

Evolution of Crop Plants

Edited by N. W. Simmonds

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Editor's introduction

The need for a book such as this became apparent to me some fifteen years ago when I was trying to read up the evolution of crops that might offer illuminating parallels with bananas and potatoes. It quickly became clear that the only compendious work was De Candolle's great book (1886) and that was out of date and pre-cytogenetic. It also became clear that, for a great many crops (and most of those I was interested in), there wasn't even an authoritative essay and, when there was, it often did not answer, or even ask, the interesting questions.

Since that time, the situation has improved, in the sense that there are now several monographs of major crops and a few valuable compendia of essays such as Sir Joseph Hutchinson's *Essays on crop plant evolution* (Cambridge, 1965). But minor crops (and even some major ones) are still very poorly served. Furthermore the literature is all too often very unbalanced: cytogeneticists, archaeologists, historians, geographers, taxonomists, agriculturists, horticulturists and plant breeders all have something to contribute to understanding but they rarely seem to understand (or even read) each other and the study that really collates all the evidence is rare indeed. One result is the almost universal tendency to think of crop plant evolution as something that happened in the past and stopped some time ago. In fact, crop evolution – genetic change in crop populations – is probably at least as rapid now as ever it has been and, in some crops, much more rapid; plant breeders are applied evolutionists (even if they have rarely noticed the fact). One might call this the 'continuum view' of crop evolution.

I concluded therefore that there was need for a work having the following characteristics. It should be comprehensive, covering all the major crops and providing at least an introduction to many minor ones. It should be authoritative, which meant that it had to be multi-authored. It should be as brief as the subject-matter allowed, so that individuals as well as libraries

would buy it. And it should allow expression of editorial prejudices in favour both of the continuum view of crop evolution and of the value of diagrams as an aid to concise presentation.

The choice of crops to be treated and the assignment of specific lengths (in the range 2,000–6,000 words) was inevitably a matter of largely arbitrary editorial decision. I tried to balance considerations of agricultural importance and depth of evolutionary understanding and hope that, in the outcome, both authors and readers will feel that a reasonable balance has been achieved.

I decided that, in the interests of coherence and brevity, a standard format would be essential. Experiments with a rather elaborate system of headings and sub-headings convinced me that crop histories were too diverse to be treated thus, so I settled upon a simple but logical sequence of six headings and left authors to adapt it to the needs of their crops. Bibliographies are, inevitably, selective and are intended to provide key- and source-references; I asked authors to refer, as far as reasonably possible, to recent comprehensive reviews for this purpose.

The arrangement of contents presented certain problems. Conventional taxonomic systems offered possibilities but there are several to choose from. Arrangements by economic use had to be discarded because of frequent multiple uses: were Brassicas to be treated as vegetables, fodders or oilseeds? In the outcome, an arbitrary alphabetical arrangement (by families and by genera within families) seemed the most practical and has been adopted; this has the joint merits of ready reference and of placing botanically related crops in proximity. Taxonomists will search in vain for authorities for Latin names and may, I fear, be critical of the omission: it was quite deliberate. Their inclusion would have added nothing to understanding of crop evolution but would have added something to length and much to labour. Taxonomy is one of the foundations of evolutionary understanding but taxonomic process and nomenclatural dispute are irrelevant.

I wondered whether to write a general introductory essay on the subject of crop evolution but decided against doing so. In this field, there is, I think, already perhaps too much generalization from too few examples. This book therefore is, in a sense, an attempt to redress the balance; it concentrates on the particular and, in doing so, reveals, I think, how insecure our knowledge often is, how much more work is needed and how often, even now, the right questions have not yet been asked.

An editor of a book such as this has no light task. Mine has been lightened by many people. My best

thanks are due to: authors, for their helpful response to editorial importunities about lengths, deadlines, contents and diagrams; many colleagues, both in Britain and abroad, for advice on possible authors and on points of detail; Messrs Longmans for their efficient, courteous and helpful guidance on technical matters; the Agricultural Research Council, the Department of Agriculture and Fisheries for Scotland and the Scottish Society for Research in Plant Breeding for their approval of the project as one which would take up some public resources; my Secretary, Miss I. M. Hayes, for her outstandingly efficient management of a formidable volume of correspondence; and my wife for her tolerance of a long stretch of week-ends committed to The Book.

