

Cotton

Gossypium (Malvaceae)

J. F. Wendel

Iowa State University, Ames, Iowa 50011, USA

Introduction

The genus *Gossypium* is unique in the annals of plant domestication in that a minimum of four similar crop plants emerged independently on opposite sides of the world. *Gossypium* includes four species that have been domesticated for their seed fibre and oil: the African-Asian diploids, *G. arboreum* and *G. herbaceum*, and the New World tetraploids, *G. hirsutum* and *G. barbadense*. These species collectively provide the world's most important textile fibre and its second most valuable oil and meal seed. Although *G. arboreum* is still an important crop plant in India and Pakistan and *G. herbaceum* is cultivated on a small scale in several regions of Africa and Asia, New World tetraploid cultivars presently dominate world-wide cotton production, having displaced the majority of Old World diploid cultivation. Primary production areas for *G. barbadense* (Extra-long staple, Pima, Egyptian cotton) include several regions of the Commonwealth of Independent States, Egypt, Sudan, India, the USA and China. *Gossypium barbadense* is favoured for some purposes because of its long, strong and fine fibres, but its relatively low yield has limited its importance to <10 per cent of total world production. Over 90 per cent of the world's cotton is supplied by modern cultivars of *G. hirsutum*, or Upland cotton. Upland cultivars currently are grown in more than 40 nations in both tropical and temperate latitudes, from 47° N in the Ukraine and 37° N in the USA to 32° S in South America and Australia (Niles and Feaster, 1984).

Modern cultivars of the four domesticated species are high-yielding, day-length neutral, annualized plants with easily ginned, abundant fibre. These 'improved' characteristics resulted from human selection, by both aboriginal and modern plant breed-

ers, from tropical, perennial ancestors with shorter, sparser fibre. Cotton has an ancient history of cultivation in both the Old and New Worlds, as documented by archaeobotanical remains, for each of the four domesticated species, that extend back several millennia or more (Lee, 1984; J. Vreeland, pers. comm.). It appears that a minimum of four independent domestications were involved in cotton development (Percy and Wendel, 1990; Wendel *et al.*, 1989, 1992). Apparently each was derived from divergent progenitors by parallel and/or convergent selection for similar agronomically favourable characteristics.

Cytotaxonomic background

Gossypium includes approximately 50 species of shrubs and small trees distributed throughout the arid or seasonally arid tropics and subtropics (Table 70.1). The most widely followed taxonomic treatments are those of Fryxell (Fryxell, 1979; Fryxell *et al.*, 1992), in which he recognizes 39 diploid ($2n = 26$) and six tetraploid ($2n = 4x = 52$) species grouped into four subgenera and eight sections. Additional species probably remain to be discovered, as recent explorations have led to the recognition of new species from Africa/Arabia (Vollesen, 1987) and Australia (Fryxell *et al.*, 1992). Extensive chromosomal evolution accompanied the diversification and geographical radiation of the genus, leading to the recognition of seven diploid genomic groups (designated A-G; the distinctness of the G genome from the C genome is questionable). These cytogenetic distinctions are based on chromosome size differences and interspecific meiotic pairing behaviour (reviewed in Endrizzi *et al.*, 1985). Tetraploid taxa are allopolyploids, containing both A-genome and D-genome nuclear contributions.

Molecular analysis of the chloroplast genome (Wendel and Albert, 1992) demonstrate that phylogenetic relationships are largely congruent with genome designations and geographical distributions (Fig. 70.1). Three major monophyletic groups of diploid species correspond to three continents: Australia (C, G genome), the Americas (D genome), and Africa (A, E, and F genome). African B-genome diploids are hypothesized to share a common ancestor with the D-genome species. In addition

Table 70.1 Classification of *Gossypium*.

