02	1.03	0.75	351.5	356
Sj V Visalia Elmer	315.6	24.8	0.91	0.87	0.58	309.3	312.4
S 9	350.3	31.5	0.95	1.12	0.7	338	344.1
Sahel 1	308.6	22.6	0.9	0.94	0.56	303.6	306.1
Samarkant Uzbek	337.7	33	0.91	1.39	0.65	324.5	331
Somon	310.5	25	0.89	0.89	0.56	304.2	307.3
Sayar 314	374.2	13.6	1.16	0.61	0.83	372.2	373.2
Sealand 542	344.3	34.6	0.91	1.33	0.67	329.2	336.7
Semu SS/G	320	38.1	0.82	1.33	0.57	302.3	311
SG 1001	357.3	36.6	0.93	1.36	0.72	339.3	348.2
SG 125	393.4	38	1.01	1.36	0.87	371.7	382.4
Sicala 3/2	356.1	12.1	1.12	0.53	0.75	354.6	355.4
Sicala 33	355.3	25.1	1.02	1.03	0.73	348	351.6
Sindos 80	320.2	21.1	0.95	0.74	0.6	315.8	318
Sj U 86	434.2	43.5	1.05	1.47	1.03	400.6	417.1
Stoneville 213	332.9	24.4	0.96	0.94	0.65	326.5	329.7
Stoneville 453	362.5	20.6	1.08	0.75	0.77	357.7	360.1
Stoneville 8751	349.2	35.8	0.92	1.25	0.69	332.6	340.8
Sahin 2000	368.8	37.4	1.02	1.44	0.77	349.5	358.9
Tomcot 22	348.1	50.9	0.77	1.73	0.64	307.4	327.1
Tomcot Cabcs	320.1	23.2	0.93	0.92	0.6	314.6	317.4
Tomcot Sphinx	360	29.2	1	0.88	0.75	349.5	354.7
Taskent 1	312.6	48.8	0.71	1.89	0.52	280.1	295.9
Taskent Uzbek	354.4	42.3	0.87	1.72	0.69	328.9	341.4
Taskent 6	333.8	24.1	0.97	0.8	0.65	327.5	330.7
TKY3304 GS316	262.1	15.8	0.8	0.61	0.41	260.1	261.1
TKY 9309	384.4	36.6	1	1.26	0.83	365.1	374.6
TKY 9409	303.5	35.1	0.8	1.33	0.52	289.8	296.6
Togo	335.6	16.8	1.02	0.63	0.66	332.8	334.2
Vulcano	323.3	11.2	1.02	0.43	0.62	322.2	322.7
Zeta 2	368.7	-0.5	1.24	0.12	0.81	368.7	368.7
Average	352.8	26.2	1.00	0.95	0.73	342.8	347.7

Strong positive correlations were found between many of the traits (Table 3.5 and Table 3.6). Under the well-watered regime, seed cotton yield was correlated ($p < 0.01$) with water-use efficiency ($r = 0.99$) and lint yield ($r = 0.94$). Similarly, lint yield was correlated with water-use efficiency ($r = 0.94$). Under the water-limited regime,

drought parameters (geometric mean productivity, harmonic mean, stress tolerance index, water-use efficiency) showed highly significant positive correlations ($r > 0.80$) with each other. Drought sensitivity index was positively correlated with yield reduction ($p < 0.01$). The stress tolerance and yield indices were also correlated ($r = 0.86$). Lint percentage did not show significant correlation with any traits except yield potential ($r = 0.52$). Negative correlations between traits tended to be much weaker ($r \leq 0.34$).

Table 3.4. Variance analysis of the data at ADU and OAE under well-watered and water-limited conditions.

	Well-watered				
	SCY (kg ha^{-1})	**LY (kg ha^{-1})**	**LP (%)**	**WUE (kg da^{-1} mm^{-1})**	
Location	2357,51	1518,22	32,97*	0,58*	
Replication	7244,88	1254,70	6,61	0,02	
Genotype	692986,67*	114850,51*	757,15*	1,80*	
Location x Genotype	278067,48	40378,81	154,82	0,71	
Error	99910,90	14862,24	37,83	0,25	
	Water-limited				
	SCY (kg ha^{-1})	**LY (kg ha^{-1})**	**LP (%)**	**WUE (kg da^{-1} mm^{-1})**	**DSI**
Location	47546.32*	10057.15*	30.44*	2.89*	0.06
Replication	14154.23	1933.00	5.41	0.13	1.14
Genotype	258791.88	47799.67	898.31*	2.76	25.57
Location x Genotype	250833.12	3412723	145.33	2.66	13.57
Error	52229.94	8090.63	49.87	0.48	8.11

