

## Wild Cotton in Northeast Brazil

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### ABSTRACT

Some additional localities for a wild tetraploid cotton, *G. mustelinum* Watt, in northeast Brazil are reported, together with field observations on this cotton in its natural habitats. The history of cotton cultivation in northeast Brazil is reviewed and *G. mustelinum* compared with cottons cultivated in the region from early Colonial times onward. *G. mustelinum* appears to be specifically distinct from the other tetraploid cottons, and it is not likely that it is a feral derivative of any commercially cultivated cotton. This little-known tetraploid may help in reconstructing the origin of the New World polyploid cottons.

THE NEW WORLD CULTIVATED COTTONS, *Gossypium hirsutum* and *G. barbadense*, are tetraploids ( $2n=4x=52$ ) which contain the A genome found in the Old World diploids *G. herbaceum* and *G. arboreum* and the D genome found in American wild diploids. In both the cultivated tetraploids and the A genome diploids the hairs on the seed coat are differentiated into long lint hairs, which become twisted on drying and can thus be spun into thread, and an undercoat of short hairs (fuzz), which have more extensive cellulose thickening and which do not twist on drying. The D genome diploids have seed hairs of various sorts but never bear lint and have never been used by man for fiber.

At one time it was thought that man had introduced a domesticated, linted A genome cotton from the Old World to the New, where it hybridized with a native D diploid to produce the tetraploids. Gerstel (1953) showed that *G. herbaceum* chromosomes were more similar to those of the New World A genome than were those of *G. arboreum*, although even *G. herbaceum* chromosomes differed from the A genome of the tetraploids by two translocations. At present it seems that the diploid most similar to the A genome progenitor of the tetraploids is *G. herbaceum* var. *africanum*, a linted, hard-seeded cotton that occurs wild in southern Africa.

The D genome diploids are today confined to the western sides of the American continents. The Mexican species, together with *G. klotzschianum* var. *dauidsonii* from the Galápagos Islands, form a group fairly closely related among themselves but

more distantly related to the Peruvian species *G. raimondii* (Phillips 1966). *G. raimondii* is the species most similar to the D genome ancestor of the tetraploids on the criteria of morphology of the seed hairs (Hutchinson, Stephens, and Dodds 1945) and chromosome pairing and chiasma formation in hybrids with the tetraploids (Phillips 1963, 1966). Furthermore, electrophoretic studies on seed proteins have shown that a synthetic mixture of proteins from *G. raimondii* and *G. herbaceum* var. *africanum* gave very similar banding patterns to proteins from *G. hirsutum* and *G. barbadense* (Cherry, Katterman, and Endrizzi 1970). However, although *G. raimondii* is the most similar extant diploid to the D genome ancestor of the tetraploids, there are more dissimilarities between the chromosomes of *G. raimondii* and the tetraploid D genome than there are between *G. herbaceum* and the tetraploid A genome (Phillips 1963).

Today the ranges of the A and D genome diploids are separated by some thousands of miles (see map, fig. 1), and the origin of the tetraploids poses a considerable phytogeographic problem. Cytogenetic data (Phillips 1963) suggested that the tetraploids are derived from a common ancestor (i.e. originated monophyletically) and that speciation occurred after the tetraploids were established. The different genome groups in *Gossypium* may have diverged when the range of an early prototype cotton became fragmented when Gondwanaland broke up into the land masses which correspond to the southern continents of today. This separation probably began in the early Cretaceous (Raven 1972). The first records of tetraploid cottons are archaeological specimens of domesticated (not wild) cot-

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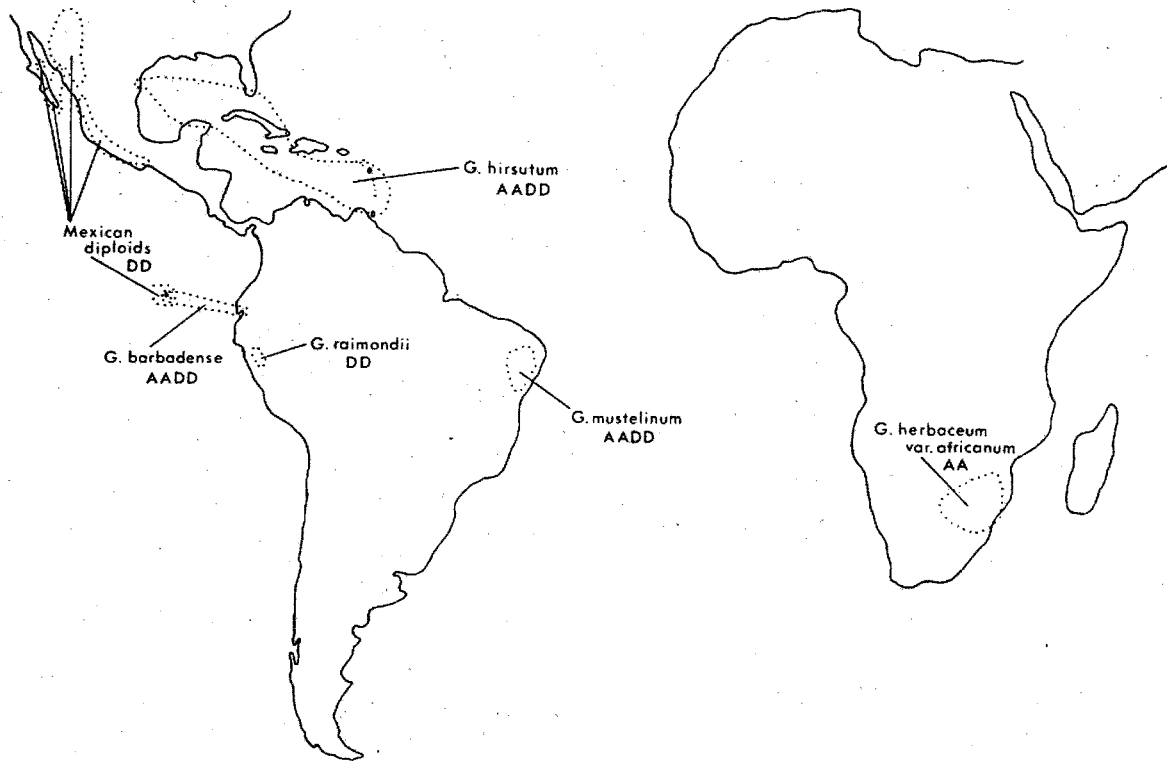


FIGURE 1. Distribution of wild forms of A and D genome diploid and New World AADD tetraploid cottons.

ton from Mexico and Peru about 3000 B.C. (Smith and Stephens 1971; Stephens and Moseley 1974). It is not possible to define more precisely the origin in time of the tetraploids, though Fryxell (1965) suggested that they may have arisen during the Pleistocene.

