Section 1.
Cotton (*Gossypium* spp.)

1. Introduction: Description and uses

Generally cotton refers to four species of the genus *Gossypium* L. apparently domesticated independently in four separate regions, in both the Old World and the New World (Sauer, 1993; Brubaker *et al*., 1999c). The word is derived from the Arabic "quotn", "kutum" or "gutum" and refers to the crop that produces spinnable fibres on the seed coat (Lee, 1984; Smith, 1995). *Gossypium* (cotton) comprises approximately 50 species worldwide in the arid to semi-arid tropics and subtropics (Fryxell, 1992; Wendel and Cronn, 2003) (Appendix 1). The cultivated species are grouped according to their level of ploidy:

- Diploids (AA) ($2n = 2x = 26$): *Gossypium herbaceum* L. and *Gossypium arboreum* L.;
- Tetraploids (AADD) ($2n = 4x = 52$): *Gossypium barbadense* L. and *Gossypium hirsutum* L.

Of these four cultivated species, *Gossypium hirsutum* and *G. barbadense* account for 95% or more of world cotton production (Jenkins, 1993; May and Lege, 1999; Zhang *et al*., 2008). Throughout this document the word cotton often is used to include both of these dominant crop species, but where the differences are significant and relevant, individual species are differentiated. *Gossypium hirsutum*, widely known as upland cotton or sometimes American, Mexican or Acala cotton, accounts for over 90% of the production. *Gossypium barbadense*, which accounts for some 5%, is commonly known as extra long-staple cotton or Pima or Egyptian cotton.

1.1. Description

A full description of the cotton plant is provided by Oosterhuis and Jernstedt (1999). Potentially perennial but typically grown commercially as annual crops, both species include plants that can grow into a bush or small tree. *Gossypium hirsutum* grows to 1.5-2 (-5) m tall and *G. barbadense* to 3 m. However, both are typically cultivated as plants approximately 1-1.5 m high, with destruction after harvesting the fruits for lint and seed. The plants have a taproot which can reach a depth of 1-3 m depending on the variety's age, soil characteristics and the management regime, and many lateral roots. Cotton plants have a prominent upright main stem, monopodial and indeterminate in growth, which bears the branches and leaves (Hanan and Hearn, 2003; Marur and Ruano, 2001, 2004; Ritchie *et al*., 2007). The number and length of axillary branches vary depending on the variety and environmental conditions.

The leaves are arranged alternately in a spiral around the axis of the main stem or branch. Phyllotaxis is 3/8 back over the last leaf. Leaves vary in size, shape, texture and hairiness. Most lamina are palmate, with several sinuses and lobes more or less defined, varying in shape from rounded to acute. The leaves are usually large and relatively hairy (Hu and Zhao, 1992; Susín *et al*., 1988; Bourland *et al*., 2003), although there are hairless, smooth-leaved varieties (Delattre, 1992); there are a large number of stomata mostly on the abaxial surface. The petiole is normally as long as the leaf lamina, and flanked by two stipules (persistent or falling early) at its juncture with the stem. Leaf characteristics differ considerably between *G. hirsutum* and *G. barbadense* (Wise *et al*., 2000).

Generally the leaves of *G. barbadense* are 3- to 7-lobed (Fryxell, 1984, 1992) and mature leaves are larger and thinner than in *G. hirsutum*. The generally 3- to 5-lobed leaves of *G. hirsutum* are mostly flat throughout development and diaheliotropic, tracking the sun to maximise light absorption. *Gossypium barbadense* leaves exhibit significant cupping or curling which reduces photoinhibition and allows for more light penetration into the plant's canopy over the course of the day. Although *G. barbadense* leaves have higher stomatal density than in *G. hirsutum*, the stomata are smaller, so there is less stomatal surface area per leaf (Lu *et al*., 1997; Wise *et al*., 2000).

Two types of branches are produced: vegetative or monopodial (continuing growth from terminal bud), and fruiting or sympodial (continuing growth from lateral bud). In terms of structure, the vegetative branches are much like the main stem. Flowers are produced only after secondary or tertiary branching. The fruiting branches develop mainly from the first axillary bud of the upper nodes of the plant. They are smaller in diameter and more horizontal than vegetative branches. The sympodial development of fruiting branches gives them a slightly zigzag appearance in contrast to the fairly straight vegetative branches.

Each fruiting branch produces six to eight solitary flower buds (called "squares") (Hutmacher, 2004). The bud is a pyramidal structure, and has three large laciniate triangular bracts surrounding the flower (as an epicalyx or involucre). Just within these bracts is the true calyx, which consists of five short sepals fused together into a cup at the lowest, widest part of the flower (McGregor, 1976). Inside the calyx are five petals separated except at the base, which form the corolla. Inside the corolla (and fused to its base) is a staminal column with many (50 to 125 or more) shortly stalked unilocular anthers distributed along it; this tubular column surrounds the elongated style. The style terminates in a club-shaped lobed stigma exserted somewhat beyond the end of the staminal column and positioned sometimes below but usually beyond the distal-most anthers. Unlike *G. hirsutum*, the *G. barbadense* stigma extends well beyond the anthers (McGregor, 1976), which increases the potential for cross-pollination.

Gossypium hirsutum flowers are of a uniformly creamy white to pale yellow colour, with cream pollen, and secrete a low volume of nectar; *G. barbadense* flowers are yellow with maroon blotches at the inner base (that serve as a nectar guide), have orange pollen, and produce more nectar of a lower sugar concentration (McGregor, 1976; Moffett, 1983).

The pistil's basal rather conical portion is the superior ovary, consisting of three to five carpels or locules. The ovary of *G. hirsutum* often has four or five carpels, each with 8 to 12 ovules, which are aligned in two parallel vertical grooves along the axile placenta (the central column where the carpels join). The capsular fruit, which splits open at maturity, is referred to as the "boll"; it is spherical or ovoid with a beak at the top, and differs among species in shape, size and colour. *Gossypium hirsutum* bolls are usually of a pale-green colour and relatively smooth with few punctate gossypol glands; those of *G. barbadense* are of darker green and conspicuously pitted with numerous glands.

The fertilised ovule develops into a seed, the epidermis of which gives rise to many single-celled seed hairs (epidermal trichomes) of two kinds: long hairs referred to as "lint" and coarser short hairs referred to as "fuzz" or "linters" (Applequist *et al*., 2001; Zhang *et al*., 2007). Differentiation between the hair types has been maximised to produce the white lint in elite cultivars. Cottonseed oil accumulates in the cytoplasm of the seed embryo cells (Gotmare *et al*., 2004); it is not associated with the gossypol glands. Descriptions of the seed are provided by Hopper and McDaniel (1999) and Ritchie *et al*. (2007), and an overview of advances in knowledge of the development of seed and fibre is provided by Ruan (2005).

The cotton plant is characterised by the presence of small lysigenous cavities known as "gossypol glands", which are found in most tissues except xylem. They contain terpenoid aldehydes in an oily water-soluble matrix, which forms an essential oil known as "gossypol" (Khan *et al*., 1999). Gossypol is toxic to non-ruminant mammals, birds, and many insects and microbes, thus providing a constitutive as well as inducible defense against herbivory and microbial attack. Glandless cotton has been developed for food purposes, but the plants are more susceptible to damage (Lusas and Jividen, 1987; Delattre, 1992). Cotton plants also have usually a single extrafloral nectary on the midvein of the underside of the leaf blade (somewhat outward from its base), and nectaries as well at the base of each involucral bract (on the outer and the inner sides). Their sugary nectar can draw insects that may provide defense against herbivory or increase it, depending on the overall management or ecological context (Adjei-Maafo and Wilson, 1983a, 1983b; Wäckers and Bezemer, 2003; Wäckers and Bonifay, 2004; Röse *et al*., 2006).

1.2. Uses

The main product of the cotton plant is fibres — their qualitative characteristics have been valued and analysed over many centuries (Vreeland, 1999; Wakelyn *et al*., 2007a, 2007b). Cotton crops provide the world's premier source for natural fibres, which are mainly used in the manufacture of a large number of textiles. Low-quality fibre can be used for manufacturing felt, mattress filling and special paper, and the processed celluose is used for various consumer products such as toothpaste, lipstick, ice cream and mayonnaise. There also is a range of applications in the chemical industry.

The seeds, even though extensively and intensively used worldwide as well, tend to be regarded as a secondary product or byproduct. The seeds are used to obtain edible oil, which is considered to be of very good quality within the range of vegetable oils (O'Brien *et al*., 2005); as chaff for livestock feed; and as high-protein cake and flour, which are used mainly for livestock feed (Section VII). The flour is sometimes used for human consumption (in low amounts, or after extraction of the gossypol or from gossypol-free varieties). Gossypol has been used as a male contraceptive (Coutinho, 2002). Cottonseed oil is of interest as a lubricant and a biofuel (Karaosmanoğlu *et al*., 1999).

The nations producing the most cotton lint and cottonseed in 2006 were China, USA, India and Pakistan (Table 1). *Gossypium hirsutum* is called long-staple cotton, and the characteristic length of its fibres is 22-36 mm. *Gossypium barbadense*, extra-long-staple cotton, has fibres usually over 35 mm in length; it is cultivated mainly in Egypt, Peru, Sudan, USA and some Central Asian countries. The combination of best agronomic practices, an increasing level of qualification of farmers, and application of technological advances has boosted unit yields. The highest yields in 2006 were 1861 kg/ha of lint, and 2793 kg/ha of cottonseed (Table 1).

Table 1. Countries with the highest yields and/or the most production of cotton lint and/or cottonseed in the 2006 growing season (FAO, 2007)

2006	Yield: kg/ha		Production: tonnes	
	lint	cottonseed	lint	cottonseed
Australia	1861	2631		
Brazil			1,210,000	1,784,672
Cambodia		2712		
China	1243	2485	6,730,000	13,460,000
India			3,563,880	7,127,760
Israel	1717	2732		
Pakistan			2,186,800	4,065,200
Syria	1409	2793		
Turkey	1646	2469	900,000	1,350,000
USA			4,498,000	6,665,900
Uzbekistan			1,171,000	2,376,200

2. Taxonomy and centers of origin, diversity and domestication

2.1. Taxonomy

The genus *Gossypium* L. is a member of the family Malvaceae, subfamily Malvoideae and tribe Gossypieae, which has about nine genera (*cf*. Seelanan *et al*., 1997). The genus emerged as a separate evolutionary lineage some 11-14 million years ago (Senchina *et al*., 2003; Wendel and Cronn, 2003). *Gossypium* has three main centres of biological diversity: Africa and the Arabian Peninsula, Australia, and Mexico (see Appendix 1); and three centres of domestication: Africa and Asia, Mesoamerica (*i.e.* Mexico and Central America), and South America. The two diploid cultivated species (*G. herbaceum* and *G. arboreum*) are from the Old World (Africa-Asia). The two tetraploid cultivated species are from the New World — Mesoamerica (*G. hirsutum*) and South America (*G. barbadense*). Although the record is less clear for Asia, each of the four cultivated species may have been domesticated independently (Sauer, 1993; Brubaker *et al*., 1999c).