** significant at 0.05 level*

Table 3.5. Correlation coefficients between the traits under well-watered conditions

Trait	SCY	LY	LP	WUE
SCY	1	0.94**	0.10	0.99**
LY		1	0.43**	0.94**
LP			1	0.09
WUE				1

**Correlation is significant at the 0.01 level.

Table 3.6. Correlation coefficients between the traits under watered-limited conditions

	SCY	LY	LP	WUE	DSI	GMP	YR	YP	HM	STI	YI
SCY	1	0.92**	0.16	0.99**	-0.34**	0.86**	-0.35**	0.82**	0.90**	0.85**	0.99**
LY		1	0.52**	0.93**	-0.29**	0.82**	-0.26**	0.79**	0.85**	0.81**	0.90**
LP			1	0.19	-0.02	0.20	0.08	0.19	0.20	0.19	0.14
WUE				1	-0.32**	0.87**	-0.32**	0.83**	0.91**	0.86**	0.98**
DSI					1	0.14	0.95**	0.21*	0.06	0.13	-0.33**
GMP						1	0.15	0.99**	0.99**	0.99**	0.87**
YR							1	0.22*	0.07	0.15	-0.34**
YP								1	0.99**	0.99**	0.83**
HM									1	0.99**	0.91**
STI										1	0.86**
YI											1

** Correlation is significant at the 0.01 level.

* Correlation is significant at the 0.05 level.

3.3.2. Analysis for Yield and Drought Parameters

Loci supported by both GLM and MLM analysis at a significance level $p \leq 0.001$ are reported here. Different sets of loci were discovered to be associated with the two watering regimes. At both locations, GLM detected a total of 20 and 16 marker-trait associations under well-watered and water limited conditions, respectively. MLM detected nine and six associations under well-water and water-limited regimes, respectively.

3.3.2.1. Association Analysis under Well-Watered Regime

Association analysis identified significant marker loci for SCY, LY, LP and WUE at both locations (ADU and OAE) under well-watered conditions. GLM and MLM methods identified 17 and three marker-trait associations, respectively, at ADU; and seven and six marker-trait associations, respectively, at OAE. All identified marker loci were highly significant ($p < 0.001$) and were major-effect loci (PVE > 10%) with a PVE value ranged from 11% to 19% (Table 3.7). The most significant marker locus (DPL247-168) was identified for SCY ($p = 0.00001$) at ADU with a high PVE value of 17%.

Of the detected marker loci at ADU, three for LP were supported by both GLM and MLM methods: DPL520-203, DPL520-289 and TMB2018-145. At OAE, all marker-trait associations except for LP were supported by both GLM and MLM methods. Moreover, TMB2018-145 was identified at both locations for LP and considered as stable QTL for LP.

Table 3.7. Yield traits-associated marker loci identified by GLM and MLM models under well-watered conditions at two locations (ADU and OAE).

ADU						
GLM				**MLM**		
Trait	Marker Locus	r^2 (%)	p	Trait	Marker Locus	p
LP	$DPL520_{203}$	17	0.00003	LP	$DPL520_{203}$	0.0002
	$TMB2018_{245}$	18	0.00005		$DPL520_{289}$	0.0007
	$DPL520_{289}$	14	0.0001		$TMB2018_{245}$	0.0008
	$TMB1427_{297}$	11	0.0008			
	$DPL181_{178}$	12	0.0008			
LY	$DPL247_{168}$	13	0.0002			
	$DPL513_{125}$	13	0.0008			
SCY	$DPL247_{168}$	17	0.00001			
	$BNL1151_{207}$	16	0.00008			
	$DPL307_{208}$	12	0.0004			
	$DPL100_{175}$	12	0.0006			
	$DPL890_{172}$	12	0.0008			

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Table 3.7. (cont.)