Subgenus STURTIA	Australian C-genome diploids (G genome in <i>G. bickii</i>)
Section Sturtia :	<i>G. robinsonii</i> , <i>G. sturtianum</i>
Section Grandicalyx :	<i>G. costulatum</i> , <i>G. cunninghamii</i> , <i>G. enthyle</i> , <i>G. exiguum</i> , <i>G. londonderriensis</i> , <i>G. marchantii</i> , <i>G. pilosum</i> , <i>G. populifolium</i> , <i>G. pulchellum</i> , <i>G. nobile</i> , <i>G. rotundifolium</i>
Section Hibiscoidea :	<i>G. australe</i> , <i>G. nelsonii</i> , <i>G. bickii</i>
Subgenus HOUZINGENIA :	New World D-genome diploids
Section Houzingenia	
Subsection <i>Houzingenia</i> :	<i>G. thurberi</i> , <i>G. trilobum</i>
Subsection <i>Integrifolia</i> :	<i>G. davidsonii</i> , <i>G. klotzschianum</i>
Subsection <i>Caducibracteolata</i> :	<i>G. armourianum</i> , <i>G. harknessii</i> , <i>G. turneri</i>
Section Erioxylum	
Subsection <i>Selera</i> :	<i>G. gossypioides</i>
Subsection <i>Erioxylum</i> :	<i>G. aridum</i> , <i>G. laxum</i> , <i>G. lobatum</i> , <i>G. schwendemanii</i>
Subsection <i>Austroamericana</i> :	<i>G. raimondii</i>
Subgenus GOSSYPIMUM :	African and Arabian diploids (A, B, E, and F genomes)
Section Gossypium	
Subsection <i>Gossypium</i> :	<i>G. arboreum</i> , <i>G. herbaceum</i> L. (A genome)
Subsection <i>Anomala</i> :	<i>G. anomalum</i> , <i>G. capitiviridis</i> , <i>G. trifurcatum</i> , <i>G. triphyllum</i> (B genome)
Section Pseudopambak	
Subsection <i>Pseudopambak</i> :	<i>G. areysianum</i> , <i>G. benadirensis</i> , <i>G. bricchettii</i> , <i>G. incanum</i> , <i>G. somalense</i> , <i>G. stocksii</i> (E genome)
Subsection <i>Longiloba</i> :	<i>G. longicalyx</i> (F genome)
Subgenus KARPAS :	New World AD-genome tetraploids
Section Karpas :	<i>G. barbadense</i> , <i>G. darwinii</i> , <i>G. hirsutum</i> , <i>G. lanceolatum</i> , <i>G. mustelinum</i> , <i>G. tomentosum</i>

to providing information on the phylogeny of the genus, the molecular data provide a framework for timing various divergence events, which allows the following interpretation of the origin and radiation of the genus.

Australian (C genome) cottons consist of sixteen species, including a group of unusual herbaceous perennials with arillate seeds from the Kimberley region (Fryxell *et al.*, 1992). Australian species comprise one branch of the earliest split in the genus, and African species are basal in the other branch. It is likely, therefore, that *Gossypium* originated in either Africa or Australia. Fossil evidence and molecular sequence divergence estimates both suggest that these two primary branches diverged perhaps 25–30 million years ago. Because the most basal branch within the Australian species is represented by *G. robinsonii* (from Western Australia), radiation of *Gossypium* in Australia most probably proceeded

eastward from the westernmost portion of the continent.

Several subgroups exist within the primarily African branch: the three B-genome species, the four E-genome species, the sole representative of the F genome and the two A-genome cultivated cottons, *G. arboreum* and *G. herbaceum*.

As shown in Fig. 70.1, a relatively early (perhaps 6–11 million years BP) long-distance dispersal from Africa led to the evolution of the New World D-genome diploids. This assemblage of thirteen primarily Mexican species probably originated in north-western Mexico, with later radiations into other regions. An early diversification among D-genome taxa was between lineages that are presently represented by a group of relatively compact, shrubby species from Baja California and an assemblage of larger shrubs and small trees from western and southern Mexico. Later range extensions arose from