About 50 species of *Gossypium* are generally recognised (see Appendix 1) (Fryxell, 1992; Percival *et al*., 1999), although some taxonomic study is still needed. About 45 of the species are diploids, which are divided into three geographical groups and corresponding subgenera; 5 species are tetraploids, which are included in one subgenus (Fryxell, 1984, 1992; Wendel and Cronn, 2003; Cronn and Wendel, 2004):

- African-Arabian group (subgenus *Gossypium*): about 14 species (possibly fewer); naturally distributed principally in Africa, also on the Arabian Peninsula, and reaching Pakistan and perhaps farther eastward (Vollesen, 1987; Fryxell, 1992; Stanton *et al*., 1994; Wendel and Cronn, 2003). One species is endemic to the Cape Verde Islands;

- Australian group (subgenus *Sturtia*): about 17 species (16 taxonomically described), naturally distributed mostly in the northwestern Kimberley region, but also in the northern tropics and in the central arid zone, with one species reaching the eastern warm-temperate zone (Fryxell *et al*., 1992; Seelanan *et al*., 1999; Brown and Brubaker, 2000);

- American group (subgenus *Houzingenia*): about 14 species (13 taxonomically described), 12 occurring naturally in western Mexico (one reaching northward into Arizona, USA) and one each in the Galapagos Islands and in Peru (Fryxell, 1988; Small and Wendel, 2000; Cronn *et al*., 2003; Álvarez *et al*., 2005; Álvarez and Wendel, 2006; Ulloa *et al*., 2006);

- American and Pacific group (subgenus *Karpas*): 5 tetraploid species; 3 naturally distributed in the Americas (one in Mesoamerica, 2 in South America), and one each in the Galapagos Islands and in the Hawaiian Islands (Small *et al*., 1998; Wendell and Cronn, 2003).

The diploid species are placed into eight cytogenetic genome groups, and the tetraploids in one group (Endrizzi *et al*., 1985; Stewart, 1995; Wendel and Cronn, 2003), shown in Table 2.

The species of the genus usually recognised taxonomically are given in Appendix 1 along with their natural geographic distributions, designated genomes, and general groupings phylogenetically (Endrizzi *et al*., 1985; Fryxell, 1992; Percival *et al*., 1999; Wendel and Cronn, 2003).

Table 2. Genome groups of *Gossypium*

Genome group	Number of species	Native distribution
A	**2**	Africa, possibly Asia
B	**3**	Africa (including Cape Verde Islands)
E	**7+**	NE Africa, Arabian Peninsula, SW Asia
F	**1**	East Africa
C	**2**	Australia
G	**3**	Australia
K	**11 (or 12)**	NW & N Australia
D	**13 (or 14)**	Americas (primarily Mexico, also Peru), Galapagos Islands
AD	**5**	Americas, Galapagos Islands, Hawaiian Islands

2.2. Major evolutionary events

DNA-sequence phylogenetic data suggest that 6-7 million years ago, following a trans-oceanic dispersal event, a D genome diverged from the African lineage that eventually gave rise to the A genome, and became a separate lineage in the Americas (primarily Mexico) (Senchina *et al*., 2003; Wendel and Cronn, 2003; Cronn and Wendel, 2004; *cf.* Graham, 2006). From another long-distance dispersal event 1-2 million years ago, a tetraploid originated through hybridisation of an African plant of the A-genome group, perhaps most closely related to the present-day species *G. herbaceum*, with a resident plant of the D-genome group, most closely related to the present-day species *G. raimondii* (Wendel *et al.*, 1992; Senchina *et al.*, 2003; Wendel and Cronn, 2003; Kebede *et al.*, 2007). The nascent disomic AD allotetraploid from that single polyploidisation event evolved into the five present-day tetraploid species (Endrizzi *et al.*, 1985; Cronn *et al.*, 1999).

Gossypium raimondii, a rare species of northwestern Peru, is considered to be the diploid with the genome that has retained the most similarity to this ancestral D-genome species (Liu *et al.*, 2001; Guo *et al.*, 2007); it is one of the more recently evolved of the DD species, having diverged in isolation as a result of a long-distance dispersal event from Mexico (Wendel and Cronn, 2003; Álvarez *et al.*, 2005). *Gossypium raimondii* has genetic similarities with *G. gossypioides*, which is a local species in southern Mexico (Oaxaca) and considered evolutionarily basal within the New World diploids. Nonetheless, *G. gossypioides* has a strikingly unusual history, involving several natural interspecific hybridisations — apparently including introgression from yet another African immigrant (evolutionarily prior to divergence of the African B, F and A genomes) (Cronn *et al.*, 2003; Cronn and Wendel, 2004; Álvarez *et al.*, 2005; Guo *et al.*, 2007).

Soon after separation of the D-genome lineage, African *Gossypium* further diverged with a long-distance dispersal event and establishment of an Australian lineage (which evolved into the three genome groups C, G and K). The lineage in Africa evolved further into four genome groups, first with divergence of the E-genome lineage, subsequently the B-genome lineage, and most recently the F- and A-genome lineages (Cronn *et al*., 2002; Cronn and Wendel, 2004).

Chloroplast and mitochondrial DNA are inherited maternally in *Gossypium* (Small and Wendel, 1999). The means and route of the relatively recent long-distance dispersal of the A-genome fruit/seed(s) and place of origin of the progenitor allotetraploid continue to be researched (Wendel and Cronn, 2003). The A and D genomes of the South American tetraploid *Gossypium mustelinum* (northeastern Brazil) are genetically most similar to the ancestral type that differentiated into the five present-day widely dispersed tetraploids (Wendel *et al*., 1994). The disseminule of an AA species may have travelled *via* sea currents from Africa to the Americas (Stephens, 1966; *cf.* Renner, 2004). Then, pollen from an American diploid (DD) species fertilised the immigrant, and chromosome doubling produced the original AADD tetraploid; the AA coloniser either did not persist or possibly established a small population that went extinct.

2.3. Domestication and early cultivation

2.3.1. Old World diploids

The cultivated AA diploids of the Old World are typically short-staple cottons, with a fibre length of less than 23 mm. These cottons can be important regionally, and still may be preferred especially in harsh or dry growing conditions (Basu, 1996; Rajendran *et al*., 2005). The two species (with *G. arboreum* as the larger crop) now provide only about 4% of world production, however, and are largely displaced in much of the Old World by the New World tetraploids.

Both AA species have been studied thoroughly using many methodologies (*e.g.* agronomic, morphological, cytogenetic, genetic, molecular) and are definitely biologically distinct, although their differences are observable in divergent suites of shared characters rather than by obvious diagnostic characters (Wendel *et al*., 1989; Stanton *et al*., 1994; Rana and Bhat, 2004; Gao *et al*., 2005; Desai *et al*., 2006; Kebede *et al*., 2007). *Gossypium herbaceum* typically has less anthocyanin (so becomes less “sun-red”), shorter leaves with shallower sinuses and broader lobes, epicalyx bracts broader and with twice as many apical teeth or lobes, smaller flowers, more rounded bolls, larger seeds and finer lint than *G. arboreum* (Abedin, 1979; Stanton *et al*., 1994). *Gossypium arboreum* has an interchromosomal translocation in comparison to the generically typical arrangement in its sister species *G. herbaceum* (Song *et al*., 1991; Desai *et al*., 2006).

Wild (non-feral) *Gossypium herbaceum* subsp. *africanum* occurs naturally in the savanna biome across southern Africa (Vollesen, 1987; Wendel *et al*., 1989; *cf.* Jürgens, 1997), whereas the domesticated plant *G. herbaceum* subsp. *herbaceum* is found disjunctly farther to the northeast, being grown mainly from Ethiopia to Central Asia, northwestern China and India (Wendel *et al*., 1989; Guo *et al*., 2006). *Gossypium arboreum* is grown primarily across Asia farther to the east, from India (where it is cultivated more than *G. herbaceum*) to Korea (Wendel *et al*., 1989; Basu, 1996; Guo *et al*., 2006). The original ranges or centres of domestication of *G. arboreum* and *G. herbaceum* subsp. *herbaceum* are unclear (Wendel *et al*., 1989; Brubaker *et al*., 1999c).

The archaeological evidence of early cotton use in the Old World is not at the species level. Circumstantially, *G. herbaceum* subsp. *herbaceum* might be from Southwest Asia (*e.g.* Abedin, 1979; Fuller, 2006) and *G. arboreum* possibly from India (Santhanam and Hutchinson, 1974). Early utilisation and probable cultivation of cotton have been reported from Pakistan before 5000 BC (Moulherat *et al*., 2002); North Arabia (Jordan) about 4450-3000 BC, but perhaps present by trade according to Betts *et al.* (1994); South India in 1500 BC (Fuller *et al*., 2004); and southern Libya in 900 BC – 500 AD (Pelling, 2005). Both species may have reached North Africa and Greater Mesopotamia before earliest historic times (Watson, 1983; Potts, 1997). Cotton and weaving are mentioned in early texts in Asia (*e.g.* India and China) and the Mediterranean region.

2.3.2. New World tetraploids

2.3.2.1. *Gossypium barbadense*

Originally wild (*i.e.* non-feral) *Gossypium barbadense* is considered to occur naturally in the dry coastal region of northern Peru and southern Ecuador (Schwendiman *et al.*, 1985; Percy and Wendel, 1990; Westengen *et al.*, 2005). The earliest archaeological evidence of the cultivation of *G. barbadense* dates to 5500 BC in northwestern Peru (Dillehay *et al.*, 2007). This cotton species was apparently domesticated and grown extensively in the northwestern Peruvian and southwestern Ecuadorian region, and was spread into the Andes and farther eastward in South America, and onward to the Caribbean and southern Mesoamerica (Brubaker *et al.*, 1999c; Vreeland, 1999; Pearsall, 2003; Westengen *et al.*, 2005; Johnston *et al.*, 2006; Dillehay *et al.*, 2007).

2.3.2.2. *Gossypium hirsutum*

Gossypium hirsutum is native in Mesoamerica, but its natural range as well as its centres of domestication and development are obscured by millennia of use (Stephens, 1967; Lee, 1984; Jones *et al.*, 1989; Wendel *et al.*, 1992; Brubaker and Wendel, 1994; Stark *et al.*, 1998; Brubaker *et al.*, 1999c; Whitmore and Turner, 2002). Collections from this large and diverse region, even of free-living plants, generally have varying characteristics of domestication rather than of a genuinely wild species — for example, having larger and more flaring capsules, larger seeds, loss of seed dormancy and of day-length sensitivity, and more and finer lint which is also more easily detachable (Hutchinson, 1951; Stephens, 1958; Fryxell, 1979). The oldest archaeological remains of *G. hirsutum*, dating to 3500-2300 BC, seem to be domesticated forms and were found in the Tehuacan Valley of central Mexico (Smith and Stephens, 1971; WWF and IUCN, 1997; *cf.* Pope *et al.*, 2001).