The place of origin of the tetraploids is also obscure, and the distribution of presumed wild forms of *G. hirsutum* and *G. barbadense* (see fig. 1) sheds little light on this. Either the A diploids or the D diploids or both must previously have been more widespread for an AD hybrid to have been produced. The most plausible assumption is that an A genome diploid spread across the Atlantic, probably by natural means and possibly at a time when the Atlantic barrier was less formidable than it is now, since Stephens (1966) has shown that seeds of *G. herbaceum* var. *africanum* are not sufficiently tolerant of salt water to survive a crossing of the present-day Atlantic. Lathrap (in press) has argued that man played a part in bringing linted cotton from Africa to the New World, and this view is difficult to refute on present evidence, though it seems unlikely on chronological grounds that this cotton was domesticated.

Whether the diploid ancestors of New World cultivated cottons spread naturally or by human intervention, it seemed possible that some traces of the early evolutionary history of the tetraploids might remain in the area between the present ranges of the A and D diploids, particularly the arid region of northeast Brazil which is climatically and ecologically rather similar to the natural habitat of *G. herbaceum* var. *africanum*. Our interest was further aroused when Brazilian workers reported a wild tetraploid cotton from northeast Brazil which differed from both *G. hirsutum* and *G. barbadense* (Neves *et al.* 1965; Aranha *et al.* 1969). In the course of a plant-collecting expedition to northeast Brazil in 1972, we were able to study the colony of wild cotton described by Neves and his colleagues and to record two additional localities for what appears to be the same taxon. In this paper we report our field observations on this wild cotton and comment on its status and possible evolutionary significance.

#### FIELD OBSERVATIONS

1. CAICÓ (Rio Grande do Norte). Neves *et al.* (1965) have given a detailed description of the

wild cotton that they found near Caicó. A single colony occurred in a steep gully cut by a stream into the slopes of the Serra da Formiga above the town of Caicó, in the Seridó district of Rio Grande do Norte. The gully was on land belonging to a small farm, about 2 km from the farmhouse, at an altitude of about 500 m. We found that the cotton plants were confined to an area only a few hundred meters long, bordering the stream. Most of the plants were very large, one trunk measuring over 20 cm in circumference a short distance above the base, and the extremely long branches (estimated at up to 8 m in length) straggled over the associated woody vegetation (*Combretum*, *Bauhinia*, *Mimosa* and other shrubs) so that the young leaves, flower buds, and fruits of the cotton were borne in the upper levels of the more or less closed canopy. In March, when we visited the site, there were very few immature capsules and only two open flowers, although most plants bore young buds. Neves *et al.* (1965) also reported finding very few flowers on their visit in September. The dry season in this area extends from July to December. This cotton may thus resemble *G. hirsutum* in that buds produced during wet weather may be shed without opening (Hutchinson, Silow, and Stephens 1947). If so, peak flowering probably occurs at the beginning of the dry season, in July.

Because the plants were so large and straggling, and the vegetation so dense, it was difficult to determine how many individuals the colony contained, but close inspection suggested there were probably only six and certainly not more than 10 mature plants. Some seedlings had managed to establish and reach the 2-3 leaf stage on moist soil at the foot of a bank along the stream, where very few herbs were present. However, we could find no plants intermediate in size between these seedlings and the very old mature specimens. These observations differ from those of Neves *et al.* (1965), who reported that the colony consisted of more than 20 individuals, including some young plants, one less than a year old. Unlike Neves and his colleagues, we concluded that the colony was not regenerating.

Although there were so few plants, the colony contained some individuals with spotted and others with unspotted corollas (a difference determined by a single major gene in other cottons). Many of the young buds had a partial or complete second whorl of bracteoles, an unusual feature possibly connected with the fact that these buds were developing outside the main flowering season.

According to people at the farm, cotton was grown on hill slopes similar to that on which the

wild colony occurs as far back as 1877, although these slopes are not cultivated today. Pearse (1921) reported that in the Seridó district of Rio Grande do Norte "until quite recently cotton was grown on the margins of rivers, brooks, etc., only so far up the slanting side of the hill from the course, as it was thought that the roots would reach into the sub-soil water level. . . . But a few years ago some cultivators made experiments with growing cotton much further up the slant, on what are called 'taboleiras,' which used to be considered too dry. These experiments have been a great success, and the practice of using these 'taboleiras' for cotton is becoming common."

2. SALGADO DO MELÃO (northern Bahia). Local people in the village of Salgado do Melão (Município de Macururé) helped us find three small colonies of wild cotton on the land of fazenda Barbosa, about 10 km from the village, at an altitude of about 300 m. In all cases the plants were growing around the margins of small pools which dried up at the end of the rainy season (fig. 2a). The three pools were a few kilometers apart, separated by stretches of typical caatinga (thorn scrub) vegetation. Around the pools *Erythrina velutina* (indicative of a high water table) joined such caatinga species as *Caesalpinia pyramidalis*, *Mimosa* sp., *Croton campestris*, *Cordia leucocephala*, *Aspidosperma pyrifolium*, and *Opuntia palmadora*. As at Caicó, the long branches of the wild cotton straggled over the surrounding shrubs. The shrubs were less dense than at Caicó, but breaks in the woody cover were filled with almost impenetrable stands of the extremely spiny *Bromelia laciniosa*. The land around the pools was not cultivated, but cattle ranged freely through the area grazing on the caatinga vegetation, including the wild cottons (immature capsules noted by us on our first visit in February had been eaten off when we returned to the site in April). The bromeliads evidently played an important part in protecting the cotton from grazing animals, since plants surrounded by bromeliads were taller and more vigorous than unprotected plants. The bromeliads also made it extremely difficult to assess the number of individuals in each population, but there seemed to be at least 18 plants and some regenerating seedlings around the first pool (Lagoa Patori), three small plants around the second pool (Lagoa dos Algodões), where our informant said that the number of cotton plants had decreased since the area had been burned to eradicate the bromeliads and improve the grazing, and a single plant by a third, unnamed pool. The largest colony contained some flowering and fruiting specimens, and these



FIGURE 2. Habitats of *G. mustelinum* in northeast Brazil. (a) Salgado do Melão. Cotton plant (arrowed) on margin of small pool, in shade of *Erythrina* tree and surrounded by spiny bromeliads. (b) São Francisco. Depauperate cotton plant (arrowed) on dry slope in center of bromeliad ring.

were very similar indeed to the Caicó plants. As at Caicó, some plants had spotted and others unspotted corollas.