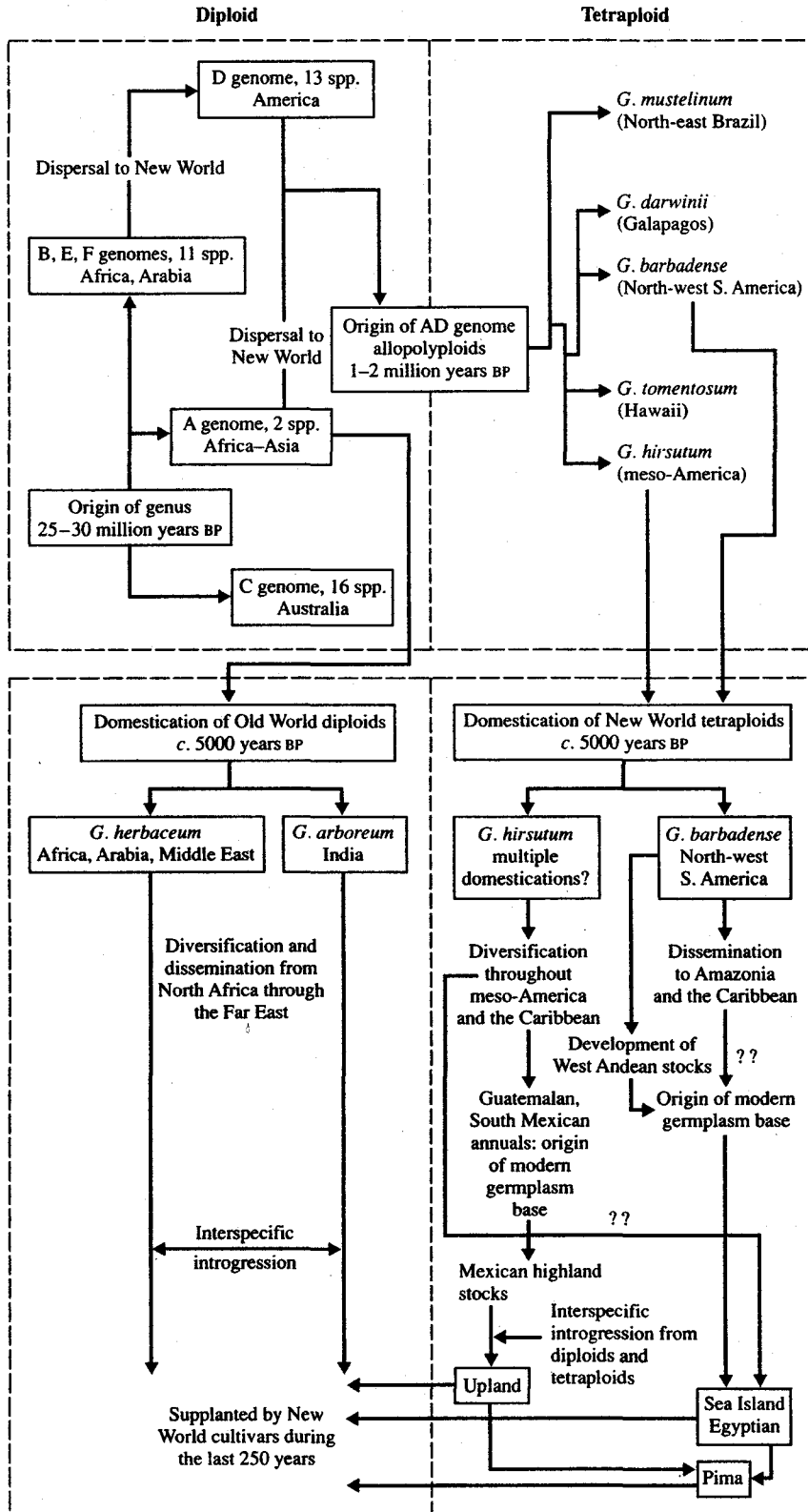


Fig. 70.1 Phylogeny of *Gossypium* (top) and the origin and diversification of the cultivated cottons (bottom).

relatively recent (probably Pleistocene) long-distance dispersals, leading to the evolution of endemics in Peru (*G. raimondii*) and the Galapagos Islands (*G. klotzschianum*; Wendel and Percival, 1990).

Ample evidence establishes that the New World tetraploid cottons are allopolyploids containing one genome that is similar to those found in the Old World, A-genome diploids and one genome similar to those found in the New World, D-genome diploids (reviewed in Endrizzi *et al.*, 1985; also see Wendel, 1989). Accordingly, genomic sympatry must have been established, at least ephemerally, at some time in the past, but the two parental genomic groups currently exist in diploid species with geographical distributions that are half a world apart. The mysteries surrounding polyploid formation have led to considerable speculation regarding the identity of the progenitor diploid species, the time of allopolyploidization and the question of polyploid monophyly (reviewed in Endrizzi *et al.*, 1985). Views vary widely with respect to the time of polyploid formation, from proposals of a Cretaceous origin, with subsequent allopatry of genomic groups arising from tectonic separation of the South American and African continents, to suggestions of very recent origins in prehistoric times involving transoceanic human transport.

Molecular evidence suggests that all polyploids share a common ancestry, lending support to the hypothesis that AD allopolyploidization occurred only once. In addition, all allopolyploids contain an Old World (A-genome) chloroplast genome, indicating that the seed parent in the initial hybridization event was an African or Asian A-genome taxon (Wendel, 1989). Molecular data also suggest a relatively recent (Pleistocene) origin of the polyploids, perhaps within the last 1–2 million years, consistent with earlier suggestions based on cytogenetic (Phillips, 1963) and ecological considerations (Fryxell, 1979).