Through intensive study of germplasm collections from the widespread complex in the region, Hutchinson (1951) distinguished six domesticated races (not botanical varieties) and one wild race based mainly on their habit and morphology, and found that these races had generally distinct geographic distributions, with the most differentiation of the domesticated types in southern Mexico:

- *morrilli* — inland montane, southern Mexican plateau and northward
- *palmeri* — Pacific slope, southern Mexico west of Isthmus of Tehuantepec
- *richmondi* — Pacific slope in Gulf of Tehuantepec region
- *punctatum* — Yucatan Peninsula, and northward on Atlantic slope, to Florida (USA) and Bahamas
- *yucatanense* — wild, northwestern coast of Yucatan Peninsula
- *latifolium* — Guatemala (both slopes) and southernmost Mexico (Chiapas), nearby areas
- marie-galante— northern Central America (Guatemala) southward to Colombia on both coasts, Caribbean region (Antilles) and northeastern Brazil

Research using isozymes (allozymes) only confirmed the distinction of Caribbean marie-galante (Wendel *et al.*, 1992); RFLP and SSR analyses have supported recognition of additional landraces (Brubaker and Wendel, 1993, 1994; Lacape *et al.*, 2007). The next most distinct lineage is *punctatum*, and then *latifolium*. Of these three major domesticated lineages (Iqbal *et al.*, 2001), marie-galante is a perennial, from which mocó cotton is still cultivated in Brazil (Freire and Moreira, 1991; Moreira *et al.*, 1995; Johnston *et al.*, 2006); punctatum and latifolium are annualised. The original Amerindian Hopi Moencopi cotton (Arizona, southwestern USA) is considered to belong to *punctatum* (Lee, 1984). Race *palmeri* is closely related to race *latifolium*, and the SSR research found *morrilli* and *richmondi* to be distinct lineages that are close to *palmeri*. *Gossypium lanceolatum* is not a distinct species but a local Mexican landrace, in the domesticated race *palmeri* (Brubaker and Wendel, 1993).

The modern studies have maintained yucatanense as a truly wild ecotype, sprawling plants which are isolated in populations along the northwestern coastal strand of Mexico's Yucatan Peninsula (Hutchinson, 1951), but perhaps occur naturally eastward even as far as Guadeloupe island in the Lesser Antilles (Ano *et al*., 1982; Lacape *et al*., 2007). Wild-like or wild populations of *G. hirsutum* are widely scattered and rare, growing near beaches or confined on small islands; such populations do not occur inland from the coast, but feral plants are found inland (Brubaker and Wendel, 1994).

2.3.2.3. Origin of upland cotton

The upland type of *Gossypium hirsutum* and derived varieties are the mainstay of the worldwide industry (May and Lege, 1999). Upland cotton is thought to have its centres of origin and diversity near the border of Mexico with Guatemala (Hutchinson *et al.*, 1947; Hutchinson, 1951; Brubaker and Wendel, 1994), apparently within *G. hirsutum* race latifolium. This type appears to have become prevalent in southeastern USA around the middle of the 18th century (Phillips, 1976; Smith *et al*., 1999). Somewhat later (about 1785), Sea Island cotton (*G. barbadense*) from the Bahamas was widely grown in the U.S. Atlantic coastal regions of Georgia and South Carolina (Brown and Ware, 1958; Smith *et al*., 1999).

The first seed stocks of the cotton arriving in USA were called Georgia green seed (Hutchinson *et al.*, 1947). This type normally grew from a ginned seed with persisting green-coloured fuzz; the Sea Island-type had hairless or bare ginned seed, placing it among the "black-seed" cottons. Sea Island cotton was cultivated in the lowlands, whereas green-seed cotton was more inland and consequently became known as upland cotton (Smith *et al*., 1999). In the 18th century similar stocks also were taken to Southeast Asia (Lee, 1984). In the 19th century further Mexican green-seed cultigens were introduced into the USA and came to be known as varieties of upland cotton (Brown and Ware, 1958; Smith *et al.*, 1999). Cotton was introduced into many tropical and subtropical countries during the U.S. civil war period (1861-1865), including Australia (Constable *et al*., 2001). Crosses between many varieties of introduced cottons have caused the worldwide expansion of upland cotton (Lee, 1984; Smith *et al.*, 1999; Iqbal *et al*., 2001). The intensive modern cotton industry only became established in Australia in the 1960s (Hearn and Fitt, 1992).

3. Agronomic requirements and practices

3.1. Abiotic environment

Although originating in the tropics and subtropics, cotton has come to be cultivated mostly in subtropical and warm-temperate zones — regions which provide more than half of world production (*cf.* Table 1). For this geographical shift to be possible as a crop, the species' photoperiod needed to change — the naturally short-day plant became a day-neutral plant that could be cultivated as an annual crop in the longer summers (Smith *et al.*, 1999).

3.1.1. Climate

The geographical distribution of the cotton crop reaches 43-45° N (Central Asia, China) but is primarily grown between 37° N and 32° S (*e.g.* Australia, northern Argentina). Temperature is the main climatic factor determining the geographic range in which cotton can be grown (Freeland *et al*., 2006). Generally the plant is highly sensitive to temperature (Reddy *et al.*, 2006). Seeds do not germinate, nor seedlings begin their activity, until the temperature rises to 15ºC; they are delayed above 38ºC. *Gossypium barbadense* seedling development in the first 2 weeks is generally not sensitive to temperatures between 15ºC and 40ºC, but 3 weeks after emergence the young plants are generally more sensitive than *G. hirsutum* (*e.g.* having fewer fruiting branches at 35º/27ºC than at 30º/22ºC, and no fruiting branches at 40º/32ºC) (Reddy *et al*., 1992b). Nonetheless, there are *G. barbadense* cultivars with heat tolerance close to that of *G. hirsutum* (Cornish *et al*., 1991; Radin *et al*., 1994; Srivastava *et al*., 1995). The optimum daytime temperature range for *G. hirsutum* is 30-35ºC, with a loss of fruit above 35ºC, and with a 50% yield reduction at 25ºC (Reddy *et al*., 1992a).

After planting *G. hirsutum*, 180-200 frost-free days are needed for normal development, with an average of 150 days of suitable temperatures (*i.e.* 1200 heat units above 15.5ºC accumulated) (Duke, 1983); for *G. barbadense*, 200-250 days are needed (Unruh and Silvertooth, 1997). Although the values differ among varieties, from the planting of cotton to 60% boll opening about 2050 heat units (degree-days or day-degrees) are the required minimum (Ritchie *et al*., 2007; OGTR, 2008).

3.1.2. Soil and water

Cotton plants are cultivated in a wide variety of soils, but the crop develops best in deep arable soils with good drainage, filled with organic matter and with a high moisture-retention capacity. Yet cotton is grown in cracking clays in some countries. Cotton is a salt-tolerant plant, with *G. barbadense* more salt tolerant than *G. hirsutum* (Ashour and Abd-El'Hamid, 1970). Salinity stress nonetheless has adverse effects on germination and emergence (Ashraf, 2002); the most common stress effect is general stunting of the plant's growth (Cothren, 1999).

Irrigation allows cultivation in poor-quality soils, with necessary moisture and nutrients provided in a controlled way. Irrigation is carried out mainly at ground level, flooding the furrows, which requires adequate leveling of the field.

At least 500 mm of rainfall is required during the growing season for dryland (non-irrigated) cotton crops. Cotton is also grown as an irrigated crop, and it is still common to use sprinklers with fixed or mobile outlets, with total coverage. The use of drip irrigation has increased, which allows a saving in water and use of soil that is less than optimum (due to its sloping surface, lack of fertility, or an excessively high salt content). Generally *G. barbadense* has similar water requirements to *G. hirsutum*; the longer growing season of *G. barbadense* may however require additional irrigation to mature its later-set bolls (Silvertooth, 2001). Carefully timing the application of water optimises the plant's vegetative growth, flowering and boll production (McWilliams, 2003). Flower and boll formation in *G. barbadense* are enhanced by a short duration of sunshine, high minimum humidity and low evaporation rate (Sawan *et al*., 2004, 2005).

3.2. Cultivation

3.2.1. Sowing

Sowing cotton is an operation that requires careful soil preparation, in order to achieve sufficient moisture, to allow favourable germination and rapid development of roots. Pre-prepared ridges are recommended, to obtain adequate drainage of water and maintain optimum temperature. The optimal sowing date is determined by temperature. Temperature is the dominant factor affecting the cotton plant's development and yield (ACCRC, 2001; Robertson *et al*., 2007). The sowing can commence when the minimum soil temperature at a depth of 10 cm exceeds 14ºC for at least 3 consecutive days. Lint yield is adversely affected if *G. hirsutum* is planted too early (due to cold temperatures) or too late (due to a shortened growing season) (Kittock *et al*., 1987). Since *G. barbadense* prefers a longer growing season (> 200 days) for yield increase it is more sensitive to delays in planting (Kittock *et al*., 1981, 1985; Silvertooth, 2001).

Acid-delinted seeds are treated with fungicides against seedling disease complexes and with insecticides to protect seedlings from sucking insect pests and wireworm soil insects (beetle larvae), and are sown at a rate of 20-25 kg/ha. Sowing is carried out with precision machines, in 4 or 6 rows with spacing of 95-105 cm to adapt to mechanical collection of bolls. A proportion of the crop is sometimes planted in an Ultra Narrow Row configuration, for example with row spacing of 30 cm and a target population of 25 to 30 plants per m^2.

Germination takes place under favourable conditions of temperature and humidity. Cotton remains in a seedling stage longer than some other crop species. Sometimes the seeds are sown under plastic, a technique that ensures high germination and enhances floral development. In Spain this practice is totally mechanised, and (depending on the year) may be applied on more than two thirds of the sown surface area.

3.2.2. Fertilisers

Phosphorus (P) and potassium (K) are applied according to soil content, at the base of the plants. Nitrogen (N) is distributed between the plant's base and top with an application rate of up to 200 or 250 units of N, depending on the environmental and crop conditions. *Gossypium barbadense* requires slightly more N, P and K per unit of lint produced (Unruh and Silvertooth, 1996). However it is more sensitive to a slight excess of N, which can stimulate higher vegetative growth and delay maturity (Silvertooth *et al*., 1995).

3.2.3. Growth regulators

Growth regulators or herbicides may be applied to control vegetative growth and development of the crop, and to assist in its harvest. Examples include a growth regulator applied early in bud/flower production to reduce internode length, increase boll retention, promote early flowering and/or produce a more open canopy, and a growth regulator applied to the crop close to harvest time to stimulate opening of mature bolls and to defoliate (Cothren, 1999; Ritchie *et al*., 2007).