WUE	$DPL247_{168}$	17	0.00002
	$BNL1151_{207}$	15	0.0001
	$DPL307_{208}$	12	0.0004
	$DPL100_{175}$	12	0.0006
	$DPL890_{172}$	12	0.0008

OAE

GLM				MLM		
Trait	Marker Locus	r^2 (%)	p	Trait	Marker Locus	p
LP	$TMB2018_{245}$	14	0.0005	LP	$BNL3545_{129}$	0.0004
	$DPL223_{269}$	15	0.0005	LY	$BNL3545_{129}$	0.0003
LY	$BNL3545_{129}$	16	0.0005	SCY	$STV023_{180}$	0.0003
SCY	$STV023_{180}$	19	0.0002		$STV023_{140}$	0.0004
	$STV023_{140}$	18	0.0002	WUE	$STV023_{180}$	0.0002
WUE	$STV023_{180}$	19	0.0001		$STV023_{140}$	0.0004
	$STV023_{140}$	18	0.0002			

3.3.2.2. Association Analysis under Water-Limited Regime

Under water limited conditions, a total of 22 marker-trait associations were identified for SCY, LY, LP and WUE at both locations. GLM and MLM detected eight and one significant loci, respectively, at ADU; and, eight and five loci, respectively, at OAE. All identified marker loci were highly significant ($p < 0.001$) and were major-effect loci (PVE > 10%) with a PVE value ranged from 12% to 18% (Table 3.8). The most significant marker locus, DPL490-241, was identified for SCY ($p = 0.00002$) at OAE with the highest PVE value of 18%. Moreover, one and five marker-trait associations at ADU and OAE, respectively, were supported by both GLM and MLM methods.

Table 3.8. Yield and drought related trait-associated marker loci identified by GLM and MLM models under water-limited conditions at two locations (ADU and OAE).

ADU						
GLM				**MLM**		
Trait	Marker Locus	r^2 (%)	p	Trait	Marker Locus	p
LP	$TMB2018_{245}$	16	0.0001	LP	$BNL3474_{175}$	0.0008
	$BNL3474_{175}$	15	0.0003			
	$TMB1295_{275}$	13	0.0006			
LY	$MGHES22_{200}$	13	0.0004			
	$BNL3594_{173}$	13	0.0007			
	$DPL405_{265}$	11	0.0007			
SCY	$MGHES22_{200}$	12	0.0006			
WUE	$MGHES22_{200}$	12	0.0006			
OAE						
GLM				**MLM**		
Trait	Marker Locus	r^2 (%)	p	Trait	Marker Locus	p
LP	$DPL322_{197}$	12	0.0007	LP	$DPL322_{197}$	0.0008
LY	$DPL490_{241}$	15	0.0001	LY	$DPL176_{275}$	0.0003
	$JESPR157_{237}$	14	0.0002		$JESPR157_{237}$	0.0008
	$DPL176_{275}$	13	0.0004	SCY	$JESPR157_{237}$	0.0005
SCY	$DPL490_{241}$	18	0.00002	WUE	$JESPR157_{237}$	0.0005
	$JESPR157_{237}$	16	0.00009			
WUE	$DPL490_{241}$	18	0.00003			
	$JESPR157_{237}$	16	0.00009			

A total of nine and four significant loci were detected by GLM and MLM models, respectively, for five drought parameters: DSI, YR, HM, STI and YI. No significant QTL was identified for GMP and YP. All detected associations were highly significant ($p < 0.001$) and major-effect (PVE > 10%) with a PVE value ranging from 11 % to 13%. The most significant association was identified for JESPR157-237 linked to YI ($p = 0.0002$).

Table 3.9. Drought parameters-associated loci identified by GLM and MLM methods.

GLM				MLM		
Trait	Marker Locus	r^2 (%)	p	Trait	Marker Locus	p
DSI	$DPL100_{160}$	12	0.0007	YI	$TMB2068_{145}$	0.0005
YR	$CIR169_{180}$	12	0.0007	YR	$CIR169_{180}$	0.0007
HM	$BNL1034_{320}$	12	0.0006	STI	$DPL541_{244}$	0.0008
	$BNL1151_{207}$	11	0.0009	DSI	$DPL100_{160}$	0.00096
STI	$BNL1151_{207}$	12	0.0006			
	$BNL1034_{320}$	12	0.0008			
YI	$JESPR157_{237}$	13	0.0002			
	$TMB2068_{145}$	13	0.0003			
	$BNL1034_{320}$	13	0.0004			

3.4. Discussion

3.4.1. Phenotypic Evaluation

In the present chapter, a germplasm panel of 99 upland cotton genotypes was characterized genetically and morphologically with 177 SSRs for four characters and seven drought parameters under two watering-regimes. This study also revealed which of the lines showed the greatest phenotypic stability under drought stress conditions.