A Pleistocene origin allopolyploid cotton has several evolutionary implications. First, morphological diversification and spread of tetraploid taxa subsequent to polyploidization must have been relatively rapid. *Gossypium mustelinum*, the sole descendant of one branch of the earliest polyploid radiation (Fig. 70.1), is restricted to a relatively small region of north-east Brazil. Both of the cultivated species (*G. barbadense* and *G. hirsutum*) are widely distributed in Central and South America,

the Caribbean and even reach distant islands in the Pacific (Solomon Islands, Marquesas, etc.). Each of these species shares recent common ancestry with island endemics that originated from additional long-distance dispersals: *G. barbadense* with *G. darwinii* (Galapagos Islands; Wendel and Percy, 1990) and *G. hirsutum* with *G. tomentosum* (Hawaiian Islands; DeJooode and Wendel, 1992). The sixth tetraploid species (after Fryxell, 1979), *G. lanceolatum* (= *G. hirsutum* race 'palmeri'), which is known only as a cultigen, is completely interfertile with *G. hirsutum*. These facts, in conjunction with a wealth of molecular evidence (Brubaker and Wendel, 1993) support the conclusion that *G. lanceolatum* is more properly considered a variant of *G. hirsutum*.

A second implication concerns the diploid parentage of the allopolyploids. A Pleistocene origin of the allopolyploids, as opposed to a more ancient origin, increases the likelihood of recognizing modern diploid lineages that contain descendants of the original genome donors. Many investigators have considered a species similar to *G. raimondii*, from Peru, as representing the closest living model of the D-genome paternal donor to the allopolyploids, although other species have been suggested (Endrizzi *et al.*, 1985; Wendel, 1989). *Gossypium raimondii* belongs to an evolutionary lineage of small trees and shrubs from southern and western Mexico (*G. laxum*, *G. lobatum*, *G. schwendimanii*, *G. aridum*, *G. gossypioides*), suggesting the taxa from which the closest descendant of the original D-genome donor may be found. The identity of the A-genome donor is also uncertain. Genomes of the only two A-genome species, *G. arboreum* and *G. herbaceum*, differ from the A subgenome of allopolyploid cotton by three and two chromosomal arm translocations respectively, suggesting that *G. herbaceum* more closely resembles the A-genome donor than *G. arboreum*.

A third implication of a Pleistocene polyploid origin concerns the biogeography of their formation. Cytogenetic data, combined with the observation that the only known wild A-genome cotton is African (*G. herbaceum* subsp. *africanum*), has been used to support the suggestion that polyploidization occurred following a transatlantic introduction of a species similar to *G. herbaceum*. While this theory is plausible, it should be pointed out that *G. herbaceum* is not the actual maternal parent, as indicated by its cytogenetic and molecular differentiation from the

A subgenome of the polyploids. Wendel and Albert (1992) raised the possibility of a pre-agricultural A-genome radiation into Asia followed by a transpacific, rather than transatlantic, dispersal to the Americas. This possibility is supported by the biogeography of the D-genome species, which are hypothesized to have originated in north-western Mexico. The relatively recent arrival of *G. raimondii* in Peru also suggests that the initial hybridization event may have taken place in meso-America rather than South America.

Early history

Little is known about the time and place of domestication of *Gossypium arboreum* and *G. herbaceum* in the Old World. Cloth fragments and yarn that date to 4300 years BP have been recovered from archaeological sites in India and Pakistan, although it is not clear which of the two species is represented in these earliest remains. *Gossypium herbaceum* is known primarily as a crop plant (grown from Ethiopia to western India), with the single exception of an endemic form from southern Africa, *G. herbaceum* subsp. *africanum*. This morphologically distinct entity, which occurs in regions far removed from historical or present cotton cultivation, has a unique ecological status in that it is fully established in natural vegetation in open forests and grasslands. Its small fruit, thick, impervious seed coats, sparse lint and absence of sympatric cultivated *G. herbaceum* suggest that *G. herbaceum* subsp. *africanum* is an indigenous wild plant. *Gossypium arboreum*, known only as a cultivated plant, has a centre of diversity in India and an extensive range from China and Korea westward into northern Africa. Wild forms of *G. arboreum* have not been verified, although presumably feral, perennial derivatives have been described. When *G. arboreum* and *G. herbaceum* are cultivated sympatrically, as in western and southern India and western China, occasional interspecific hybrids arise, yet the integrity of each species remains over time (Hutchinson *et al.*, 1947). Interspecific hybrids are fertile, but F₂ and later generation progenies are characterized by a high frequency of non-germinable seeds, moribund seedlings or other aberrant recombinant types. *Gossypium arboreum* and *G. herbaceum* also differ by a single reciprocal translocation (Endrizzi *et al.*, 1985).