Local people did not use the wild cotton, but said it had been in the area as long as anyone could remember (some of our informants claimed to be over 80 years old).

3. SÃO FRANCISCO (northern Bahia). Another colony of wild cotton was found on the land of fazenda São Francisco, near the small village of São Francisco (also in the Município de Macururé), not far from Salgado do Melão but in a very different ecological situation (fig. 2b). There were no pools or streams in the immediate vicinity, no indication of a high water table, and the whole area was extremely dry and very open. The typical shrubs of dry caatinga, *Caesalpinia pyramidalis*, *Mimosa* sp., *Cnidioscolus phyllacanthus*, *Croton* sp., and the characteristic cacti xique-xique and facheiro (*Pilosocereus* spp.) were widely spaced and between were dense stands of spiny bromeliads (*Encholirium*

sp.). The cotton was even more markedly associated with bromeliad rings here than at Salgado do Melão, and again some cotton plants had been damaged by browsing animals. The plants were extremely depauperate, none more than 1 m tall, and with more anthocyanin pigmentation than plants at the other localities. The population was again small (about 10 plants), and the only flower present had a faint corolla spot. In other characters the plants agreed well with those from Caicó and Salgado do Melão.

According to the owner, wild cotton had been growing on this site when he acquired the fazenda in the 1950's. He was still growing cotton when we visited him, but on lower land, where there was more available water.

### IDENTITY OF THE WILD COTTON IN NORTHEAST BRAZIL

From their studies on plants raised from seed from the Caicó population, Aranha *et al.* (1969) concluded that this cotton differed morphologically from the other two linted New World<sup>a</sup> cottons, *G. hirsutum* and *G. barbadense*, and consequently described it as a new species, *G. caicoense*. Fryxell (personal communication) pointed out that the Caicó cotton was, in his opinion, identical with a wild cotton collected by Gardner near Crato, in the state of Ceará, in 1838 and also described as a distinct species, *G. mustelinum* Miers ex Watt (Watt 1907). Figure 3 shows some of the salient characters of Gardner's material and ours. Although collected nearly 150 years apart, the specimens are very similar in leaf shape and dissection, the presence of numerous many-branched stellate hairs on both surfaces of the leaves, the small, beaked capsules, the sparse, short, brownish lint, and the reddish-brown fuzz on the seeds. They differ chiefly in the unspotted corollas of Gardner's specimens and in the number of bracteole teeth: 14-16 in Gardner's material, 5-9 in plants from Caicó and São Francisco, 9-15 in plants from Salgado do Melão. We agree with Fryxell that *G. caicoense* Aranha *et al.* is a later synonym of *G. mustelinum* Miers ex Watt, and that *G. mustelinum* is the valid name for this cotton at the specific level.

This interpretation raises the question of whether *G. mustelinum* is specifically distinct from *G. hirsutum* and *G. barbadense*. *G. hirsutum* and *G. barbadense* can be separated by a number of qualitative and quantitative characters, of which the most useful include foliar hair pattern, corolla length, certain staminal characters, presence or absence of fringe

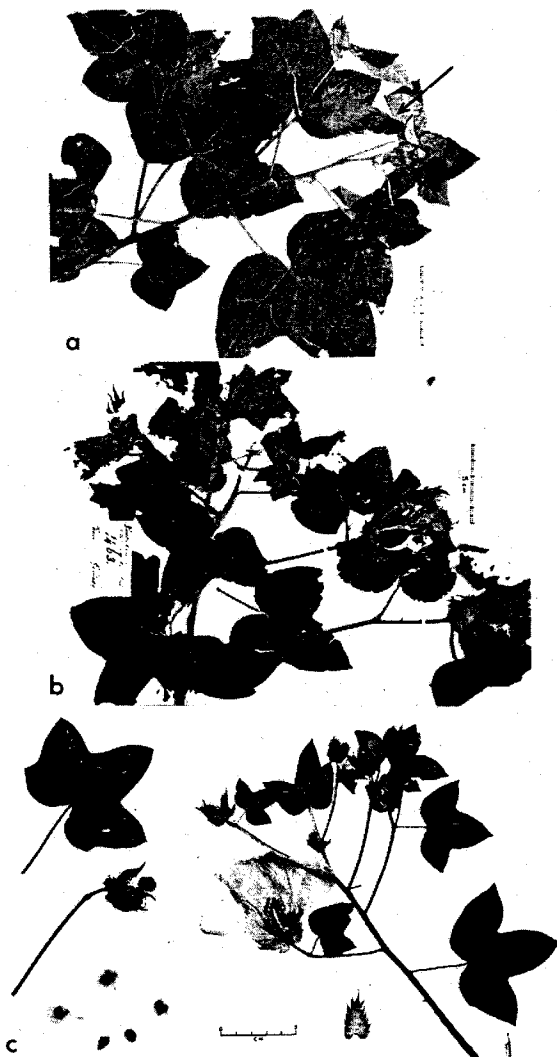


FIGURE 3. Herbarium material of *G. mustelinum* collected by Gardner (1838) and the Reading University expedition (1972). (a) Gardner's material from the type locality at Crato showing a flower (arrowed). (b) the same, showing mature capsules and seed. (c) our material from Caicó (at left) and Salgado do Melão (at right).

hairs on the floral nectary, and some capsule characters (Stephens 1967). As can be seen from table 1, *G. mustelinum* resembles either *G. barbadense* or *G. hirsutum* when these characters are considered individually, but is distinguished from both by its overall combination of diagnostic characters. It is most similar to Mocó, a local perennial form of *G. hirsutum* var. *marie-galante* grown over much of northeast Brazil, and indeed *G. mustelinum* has frequently been included in *G. hirsutum* var. *marie-galante* (e.g. Hutchinson, Silow and Stephens