3.3. Biotic environment

3.3.1. Vesicular arbuscular mycorrhizae (VAM)

In most soils successful growth of cotton crops depends on the interaction with mycorrhizal fungi (Youssef and Mankarios, 1974; ACCRC, 2002; Nehl and Allen, 2004). The fungi (*e.g. Glomus mosseae*) grow intercellularly in the root cortex. They form vesicular arbuscules with the plasma membrane in the cortical cells, which are the sites of mineral exchange from the fungus to the plant and carbohydrate exchange from the plant to the fungus. Improvement in phosphate uptake is the main advantage for the cotton plants. VAM fungi also can reduce incidence and severity of diseases of the plants (Hu and Gui, 1991; Liu, 1995).

3.3.2. Pests

Pest and disease control is a highly significant cost (Oerke, 2006), and repeated applications of insecticides and fungicides may be employed. Numerous insect pests feed on cotton (Matthews, 1989; Delattre, 1992). Insects that are natural enemies of the pests are encouraged as part of integrated pest management systems. Cultivation of varieties with genetically engineered resistance to some insects has been a major advance in management of the crop against some major pests.

Arthropod pests may affect boll production or fibre quality. Aphids (*Aphis gossypii*, *A. craccivora*, *Myzus persicae*) and the silverleaf whitefly *Bemisia tabaci* are the usual pests which most affect fibre quality, producing sticky cotton with dark stains if not controlled late in the season. The pink bollworm *Platyedra gossypiella*, various Hemiptera such as *Lygus* bugs, and various mites such as the two-spotted spider mite *Tetranychus urticae* also diminish fibre yield and quality. Important pests affecting boll production include cotton bollworms (*Helicoverpa armigera*, *H. punctigera*), and the spiny bollworm

Earias insulana mainly reduces fibre production. Lepidoptera such as the beet armyworm *Spodoptera exigua* and Egyptian cotton leafworm *Spodoptera littoralis* are less common. The cotton boll weevil *Anthonomus grandis* is a highly aggressive pest in some areas. Other important pests include the leafhopper *Empoasca lybica* (the cotton jassid).

Gossypium barbadense has some resistance to *Earias* spp. (Reed, 1994), jassids (Matthews, 1994) and spider mites, possibly due to its higher content of gossypol than *G. hirsutum* (engonca *et al*., 1986; Matthews and Tunstall, 1994).

Nematodes that may be damaging in some regions or areas include particularly the root-knot nematodes *Meloidogyne incognita* (as well as *M. acronea*), reniform nematode *Rotylenchulus reniformis*, lance nematodes *Hoplolaimus columbus* (and several other spp.) and sting nematode *Belonolaimus longicaudatus* (Robinson, 1999), and as well associated ring nematodes *Criconemella* spp., spiral nematodes *Helicotylenchus* spp., needle nematode *Longidorus africanus*, stunt nematodes *Merlinius* spp. and *Tylenchorhynchus* spp., stubby-root nematodes *Paratrichodorus* spp., pin nematode *Paratylenchus hamatus*, lesion nematodes *Pratylenchus* spp., spiral nematodes *Scutellonema* spp., and American dagger nematodes — the *Xiphinema americanum* group.

3.3.3. Diseases

Among cotton diseases (Kirkpatrick and Rothrock, 2001), the most prominent is Verticillium wilt, which is caused by *Verticillium dahliae*. This fungal disease is extensively distributed in areas where *G. hirsutum* is cultivated; conventionally bred resistant varieties are available in Australia (OGTR, 2008). Other diseases, such as damping off, are caused by a complex of pathogens that have a major effect on the crop. The main causative agents are *Rhizoctonia solani*, *Pythium ultimum*, *Thielaviopsis basicola* and *Fusarium* spp.

Many other fungi have been associated with diseases of cotton, either as the primary agents or secondary invaders: *Alternaria* spp., *Ascochyta gossypii*, *Aspergillus flavus*, *Brasilomyces malachrae*, *Cladosporium herbarum*, *Fusarium* spp. (*e.g. F. oxysporum* f. sp. *vasinfectum*), *Glomerella gossypii* (anamorph *Colletotrichum gossypii*), *Lasiodiplodia theobromae* (synonym *Diplodia gossypina*), *Leveillula taurica* (anamorph *Oidiopsis haplophylli* [synonyms *O. gossypii*, *O. sicula*]), *Macrophomina phaseolina*, *Mycosphaerella* spp., *Nematospora* spp., *Phakopsora gossypii*, *Phymatotrichopsis omnivora*, *Phytophthora* spp., *Puccinia cacabata* and *P. schedonnardi*, *Pythium* spp. and *Sclerotium rolfsii*.

Boll rot caused by these diseases leads to serious production losses. Damage is more severe in crops cultivated with high humidity and low light intensity, and it increases if the bolls have mechanical lesions. Mainly, the damage these fungi cause is the contamination of fibres, especially if open bolls remain exposed to rain or high humidity for a long period. In addition to causing undesired discolouring of the fibre, these agents may give rise to enzyme degradation in some basic components, as frequently occurs in cellulose.

Other diseases of cotton are caused by bacteria, for example *Xanthomonas campestris* pv. *malvacearum*, and by viruses, for example abutilon mosaic geminivirus, cotton leaf crumple geminivirus, cotton leaf curl geminiviruses, cotton yellow mosaic geminiviruses and cotton anthocyanosis virus. Cotton bunchy top, cotton leaf mottle and cotton leaf roll diseases are of unknown etiology.

3.3.4. Weeds

Weed control in cotton fields is of considerable importance, and is carried out with mechanical methods by passing through the crop rows, and by chemical methods. Many different herbicides are employed in the cultivation of cotton, with their application during pre-sowing and/or pre-emergence of seedlings or less frequently in post-emergence (Table 3). Integrated weed management measures reduce reliance on single herbicide groups, and include crop rotations and farm hygiene to prevent weed seed spreading (Charles, 2002; Roberts and Charles, 2002). The cultivation of varieties with herbicide tolerance developed by genetic engineering has also significantly improved weed management of the crop.

The commonly occurring and the most troublesome weeds vary considerably by region and management practices. Genera often having species of notable concern in areas are listed in Appendix 2.

Table 3. Timing of application of various herbicides

Land inclusion and pre-sowing
Pre-sowing
Pre- and post-sowing
Immediately post-sowing
Pre-sowing and pre-emergence
Pre-emergence
Pre- and post-emergence
Immediately post-sowing, and post-emergence
Post-emergence

3.4. *Harvest and processing (ginning, crushing)*

To facilitate harvest and subsequent ginning (freeing up of fibres from seed to obtain the lint), the plant is defoliated by means of a chemical treatment. This improves cleanliness and the quality of the fibres. Mechanised harvest is done by means of spindle picker machines in two or four rows.

A final step is ginning the cotton in saw gins, to make bales classified according to grade and length of fibre. The separated cottonseed is further processed, first by separating the hulls from the kernels. The kernels are crushed, and the oil extracted and processed for use in human food or other products. The hulls are used for livestock feed or industrial products, and the remainder of the kernel (which is high in protein) is converted into cottonseed meal for livestock. In the case of *G. hirsutum*, the fuzzy seed (*i.e.* seed with linters) is delinted, *i.e.* processed mechanically or chemically to remove the linters. These residual short fibres are used for a variety of purposes, such as a cellulose base for food or other consumer products. To maintain its superior fibre quality, the picking and ginning techniques for *G. barbadense* cotton are different than those used for *G. hirsutum*. As *G. barbadense* does not produce linters, its seed exists either as the unprocessed “seed cotton” or processed black seed.

3.5. *Crop rotation*

Cotton crop rotation is usually carried out by alternating with other traditional crops in the area. However, in contrast to best agricultural practices, sometimes cotton is planted in the same field again, for 2 years or longer. The number of repetitions is hindered by the damage to the crop caused by diseases, especially *Verticillium* wilt.

4. Reproductive Biology, Dispersal and Establishment

4.1. Floral biology, pollination and development of seeds

The sequence of flowering is from the lower to the upper part of the plant, and from the centre to the outside. Anthesis takes place 25-30 days after the appearance of the floral bud. Secretion of bracteal (extrafloral) nectar starts 5-6 days before flowering and initially peaks on the day of anthesis (Adjei-Maafo and Wilson, 1983a; Wäckers and Bonifay, 2004). On the day preceding anthesis the corolla extends well above the bracts, and early the following morning the large flower opens and secretion of floral nectar begins (Waller *et al*., 1981); the petals turn dark pinkish and wilt by evening of the same day (Fryxell, 1979; Waller *et al*., 1981; Eisikowitch and Loper, 1984; Sanchez and Malerbo-Souza, 2004). The anthers open soon after the flower and shed their pollen grains, some 900-350 per anther; the grains are spheroidal and very large (100-140 µm diameter), with *G. barbadense* having larger grains than *G. hirsutum* (Srivastava, 1982; Wetzel and Jensen, 1992; Kakani *et al*., 1999; Sava kan, 2002; Watanabe *et al*., 2006). The stigma generally is receptive at anthesis (McGregor, 1976).

Self-pollination usually takes place. As the pollen grains are large, heavy and somewhat sticky, dissemination by wind is absent or negligible (McGregor, 1976; Umbeck *et al*., 1991; Borém *et al*., 2003). Under humid laboratory conditions, Richards *et al*. (2005) found that about 90% of the pollen grains were viable after 8 hrs, nearly 31% still viable after 16 hrs and about 7.5% viable after 32 hrs, but after 8 hrs on the proboscis of *Helicoverpa armigera* moths, pollen grains were about 81% non-viable.

Although cotton is mostly self-pollinating, in the presence of suitable insect pollinators it is also cross-pollinating at generally low levels, which improves yields (McGregor, 1976; Tanda, 1984; Mamood *et al*., 1990; Rhodes, 2002; Sanchez and Malerbo-Souza, 2004; Llewellyn *et al*., 2007). The species pool and concentration of pollinators vary according to region, location, season and timing. The extent of spontaneous (unaided) or natural outcrossing thus depends greatly upon local insect populations, including introduced and native species (Moffett *et al*., 1976; Berger *et al*., 1988; Freire *et al*., 2002; Rhodes, 2002; Sanchez and Malerbo-Souza, 2004; Danka, 2005; Van Deynze *et al*., 2005; Llewellyn *et al*., 2007). Nectar from the extrafloral bracteal nectaries (epicalyx) is more accessible than nectar from the floral nectaries inside the calyx, so flower visitors are not always potential pollinators (Moffett *et al*., 1975; McGregor, 1976; Tsigouri *et al*., 2004; Danka, 2005). Bumble bees (*Bombus*), honey bees (*Apis*), *Anthophora*, *Melissodes* and *Halictus* bees and *Scolia* wasps are important pollinators in some areas (McGregor, 1976; Free, 1993; Delaplane and Mayer, 2000). *Apis mellifera* can be an important pollinator, but it does not prefer *Gossypium* pollen (McGregor, 1976; Eisikowitch and Loper, 1984; Vaissière *et al*., 1984; Waller *et al*., 1985; Loper, 1986; Vaissière, 1991; Vaissière and Vinson, 1994; Danka, 2005; Van Deynze *et al*., 2005). In using insecticides to manage the crop, mitigation measures are taken to preserve the pollinator populations, for example by not applying insecticides during the effective period of flowering (Delattre, 1992; Bourland *et al*., 2001; Sekloka *et al*., 2007).