The lack of wild *G. arboreum* and the extreme geographical separation between *G. herbaceum* subsp. *africanum* and cultivated forms of either species have led to speculation regarding the origin of the two species. One widely held view is that *G. arboreum* arose from *G. herbaceum* early in the history of diploid cotton cultivation (Hutchinson *et al.*, 1947). An alternative hypothesis is that *G. arboreum* and *G. herbaceum* diverged prior to domestication. Fryxell (1979), for example, argues that the genetic differences between the two species are too great to have arisen during the relatively brief period in which domesticated cottons have existed. Recent molecular evidence (Wendel *et al.*, 1989) supports this later hypothesis: the genetic similarity between *G. arboreum* and *G. herbaceum* is lower than for documented progenitor-derivative and crop-ancestor species pairs. These data, and the genetic and cytogenetic observations listed above, support the hypothesis that cultivated *G. arboreum* and *G. herbaceum* were independently domesticated from different wild ancestors.

Considerably more detail is available regarding the origins of domesticated *G. barbadense*. A diverse array of archaeobotanical remains, such as seed, fibre, fruit, yarn, fishing nets and fabrics has been recovered from central coastal Peru, dating to 5500 years BP (J. Vreeland, pers. comm.). The relatively primitive fruit and fibre properties and location of these remains support the general belief that original domestication occurred in north-western South America (Hutchinson *et al.*, 1947). This hypothesis is supported by molecular evidence (Percy and Wendel, 1990), which implicates a genetic centre of diversity that is congruent with the geographic distribution of wild populations. Trans-Andean and northward migrations are thought to have occurred later, leading to the development of Caribbean forms and the distinctive 'kidney-seeded' cottons of Amazonia and northern South America (Percy and Wendel, 1990).

Gossypium hirsutum has a large indigenous range encompassing most of meso-America and the Caribbean, where it exhibits a diverse array of morphological forms spanning the wild-to-domesticated continuum. The oldest archaeobotanical remains are from the Tehuacan valley of Mexico, dating from 4000 to 5000 years BP (this estimate should be considered tentative until additional stratigraphic

and carbon-14 dating information become available; P. Fryxell and J. Vreeland, pers. comm.). These cottons apparently were introduced domesticated forms, suggesting that *G. hirsutum* was initially domesticated earlier. Wild or feral populations are widely distributed throughout the range of the species, thus providing few clues for ascertaining the time and place of original domestication. In addition, there is no single centre of diversity. Rather, two geographically broad centres of diversity are evident: one in southern Mexico–Guatemala and the other in the Caribbean (Wendel *et al.*, 1992).

One cannot discount the possibility that *G. hirsutum* may have been domesticated more than once, in more than one part of its native range, and at different times. Most who have considered the problem suggest that the modern, highly improved Upland cultivars, which currently dominate world cotton commerce, were developed from local, semi-domesticated progenitors in a centre of diversity near the Mexican–Guatemalan border (Hutchinson *et al.*, 1947). This scenario is supported by genetic data, which demonstrate that the germplasm of modern cultivars traces to Mexican highland stocks, which in turn, were derived from material originally from southern Mexico and Guatemala (Wendel *et al.*, 1992). An independent domestication for the ‘Hopi cottons’ of the American Southwest is suggested by Lee (1984), who traces these to wild northern Mexican ancestors. Cultivated forms of the morphologically distinctive *G. hirsutum* race ‘marie-galante’, from the northern part of South America and many Caribbean islands, may have been derived from northern Colombian stock or from introgression between West Indian wild forms of *G. hirsutum* and introduced *G. barbadense* (Lee, 1984). This latter possibility is consistent with molecular evidence, which shows that introgression of *G. barbadense* genes into *G. hirsutum* has been common in a broad area of sympatry in the Caribbean (Wendel *et al.*, 1992).

Recent history

European exploration of the New World led to ‘discovery’ of strains that were vastly superior to Old World cottons in many agronomic features. The indigenous Old World diploids were thus gradually supplanted by superior tetraploid cottons, first by

perennial forms of both *G. hirsutum* and *G. barbadense*, and, more recently and at an increasing rate, by modern annual varieties. The following account chronicles the multicultural development and globalization of modern tetraploid cotton cultivars.

All modern extra long staple cultivars (*G. barbadense*) are believed to have originated with the Sea Island cottons that appeared in the offshore islands of the south-east USA in the late eighteenth century. Although Sea Islands cotton’s origin is obscure, it clearly has a complicated parentage that includes germplasm from the north-western South American centre of diversity and possible inputs from West Indian forms of *G. barbadense* and *G. hirsutum* (Meredith, 1991; Niles and Feaster, 1984; Percy and Wendel, 1990). Despite its high-quality lint, the late maturity of Sea Island cotton made it especially susceptible to the boll weevil, and commercial production ceased during the early decades of this century. Some modern derivatives are still sporadically grown in various regions of the world, including several West Indian islands and Egypt.