1947). In figure 4, measurements made in northeast Brazil on backyard plants of kidney cotton (*G. barbadense*), field plants of Mocó and Upland cotton (*G. hirsutum*), and *G. mustelinum* are plotted in the form of a scatter diagram. This shows clearly the similarity between *G. mustelinum* and Mocó in the characters used for the diagram, and the intermediate position of both with respect to kidney and Upland cotton. In this connection, it is interesting that both Stephens (1967) and Boulanger and Pinheiro (1971) have suggested that Mocó shows evidence of introgression from *G. barbadense* into *G. hirsutum*. Such introgression might account for the reduced number of bracteole teeth in Mocó, since experimental  $F_2$ 's from *hirsutum* x *barbadense* crosses show transgressive segregation with the number of bracteole teeth tending to be less than in either parent (Stephens 1967). *G. mustelinum* also usually has few bracteole teeth.

*G. mustelinum* does, however, have certain characters not found in other cottons in northeast Brazil. These include the marked beak on the capsule and the short, rather sparse, brownish lint (which is silky in texture like the lint of *G. barbadense*). Figure 5 shows seed and lint characteristics of *G. mustelinum* and the cultivated cottons of northeast Brazil. The lint hairs of *G. mustelinum* were examined microscopically and found to be convoluted, but there appeared to be fewer convolutions per hair than in present-day cultivated cottons. A commercial buyer of cotton in northeast Brazil to whom we showed our specimens considered that the lint of *G. mustelinum* could be spun, with some difficulty, but would produce a weak thread. Beaked capsules and sparse lint which is not uniform in color are found in wild (as opposed to feral) forms of both *G. barbadense* and *G. hirsutum* (Stephens, personal communication). Colored fuzz, present in *G. mustelinum*, is likewise characteristic of wild tetraploid cottons, but occurs too in cultivated Verdão in northeast Brazil. Verdão appears to be derived from hybridization between Upland, which has white fuzz, and Mocó, which has no fuzz itself but carries the gene for colored fuzz (Harland 1933; Boulanger and Pinheiro 1971). Aranha *et al.* (1969) claimed their wild cotton had hairs on the sutures of the capsules, a character found in D diploids but in none of the tetraploid cottons. We could find no hairs on the sutures of any of the capsules of *G. mustelinum* that we examined, though small amounts of lint did tend to catch on the slightly rough sutures.

*G. mustelinum* is thus most easily distinguished from cultivated forms of *G. hirsutum* and *G. bar-*

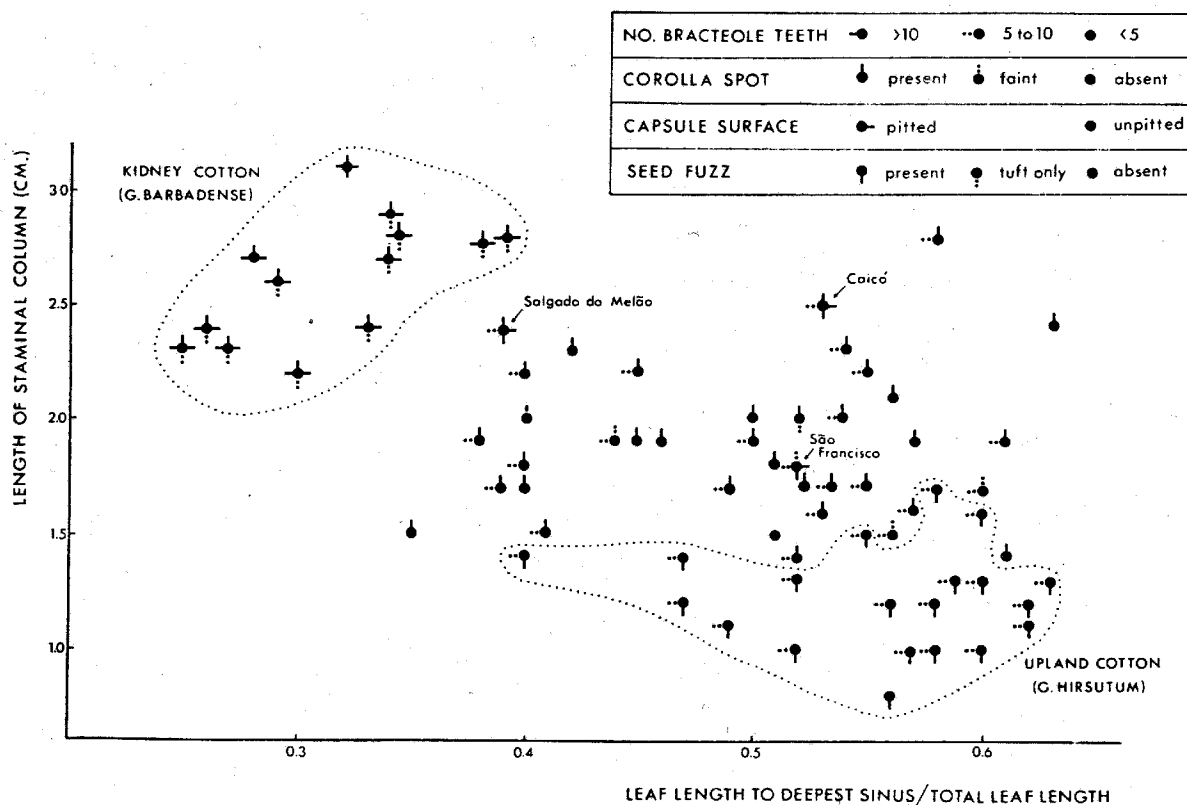


FIGURE 4. Scatter diagram comparing *G. mustelinum* and Moco (*G. hirsutum* var. *marie-galante*) with kidney cotton (*G. barbadense*) and annual Upland cotton (*G. hirsutum*). The limits of variation in kidney and Upland cotton are indicated by the dotted lines. *G. mustelinum* and Moco are represented by the symbols excluded from the dotted areas. Symbols for *G. mustelinum* are arrowed.

TABLE 1. Comparison of morphological characters in wild and cultivated cottons in northeast Brazil.