Isolation of test plots or the crop thus depends on the presence and flight distances of the insect pollinators, and the result desired (Llewellyn *et al*., 2007). Conditions and objectives vary tremendously. Pollen-mediated gene flow declines steeply, typically being below 1% beyond 10 m from the source (Van Deynze *et al*., 2005). From experiments, isolation distances suggested for field tests include 8-10 m (Turkey) (Sen *et al*., 2004); 10 m (Greece) (Xanthopoulos and Kechagia, 2000); 20 m (Brazil) (Freire, 2002a); 33 m (India) (Singh and Singh, 1991); and 60 m (China) (Zhang *et al*., 2005). Barriers composed of other cotton can be effective (Simpson and Duncan, 1956); in Australia the accepted practice has been a distance of 20 m with a cotton buffer or 50 m of bare ground, but somewhat larger distances may be preferable sometimes (Llewellyn *et al*., 2007). Border rows of *Zea mays* 4 m wide reduced cotton cross-pollination in Brazil from 15% to 5%, and an isolation distance of 100 m has been recommended when maize barriers are used (Castro *et al*., 1982; Freire, 2005).

As the field area under cultivation for cotton increases or the goal in separation becomes more strict, the recommended isolation distance increases, or there are large regions of exclusion. The OECD Seed Schemes recommend separation distances of 200 m for production of Certified commercial seed of *G. hirsutum* and 600 m for *G. barbadense*, and separation distances of 600 m and 800 m respectively for Basic (*i.e.* Foundation) seed (OECD, 2008). Suggestions for isolation of cotton crop fields in Brazil, depending on the objective, are a distance of 250 m or 800 m (Freire, 2005). In some situations an isolation distance of 1000 m (1 km) or more may be necessary (Australia) (Llewellyn *et al.*, 2007). Van Deynze *et al.* (2005) found 0.04% pollen-mediated gene flow at 1625 m (California, USA). In Hawaii, large-scale production of Bt cotton is prohibited to avoid crossing with the endemic *Gossypium tomentosum* (Hawkins *et al.*, 2005). In Northeast Brazil, to safeguard the few extant wild populations of the endemic *Gossypium mustelinum*, a mapped zone of exclusion of cotton cultivation of at least 3 km has been proposed (Barroso *et al.*, 2005; Freire, 2005).

Suitable pollen grains that have been deposited on the surface of the large sticky stigma *via* self-pollination or cross-pollination germinate within 30 min (Pundir, 1972). There is some sensitivity to the genotypic origin of the pollen, with effects ranging from positive to negative, even to incompatibility between some strains of *G. hirsutum* (McGregor, 1976; Gawel and Robacker, 1986; Pahlavani and Abolhasani, 2006). The pollen tube typically grows through the style for 12-30 hrs to the ovary and ovule, after which fertilisation is completed. Cell division in the zygote takes place 4-5 days after anthesis.

The young seed commences with fertilisation. Normal development follows a sigmoid curve, with the most rapid growth of the seeds and boll (fruit) occurring from about the 7th day to 18th day after anthesis (Oosterhuis and Jernstedt, 1999). Definitive size of the ovoid seed is reached about 25 days after anthesis. Boll development is characterised by three phases: enlargement, filling and maturation. Initially as the seeds grow the cotton fibres elongate; both seeds and fibres give maximum volume to the boll. Each fibre develops from a single epidermal cell of the seed coat. After 3 weeks, the boll-filling phase begins, with cellulose deposited inside the lumen of the elongated fibres. The filling phase continues into the 6th week, then the boll maturation phase begins and the boll dries out (Ritchie *et al.*, 2007).

Each mature boll has three to five locules or “locks”, within which are the seeds surrounded by their fibres. The average number of seeds in a boll depends on many factors, including genotype, location of the boll on the plant, and stresses during plant development and growth; roughly 20 to 35 (even 45) seeds per boll can be typical. Post-fertilisation failure can result in the development of “motes”, embryos that do not ripen into mature seeds but develop partially, including growth of immature fibres of various lengths that complicate lint production (Bolek, 2006).

4.2. Dispersal

The dispersal ability of the genus *Gossypium* is apparent from its unusual evolutionary history, including various trans-continental dispersal events and several interspecific hybridisations resulting in new lineages. For example, within the last 1-2 million years, there have been long-distance dispersals of the progenitor of *Gossypium darwinii* from South America to the Galapagos Islands, and the progenitor of *Gossypium tomentosum* from Mesoamerica to the Hawaiian Islands, and in each case, the tetraploid coloniser evolved into an endemic species that became well established, dispersing to various islands within its archipelago (Wendel and Percy, 1990; Sherwood and Morden, 2004).

Over the several millennia that early peoples achieved domestication and expansion in cultivation of *Gossypium*, the four utilised species were spread beyond their natural centres of origin and diversity to new regions (Brubaker *et al.*, 1999c), and sometimes have become established and free-living or naturalised to varying degrees. In this way the genuinely wild distributions of the domesticated species were obscured (Stephens, 1958). The region where wild (non-feral) *Gossypium barbadense* occurs in South America is rather clear (Westengen *et al.*, 2005), but the original range of *G. hirsutum* in Mesoamerica (and perhaps the Caribbean) is quite unclear (Stephens, 1958; Brubaker and Wendel, 1994). Similarly, the original centres or ranges of *G. arboreum* and *G. herbaceum* subsp. *herbaceum* are obscure.

The dispersal of seeds varies in different areas or settings and situations and from one season to another (OGTR, 2008). In a natural setting, wind, water and birds may serve as dispersal agents (Stephens, 1958, 1966; HEPX, 2007). In an agricultural setting, greater dispersal of cottonseed generally may occur during transport (Addison *et al*., 2007), stock-feeding (Coppock *et al*., 1985; Sullivan *et al*., 1993a, 1993b) or adverse weather conditions, and rarely by animals (Smith, 1995).

4.3. Seed dormancy and germination

Although *Gossypium* seeds can have a natural capability of 2-3 months of innate or induced dormancy, "hard" seeds are undesirable for crop production, and the trait has been minimised or completely eliminated in modern cultivars through domestication and selective breeding (Stephens, 1958; Hopper and McDaniel, 1999; Paiziev and Krakhmalev, 2006; OGTR, 2008).

The quality or vigour (potential for rapid, uniform emergence of seedlings) of *G. hirsutum* seeds can vary between seed lots (Hopper and McDaniel, 1999). Factors such as chemical composition of the mature seed and pre-harvest environmental conditions contribute to the relative quality of cottonseed. Selection to improve seedling vigour has been incorporated into *G. hirsutum* breeding programs (Bourland, 1996).

Germination depends largely on the type of cottonseed (Eastick and Hearnden, 2006). The *G. hirsutum* black seed used for planting (*i.e.* ginned and acid-delinted seed) has the highest germination rate. New seed has a low germination rate, attributed to mechanical hindrance of cotyledon emergence by the surrounding fibres. Fuzzy seed (*G. hirsutum*) has an intermediate germination rate.

The type of habitat that the seed is dispersed into affects germination. An experimental study on spread and persistence of *G. hirsutum* (Eastick and Hearnden, 2006) found germination highest in disturbed habitats such as stockyards and the edges of waterways, especially if the seed had been buried, and much less likely in undisturbed habitats and roadside sites. The experiments aimed to maximise germination and initial establishment of seedlings by sowing seeds into cleared ground, lightly burying the seeds and then hand-watering. Subsequent persistence and recruitment at a site were solely dependent on the habitat.

4.4. Weediness and naturalisation

Gossypium hirsutum and *G. barbadense* can occur as escapes from agriculture. Cotton can become feral and naturalise locally in suitable areas in many regions. Nonetheless cotton has been grown as a crop for decades to centuries in many countries without being reported as strongly invasive or a serious weed (*e.g.* Holm *et al*., 1979, 1997; Randall, 2002; Weber, 2003). Abiotic and biotic factors determine whether introduced *Gossypium* will establish in the particular environment, including the length of the growing season and severity of a cold or a dry season, rainfall, soil type, competition from other plants, herbivory (by insects and other animals), and physical destruction such as stock trampling or fire (Eastick and Hearnden, 2006).

Recently the weediness and naturalisation potentials of cotton were thoroughly reviewed for cotton-growing regions in Australia (OGTR, 2008). The crop species were not considered to threaten agricultural productivity, or native biodiversity (Tothill *et al*., 1982; Lazarides *et al*., 1997). *Gossypium hirsutum* has been grown since the 1960s or 1970s in a number of places in northern Australia. Isolated naturalised populations of *G. hirsutum* and *G. barbadense* occur, including within conservation areas (Sindel, 1997; Eastick, 2002).

Cotton volunteers are found in all Australian cotton-growing areas and are relatively common where cottonseed is used as livestock feed (Eastick and Hearnden, 2006). Typically such volunteers are grazed by livestock and/or killed by roadside management practices, limiting their potential to persist and reproduce (Eastick and Hearnden, 2006; Addison *et al*., 2007).

Surveys in 2002, 2004 and 2005 along Australian routes for transporting ginned *G. hirsutum* seed for stockfeed indicated that plants infrequently established in the roadside environment, mostly as transient populations despite more than 12 years of using the routes (Addison *et al*., 2007). *Gossypium hirsutum* volunteers tended to establish in highly and regularly disturbed environments.

In another study (Eastick, 2002; Eastick and Hearnden, 2006), persistence of *G. hirsutum* plants for more than 1–2 years was found only in habitats having increased availability of water and/or nutrients, such as cattle yards. Although the cotton plants in cattle yards might grow to reproductive maturity, persistence and seed dispersal were limited by trampling and grazing; no volunteers were found in undisturbed bush habitats surrounding the areas.

A rigorous model has been developed to predict the regions in Australia that are climatically suitable for long-term survival of feral cotton (Rogers *et al*., 2007; OGTR, 2008). The modelling program predicted that the winter temperatures in current Australian cotton-growing areas are too cold to support the establishment of permanent populations. The model indicated that dry stress is the major limiting factor in northern Australia, and predicted potential naturalisation of cotton with matching climates on the northeastern coast. Soil fertility, plant competition and fire were identified as factors that could reduce the probability of permanent populations establishing.