The complexity and international character of the development of modern *G. barbadense* varieties is exemplified by the origin of ‘Egyptian’ cotton. Subsequent to the rise of Sea Island cotton and its dissemination to the Old World, Egyptian cotton was developed, in Cairo during the mid-1800s, from hybridization of a perennial Peruvian *G. barbadense* (known as Jumel’s tree cotton) with Sea Island cotton. Jumel’s tree cotton may have reached Africa from the Mediterranean region via a Spanish trade route from western South America. Later Egyptian varieties were developed from derivatives of this and other hybridizations with Sea Island cotton. It is from this heterogeneous assemblage that modern American, Egyptian and Russian extra long staple cottons were derived.

Historical data are quite detailed concerning the origin of the currently dominant Pima varieties of *G. barbadense*. Early varieties (pre-1950) were based on a relatively narrow germplasm base consisting almost entirely of several Egyptian strains. More recent cultivars (the Pima S series), which are developed to increase yield, adaptability and heat tolerance, were derived from a complex series of crosses involving descendants of Egyptian and Sea Island cottons and the Peruvian landrace ‘Tanguis’, as well as cultivars of *G. hirsutum*, which were

deliberately introgressed into *G. barbadense*. The present-day gene pool of modern *G. barbadense* cultivars, although significantly enriched by this interspecific introgression (Meredith, 1991; Percy and Wendel, 1990), contains only an average amount of genetic variability when compared with other crop plants (Doebley, 1989).

The origin and development of the highly productive, modern cultivars of *G. hirsutum* entailed several stages (Meredith, 1991; Niles and Feaster, 1984). Early introductions into the cotton belt of the USA apparently originated either directly from several parts of the indigenous range of the species, including the Caribbean, Mexico and Central America, or indirectly via reintroduction of Asian, Mediterranean or Levantine stocks collected and disseminated during the European colonial period. Relatively little is known regarding the proportional contribution of germplasm from various potential source areas (Caribbean, Mexico, Central America) into these early stocks.

Historical records provide more detail about the rise of cotton cultivation in the south-eastern USA during the late eighteenth and early nineteenth centuries (Niles and Feaster, 1984). Commercial-scale plantings began in earnest in the late 1700s, when two categories of cultivars, 'green seed' and 'black seed', predominated. The green-seeded stocks had longer, finer lint, higher yield and better disease resistance than the black-seeded stocks, but their adherent lint was difficult to gin. The invention of Whitney's saw gin allowed the green-seeded stocks to predominate until the daylength neutral Mexico highland stocks were introduced, beginning in the early 1800s. These new Mexican stocks were intentionally and perhaps unintentionally introgressed with the local green seed and black seed stocks, leading to the development of hybrids with vastly improved lint characteristics, yield, disease resistance and ease and earliness of harvest.

Further augmentation of the modern crop involved a series of additional, deliberate introductions, beginning in the early 1900s, in response to the devastation brought on by the boll weevil. Circumventing crop losses due to the boll weevil became a priority, so earlier maturing varieties were highly desired, as were cultivars adapted to the specific ecological conditions of the main cotton-growing regions of the USA. This led to the development of four basic categories of Upland cultivars (Acala, Delta, Plains,

Eastern), whose modern derivatives account for the majority of Upland cotton grown world-wide (Niles and Feaster, 1984; Meredith, 1991).

In the USA, Acala cultivars are grown primarily in irrigated regions of western Texas, New Mexico, and the San Joaquin valley of California. Acalas have a complicated breeding history involving Mexican stocks from the area surrounding Acala and Tuxtla in Chiapas, Mexico, with subsequent inputs of germplasm from a synthetic interspecific 'triple hybrid' (doubled [*G. arboreum* × *G. thurberi*] × *G. hirsutum*) and perhaps *G. barbadense* (Niles and Feaster, 1984; Meredith, 1991). Delta cottons, grown in the Mississippi delta, Arizona, southern California and elsewhere, can be traced to a mid-1880s Mexican introduction. Plains cottons, grown largely in northern Texas and Oklahoma, were derived from Mexican introductions with subsequent input of 'Kekchi' germplasm collected in Guatemala during the first decade of the twentieth century. The last group of modern cultivars, the Eastern group (e.g. the Coker family), is a heterogeneous assemblage of largely unknown pedigree. They are thought to consist primarily of selections from nineteenth and twentieth century Mexican introductions, perhaps with introgressed *G. barbadense* germplasm.