We, that is, the editor and authors collectively, hope the work will prove useful. Certainly, it attempts to do something not attempted since De Candolle. Readers must judge of our success and it goes without saying that we shall be pleased to have comments and criticisms for incorporation in any possible revision. We should like to think that the work, lying as it does between the scholarly and the practical, may help in the understanding of past, present and future of our crops. Their future, in a world already hungry and becoming hungrier, is a matter of vital human importance; if we shall have established the essential continuity, linked the scholarly and the practical and shown that past, present and future illuminate each other, we shall be well content.

N. W. Simmonds
Edinburgh
November 1974

Front Board illustrations

Illustrations from the Herbals in the Herbarium Library, Royal Botanical Gardens, Kew

Bananas – Gerard, Herball 1636

Potatoes – Parkinson, Paradisus Terestris 1629

Maize – Mattioli, Herbarz 1562

Back Board illustrations

Bananas – The Jamaica Banana Board

Potatoes – Potato Marketing Board

Maize – Pioneer Hi-Bred International, Inc.

Contents

Editor's introduction
List of Authors

Chapter	Botanical names	Crop	Page
15	Convolvulaceae <i>Ipomoea</i>	Sweet potato	42
16	Cruciferae <i>Brassica campestris</i>	Turnip, etc.	45
17	<i>Brassica oleracea</i>	Cabbage, kale, etc.	49
18	<i>Brassica napus</i>	Swede, rape, etc.	53
19	<i>Brassica</i> spp. and <i>Sinapis alba</i>	Mustards	56
20	<i>Raphanus</i>	Radish	60
21	<i>Rorippa</i>	Watercress	62
22	Cucurbitaceae <i>Cucumis</i> , <i>Cucurbita</i> , <i>Citrullus</i> , <i>Lagenaria</i>	Cucurbits	64
23	Dioscoreaceae <i>Dioscorea</i>	Yams	70
24	Euphorbiaceae <i>Aleurites</i>	Tung	74
25	<i>Hevea</i>	Rubber	77
26	<i>Manihot</i>	Cassava	81
27	<i>Ricinus</i>	Castor	84
28	Gramineae <i>Avena</i>	Oats	86
29	<i>Eleusine</i> , <i>Pennisetum</i>	Milletts	91
30	<i>Hordeum</i>	Barley	93
31	<i>Oryza</i>	Rice	98
32	<i>Saccharum</i>	Sugarcane	104
33	<i>Secale</i>	Rye	108
34	<i>Sorghum</i>	Sorghum	112
35	<i>Triticosecale</i>	Triticale	117
36	<i>Triticum</i>	Wheats	120
37	<i>Zea</i>	Maize	128
38	Various genera	Temperate grasses	137
39	Various genera	Tropical and subtropical grasses	142
40	Grossulariaceae <i>Ribes</i>	Currants	145
41	Lauraceae <i>Persea</i>	Avocado	148
1	Agavaceae <i>Agave</i>	Sisal	1
2	Amaranthaceae <i>Amaranthus</i>	Amaranths	4
3	Anacardiaceae <i>Mangifera</i>	Mango	7
4	Araceae <i>Alocasia</i> , <i>Colocasia</i> , <i>Cyrtosperma</i> , <i>Xanthosoma</i>	Aroids	10
5	Bombacaceae <i>Ceiba</i>	Kapok	13
6	Bromeliaceae <i>Ananas</i>	Pineapple	14
7	Camelliaceae <i>Camellia</i>	Tea	18
8	Caricaceae <i>Carica</i>	Papaya	21
9	Chenopodiaceae <i>Beta</i>	Beet	25
10	<i>Chenopodium</i>	Chenopods	29
11	Compositae <i>Carthamus</i>	Safflower	31
12	<i>Chrysanthemum</i>	Pyrethrum	33
13	<i>Helianthus</i>	Sunflower	36
14	<i>Lactuca</i>	Lettuce	39