5. Genetics and Hybridisation

Germplasm resources of *Gossypium* have been described in detail (Percival *et al*., 1999). The various objectives followed in breeding cotton and the technology used are dependent on factors such as biological constraints and abiotic stress resistances, and other factors such as market demands (Niles, 1980; Calhoun and Bowman, 1999; Mergeai, 2006a). A survey of breeders in 2000 showed that most of the breeding work in *G. hirsutum* involved crossing closely related parents followed by backcrossing or reselecting from existing crosses, with less than 3% of the breeding material coming from non-*G. hirsutum* sources (Bowman, 2000). In Australia breeding has contributed about 45% to the improvements in yield since 1983 (Constable *et al*., 2001).

5.1. Genomes

Gossypium species are classified into eight diploid genomic groups and one tetraploid group (Section II, Table 2) based on cytogenetics, along with their capability to form viable or fertile interspecific hybrids experimentally (Edwards & Mirza 1979; Endrizzi *et al*. 1985; Stewart 1995). Generally species within a group can form hybrids with normal meiotic pairing and at least some F_1 fertility, whereas crosses between groups rarely form hybrids, and if so they have meiotic abnormalities and are infertile.

The D genome is the smallest, with a mean 2C nuclear DNA content of 1.81 picograms, and the A genome is almost twice as large — 3.47 pg; the mean DNA content of the AD-genome tetraploids is nearly additive, with 4.91 pg, and suggests a small loss of DNA subsequent to polyploidisation (Hendrix and Stewart, 2005; Grover *et al*., 2007, 2008). The size difference in diploid genomes (and the tetraploid subgenomes) is primarily a result of differential amplification of repetitive DNA transposable elements (Hawkins *et al*., 2006).

In the allotetraploid crop species ($2n = 4x = 52$), the A group's generally larger 13-chromosome set can be distinguished from the D group's generally smaller 13-chromosome set and the individual chromosomes in each subgenome identified (Muravenko *et al*., 1998; Rong *et al*., 2004; Wang *et al*., 2006). In *G. barbadense*, the A-genome chromosomes average 4.20 µm in length, with the largest seven being 4.34 µm or more (the full range is 2.23 to 5.81 µm), whereas the D-genome chromosomes average 3.29 µm long (and range from 1.76 to 4.25 µm) (Muravenko *et al*., 1998). The 13 individual chromosomes of the A-genome diploid ($2n = 2x = 26$) species *G. arboreum* have been identified and correlated with their counterparts in the A subgenome of *G. hirsutum* (Wang *et al*., 2008).

Comprehensive overviews of the results from recent genomic investigations of *Gossypium* have been provided (Preetha and Raveendren, 2008; Zhang *et al*., 2008). The most complete tetraploid genetic map so far (from *G. hirsutum* × *G. barbadense* F_2s) comprises 2584 loci, at an average inter-marker distance of 1.72 cM (~ 606 kbp), in 26 linkage groups — thus covering all 13 individual chromosomes of each subgenome (Rong *et al*., 2004). Genetic linkage maps of the *G. arboreum* genome have been made and correlated with the A subgenome of *G. hirsutum* (Desai *et al*., 2006; Ma *et al*., 2008).

Based on a mean 2C nuclear DNA content of 4.93 pg for *G. hirsutum*, the haploid DNA (1C-value) is estimated to be 2410 Mbp (Hendrix and Stewart, 2005). An international coalition of researchers has plans underway to completely sequence the nuclear genome of *G. hirsutum* (Chen *et al*., 2007), first by sequencing the ancestrally close D-genome relative *G. raimondii*, which has a much smaller genome (1C of 880 Mbp) (Hendrix and Stewart, 2005). The complete nucleotide sequences of the chloroplast genomes of *G. hirsutum* (Lee *et al*., 2006) and *G. barbadense* (Ibrahim *et al*., 2006) have been determined.

The complexity in the *Gossypium* genome occurs in a multitude of diverse dimensions. The diploid genus itself is considered a paleopolyploid (as is possibly the case for most angiosperms). An ancient polyploidisation event (whole genome duplication) (perhaps $2n = 14$ to $2n = 28$) appears to have occurred 13-15 (-30) million years ago in the Malvaceae lineage that evolved into what is treated as the emergent diploid genus *Gossypium* ($2n = 26$) (Muravenko *et al*., 1998; Brubaker *et al*., 1999a; Wendel and Cronn, 2003; Blanc and Wolfe, 2004; Rong *et al*., 2004, 2005; Ma *et al*., 2008). Consequently, genes were duplicated in that ancient originating event, the species continued genomic and genic evolution (Small *et al*., 2004), and genes were duplicated again in the rather recent formation of the allotetraploid lineage that has provided the two predominant crop species.

The functioning and evolutionary fortune of the plethora of counterpart genes (homoeologs) subsequent to the *Gossypium* allopolyploidisation event have been receiving substantial investigation. A broad array of divergent outcomes can occur, in some cases immediately with the onset of the genome doubling (and gene duplicating) event, in other cases during the long course of evolutionary time (Wendel and Cronn, 2003; Adams and Wendel, 2004; Adams, 2007; Liu and Adams, 2007; Wang *et al*., 2007; Flagel *et al*., 2008). Paterson (2005) has sketched how some cotton QTLs for crop improvement relate to such homoeologs.

5.2. Intraspecific crossing

Typically, the profitability of production mostly depends on lint yield, so the ultimate objective of many breeding programs is to increase it. Using intraspecific hybrid vigour to increase the yield has long been an objective (Zhang and Pan, 1999). Lint yield is a complex trait under complex genetic and environmental interactions, requiring a good balance among yield components. Heterosis has not been easy to employ due to the lack of an efficient crossing system. Many male-sterile systems have been explored (Percy and Turcotte, 1991; Basu, 1996), but male steriles and their restorer factors often have not been stable in different environments. Heterosis is not used commercially except where a large labor force can make emasculations and crosses by hand. At least 40% of cotton production in India has been derived from intraspecific hybrids of *G. hirsutum* (Chaudhry, 1997). Meredith (1999) reported an average useful heterosis of 21.4% (or 276 kg/ha) for F_1 hybrids and 10.7% for F_2 hybrids, although heterosis for fibre properties averaged only 0-2% for most characteristics.

5.3. Interspecific crossing

Under intensive experimental conditions, species in a few other genera of Malvaceae have been reported to form fertile hybrids with *Gossypium* (Mehetre *et al*., 1980), but spontaneous intergeneric hybridisation is highly improbable. Within the genus *Gossypium*, the sexual transmission of genetic material of cultivated cottons *via* pollen has been possible to certain of the species. For improvement of the main crops, *Gossypium* species can be grouped into three gene pools based on their ability to generate fertile hybrids and homoeologous recombination (Stewart, 1995; Percival *et al*., 1999).

Most cultivated cotton is tetraploid (primarily *G. hirsutum*), and thus relatively incompatible with the diploid species — normally plants from these two groups do not hybridise spontaneously and produce fertile offspring, and experimental crosses are difficult and require complex breeding schemes (Mergeai, 2006b). Moreover, experimental F_1 hybrids between the genome groups of diploids are nearly always sterile, or are weak (Endrizzi *et al*., 1984, 1985; Brown and Brubaker, 2000; Cronn and Wendel, 2004).

5.3.1. Primary gene pool — the tetraploids

The tetraploid (AADD) species are sexually compatible, which accords with their differentiation following a hybridisation event only 1-2 million years ago; since then they have diverged into three evolutionary lineages (Wendel and Cronn, 2003). The primary gene pool comprises the subgenus *Karpas*: the three wild tetraploid species (*G. mustelinum*, *G. darwinii*, *G. tomentosum*) and the wild, commensal, landrace, cultigen and feral *G. barbadense* and *G. hirsutum*. Experimental crosses among these entities are rather easy and genetic recombination frequency is high; favourable traits have been incorporated from this gene pool (particularly from *G. hirsutum* and *G. barbadense*) into the modern crops (Endrizzi *et al*., 1984, 1985; Meredith, 1991; Stewart, 1995; Percival *et al*., 1999).

5.3.1.1. Spontaneous hybridisation of tetraploids in the New World

Native populations of the three completely wild tetraploid species are widely separated biogeographically (Appendix 1). Moreover, the clearly genuinely wild native populations of *G. barbadense* and *G. hirsutum* are also completely separated from the other three species, and from each other (Brubaker and Wendel, 1994; Westengen *et al*., 2005; Johnston *et al*., 2006). Thus, fully natural hybridisations do not occur among the tetraploids; however, spontaneous (unaided) hybridisation might occur when cultivated plants are brought within range of these wild species or primordially wild populations. Spontaneous hybridisation between various other populations or plants of the cultivated species also may occur.

5.3.1.2. Gossypium mustelinum

Gossypium mustelinum is a local, very rare endemic in semi-arid northeastern Brazil (Freire *et al*., 1998; Batista *et al*., 2005; Barroso *et al*., 2006; WWF and IUCN, 1997), and is considered most similar to the original allotetraploid progenitor (Wendel *et al*., 1994). Experimentally, *G. mustelinum* can form fertile F_1 as well as F_2 hybrids and backcrosses with *G. hirsutum*, and to some extent with *G. barbadense* (Freire, 2002b; Freire *et al*., 2002; Gardunia *et al*., 2007). The evidence of spontaneous introgression in Brazil is uncertain, and relates particularly to *G. hirsutum* (Wendel *et al*., 1994; Freire, 2002a; Freire *et al*., 2002; Borém *et al*., 2003; Johnston *et al*., 2006).

5.3.1.3. Gossypium darwinii

Gossypium darwinii is a widespread endemic in the Galapagos Islands, and is considered most closely related to *G. barbadense* (Wendel and Percy, 1990; Lacape *et al*., 2007). The *Gossypium barbadense* that settlers brought to the Galapagos apparently included plants that earlier had introgressed with *G. hirsutum*. The introduced domesticated cotton has not become widely naturalised, but spontaneous gene flow has occurred into *G. darwinii* (Wendel and Percy, 1990). Experimentally, F_2 hybrids produced from crosses of *G. barbadense* and *G. darwinii* are fertile and vigorous.

5.3.1.4. Gossypium barbadense and *Gossypium hirsutum*

The original native habitat of *G. barbadense* is considered to be the dry coastal region of northern Peru and southern Ecuador (Schwendiman *et al.*, 1985; Percy and Wendel, 1990; Westengen *et al.*, 2005). The original native habitat of *Gossypium hirsutum* is considered to involve central Mesoamerica (Hutchinson, 1951; Stephens, 1958; Brubaker and Wendel, 1994). The natural distribution of *G. hirsutum* as a wild species is particularly obscure because of millennia of early use, domestication and expanded cultivation.

Many of the advanced stocks of commercial *G. barbadense* have benefited from the introgression of *G. hirsutum* characteristics by plant breeding (Wang *et al.*, 1995). Reciprocally, introgression of *G. barbadense* into *G. hirsutum* has exploited (for example) the excellent fibre qualities of the former. However, the hybrid vigour resulting is associated with excessive vegetative growth and late maturity, which make adaptation of such hybrids limited to those areas with a long growing season. This problem was reduced by obtaining precocious, short-growing season *G. barbadense*-types that may be used to produce the F_1 hybrids with *G. hirsutum* (Feaster and Turcotte, 1980).