The genotypes showing the least change in seed cotton yield under drought stress were: Zeta 2 (0%), Delcerro (-2%), Nazilli 87 (-3%), and DAK 66/3 (-4%). Lint yield was fairly stable under drought stress in three of the same genotypes: Zeta 2 (+2%), Delcerro (-1%), DAK 66/3 (-3%) and Vulcano (-3%). Lint percentage was not altered much by watering regime. In Stoneville 213 and Vulcano, LP increased 8 to 9% under drought stress indicating the potential of these cultivars to adapt to drought conditions. Water-use efficiency increased in all genotypes under drought stress. The top performing genotypes were, of course, those which had little change in yield under drought: Zeta 2 (100%), Delcerro (100%), Nazilli 87 (91%) and DAK 66/3 (88%).

Under drought conditions, Np Ege 2009 (525 kg ha^{-1}), Nazilli M39 (452 kg ha^{-1}), Sj U 86 (434 kg ha^{-1}), Barut 2005 (430 kg ha^{-1}), Nazilli 143 (429 kg ha^{-1}), and Np

Ozbek 100 (426 kg ha^{-1}) had the highest yield potential. In contrast, yield reduction ($\bar{x}$ = 26%) was lowest in: Zeta 2 (0%), Delcerro (2%), Nazilli 87 (3%), and DAK 66/3 (4%). Yield index was higher than the average value of 1 in sixty-three genotypes. The best genotypes were Np Ege 2009 (1.3) and DAK 66/3 (1.3).

High ($\geq$ 1) and low ($\leq$ 1) drought sensitivity index ($\bar{x}$ = 0.95) indicates susceptibility and tolerance against drought stress, respectively. Fifty-six genotypes showed some level of drought tolerance. The top five genotypes were Zeta 2 (0.1), Nazilli 87 (0.2), DAK 66/3 (0.3), Niab 999 (0.3), and Delcerro (0.3). Forty-three genotypes did not show a significant level of drought tolerance. The most sensitive cultivars were: Taskent 1 (1.9), Tamcot 22 (1.7), Taskent Uzbek (1.7) and Coker 208 (1.5).

Stress tolerance index ($\bar{x}$ = 0.7) was highest in Np Ege 2009 (1.6), Nazilli M39 (1.2), Barut 2005 (1.1), and Nazilli 143 (1.1). Harmonic mean ($\bar{x}$ = 343) and geometric mean productivity were highest in the same genotypes: Np Ege 2009 (495 and 510 kg ha^{-1}, respectively), Nazilli M39 (437 and 444), Barut 2005 (421 and 425).

Stoneville 453, Caroline Queen, Sayar 314, Cukurova 1453, Nazilli 84, Nazilli 87, Ersan 92 and Ege 7913 are widely grown in Turkey (Cukobirlik 2017). Two of these cultivars (Ersan 92 and Nazilli 87) performed well in our study under drought conditions. Our study identified several other genotypes with good drought tolerance. For example, yield component traits were fairly stable in DAK 66/3, Ms 30/1, Zeta 2, Delcerro, Delcerro Ms, Niab 999 and Vulcano under water-limited conditions. Changes in climate, such as temperature and precipitation, can have profound impacts on agricultural production including cotton yield (ITC 2011). Cotton genotypes that show little change in yield-based traits between well-watered and water-stress conditions may be more adaptive and less susceptible to unforeseen changes in climate.

3.4.2. Association Analysis for Yield and Drought Parameters

Many QTL analyses related to fiber and yield traits under different environments have been published for cotton (B. Wang et al. 2007; T. Zhang et al. 2013; Qin et al. 2015; H. Wang et al. 2015; Shi et al. 2015; Jamshed et al. 2016; R. Liu et al. 2018; C. Zhang et al. 2019; Shi et al. 2020). In comparison, drought tolerance in cotton has been considered in only a few reports (Saranga et al. 2001; Saranga et al.

2004; Saeed et al. 2011; Zheng et al. 2016; Abdelraheem et al. 2018; Hou et al. 2018; H. Li et al. 2019; B. Li et al. 2020).

Abdelraheem, Fang, and Zhang (2018) investigated drought tolerance related QTLs under field and greenhouse evaluations in a RIL population consisting of 97 individuals generated from a cross between TM1 and NM24016 lines. They detected 49 and 61 QTL for fiber quality and agronomic traits under drought conditions using a total of 1004 polymorphic loci produced by SSR, GBS-SNP and RGA-AFLP markers. In another study, Shukla et al. (2021) performed QTL analysis in an intra-specific cross population from susceptible and tolerant parents against water stress. They identified 19 QTLs: five for nitrate reductase activity, five for relative water content, four for chlorophyll stability index, four for proline content and one for total chlorophyll content, using 1116 GBS-SNP and 782 SSR markers. In other work, Sang et al. (2017) identified 15 SSR marker loci related to drought tolerance traits in a natural Upland cotton population using 74 SSR markers under an osmotic drought test.