Contents

Chapter	Botanical names	Crop	Page	Chapter	Botanical names	Crop	Page
	Leguminosae				Piperaceae		
42	<i>Arachis</i>	Groundnut	151	68	<i>Piper</i>	Pepper	234
43	<i>Cajanus</i>	Pigeon pea	154		Polygonaceae		
44	<i>Cicer</i>	Chickpea	157	69	<i>Fagopyrum</i>	Buckwheat	235
45	<i>Glycine</i>	Soybean	159		Rosaceae		
46	<i>Lens</i>	Lentil	163	70	<i>Fragaria</i>	Strawberry	237
47	<i>Medicago</i>	Alfalfa	165	71	<i>Prunus</i>	Plum, cherry, almond	242
48	<i>Phaseolus</i>	Beans	169	72	<i>Malus, Pyrus</i>	Apple, pear	247
49	<i>Pisum</i>	Pea	172	73	<i>Rubus</i>	Blackberry, raspberry	251
50	<i>Trifolium</i>	Clovers	175		Rubiaceae		
51	<i>Vicia</i>	Broad bean	179	74	<i>Cinchona</i>	Quinine	255
52	<i>Vigna</i>	Cowpea	183	75	<i>Coffea</i>	Coffees	257
	Liliaceae				Rutaceae		
53	<i>Allium</i>	Onion, etc.	186	76	<i>Citrus</i>	Citrus	261
	Linaceae				Solanaceae		
54	<i>Linum</i>	Flax, linseed	190	77	<i>Capsicum</i>	Peppers	265
	Malvaceae			78	<i>Lycopersicon</i>	Tomato	268
55	<i>Abelmoschus</i>	Okra	194	79	<i>Nicotiana</i>	Tobacco	273
56	<i>Gossypium</i>	Cottons	196	80	<i>Solanum melongena</i>	Eggplant	278
	Moraceae			81	<i>Solanum tuberosum</i>	Potato	279
57	<i>Artocarpus</i>	Breadfruit	201		Sterculiaceae		
58	<i>Cannabis</i>	Hemp	203	82	<i>Cola</i>	Cola	284
59	<i>Ficus</i>	Fig	205	83	<i>Theobroma</i>	Cacao	285
60	<i>Humulus</i>	Hop	209		Tiliaceae		
	Musaceae			84	<i>Corchorus</i>	Jute	290
61	<i>Musa</i>	Banana	211		Umbelliferae		
	Myrtaceae			85	<i>Daucus</i>	Carrot	291
62	<i>Eugenia</i>	Clove	216		Vitaceae		
	Oleaceae			86	<i>Vitis</i>	Grape	294
63	<i>Olea</i>	Olive	219		Various genera	Timber trees	298
	Palmae			88	Various genera	Minor crops	301
64	<i>Cocos</i>	Coconut	221		Index of authors		
65	<i>Elaeis</i>	Oil palm	225		Index of scientific names		
66	<i>Phoenix</i>	Date	229		Index of common names		
	Pedaliaceae						
67	<i>Sesamum</i>	Sesame	231				

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Sisal and relatives

Agave (Agavaceae-Agaveae)

J. F. Wienk

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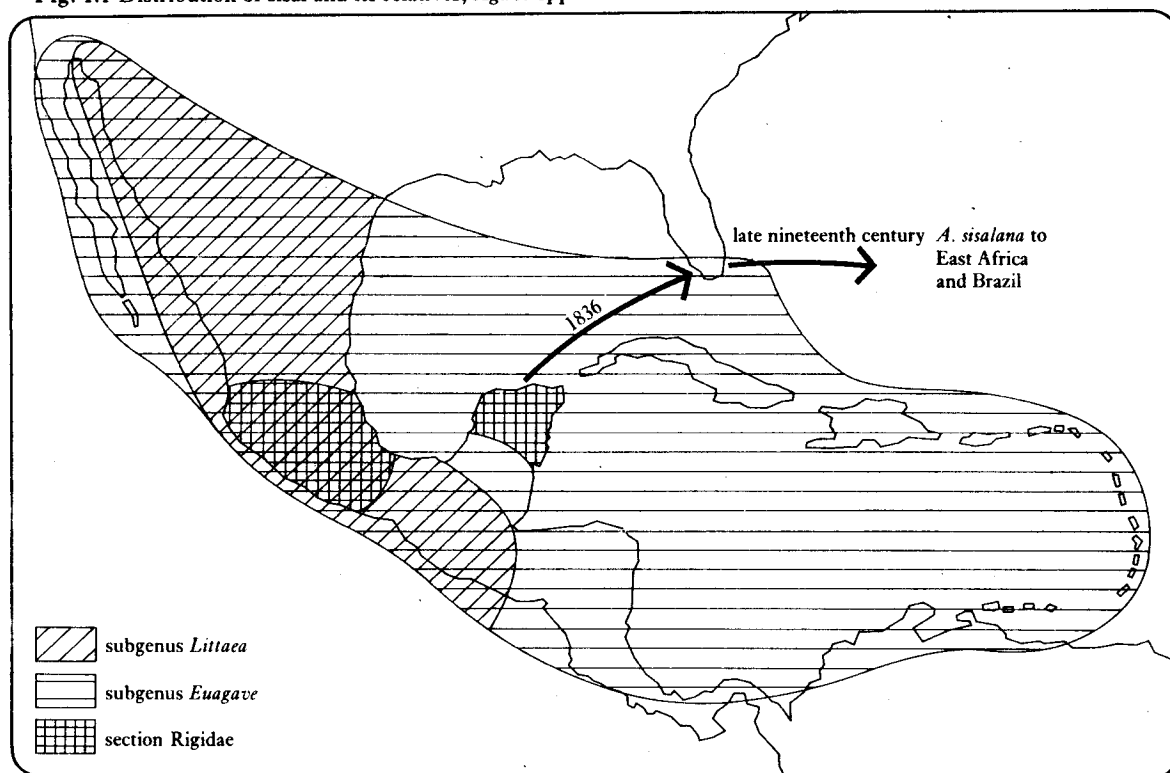
1 Introduction