	<i>G. barbadense</i> var. <i>brasiliense</i>	<i>G. mustelinum</i>	var. <i>marie-galante</i>	<i>G. hirsutum</i>	var. <i>latifolium</i>
Local name	Rim de boi (kidney cotton)	Algodão bravo (wild cotton)	Moco	Verdão	Herbaceo (Upland cotton)
Leaves	$\frac{2}{3}$ cut	$\frac{1}{2}$ to $\frac{2}{3}$ cut	$\frac{1}{2}$ to $\frac{2}{3}$ cut	$\frac{1}{2}$ to $\frac{2}{3}$ cut	$\frac{1}{2}$ cut or less
Leaf pubescence	$\pm$ glabrous	Stellate hairs numerous, >5- branched	Stellate hairs few, <5- branched	Stellate hairs few, <5- branched	Stellate hairs few, <5- branched
Bracteolet teeth	10-17	5-15	3-9	3-9	7-12
Corolla length (cm)	6.5-8.0	3.5-5.5	4.0-7.5	3.0-5.0	3.0-5.0
Corolla spot	Present	Variable	Present	Variable	Absent
Fringe hairs on floral nectary	Absent	Absent	Present	Present	Present
Staminal column	Long	Long	Short	Short	Short
Filaments	All short	Upper slightly longer than lower	Upper long, lower short	Upper long, lower short	Upper long, lower short
Capsule shape	Acuminate	Beaked	Variable	Rounded	Rounded
No. locules	3	3-4	3-4	4	4
Capsule pitting	Pitted	Pitted	Smooth	Smooth	Smooth
Lint color	White	Brownish	White	White	White
Lint length (mm)	25-32	15-20	32-45	up to 35	20-30
Lint quantity	Abundant	Sparse	Abundant	Abundant	Abundant
Lint hair convolutions	Many	Few	Many	Many	Many
Lint texture	Fine, silky	Fine, silky	Fine, silky	Fine, silky	Coarse
Fuzz	Absent	Green to brown	Absent	Green to brown	White

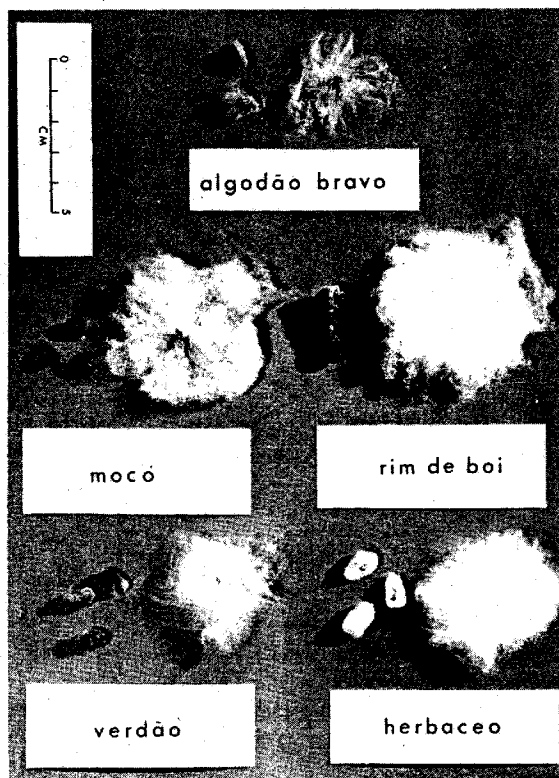


FIGURE 5. Seed and lint characters in *G. mustelinum* (algodão bravo) and the common cultivated cottons of northeast Brazil: Mocó (*G. hirsutum* var. *marie-galante*), Rim de boi (kidney cotton, *G. barbadense*), Verdão (*G. hirsutum*), and Herbáceo (Upland cotton, *G. hirsutum*).

*badense* by its 'primitive' fruit and seed characters. We have not ourselves compared *G. mustelinum* with wild forms of *G. hirsutum* and *G. barbadense*, but Stephens (personal communication) has done so and considers that it is taxonomically distinct from both. It may also be reproductively isolated, since although  $F_1$  hybrids of *G. mustelinum* with both *G. hirsutum* and *G. barbadense* are fertile,  $F_2$  segregates of crosses with *G. hirsutum* and with *G. barbadense* var. *darwinii* show the breakdown and sterility characteristic of interspecific crosses in *Gossypium* (Stephens 1967 and personal communication; Gridi-Papp personal communication).

## OVERALL DISTRIBUTION OF *G. MUSTELINUM*

Recent collections of *G. mustelinum* suggest that this species is widely, although sporadically, distributed throughout much of northeast Brazil (see map, fig. 6). Beside the localities recorded by Neves *et al.* (1965) and by us, Stephens (personal

communication) and Fryxell (personal communication) have received seed of *G. mustelinum* from Belo Vale, near the mouth of the Paraguaçu river in Bahia. *G. mustelinum* may also still survive in its type locality at Crato, in Ceará. We could find no one with any knowledge of wild cottons when we spent about a week in the area in 1972, but in 1963 Neves *et al.* (1968) collected a peculiar cotton on the slope of the Chapada do Araripe, near Crato. They did not state whether it was wild or cultivated, but they did comment on its unspotted corolla, seeds with chestnut fuzz, and small, pointed bolls with 3-4 locks. They were unable to decide whether it belonged to *G. hirsutum* or *G. barbadense*, and compared it with Watt's (1907) description of *G. mustelinum*.

There are also a number of other published records of wild cotton in northeast Brazil, spanning some 200 years, but unfortunately not accompanied by herbarium specimens. We have listed some of the more detailed of these in table 2. Wild cotton is reported most frequently from the Seridó district of Rio Grande do Norte, though these reports are all fairly recent. It is also doubtful whether they all refer to *G. mustelinum* in the sense that we are using that name, since several mention coarse lint and seeds without fuzz, whereas all our material had fine silky lint and fuzzy seeds. Feral forms of cotton may establish and survive for a number of years in open or disturbed habitats, and it is virtually impossible to distinguish these from wild cottons without very complete descriptions. Bittencourt's account of wild cotton from the Rio Contas, quoted by Neves and Junqueira (1965), is interesting because of its early date, because it agrees with our material in all characters mentioned except the rough (áspero) lint, and because the Rio Contas is less than 200 km south of a known locality for *G. mustelinum* (see map, fig. 6).