The preceding abbreviated history suggests that the modern Upland cotton gene pool was derived from a complex admixture of numerous introductions from a variety of sources. It is widely believed, however, that much of the early germplasm (e.g. 'green seed' and 'black seed') was replaced by a limited number of later Mexican introductions during the nineteenth and twentieth centuries. That a relatively severe genetic bottleneck accompanied the development of modern Upland cultivars is evidenced by molecular data (Wendel *et al.*, 1992), although in comparison with other crop plants, modest levels of genetic variation remain in commercially important breeding populations.

Prospects

After a period of decline due to problems associated with pests and competition from synthetic textiles, cotton's importance as a world crop has increased steadily in recent years. This trend is likely to continue as strains adapted to an expanding array

of agroecological settings are developed. Because modern mechanized production entails relatively heavy chemical inputs, e.g. fertilizers, fungicides, insecticides and herbicides, current objectives in cultivar improvement programmes include not only the traditional goals of increasing yield, fibre quality, earliness, disease resistance and diminution of plant size, but also objectives designed to ameliorate environmental damage associated with cotton production. Increased effort is also likely to be directed at improving salinity and stress tolerance, water-use efficiency and the quality and diversity of uses of cotton seed as a food and feed plant (e.g. low gossypol, high protein, high oil); the latter has received relatively little attention because the market value of cotton as a meal and oilseed is a quarter to a third of its value as a source of lint (Niles and Feaster, 1984). Hybrid cotton has received considerable attention during the last couple of decades (Davis, 1978; Niles and Feaster, 1984), but to date it has found commercial success only on a limited scale in India. Additional development of hybrid cotton will facilitate exploitation of the heterosis and novel genetic combinations that accompany synthesis of interspecific and intraspecific hybrids. The principal economic limitation is the expense of F₁ seed production; hand pollination is required because natural pollinators are usually insufficient to ensure a full crop.

Future genetic improvement programmes will continue to exploit the diverse reservoir of germplasm represented by wild and feral *Gossypium*. To date, diploid species have contributed genes for fibre strength, disease resistance, glandless seed (lacking gossypol, which is toxic to mammals), cytoplasmic male sterility and fertility restoration, whereas genes for disease resistance, nectariless and glandless cotton have been deliberately introduced from wild and feral tetraploids. These genetic improvements of Upland cotton, involving intentional interspecific introgression from a minimum of two tetraploid and four diploid *Gossypium* species (Meredith, 1991; Niles and Feaster, 1984), were obtained through classical genetic and plant breeding approaches. Further exploitation of both wild *Gossypium* and more phylogenetically distant sources of germplasm will involve genetic engineering (Stewart, 1991). This promise is being realized, as efficient transformation systems have been developed, and herbicide-tolerant

and insect-resistant transgenic cultivars have been synthesized (Bayley *et al.*, 1992; Cousins *et al.*, 1991).

Acknowledgement

The author wishes to acknowledge gratefully P. Betting, J. Stewart, P. van der Wiel and J. T. Walker for helpful comments on the manuscript. Special thanks are due to J. T. Walker for his good offices and various contributions. Financial support for the author's research was provided by the National Science Foundation.

References

- Bayley, C., Trolinder, N., Ray, C., Morgan, M., Quisenberry, J. E. and Ow, D. W. (1992) Engineering 2, 4-D resistance into cotton. *Theor. appl. Genet.* **83**, 645-9.
- Brubaker, C. L. and Wendel, J. F. (1993). Molecular evidence bearing on the specific status of *Gossypium lanceolatum* Todaro. *Genet. Res. Crop. Evol.* **40**, 165-70.
- Cousins, Y. L., Lyon, B. R. and Llewellyn, D. J. (1991). Transformation of an Australian cotton cultivar: prospects for cotton improvement through genetic engineering. *Aust. J. Plant Physiol.* **18**, 481-94.
- DeJode, D. R. and Wendel, J. F. (1992). Genetic diversity and origin of the Hawaiian Islands cotton, *Gossypium tomentosum*. *Am. J. Bot.* **79**, 1311-19.
- Davis, D. D. (1978) Hybrid cotton: specific problems and potentials. *Adv. Agron.* **30**, 129-57.
- Doebley, J. F. (1989) Isozymic evidence and the origin of crop plants. In D. E. Soltis and P. S. Soltis (eds). *Isozymes in plant biology*. Dioscorides Press, Portland, OR, pp. 165-86.
- Endrizzi, J. E., Turcotte, E. L. and Kohel, R. J. (1985). Genetics, cytology, and evolution of *Gossypium*. *Adv. Genet.* **23**, 271-375.
- Fryxell, P. A. (1979) *The natural history of the cotton tribe*. Texas A&M University Press, College Station, TX.
- Fryxell, P. A., Craven, L. A. and Stewart, J. McD. (1992) A revision of *Gossypium* sect. *Grandicalyx* (Malvaceae), including the description of six new species. *Syst. Bot.* **17**, 91-114.
- Hutchinson, J. B., Silow, R. B. and Stephens, S. G. (1947) *The evolution of Gossypium*. Oxford University Press.
- Lee, J. A. (1984) Cotton as a world crop. In R. J. Kohel and C. L. Lewis (eds), *Cotton*, Agron. Monogr. **24**, 1-25, Crop Sci. Soc. Am., Madison, WI.