Several species of *Agave* are cultivated for their leaf fibres which provide over 90 per cent of the hard fibres of commerce. The most important one is *A. sisalana*, sisal, followed by *A. fourcroydes* or henequen; *A. cantala*, yielding maguey or cantala, and *A. letonae*, Salvador henequen, are grown to a limited extent. These four species are usually referred to as long-fibre

agaves as against the brush-fibre yielding *A. lecheguilla* and *A. funkiana*. *A. amaniensis*, blue sisal, and *A. angustifolia*, dwarf sisal, though of no commercial importance themselves, are valuable as parents in breeding long-fibre agaves.

The cultivated agaves are xerophytic, tropical monocarpic perennials with large, stiff, fleshy, persistent leaves arranged in basal rosettes. They are propagated vegetatively by means of suckers or bulbils, the latter arising on the massive inflorescences after the flowers have fallen; most cultivated species seldom fruit. Harvesting the fibre-containing leaves of sisal, henequen, cantala and Salvador henequen is begun when the lowest leaves that start withering have attained a certain minimum size; only the lower leaves are cut. Cutting is then carried out annually until the plants flower. The fibre is extracted mechanically by decortication but cantala leaves are mostly retted. The brush fibres are produced by scraping the immature leaves of the central bud which is cut when the plants are six years old; the plants will continue to produce central buds, which may be cut twice a year, for another six years. World production of agave fibres in 1972 was estimated at about 760 kt of which 600 kt

Fig. 1.1 Distribution of sisal and its relatives, *Agave* spp.



was sisal. The brush fibres are of little importance.

The agaves are tropical by origin and there are very few commercial plantations outside the tropics. The major sisal producers are Brazil, Tanzania, Mozambique, Angola, Kenya, Madagascar and Haiti. Henequen is grown only in some Central American and Caribbean countries, with Mexico and Cuba accounting for over 95 per cent of total production. Cantala is grown mainly in the Philippines, Salvador henequen in El Salvador and *A. lecheguilla* and *A. funkiana* in Mexico. The fibres of sisal, henequen, cantala and Salvador henequen form the raw material for cordage of which agricultural twines are the most important.

For a general review of economic botany see Pursel-glove (1972).

2 Cytotaxonomic background

The fibre-bearing agaves belong to a small group of a large and complex genus. The long-fibre types are classified in subgen. Euagave sect. Rigidae, the brush-fibre kinds in subgen. Littaea. The greatest variability in the genus exists in Central Mexico and the widest distribution is found among the members of Euagave. The section Rigidae is more or less confined between latitudes of 15° and 25°N (Fig. 1.1).

The basic chromosome number of the genus is $x = 30$. A polyploid series, complicated by aneuploidy, occurs and somatic chromosome numbers have been found to range between $2n = 58$ and $2n = 180$. The wild and cultivated forms of the section Rigidae include diploids, triploids, tetraploids and pentaploids. This cytological complexity, coupled with vegetative propagation, may well account for the large number of morphologically more or less distinct taxa. The chromosome numbers of the most important species cultivated for fibre or used for breeding long-fibre hybrids are as follows:

Name	2n
<i>A. sisalana</i>	$5x = ca. 138-149$
<i>A. fourcroydes</i>	$5x = ca. 140$
<i>A. cantala</i>	$3x = 90$
<i>A. amaniensis</i>	$2x = 60$
<i>A. angustifolia</i>	$2x = 60$

Chromosome numbers of *A. letonae*, *A. lecheguilla* and *A. funkiana* are unknown.