There is also the intriguing possibility that *G. mustelinum* has a far wider distribution than this, reaching western South America. Watt (1907) cited a specimen from Colombia (J. F. Hutton, No. 749, 'Flora Neogranadina - Caucaña (La Paila)') which he considered the same species as Gardner's material, and Stephens (1945) worked with a strain identified as *G. mustelinum* Miers and collected wild in Colombia by F. J. Pound. The specimen to which Watt referred seems to be I. F. Holton's No. 749, in the herbarium of the Royal Botanic Gardens, Kew, which has been identified, in Watt's handwriting, as *G. mustelinum*. The specimen consists of a small branch bearing two three-lobed leaves with numerous many-branched stellate hairs on both

surfaces, a flower, and a very young fruit. The androecium of the flower is not displayed, and there are no seeds or mature fruits. It is difficult to be certain to what species this specimen belongs, but it may well be *G. barbadense*. We have seen no specimens of the material collected by Pound.

### WILD VERSUS FERAL STATUS OF *G. MUSTELINUM*

If it is a truly wild cotton, *G. mustelinum* could be an interesting link in the evolutionary history of the tetraploids. On the other hand it could be argued that *G. mustelinum* is a feral cotton, which has re-

acquired the 'wild' characteristics of small beaked bolls and short sparse lint which enable it to survive in competition with natural vegetation. All the colonies of *G. mustelinum* that we saw were on land belonging to farms (although not necessarily cultivated), and the colony at Caicó occurred in a situation very reminiscent of Pearse's (1921) description of the conditions under which cotton was cultivated at the turn of the century.

It is also possible that cottons escaped from cultivation might establish themselves in the caatinga some distance from the nearest cultivated field. Over most of northeast Brazil it is common practice to

TABLE 2. Reports of wild cotton in northeast Brazil prior to 1960.

Locality	Date	Authority	Description
<b>RIO GRANDE DO NORTE</b>			
Mountains around valley of Seridó, near Caicó.	1913	Green (1916)	Samples of ' <i>G. mustelinum</i> ' and ' <i>G. vitifolium</i> ' collected on the same slope, in a place which indicated they were truly wild, not escapes. (From the sense in which these species names were used at this time, it can be inferred that one of Green's cottons had fuzzy seeds and the other did not.)
Seridó district (Fazenda São Nicolau)	1920-21	Pearse (1921)	Growing in almost inaccessible parts of the mountains. Lint creamy, fine, pretty strong, but short. Seed small, with 'peculiar spike'; some bluish-green, some almost without fuzz. Said to have been on the fazenda since it was bought in 1807.
Arid mountains of interior	c. 1933	Harland (1933,1970)	'Macaque' cotton, regarded as truly wild on the basis of its morphological characters. Lint khaki, excessively short and coarse. Considered as the wild prototype of Mocó (hence seeds without fuzz?).
<b>CEARA</b>			
Crato	1838	Gardner (herbarium specimens)	'In the woods.' Lint brownish, fine, short and fairly sparse. Seeds with rich brown fuzz. Capsules beaked.
<b>BAHIA</b>			
Rio Contas	1797	Bittencourt (cited in Neves and Junqueira 1965; and Stephens and Phillips 1972)	"... two kinds of wild cotton which are found abundantly in the caatingas along the margin of the rio das Contas, both having the same properties as the cotton of India in the seeds as well as the shrubs, only with the difference that one of these species has brown wool which is rough through lack of cultivation." (Bittencourt's 'cotton of India' had fuzzy seeds.)



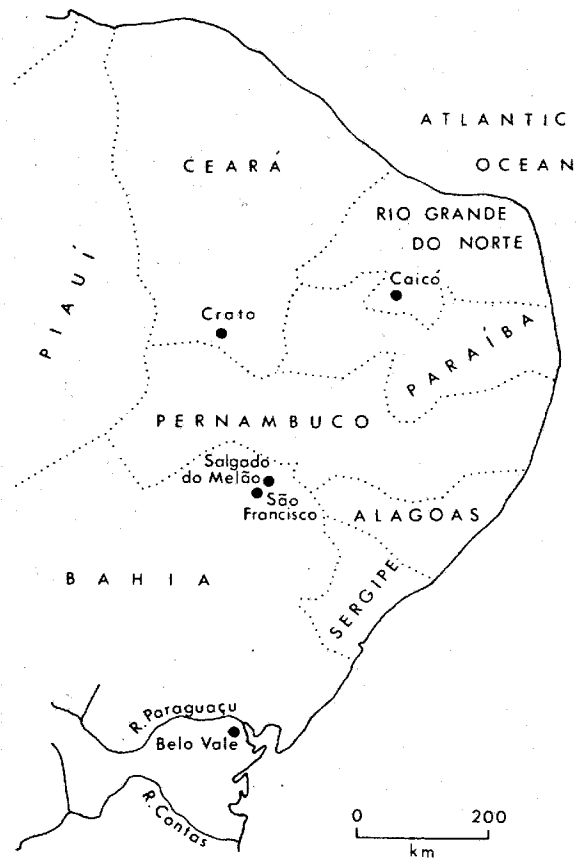


FIGURE 6. Sites from which *G. mustelinum* has been collected in northeast Brazil.

turn cattle loose in fields of perennial cotton when the harvest is completed. The cattle graze off the leaves remaining on the plants, and it is claimed that this reduces the number of insect pests carried over to the next growing season. Any unharvested bolls would presumably be ingested as well for Pearse (1923) photographed a cow in Ceará eating about 9 lb of ginned cotton from an unattended bale. Cattle are also allowed to range freely through the caatinga in search of grazing, so the small pools such as those at Salgado do Melão would be favored resting places where seeds excreted in the dung might germinate under the relatively moist conditions. Birds are another possible agent of seed dispersal. Stephens (1971) reported experiments which showed that hard-seeded cottons could be retained in the gut of killdeer for several days without becoming inviable, and on the Galápagos Islands Stephens and Rick (1966) reported that Galápagos finches frequently used linted cottons for nest build-

ing and that viable cotton seeds could be recovered from abandoned finch nests.

It is therefore possible that cotton has escaped from cultivation in northeast Brazil: the question is whether *G. mustelinum* is sufficiently similar to any cotton cultivated in Brazil now or in the past for it to seem probable that it is feral rather than primitively wild.