In the present study, an association analysis combining drought tolerance and yield parameters was conducted under both well-watered and water-limited regimes. A total of 26 different SSR markers were linked significantly for all yield and drought parameters in *G. hirsutum* under both watering regimes. Among them, 13 markers were identified under well-watered and 9 markers under water-limited conditions. These 26 SSRs were widely distributed on 17 chromosomes without any tendency for A or D chromosomes.

Several marker loci were associated with more than one trait which was expected given the related nature of quantitative traits. Under water-stress conditions, BNL1151 (on A11) was associated with four traits (SCY, WUE, STI and HM), JESPR157 (on A8 and D8) was associated with four traits (SCY, LY, WUE and YI), and DPL247 (on D05) was linked to three traits: SCY, WUE and LY. These markers could potentially lie within genomic regions controlling drought tolerance.

Furthermore, we identified completely different sets of marker loci for the traits (except LP) under the two watering regimes suggesting that different alleles may be activated in response to drought conditions.

Interestingly, the TMB2018 marker locus linked to LP was detected by both association models under water limited and well-watered conditions. Therefore, it can be considered as a stable and reliable QTL for cotton yield. Moreover, marker loci with

high PVE and positive effects could be useful for marker-assisted selection of yield and drought tolerance traits under water-limited conditions. For example, DPL490 had a relatively strong effect (PVE = 18%) on seed cotton yield (SCY), lint yield (LY) and water-use efficiency (WUE) suggesting that this marker could be useful for increasing yield under water stress conditions.

3.4.2.1. Comparison with Previous Studies

One way of targeting potentially useful loci for marker-assisted selection is to compare our results with those of previous QTL analyses using these trait-associated SSR markers. BNL1151 was reported as associated with fiber uniformity by Wang et al. (2017), however, we identified it for four yield and drought related traits: seed cotton yield, water use efficiency, stress tolerance index, and harmonic mean productivity. BNL3545, associated with lint yield and lint percentage in our study, was previously reported for fiber elongation (Deng et al. 2019) and seed cotton weight (R. Liu et al. 2018). The marker DPL405, associated with lint yield in our study, was reported to be associated with fiber length (Zhang et al. 2012) and micronaire (Tan et al. 2015) in previous studies. BNL1034 was linked to drought related parameters in our study (stress tolerance index, harmonic mean productivity, and yield index), however, it was reported for dry root weight (Abdelraheem, Fang, and Zhang 2018), lint yield (Pauli et al. 2016), fiber length (Wang et al. 2017), leaf shape (Song et al. 2005) and seed cotton yield (Adawy et al. 2008) in previous studies. Lastly, BNL3474 was identified for fiber traits (fiber elongation, fiber strength and fiber uniformity) by Tang et al. (2015), however, it associated with lint percentage in a previous study (Chen, Qian, and Guo 2010) and in our study as well. BNL3594 was reported for osmotic potential (El-moghny et al. 2017), fiber length (Qin et al. 2015) and fiber strength (Jamshed et al. 2016; Qin et al. 2015), however, we identified it for lint yield. Given their potential linkage to multiple important traits, these markers are significant targets for marker-assisted selection in cotton breeding.

3.4.2.2. Exploration of Putative Candidate Genes

The genomic locations of the significant identified markers were investigated to explore hypothetical candidate genes around the region. Twelve QTL-associated marker sequences had significant similarity with 15 genomic locations in the cotton reference genome (*G. hirsutum* v2.1 GCF_007990345.1).

DPL890, linked to seed cotton yield in our study, has similarity with a beta-amylase 8 isoforms gene (Loc107944311) on chromosome D12. It was reported by Todaka et al. (2000) that water deficiency affects carbohydrate metabolism specifically enhancing beta-amylase activity to increase sugar content in cucumber cotyledons. Moreover, it was shown that high beta-amylase activity was related to high germination capacity and it could be used as an indicator of vigor strength during germination (Nandi 1995). Therefore, DPL890 could be a candidate gene-molecular marker for seed yield in cotton.