3 Early history

The cultivated agaves originated from wild ancestors in Central America and Mexico but their precise botanical origins are unknown. *A. fourcroydes* and *A.*

letonae were used in pre-Columbian times and the former was extensively cultivated on the Yucatan peninsula of Mexico by the Maya Indians.

Nothing is known about the primary ancestors of the cultivated polyploid species, *A. sisalana*, *A. fourcroydes* and *A. cantala* and the nature of their ploidy (whether auto- or allo-) is still obscure. Moreover, the concept of species in *Agave* leaves much to be desired. Traditional taxonomy has erected many specific names on poorly understood leaf variation (Gentry, 1972). Therefore the confusion is bound to be great and many of the listed species might in fact be synonyms.

Though the Aztec codices illustrate numerous basic and exotic uses of the plants, agaves are not known as fossils. On the other hand the arid and semi-arid conditions of the agaves' natural habitat and their monocarpic habit are likely to have slowed down evolution considerably. The sexual generation time is long and of uncertain outcome; seedling survival is possible only during favourable rainy periods. If the monocarpic parent, with its one burst of flowers and seeds, does not leave progeny, only the suckers have another chance to leave sexual offspring. Sexual generations in such cases can be two, three or more times longer than the monocarpic lifecycle might indicate. Thus gene assortment and recombination may be infrequent; some agave clusters encountered in Central Mexico are perhaps hundreds of years old and still without obvious seeded progeny. However, fragmented distributions may have enhanced the distinctness of such colonies. In other crops, mutation and reassortment of genes in isolation have resulted in new genotypes which, in time, have become genetically distinct from former contemporaries, have lost genetic compatibility and have evolved eventually as distinct species. But whether this applies to the agaves is very much a matter of speculation.

Self- and cross-pollination may occur. The heavy, sticky pollen is shed before the stigma becomes receptive but flowering progresses acropetally and weeks can elapse before the uppermost flowers of the massive inflorescence have opened, so that all stages from the closed bud to the receptive stigma can be encountered. The nectar exuded in the flower tube during anthesis attracts numerous insects (particularly wasps and bees, which are probably the commonest pollinators); bats may also be pollinators. Pollen may also fall by gravity onto the exposed stigmata of lower flowers.

4 Recent history

A. sisalana was taken to Florida from Yucatan in 1836 and it was from this source that many countries cultivating the species obtained their original material. In 1893, sisal bulbils were sent via Hamburg to Tanga in (then) German East Africa, now Tanzania. This introduction was the foundation of the East African sisal industry. The plant was introduced into Brazil (presently the largest producer) at the end of the nineteenth century (Fig. 2.1).

A. fourcroydes has been introduced into many tropical countries but it has never been grown very successfully outside Yucatan.

A. cantala was taken in the early years of the Spanish settlement to the Philippines and later to Indonesia. A wild form is found on the west coast of Mexico but this plant is smaller than the cultivated one now grown in the Far East which must have arisen as the result of human selection.

A. letonae is not known outside El Salvador; *A. funkiana* is found in a very restricted area in the Jaumave valley in Mexico; and *A. lecheguilla* occurs wild in Mexico and in Texas where it is not used commercially.

A. amaniensis was found growing in secondary vegetation at the East African Agricultural Research Station, Amani, Tanzania after the First World War. Its origin is not known but it may have been introduced during German times. It was found to be an undescribed species.

A. angustifolia is found in many tropical countries where it is planted as an ornamental. It has become naturalized in India.

Attempts to improve the long-fibre agaves through breeding have been made in various countries. Such work was initiated in Algeria, Brazil, Indonesia, the Philippines, Puerto Rico, Kenya and Tanzania but, with the exception of that in East Africa, it has not led to useful results and appears not to have been continued. A breeding programme began in Tanzania in 1929; in Kenya, work started fairly recently, so that it is still too early for results.