### GOSSYPIMUM MUSTELINUM AS AN ESCAPED DERIVATIVE OF MOCÓ

Of all the cottons presently cultivated in northeast Brazil, Mocó is the most similar to *G. mustelinum* (see table 1 and fig. 4). Stephens and Phillips (1972) have argued persuasively that Mocó developed from West Indian forms of *marie-galante* cottons introduced into Brazil by French or Dutch colonists. West Indian *marie-galante* is in turn thought by Stephens (1967) to be derived in part from West Indian wild forms of *G. hirsutum* which crossed with perennial forms of *G. barbadense* introduced by the Caribs. If this pedigree is correct, then it is possible that cultivated *marie-galante* carries genes for certain 'wild' characters (e.g. beaked capsules, hard seed, and sparse, short, brownish lint), expression of which might be masked in the cultivated forms, since homozygotes segregate out much less frequently in tetraploids than in diploids. These 'wild' characters might then be reestablished in feral forms by selection, rather than by the more random process of back-mutation.

Neves *et al.* (1968), on the other hand, thought that Mocó was not introduced from the West Indies but was indigenous and probably derived from an earlier cultivated cotton of the Seridó region. Although Mocó is the cotton most widely cultivated today in the arid interior of the northeast, it was not recognized as a distinct type until the middle of the 19th century (Stephens and Phillips 1972). Mocó cultivation in the Seridó region of Rio Grande do Norte began only in the closing decades of the 19th century (Neves *et al.* 1968), and it was not until the beginning of the 20th century that the superior drought tolerance of Mocó enabled it to replace the perennial forms of *G. barbadense* hitherto cultivated in the northeast (Boulanger and Pinheiro 1971). Gardner's specimens prove that *G. mustelinum* occurred in Ceará in 1838, before Mocó was described from the area, and other reports of wild cotton in northeast Brazil suggest *G. mustelinum* may be traced back even earlier (see table 2). On chronological grounds, therefore, *G. mustelinum* cannot be a feral derivative of commercially grown Mocó.

## GOSSYPIMUM MUSTELINUM AS AN ESCAPED DERIVATIVE OF COTTONS CULTIVATED IN THE 17TH TO 19TH CENTURIES

Plantation cultivation of cotton in northeast Brazil goes back to the early stages of European colonization. The French were growing cotton in Maranhão by 1614 (Stephens and Phillips 1972), while the Dutch controlled the coast of northeast Brazil from 1632 to 1654 and established plantations there (Stephens 1967). During the 17th and 18th centuries cotton played little part in world trade but was widely grown for local use in Brazil. The European population at that time was thinly scattered over an immense area, on fazendas, in small villages around mines and salt works, in army posts, etc. Each community had to be virtually self-sufficient, and all raised cotton for making thread, hammocks, clothes, towels, sacks, bedding, lamp wicks, and other necessities, fed the seeds to their livestock, and used the rest of the plant for forage and for medicinal purposes (Neves and Junqueira 1965). The Industrial Revolution in England led to a dramatic increase in the demand for cotton: Maranhão exported 130 sacks (sacas) of cotton to Europe in 1760, 28,000 sacks in 1800, and 78,300 sacks in 1830 (Neves and Junqueira 1965). The northeast outstripped Maranhão as a cotton-producing region in the 19th century, and commercial cultivation of cotton developed also in Bahia and Minas Gerais along the São Francisco river. Throughout the area, the crop consisted of perennial cottons, cultivated for two to six years and abandoned when their yield declined. New land was then cleared by burning (Neves and Junqueira 1965).

Brazilian cotton exports declined as dramatically as they had soared when the United States became a cotton exporter. The cottons grown in the United States were fuzzy-seeded Upland types, apparently derived in part from Philip Miller's green-seeded cotton which was introduced to Georgia in 1734. Fuzzy-seeded cottons could not be delinted by the roller gins available in the 18th century, and it was not until the saw gin was invented in the 1790's that they came into their own (Stephens 1944). The American Civil War (1863-65) caused a brief resurgence in Brazilian cotton production, and American annual cottons, both Sea Island (*G. barbadense*) and Upland (*G. hirsutum*), were introduced by the British, along with improved gins and better cultural techniques (Neves and Junqueira 1965). When cotton exports from the United States were resumed

after the Civil War, Brazilian production declined again. Slavery was abolished in Brazil in 1888, and abolition was a final blow to the owners of many large cotton plantations (Pearse 1921).

This history of shifting cultivation, abandoned plantations, and sudden dramatic decreases in demand for Brazilian cotton would afford plenty of opportunities for cottons to become feral. Unfortunately it is not easy to establish the identity of morphological characteristics of the cottons grown in Brazil from the 17th to 19th centuries. There was undoubtedly considerable exchange of cottons between Brazil and the West Indies at this time (Sea Island cotton seems to have developed, at least in part, from Pernambuco seed). Von Rohr (cited in Watt 1907; see also Fryxell 1969 for identification of Von Rohr's cottons) and Edwards (cited in Stephens 1944) have described West Indian cotton cultivation around 1790. The plantations apparently consisted mostly of various forms of kidney cotton (*G. barbadense*) intermixed with free-seeded *G. barbadense* and several distinct races of *G. hirsutum* var. *marie-galante*. Equivalent mixtures may have been grown in Brazil, but there are no unequivocal references to *G. hirsutum* in Brazil until the annual Uplands were introduced in the mid-19th century. Verdão was described shortly thereafter (Watt 1907). According to Boulanger and Pinheiro, the cotton cultivated throughout the semi-arid northeast in the 19th century was kidney cotton, often mixed with a perennial free-seeded form of *G. barbadense* called Quebradinho. Stephens and Phillips (1972) suggested that Bittencourt's 'Cotton of India' and Câmara's 'Siam Cotton,' cultivated in Brazil at the end of the 18th century, might be *G. hirsutum* var. *marie-galante*, but they themselves considered this hypothesis far from conclusively demonstrated.