Fig

Ficus carica (Moraceae)

Daniel Zohary

The Hebrew University of Jerusalem, Israel

- Meredith, W. R. (1991). Contributions of introductions to cotton improvement. In H. L. Shands and L. E. Wiesner (eds), *Use of plant introductions in cultivar development*, Part 1. Crop Sci. Soc. Am., Madison, WI, pp. 127–46.
- Niles, G. A. and Feaster, C. V. (1984) Breeding. In R. J. Kohel and C. F. Lewis (eds), *Cotton*, Agron. Monogr., 24, 201–31. Crop Sci. Soc. Am., Madison, WI.
- Percy, R. G. and Wendel, J. F. (1990) Allozyme evidence for the origin and diversification of *Gossypium barbadense* L. *Theor. appl. Genet.* 79, 529–42.
- Phillips, L. L. (1963). The cytogenetics of *Gossypium* and the origin of New World cottons. *Evolution* 17, 460–9.
- Stewart, J. McD. (1991) *Biotechnology of cotton*. CAB International, Wallingford, UK.
- Vollesen, K. (1987). The native species of *Gossypium* (Malvaceae) in Africa, Arabia and Pakistan. *Kew Bull.* 42, 337–49.
- Wendel, J. F. (1989) New World cottons contain Old World cytoplasm. *Proc. Natn. Acad. Sci. USA* 86, 4132–6.
- Wendel, J. F. and Albert, V. A. (1992) Phylogenetics of the cotton genus (*Gossypium* L.): character-state weighted parsimony analysis of chloroplast DNA restriction site data and its systematic and biogeographic implications. *Syst. Bot.* 17, 115–43.
- Wendel, J. F., Brubaker, C. L. and Percival, A. E. (1992). Genetic diversity in *Gossypium hirsutum* and the origin of Upland cotton. *Am. J. Bot.* 79, 1291–1310.
- Wendel, J. F., Olson, P. D. and Stewart, J. McD. (1989). Genetic diversity, introgression, and independent domestications of Old World cultivated cottons. *Am. J. Bot.* 76, 1795–1806.
- Wendel, J. F. and Percival, A. E. (1990). Molecular divergence in the Galapagos Island–Baja California species pair, *Gossypium klotzschianum* Anderss. and *G. davidsonii* Kell. *Plant. Syst. Evol.* 171, 99–115.
- Wendel, J. F. and Percy, R. G. (1990). Allozyme diversity and introgression in the Galapagos Islands endemic *Gossypium darwinii* and its relationship to continental *G. barbadense*. *Biochem. Syst. Ecol.* 18, 517–28.

Introduction

The fig, *Ficus carica*, is one of the classic fruit crops of the Mediterranean basin. Together with the olive, grape-vine and the date palm, figs initiated horticulture in this part of the world. Also today fig production is centred in the Mediterranean region. The only large-scale planting outside this area is in the USA (mainly California). Small quantities are produced also by Australia, South Africa, Mexico, Brazil and Argentina. In most places figs are grown for local consumption. However, Greece, Turkey, Italy, Spain, Algeria and California also produce large amounts for export (mainly as dry figs, pastes and canned fruits). World annual fig production is estimated to be 250,000 t.

Ficus carica is a small (4–7 m tall), functionally dioecious tree. Wild populations contain more or less equal proportions of female and of male individuals and they reproduce entirely from seed. Under cultivation the grower maintains desired genotypes by vegetative propagation – usually by rooting of twigs and occasionally also by grafting. Female clones are cultivated. Hundreds of distinct cultivars are recognized (Condit, 1955) and different segments of the Mediterranean basin harbour distinct groups of local clones. Fig cultivars fall into the following two groups:

1. *Smyrna figs*. These clones, like their wild counterparts, still require pollination for fruit setting. The fruits are caducous: if not pollinated they drop soon after anthesis. Some 115 varieties have been described in this group (Condit, 1955; Storey, 1975).
2. *Common figs*. These are parthenocarpic cultivars. Their fruits persist and mature without pollination. It is the larger group of cultivars. Some 500 varieties