In East Africa the objects of breeding were a more rapidly growing, long-fibre agave with a higher leaf-number potential than sisal; in most other respects the improved agave should resemble the sisal plant. These include: (a) smooth (non-spiny) leaf margins; (b) long heavy and rigid leaves of good configuration; (c) mean fibre yield per leaf not less than that of sisal; (d) adaptability and resistance to pests and diseases; and (e) fibre quality comparable with that of sisal (Lock, 1969).

The polyploid species *A. sisalana*, *A. fourcroydes* and *A. cantala*, with a narrowly clonal genetic base,

offer little scope for breeding. Fertility is very low and their sexual offspring, if any, invariably have spiny leaf margins; moreover, variation as to growth rate and leaf-number potential is too little to permit selection of more productive plant types.

Though the East African work showed that various interspecific crosses were successful it soon became evident that hybrids between the diploids, *A. amaniensis* and *A. angustifolia*, showed most promise. The results of reciprocal crosses proved that the high rate of leaf production and the high leaf-number potential of *A. angustifolia* can be combined with the long non-spiny leaves of *A. amaniensis*. Most of the F_1 hybrids are fertile, can be selfed, intercrossed or backcrossed with other species and fertility is not lost after further breeding. The first hybrid seedlings were planted in 1936. To improve leaf length the longer lived ones were backcrossed to *A. amaniensis* and some were selfed or backcrossed to *A. angustifolia*. Most selections from among the second-generation hybrids were from selfings or backcrosses to *A. amaniensis*. The results so far show that it is not difficult to obtain high-yielding hybrids with rigid leaves and smooth leaf margins. The greatest difficulty lies in the size and the shape of the leaves; they are often too light or too short, corrugated or otherwise unacceptable. Improvement of leaf characteristics was approached by backcrossing selected second-generation hybrids to *A. amaniensis* and by intercrossing. Although improvement appeared to be possible, further backcrossing has meant a lower rate of leaf unfurling and reduction of leaf-number potential.

The most outstanding clone selected so far, one which meets most of the selection criteria, is hybrid no. 11648, a product of the backcross (*A. amaniensis* \times *A. angustifolia*) \times *A. amaniensis* (Wienk, 1970).

5 Prospects

The long-fibre agave hybrids selected so far are not yet ideal and more work is needed to correct their shortcomings. A serious defect is susceptibility to *Phytophthora* rot, a disease not known in sisal, henequen or cantala. Both *A. amaniensis* and *A. angustifolia* are susceptible and so are their progeny. Though some variation in susceptibility is present among their hybrids, highly-resistant clones are unlikely to be obtained without introducing resistance from other species. *Agave decipiens*, a tetraploid with $2n = 120$, has so far appeared to be completely resistant; it is sexually fertile but its leaves are very short and spiny and of such configuration that at least two generations will be required to obtain an acceptable leaf shape. Chromosome doubling may be

required at some stage. The resistance might also be introduced to *A. sisalana*.

Whether Tanzania's breeding programme will be continued much longer must depend upon the economic future of the agave fibres. Because of inroads made by synthetics, the future has recently looked very bleak. Sisal production in Tanzania, once the world's largest single producer, declined in the period 1965-72 from 218 to 157 kt/yr. Recently, prices have risen considerably but it remains to be seen whether the rise will provide enough incentive to invest in a long-term programme such as agave breeding; in the past, such fluctuations have always been of short duration, causing production to increase and prices to drop again.

If breeding is carried on, it seems likely that the present limited circle of aneupentaploid *sisalana* clones will be replaced by complex 'interspecific' hybrids, perhaps diploid, perhaps polyploid in constitution.

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Grain amaranths

Amaranthus spp. (Amaranthaceae)

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1 Introduction

The three grain Amaranth species are robust annual herbs that were domesticated prehistorically in the highlands of tropical and subtropical America. The tiny seeds are popped or parched and milled for flour or gruel. In taste, nutritional value and yield, the grain compares favourably with maize and other true cereals. However, the crop has declined to a vanishing relic in its homeland; far more Amaranth grain is now produced in Asia (especially in India) than in the Americas. For general reviews of economic botany, see Singh (1961) and Sauer (1967).

2 Cytotaxonomic background

The cultivated species and their probable native regions are:

- 1 *A. hypochondriacus* (= *A. frumentaceus*, *A. leucocarpus*, etc.) of north-western and central Mexico.
- 2 *A. cruentus* (= *A. paniculatus*, etc.) of southern Mexico and Central America.
- 3 *A. caudatus* of the Andes. In the Argentine Andes, the typical form is grown together with a conspicuous mutant that produces club-shaped inflorescence branches with determinate growth, a trait unknown in wild Amaranths. This mutant has commonly been given specific rank (as *A. edulis*) but may better be treated as *A. caudatus* ssp. *mantegazzianus* (Hanelt, 1968).