Despite these commercial breeding successes, introgression of *G. hirsutum* into *G. barbadense* is conspicuously low in germplasm collections from Mesoamerica and the Caribbean where *G. barbadense* has been grown with the predominant *G. hirsutum* since prehistoric times (Brubaker *et al.*, 1993; Westengen *et al.*, 2005). The relative absence of introgression into *G. barbadense* may result from various isolating mechanisms, involving plant reproductive biology, agroecology and ecology (Percy and Wendel, 1990; Brubaker *et al.*, 1993; Jiang *et al.*, 2000; Freire *et al.*, 2002; Borém *et al.*, 2003; OGTR, 2008). In contrast, introgression of *G. barbadense* into *G. hirsutum* under such conditions is relatively common (Wendel *et al.*, 1992; Brubaker *et al.*, 1993; Brubaker and Wendel, 1994). Isozyme analysis found the most introgression into *Gossypium hirsutum* race marie-galante (Brubaker and Wendel, 1994; Brubaker *et al.*, 1999c), but SSR analysis of several samples of marie-galante from the Caribbean and mocó from Brazil did not detect such introgression (Lacape *et al.*, 2007; *cf.* Freire *et al.*, 2002; Borém *et al.*, 2003).

5.3.1.5. Gossypium tomentosum

Gossypium tomentosum is endemic in the Hawaiian Islands, and apparently the closest relative to *G. hirsutum* (DeJoode and Wendel, 1992; Hawkins *et al.*, 2005; Waghmare *et al.*, 2005; *cf.* Westengen *et al.*, 2005). The flowers of *G. tomentosum* reportedly are receptive at night rather than during the day and pollinated by moths, not bees (Stephens, 1964; Fryxell, 1979). Feral *Aethina concolor* beetles enhance its self-pollination, and perhaps effect cross-pollination (Burraston *et al.*, 2005; Burraston and Booth, 2006). Spontaneous movement of genetic material from cultivated *G. hirsutum* to the wild endemic remains speculative (*cf.* Waghmare *et al.*, 2005). Also, despite morphological suggestion of spontaneous hybrids between naturalised *G. barbadense* and the wild endemic (Stephens, 1964; Münster and Wieczorek, 2007), no allozyme evidence of introgression has been found (DeJoode and Wendel, 1992).

5.3.2. Secondary and tertiary gene pools — the diploids

All species in these gene pools are diploids. In addition to cytological barriers to hybridisation, varied physiological barriers exist between the diploids and *G. hirsutum*, the usual focus for improvement. *In vitro* culture of ovules partly solves the problem (Stewart and Hsu, 1978). Three main breeding strategies (Mergeai, 2006b) have been devised to overcome sterility barriers and can lead to successful introgression of desirable traits (Endrizzi *et al.*, 1985; Meredith, 1991; Stewart, 1995). In two schemes, crossing a diploid and *G. hirsutum* results in sterile triploids (3*x*), with few rare exceptions (Brown, 1951; Meyer, 1974). Hexaploids (6*x*) are then made (using colchicine) by chromosome doubling of the triploid genome. The hexaploid can then be crossed with a different diploid and result in a tri-species tetraploid hybrid. Or, *G. hirsutum* can be crossed with the hexaploid; the resultant pentaploids (5*x*) can be self-crossed, or crossed again with *G. hirsutum*, resulting in a tetraploid.

The secondary gene pool includes the evolutionarily closer diploids, thus comprising the D-genome species (subgenus *Houzingenia*) and the A-genome species, as well as the African B- and F-genome species (Appendix 1) (Phillips, 1966; Phillips and Strickland, 1966; Wendel and Cronn, 2003).

Bridge-crosses between two diploid species, induced genome doubling, and then crossing with *G. hirsutum* are another useful strategy for gene transfer (Mergeai, 2006b). Such an approach using the A-genome and D-genome species produces synthetic AD tetraploids, which may be readily crossed with *G. hirsutum*. Genes from the A or D genome may thus be transferred to the upland cotton crop (Stewart and Stanton, 1988; Saravanan *et al.*, 2007). For example, the ATH tri-species hybrid (*G. arboreum* × *G. thurberi*) × *G. hirsutum* has been used to introduce fibre strength.

The tertiary gene pool includes the evolutionarily distant diploids, thus comprising the African-Arabian E-genome species, and the Australian C-, G- and K-genome species (Appendix 1) (Wendel and Cronn, 2003). Potential exploitation of desirable traits/genes in this gene pool (as well as evaluation of transgene diffusion potential) have stimulated considerable research in the Australian subgenus *Sturtia* (Brown *et al.*, 1997; Zhang and Stewart, 1997; Brubaker *et al.*, 1999b; Brown and Brubaker, 2000). Desirable traits include gossypol-free seeds, which occur in both the C- and G-genome species.

It has not been possible to obtain hybrids of *G. hirsutum* with the G-genome species, whereas hybrids can be obtained readily with the C-genome species; the situation is intermediate and variable with the K-genome species (Brown and Brubaker, 2000). The experimental hybrids among the species of subgenus *Sturtia* range from being totally infertile, to having some meiotic fertility in backcrosses but the plants are weak (Brown *et al.*, 1997; Brown and Brubaker, 2000). The first gene from the tertiary gene pool introgressed into *G. hirsutum* came from the C genome's *G. sturtianum*, and involved control of terpenoid aldehyde methylation (to reduce gossypol formation) (Bell *et al.*, 1994). Although *G. sturtianum* is the species in subgenus *Sturtia* that crosses most readily with *G. hirsutum*, the F_1 is completely infertile.

6. Biotechnology and genetic transformation

The efforts to domesticate and improve cotton span millennia, from selection and conventional breeding, to chemical and radiation mutagenesis, to advanced biotechnological techniques. Some of the traits of continuing interest to incorporate into cultivated cottons include disease and insect resistances and drought and salt tolerances for the crop, whereas other traits are focused on improving the crop's products (Basu, 1996; Paterson and Smith, 1999; Wilkins *et al.*, 2000; Jenkins and Saha, 2001; Hake, 2004). Embryo rescue is employed to obtain plants from interspecific hybridisations that will abort (Mehetre and Aher, 2004). A research focus in the 1960s and 1970s was development of new cell culture methods. Callus cultures were the starting point to isolate protoplasts, with a view to making wide crosses *via* protoplast fusion with sexually incompatible germplasm (Carlson *et al.*, 1972). Price *et al.* (1977) first defined the conditions for establishment of callus cultures, from six cotton species. The first report of a cell culture system to obtain somatic embryos from cotton callus cultures was by Price and Smith (1979), and improvements have continued (Kumar and Tuli, 2004; Sakhanokho *et al.*, 2004; Sun *et al.*, 2006).

The main vector used for introducing particular genes into cotton is *Agrobacterium tumefaciens*, with the first reports of transformations in the nuclear genome by Umbeck *et al.* (1987) and Firoozabady *et al.* (1987). A gene-transfer system was developed culturing *Agrobacterium* with sections of 6- to 7-day-old cotton-seedling hypocotyls (Fillatti *et al.*, 1989). The *Agrobacterium*-mediated approach continues to be of major utility (Wilkins *et al.*, 2004). The first report of cotton plants transformed using projectile bombardment was by Finer and McMullen (1990), which was followed by genotype-independent particle bombardment of four cultivars (McCabe and Martinell, 1993). The bombarded cells are grown in tissue culture to differentiate and develop into shoots or whole plants. A major problem has been achieving regeneration — only a limited number of cotton varieties (*i.e.* genotypes) regenerate relatively easily. Transformation has also been achieved in the chloroplast genome (Kumar *et al.*, 2004).

Insect-resistant and herbicide-tolerant cotton varieties have been developed by means of genetic engineering and are commercially grown in a number of countries. The first agronomically important gene inserted into cotton was for insect resistance, *cry1Ab* from *Bacillus thuringiensis* (Bt) (Perlak *et al.*, 1990). Other insecticidal genes from Bt have been introduced (especially *cry1Ac* and *cry2Ab*, and more recently *vip3A*), which encode particular proteins selectively toxic to various Lepidopteran pests. An insecticidal gene *AaHIT* from the scorpion *Androctonus australis* is also being explored in transgenic cotton against some lepidopterans (Wu *et al.*, 2008).

Cotton lines have been genetically engineered to tolerate the herbicides bromoxynil, glufosinate ammonium, glyphosate or sulfonylurea. Transgenic cottons in commercial production include plants having stacked transgenes, for example a Bt (Cry1Ac + Cry2Ab) + glyphosate-tolerant cotton.

With continuing development, there are likely to be transgenic cottons improved in other ways, for example with fibres that are stronger (Zhu *et al.*, 2006; Shang-Guan *et al.*, 2007) or have non-crease characteristics similar to polyester (John and Keller, 1996); or with seeds that are gossypol-free (Sunilkumar *et al.*, 2006) or with improved oil composition (Chapman *et al.*, 2001; Liu *et al.*, 2002).

7. Human health and biosafety

Cottonseed oil has been in common use since at least the middle of the 19th century (Jones and King, 1993). Cottonseed meal or flour is also sometimes used for human consumption when derived from gossypol-free varieties, or if the gossypol has been extracted or is present in the food at low levels. Information on processing of cottonseed (of both *G. hirsutum* and *G. barbadense*) and its major products (oil, meal, hulls and linters) and their composition including the key food and feed nutrients, toxins and anti-nutrients have been summarised by the OECD (2004).

Cottonseed is a valuable foodstuff for cattle, combining high energy, high fibre and high protein (Ensminger *et al.*, 1990b), and is used as whole seed, hulls, flour and cake. The whole seed of *G. hirsutum* also includes linter fibers (~ 10% of seed weight), which are nearly pure cellulose and highly digestible. The seed oil gives it high energy value (Coppock *et al.*, 1985). Cattle and sheep are fed cottonseed hulls as an important source of roughage. The hulls are removed from whole seed, and composed mainly of hemicellulose and lignin, with the linters remaining attached. Gin trash is also fed to ruminants, and has 90% of the food value of the hulls (Ensminger *et al.*, 1990a).

Extracts of cotton plants have been used medicinally (*e.g.* Sawyer, 1955; Hasrat *et al.*, 2004). Because of its several physiological effects, the medical potential of gossypol is being investigated (Dodou *et al.*, 2005), and it has been used as a male contraceptive (Coutinho, 2002).

7.1. Toxins

Cotton plants contain compounds that can have adverse effects on human and animal health (OGTR, 2008). Cotton tissue, particularly the seeds, can be toxic when ingested in large quantities because of the anti-nutritional and toxic compounds (Abou-Donia, 1976; Tumbelaka *et al.*, 1994; Smith, 1995). Most important with respect to human health and biosafety are gossypol, which is a terpenoid aldehyde, and cyclopropenoid fatty acids (CPFAs), as well as tannins.