DPL223, linked to lint yield in this study, aligned significantly to an auxin responsive protein IAA11 (Loc107952733) on chromosome D07. Several reports indicated that auxin response factors have potential roles in plant development and drought tolerance mechanisms (Bouzroud et al. 2018; Shani et al. 2017; Salehin et al. 2019). Moreover, several studies showed that auxin as a phytohormone has positive roles in cotton fiber development such as fiber cell initiation and fiber elongation (T. Zhang et al. 2015; Y. Zhang et al. 2017; Xiao, Zhao, and Zhang 2019). Therefore, this marker locus may have a role in fiber development, thus, indirectly it could be used in breeding of lint yield in cotton.

STV023, also associated with seed cotton yield in our study, was placed 73 bp downstream of the vicilin-like seed storage protein, At2g28490, gene (Loc107954241) on chromosome A07. Vicilins are one of two main seed storage proteins in cottonseed (Hu et al. 2011; Z. He et al. 2021) and serve as a nutrient reservoir. Thus, the QTL associated with STV023 may be this seed storage protein gene.

DPL520, associated with lint potential in our study, was found 570 bp downstream of a calcium-dependent protein kinase 21-like protein gene (Loc121218699) and approximately 3 kb upstream of a lactoylglutathione lyase GLX1-like protein gene (Loc121218700) on chromosome D06. Calcium-dependent protein kinases have been well-characterized in many plants and have functions in plant

responses and transductions of signals through the cell network (Gao et al. 2018) by phosphorylating various proteins such as ion channels, enzymes and transcription factors (Yip Delormel and Boudsocq 2019). Moreover, Huang et al. (2008) cloned and characterized a *G. hirsutum* calcium dependent protein kinase-1 gene (GhCPK-1) in transgenic Arabidopsis lines and showed that GhCPK-1 has function on fiber elongation in cotton. Therefore, the DPL520 marker locus could be a strong candidate gene marker and may be useful in breeding for fiber yield in cotton. A lactoylglutathione lyase, also known as glyoxalase I, catalyzes the first step of detoxification of methylglyoxal (Liu and Gronenborn 2012) and has been reported as involved in the response mechanisms of plant abiotic stress (Sankaranarayanan et al. 2017). Therefore, the associated genomic region could be a potential QTL for lint yield and abiotic stress tolerance in cotton.

BNL1034, linked to drought parameters in our study, was aligned and overlapped with a protease-do-like protein gene (Loc107924195) on chromosome A11 which has a serine-type endopeptidase activity, thus, can have possible roles in degradation of damaged proteins (Gaudet et al. 2011). In one study, it was shown that endopeptidase activity increased under stress condition in cotton (Gai et al. 2008). Therefore, this locus could be a potential QTL involved in drought stress mechanisms in cotton.

BNL1151, associated with drought parameters in our study, had similarity to the sequence of the 60s ribosomal protein L19-1 gene (Loc107923932) on chromosome A11 which has very important activity in the translation process of cells such as RNA binding, structural constituents of ribosomal machinery (Gaudet et al. 2011) and stress signaling (Wool 1996; Warner and McIntosh 2009; Nagaraj et al. 2016). This is expected because water deficiency directly decreases protein synthesis in plant cell which is known as stress induced-loss of polysomes (Dhindsa and Bewley 1976; Alqurashi et al. 2018). Therefore, this marker region can be associated with water stress-induced protein synthesis.

JESPR157, associated with seed cotton yield, lint yield and water use efficiency in the present study, was aligned to a zinc finger CCCH domain-containing protein-19 (Loc107909066) gene on chromosomes A08 and D08. CCCH domain-containing proteins are transcription factors found in a wide-range of organisms and have multiple roles in plant growth and many abiotic stress responses such as heat, drought and salt

(Y. Guo et al. 2009; Pi et al. 2018). There is ample evidence that zinc finger gene families are involved in initiation, elongation and development of cotton fibers (Salih et al. 2016; 2019; Padmalatha et al. 2012; Thyssen et al. 2014). This may indicate that JESPR157 could lie in a QTL responsible for fiber development in cotton.

TMB2018 which was considered to be a stable LP and drought related QTL in our study, was found in an uncharacterized gene within the cotton genome, however, a heat stress transcription factor-like protein gene was found approximately 12 kb upstream of the locus. Heat stress transcription factors regulate the expression of heat shock proteins in response to heat stress factors (M. Guo et al. 2016). Moreover, heat shock transcription factors were reported to have roles in fiber development of cotton (J. Wang et al. 2014). Therefore, TMB2018 may be part of a QTL responsible for regulation of fiber development under drought stress in cotton.