It thus does not seem that *G. mustelinum* could be a feral derivative of a *marie-galante* cotton ancestral to Mocó. Nor, since there are no records of *G. hirsutum* in northeast Brazil prior to 1850, is *G. mustelinum* (already present in Ceará in 1838) likely to be a stabilized derivative of hybridization between *G. hirsutum* and *G. barbadense*, even though *G. mustelinum* is intermediate in many of its characters. The variability shown by *G. mustelinum* in number of bracteole teeth and spotting of the corolla is not surprising, since isolated populations of a tetraploid would carry appreciable amounts of genetic variation which could be expressed when outcrossing was restricted by small population size. In other characters the scattered populations of *G. mustelinum* are surprisingly uni-

form, and appear to have remained so over nearly 150 years. This uniformity is not what one would expect if *G. mustelinum* were a chance hybrid, synthesized independently in its various localities and perpetuating itself by inbreeding or crossing between sister plants.

It also seems unlikely that *G. mustelinum* is a feral derivative of cottons grown commercially in Brazil before *G. hirsutum* was introduced. These would probably not have included fuzzy-seeded types, since the saw gin was not introduced into Brazil until the 1820's (Neves and Junqueira 1965). Furthermore, the uneven, fading, brownish color of the lint of *G. mustelinum* and other wild tetraploid cottons seems to be one of the first features to be selected against in domesticated cotton (Stephens, personal communication). Kidney cotton and Quebradinho (both forms of *G. barbadense*) may sometimes have chestnut or brown lint (these forms are often called 'macaco' (monkey) cottons). However, this lint is a clear, uniform brown, not the uneven fading color of *G. mustelinum*. Feral cottons usually retain the clear lint color of their domesticated ancestors (Stephens, personal communication), so on these grounds too it is unlikely that *G. mustelinum* is an escaped commercial cotton.

It is possible that *G. mustelinum* is a relic of an earlier, precommercial phase of cotton cultivation in Brazil, perhaps used in contexts where the poor spinning qualities and poor color of its lint did not matter. Stephens (1965) quoted some observations on West Indian cotton published by Raynal in 1774: "There are found in the American Islands, cotton trees of different sizes, which spring up and grow without attention, above all in low-lying areas and salt marshes. Their fibre is more or less red in colour, very fine, but so short that one would not know how to spin it. It is not carried to Europe, although it could be usefully employed in the making of hats. The little that one troubles to gather serves locally for the making of mattresses and pillows." Apparently unginmed cotton seed was commonly used for stuffing pillows and mattresses in early Colonial days (Stephens 1971), and this use provides one obvious means by which a 'primitive' cotton with poor-quality lint could have been widely distributed during the early stages of European exploitation of the New World. A primitive cotton of this sort might also have been able to establish itself as a component of the natural vegetation in such widely separated areas as northeast Brazil and Colombia while feral forms of more fully domesticated cottons would not survive for long.

## GOSSYPIMUM MUSTELINUM AS A RELIC OF BRAZILIAN INDIAN CULTIVATED COTTON

The first Europeans to visit Brazil recorded that cotton was cultivated by the local people, and many of these early records have been gathered by Watt (1907). Magellan, in 1519, reported that the Indians of Brazil used "vegetable down" in making their beds and spinning threads. De Lery, who lived in Brazil from 1557 to 1558, described cotton shrubs with seeds "close joined and verie much pressed together, after the form of a man's kidnie"—the first identifiable record of kidney cotton. In 1570-1587 de Souza noted that cotton cultivated by the Indians in Bahia was cleaned with a hoe two or three times a year.

The Indians of northeast Brazil were not culturally highly advanced. One of the few groups to practice agriculture was the Cariri, who grew maize, beans, manioc, and cotton, slept in hammocks, and may have had a simple loom (Lowie 1946). The documented habitats of the Cariri correspond surprisingly well with the known localities of *G. mustelinum*: around Crató in 1670, along a segment of the São Francisco river very close to Salgado do Melão and São Francisco in 1759, and near the lower part of the Paraguaçu river in 1740. The Cariri are now extinct, and the chances of finding out more about the cottons they cultivated or exploited must be very slim. It is, however, possible that they used *G. mustelinum* as well as or instead of kidney cotton, and may have spread it further over their territory, though their primitive agricultural techniques presumably had little effect in changing the 'wild' characteristics of *G. mustelinum*.

## GOSSYPIMUM MUSTELINUM AS A GENUINELY WILD (NEVER DOMESTICATED) COTTON

The arguments presented above virtually eliminate the suggestion that *G. mustelinum* is a feral derivative of any cotton cultivated commercially in Brazil now or in the past, though it could be a relic of a backyard cotton, little changed by human selection and used by the Brazilian Indians or early colonists, perhaps for purposes other than spinning or weaving. Although more intensive collecting in northeast Brazil may well produce additional localities for *G. mustelinum*, our impression is that it is a declining species, unable to survive the grazing of the introduced cattle and goats and the consequent changes in management of the caatinga vegetation.

*G. mustelinum* is also difficult to maintain in experimental cultivation, and many details of its relationships to the other tetraploids remain to be worked out, but the consensus of opinion among those who have seen it in the field and worked with it experimentally is that it is a genuinely wild cotton, specifically distinct morphologically and perhaps genetically from both *G. hirsutum* and *G. barbadense* and not derived from cultivated forms of either.

These conclusions raise a whole series of further questions which can be answered only by further field and experimental work. Does *G. mustelinum* really occur in Colombia as well as in northeast Brazil? If so, it would have a surprisingly extensive range for a wild cotton and would furnish correspondingly less information on when and where the A and D genome diploids came into contact. Does *G. mustelinum* show the same end arrangements of the A genome chromosomes as the other tetraploids? If so, this is further evidence for the monophyletic origin of the polyploid cottons. If not, is the A genome of *G. mustelinum* more similar or less similar than that of the other tetraploids to the A genome of *G. herbaceum*? Similarly, does *G. mustelinum* differ from the other tetraploids in the

closeness of its cytogenetic relationship to the D genome diploid, *G. raimondii*? When the answers to these questions are available, then we may be able to speculate further about the origins of the tetraploid cottons. For the moment, however, these records of a wild tetraploid cotton in northeast Brazil serve to support the current hypotheses that a linted, undomesticated A genome cotton spread across the Atlantic and hybridized with a D diploid somewhere in northern South America.

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Biologists wishing to visit Bolivia might like to consider staying at the Inca Hostel, Casilla 1514, Cochabamba, Bolivia. As the accommodations are limited, inquiries should be made as far in advance of the proposed visit as possible.

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