The gossypol and CPFAs in cottonseed limit its use as a protein supplement in animal feed. Ruminants are less affected because these compounds are detoxified by digestion in the rumen (Kandylis *et al*., 1998). Cottonseed as a stockfeed is limited to a relatively small proportion of the diet, and must be introduced gradually to avoid the potentially toxic effects (Blasi and Drouillard, 2002).

Because *Gossypium barbadense* cottonseed possesses almost no linters, it is digested differently by cattle than *G. hirsutum*. The nearly naked seeds are thought to sink in the rumen and so be less masticated and digested (Coppock *et al*., 1985; Sullivan *et al*., 1993a, 1993b; Zinn, 1995; Solomon *et al*., 2005). To improve digestibility of *G. barbadense* seed it is often cracked prior to feeding even though this increases the exposure to gossypol. Cows that consumed cracked *G. barbadense* seed at ~ 7.5% of their diet had reduced fertility (Santos *et al*., 2003).

7.1.1. Gossypol

Gossypol is found primarily in the pigment glands of the roots, leaves, flower buds and seeds (Smith, 1961, 1967). It is toxic to non-ruminant mammals, birds, and many insects and microbes; in mammals the toxic effects can include reduced appetite, body weight loss and dyspnea (Berardi and Goldblatt, 1980). Gossypol can render lysine metabolically unavailable and impact on the normal functioning of mitochondria (Yannai and Bensal, 1983; Cuellar and Ramirez, 1993; Risco *et al*., 1993).

Although glandless cotton has been developed for food purposes, the plants are more susceptible to pests (Delattre, 1992). Inactivation or removal of gossypol and CPFAs during processing has enabled use of cottonseed meal for catfish, poultry and swine (Jones and Wedegaertner, 1986; Lusas and Jividen, 1987).

Gossypol exists as two different isomers (mirror-image forms of the same compound), which are in different proportions in *G. barbadense* and *G. hirsutum* (Stipanovic *et al*., 2005). *Gossypium barbadense* has more of the (–)-gossypol form (Sullivan *et al*., 1993b), which has greater biological activity. The isomers have different toxicity levels and the toxicity varies in different animals (Wang *et al*., 1987; Bailey *et al*., 2000; Lordelo *et al*., 2005, 2007).

Both isomers exist in free and bound forms. In intact whole cottonseed, gossypol is in the free form. The free form is more biologically active, whereas the bound form is generally not released in the rumen. In ruminants, with well-developed rumen microflora, free gossypol is converted to bound gossypol, thus preventing its entering the bloodstream (Santos *et al*., 2002). During the processing of whole cottonseed, gossypol partitions into meal and oil components. Most of the gossypol in meal becomes bound to proteins, thus becoming less toxic.

The levels of gossypol and related terpenoids in cottonseed vary (0.4–2.0 %) by species, variety, fertiliser application, and environmental conditions including biotic pressure from insects and diseases (Bell, 1986). The amount of gossypol in *G. barbadense* is generally higher than in *G. hirsutum* and with more of the gossypol in the free form, which reduces the amount of cottonseed of *G. barbadense* that can be recommended for cattle feed (Kirk and Higginbotham, 1999).

7.1.2. Cyclopropenoid fatty acids

Cyclopropenoid fatty acids (CPFAs) are present in the cotton seeds, and tannins in the leaves and flower buds (Chan *et al*., 1978; Lane and Schuster, 1981; Mansour *et al*., 1997); both are thought to act as deterrents to insects. CPFAs such as malvalic, sterculic and dihydrosterculic acids constitute approximately 0.5–1.0% of the total lipid content of the seed (Schneider *et al*., 1968). The level of CPFAs is generally higher in *G. hirsutum* than *G. barbadense* (Frank, 1987).

CPFAs are anti-nutritional compounds, which interfere with the metabolism of saturated fats (Rolph *et al*., 1990; Cao *et al*., 1993). They are destroyed by the processing of cottonseed oil for use in margarine or salad oil for humans, but in less-processed animal feed CPFAs can cause unwanted effects (Goodnight and Kemmerer, 1967; Hendricks *et al*., 1980; Tumbelaka *et al*., 1994).

7.2. Allergens

Processed cotton fibre contains over 99% cellulose (Wakelyn *et al*., 2007a, 2007b), and is used widely in pharmaceutical and medical applications because of its low capacity to cause irritation. Inhalation of cotton dust by mill workers can cause an asthma-like condition called byssinosis (Nicholls, 1992), which may be complicated by fungal contamination of the cotton dust (Salvaggio *et al*., 1986).

Appendix 1. *Gossypium* species[1]

Species	Genome	Distribution
G. arboreum L.	A_2	Asian cultigen
G. herbaceum L. subsp. *herbaceum*	A_{1-1}	NE African - Central Asian cultigen
G. herbaceum subsp. *africanum* (G. Watt) Vollesen [synonym *G. herbaceum* var. *africanum* (G. Watt) J.B. Hutch. ex S.C. Harland]	A_{1-2}	southern Africa
G. longicalyx J.B. Hutch. & B.J.S. Lee	F_1	C-E Africa
G. triphyllum (Harv.) Hochr.	B_2	SW Africa
G. anomalum Wawra ex Wawra & Peyr.	B_1	SW & N sub-Saharan Africa
G. capitis-viridis Mauer	B_3	Cape Verde Islands
G. trifurcatum Vollesen[2]	?	NE Africa
G. stocksii Masters	E_1	Somalia to Pakistan
G. areysianum Deflers	E_3	Arabia
G. incanum (O. Schwartz) Hillcoat	E_4	Arabia
G. somalense (Gürke) J.B. Hutch.	E_2	NE Africa
G. benadirense Mattei	E	NE Africa
G. bricchettii (Ulbrich) Vollesen	E	NE Africa
G. vollesenii Fryxell	E	NE Africa
G. robinsonii F. Muell.	C_2	W Australia
G. sturtianum J.H. Willis var. *sturtianum*	C_1	C to E Australia
G. sturtianum var. *nandewarense* (Derera) Fryxell	C_{1-n}	E Australia
G. bickii Prokh.	G_1	N-C Australia
G. australe F. Muell.	G_2	NW Australia
G. nelsonii Fryxell	G	N-NE Australia
G. cunninghamii Todaro	K	N Australia
G. anapoides J.M. Stewart, Craven & Wendel, ined.? [3]	K	NW Australia
G. costulatum Todaro	K	NW Australia
G. enthyle Fryxell, Craven & J.M. Stewart	K	NW Australia
G. exiguum Fryxell, Craven & J.M. Stewart	K	NW Australia
G. londonderriense Fryxell, Craven & J.M. Stewart	K	NW Australia
G. marchantii Fryxell, Craven & J.M. Stewart	K	NW Australia
G. nobile Fryxell, Craven & J.M. Stewart	K	NW Australia
G. pilosum Fryxell	K	NW Australia
G. populifolium (Bentham) F. Muell. ex Todaro	K	NW Australia
G. pulchellum (C.A. Gardner) Fryxell	K	NW Australia

Species	Genome	Distribution
G. rotundifolium Fryxell, Craven & J.M. Stewart	K	NW Australia
G. gossypioides (Ulbrich) Standley	D_6	W Mexico
G. armourianum Kearney	$D_{2\text{-}1}$	NW Mexico (Baja California)
G. harknessii Brandegee	$D_{2\text{-}2}$	NW Mexico (Baja California)
G. turneri Fryxell	D_{10}	NW Mexico
G. laxum L.L. Phillips	D_8	CW Mexico
G. aridum (Rose & Standley) Skovsted	D_4	NW-SW Mexico
G. lobatum Gentry	D_7	CW Mexico
G. schwendimanii Fryxell & S.D. Koch	D_{11}	CW Mexico
G. thurberi Todaro	D_1	NW Mexico, Arizona
G. trilobum (Sessé & Moc. ex DC.) Skovsted	D_9	W Mexico
G. davidsonii Kellogg	$D_{3\text{-}d}$	NW Mexico (Baja California)
G. klotzschianum Andersson	$D_{3\text{-}k}$	Galapagos Islands
G. raimondii Ulbrich	D_5	NW Peru
G. hirsutum L.[4]	$(AD)_1$	Mesoamerica
G. tomentosum Nuttall ex Seemann	$(AD)_3$	Hawaii
G. barbadense L.	$(AD)_2$	W South America
G. darwinii G. Watt	$(AD)_5$	Galapagos Islands
G. mustelinum Miers ex G. Watt	$(AD)_4$	NE Brazil

[1] Mostly after Endrizzi *et al.* (1984), Fryxell (1992), Fryxell *et al.* (1992) and Percival *et al*. (1999).

[2] *Gossypium trifurcatum* was described by Vollesen (1987) and is accepted by Fryxell (1992). Percival *et al*. (1999) indicated that it might belong in the genus *Cienfuegosia*, but cpDNA analysis by Rapp *et al*. (2005) supports its placement in *Gossypium*.

[3] *Gossypium anapoides* has been noted in recent literature (Stewart *et al*., 1997; Zhang and Stewart, 1997; Brubaker *et al*., 1999b; Percival *et al*., 1999; Brown and Brubaker, 2000; Cronn and Wendel, 2004), but it may (as yet) not have been published as a new species in accord with the *International Code of Botanical Nomenclature*.

[4] *Gossypium lanceolatum* Todaro is not a distinct species, but instead considered to be a local Mexican landrace — in domesticated *Gossypium hirsutum* race palmeri (Brubaker and Wendel, 1993).

Appendix 2. Genera of weeds regionally common in cotton

Dicotyledons	**Monocotyledons**
Abutilon	*Alopecurus*
Achyranthes	*Cenchrus*
Alternanthera	*Commelina*
Amaranthus	*Cynodon*
Boerhavia	*Cyperus*
Capsella	*Dactyloctenium*
Celosia	*Digitaria*
Chamaesyce (*Euphorbia*)	*Echinochloa*
Chenopodium	*Eleusine*
Convolvulus	*Leptochloa*
Croton	*Lolium*
Datura	*Panicum*
Desmodium	*Paspalum*
Diplotaxis	*Poa*
Fumaria	*Rottboellia*
Geranium	*Setaria*
Heliotropium	*Sorghum*
Hibiscus	
Ipomoea	
Matricaria	
Merremia	
Oxalis	
Papaver	
Parthenium	
Pavonia	
Plantago	
Polygonum	
Portulaca	
Raphanus	
Ridolfia	
Senna (*Cassia*)	
Sesbania	
Sida	
Sinapis	
Solanum	
Stellaria	
Trianthema	
Tribulus	
Urtica	
Xanthium	

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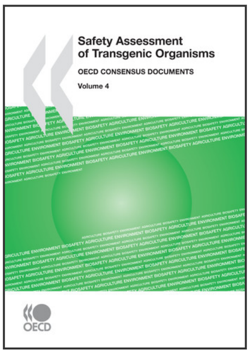

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