TMB1295, associated with LP in our study, had high similarity to a region approximately 3 kb downstream of grim reaper-like protein gene sequence (Loc107902920) on chromosome D05. Grim reaper proteins function in cell death regulation through the signal transduction network in response to stress factors (Wrzaczek et al. 2015; Wrzaczek et al. 2009). Thereby, it is expected that the TMB1295 genomic region may be related to a cell death mechanism induced by water stress.

BNL3594, associated with drought parameters, was found in an uncharacterized protein sequence. However, ALA-interacting subunit-2 gene (Loc121218672) and F-box protein At5g46170-like gene (Loc121218673) on chromosome D06, which has possible role in heat acclimation in response to heat stress (Lim et al. 2006) were present approximately 4 kb upstream and downstream of the marker, respectively. This could be a QTL which may have possible indirect roles in drought related mechanisms because water deficiency can be result from ambient heat stress (Lamaoui et al. 2018).

BNL3545, linked to lint traits in our study, had similarity to a region approximately 4 kb upstream of the NLP9-like protein isoform X1 (Loc10797456) gene sequence and approximately 3 kb downstream of the NAC domain-containing protein 62-like gene (Loc107927358) sequence on chromosome A02. NLP proteins and NN-like proteins are member of a transcription factor family containing a nitrate-responsive domain and are reported to be associated with nitrate signaling and response

mechanisms in higher plants (Schauser et al. 1999; Schauser, Wieloch, and Stougaard 2005; Castaings et al. 2009; Konishi and Yanagisawa 2013; 2019; Jagadhesan et al. 2020). NAC transcription factors make up a large protein family having multiple functions in the reprogramming of gene transcription in response to stress factors in plants (Nuruzzaman, Sharoni, and Kikuchi 2013). Moreover, it was shown that NAC genes had roles in secondary cell wall synthesis in fiber development and in stress response mechanisms in cotton (H. Sun et al. 2018). Therefore, the BNL3545 genomic region may be part of a significant QTL for fiber development under drought stress and could be a useful candidate gene-marker for fiber breeding in cotton.

DPL100, associated with drought parameters in our study, was aligned approximately 2 kb upstream of a transcription factor TCP-17 like protein gene (Loc107951214) on chromosome A12. It was reported that transcription factor TCP-17 proteins have roles in regulation of gene expressions for leaf development and senescence in plants (Koyama, Sato, and Ohme-Takagi 2017; Riechmann et al. 2000). Some of the TCP transcription factors are negative regulators for leaf growth and favor aging in plant development. There are several studies reporting possible roles of TCP proteins in cotton fiber development (Hao et al. 2012; M.-Y. Wang et al. 2013; K. Zheng et al. 2018; X. Liu et al. 2015). In one study, Wang et al. (2013) overexpressed a *G. hirsutum* TCP transcription factor gene in Arabidopsis. This resulted in a remodeled auxin level and distribution which indicated that the GhTCP transcription factor is responsible for fiber development through regulating auxin in Upland cotton. Moreover, it is noteworthy that the DPL223 marker locus, also found in an auxin-responsive protein gene sequence, was linked to lint yield in our study. Taken together, the DPL100 marker locus may be a QTL that controls fiber growth through auxin-mediated pathways and could be useful marker loci for fiber development in cotton breeding.

While our work has revealed potential candidate genes for the detected QTLs, these candidates must be further investigated and their effects on the traits should be confirmed by genetic analysis in future studies. Such work will also provide further insight on drought and yield related mechanisms in cotton.

CHAPTER 4

CONCLUSION

In conclusion, we identified 58 and 26 different SSR marker loci associated with fiber and plant structure traits and drought and yield components under two watering regimes. Our study is unique in looking at drought and yield traits under both well-watered and water-limited conditions. To our knowledge, most of the loci associated with the aforementioned traits were newly identified, highly significant major-effect MTAs. Moreover, we highlighted eight stable MTAs within all significantly identified loci (Table 4.1). Of them, BNL3502 was detected as a highly stable marker trait association for FE.

Table 4.1. Stable MTAs for fiber, yield and plant structure traits in this study.

Trait	**Marker**	
1st PBR	DPL088	under both locations
EAR	DPL080	under both regimes, both models
FE	**BNL3502**	both locations, both regimes, both models
FL	DOW070	both regimes
FS	DPL405	both locations, both regimes
PH	BNL2496	both regimes, both models

(Cont. on the next page)

Table 4.1. (cont.)

	MGHES22	both regimes, both models
TBN	BNL3502	both regimes
	BNL1151	both regimes
LP	TMB2018	both regimes both locations

The association mapping results together with the genetic diversity outcomes should facilitate the introgression of quantitative trait loci and the development of drought tolerant cotton lines with high yield. The significant, major effect marker loci and highly vigorous, tolerant genotypes may be useful in breeding programs to develop new cotton varieties with enhanced genetic diversity as well as drought tolerance.

APPENDIX A

Table 1. Accepted Gossypium species (Source: POWO 2021). Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. (Source: www.plantsoftheworldonline.org/)

Gossypium anapoides J.M.Stewart, Craven, Brubaker & Wendel
Gossypium anomalum Wawra & Peyr.
Gossypium arboreum L.
Gossypium areysianum Deflers
Gossypium aridum (Rose & Standl.) Skovst.
Gossypium australe F.Muell.
Gossypium barbadense L.
Gossypium bickii (F.M.Bailey) Prokh.
Gossypium bricchettii (Ulbr.) Vollesen
Gossypium californicum Mauer
Gossypium contextum O.F.Cook & J.W.Hubb.
Gossypium costulatum Tod.
Gossypium cunninghamii Tod.
Gossypium darwinii G.Watt
Gossypium dicladum O.F.Cook & J.W.Hubb.
Gossypium ekmanianum Wittm.
Gossypium enthyle Fryxell, Craven & J.M.Stewart
Gossypium exiguum Fryxell, Craven & J.M.Stewart
Gossypium gossypioides (Ulbr.) Standl.
Gossypium harknessii Brandegee
Gossypium herbaceum L.
Gossypium hirsutum L.
Gossypium hypadenum O.F.Cook & J.W.Hubb.
Gossypium incanum (O.Schwartz) Hillc.
Gossypium irenaeum Lewton

(Cont. on the next page)

Table 1. (cont.)

Gossypium klotzschianum Andersson
Gossypium laxum L.Ll.Phillips
Gossypium lobatum Gentry
Gossypium londonderriense Fryxell, Craven & J.M.Stewart
Gossypium longicalyx J.B.Hutch. & B.J.S.Lee
Gossypium marchantii Fryxell, Craven & J.M.Stewart
Gossypium morrilli O.F.Cook & J.W.Hubb.
Gossypium mustelinum Miers ex G.Watt
Gossypium nelsonii Fryxell
Gossypium nobile Fryxell, Craven & J.M.Stewart
Gossypium patens O.F.Cook & J.W.Hubb.
Gossypium pilosum Fryxell
Gossypium populifolium (Benth.) F.Muell. ex Tod.
Gossypium pulchellum (C.A.Gardner) Fryxell
Gossypium raimondii Ulbr.
Gossypium robinsonii F.Muell.
Gossypium rotundifolium Fryxell, Craven & J.M.Stewart
Gossypium schwendimanii Fryxell & S.D.Koch
Gossypium somalense (Gürke) J.B.Hutch., Silow & S.G.Stephens
Gossypium stephensii J.P.Gallagher, C.E.Grover & Wendel
Gossypium stocksii Mast.
Gossypium sturtianum (R.Br.) J.H.Willis
Gossypium thurberi Tod.
Gossypium timorense Prokh.
Gossypium tomentosum Nutt. ex Seem.
Gossypium trifurcatum Vollesen
Gossypium trilobum (DC.) Skovst.
Gossypium triphyllum (Haw.) Hochr.
Gossypium turneri Fryxell
Gossypium vollesenii Fryxell

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Baytar, Asena Akkose, Ceng Peynircioğlu, Volkan Sezener, Huseyin Basal, Anne Frary, Amy Frary and Sami Doğanlar. "Identification of stable QTLs for fiber quality and plant structure in Upland cotton (G. hirsutum L.) under drought stress." Industrial Crops and Products 124 (2018): 776-786.

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Education

PhD. (2021), Department of Molecular Biology and Genetics, Izmir Institute of Technology, Izmir, Turkey (GPA: 3.86/4.00). Thesis Title: "Molecular Genetic Analysis in Cotton (*Gossypium hirsutum* L.)"

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Publications

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Awards

2021, AOSB Sanayi Odaklı Ar-Ge ve İnovasyon Proje Yarışması Türkiye 2.si, Proje Başlığı: "Türk Pamuk Çeşitlerinde Kuraklık Toleransı ve Lif Kalite Özelliklerinin İlişkilendirme Analizleri"

2021, Uşak Üniversitesi TTO 2. Ar-Ge ve Tasarım Proje Pazarı Türkiye 3. sü, Proje başlığı: "CRISPR-Cas9 Sistemi ile Pamukta Gossipol Biyosentezi için Genom Düzenlemesi"