The wild species that appear most closely related to the above are, respectively:

- 1 *A. pomellii*, a pioneer of canyons, desert washes and other open habitats in the western Cordillera of the Americas. An aberrant form with indehiscent utricles has sometimes been given specific rank as *A. bouchonii*.

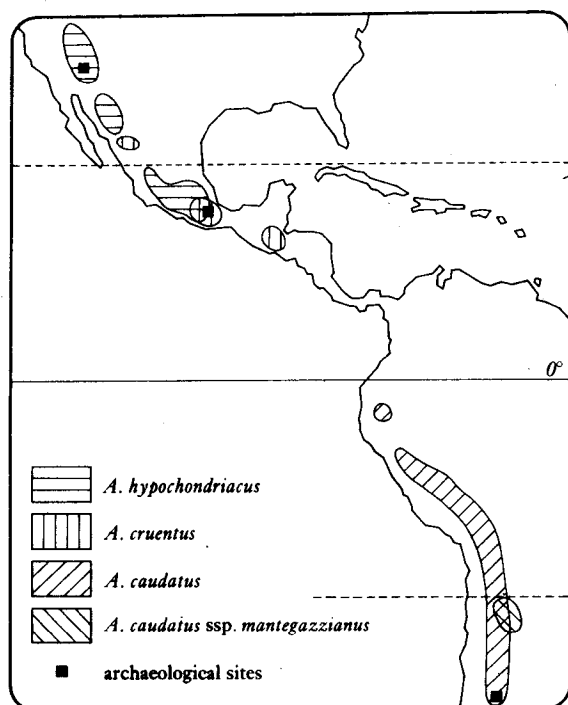


Fig. 2.1 Distribution of the grain amaranths, *Amaranthus* spp.

- 2 *A. hybridus* (= *A. chlorostachys*, *A. patulus*, etc.), a riverbank pioneer of moister regions of eastern North America and the mild highlands of Central America.
- 3 *A. quitensis*, a riverbank pioneer of highland and subtropical South America.

All six species are diploids, with $2n = 2x = 32$ consistently reported except that counts of both 32 and 34 are reported for *A. cruentus* and *A. powellii*. Pal and Khoshoo (1974) suggest derivation of *A. cruentus* from *A. powellii* on the basis of their counts of $2n = 34$ for both, but comparative morphology of the species does not support this. Counts of both 32 and 34 are also reported in other sections of the genus, varying between closely related species and within certain species without apparent taxonomic meaning (Grant, 1959; Khoshoo and Pal, 1970).

Many interspecific hybrids, both spontaneous and artificial, have been reported among the grain species and their wild relatives (Murray, 1940a; Grant, 1959). Some experimental hybrids show heterosis and nearly normal meiosis but are partially sterile; others have abnormal growth and are totally sterile, including *A. caudatus* \times *A. hypochondriacus* (Khoshoo and Pal,

1970; Pal and Khoshoo, 1972, 1974). Introgression between the last two species has not been reported where they are cultivated together.

No spontaneous polyploids are known among the grain *Amaranthus* but colchicine-induced autotetraploids and amphiploids have been bred from some of them. Seed weight in the tetraploids is about double that of the diploids, suggesting agro-economic potential (Murray, 1940b; Pal and Khoshoo, 1968).

Amaranthus are characteristically wind pollinated but the grain species with colourful inflorescences are occasionally visited by bees (Khoshoo and Pal, 1970). The grain species and their close relatives are monoecious and self-fertile. Arrangement and sequence of anthesis of the unisexual flowers favour a combination of self- and cross-pollination. Each of the many cymes of the inflorescence is initiated by a single staminate flower followed by an indefinite number of pistillate flowers, often over a hundred. Stigmas of the earliest pistillate flowers are receptive before the staminate flower opens; most of the later pistillate flowers develop after the staminate flower has abscised. However, cymes of different ages are present on each indeterminate inflorescence and pollen transfer among them probably makes selfing more common than crossing.

3 Early history

Wild amaranth seeds were commonly gathered by many prehistoric American Indian peoples. The wild seeds are as nutritious and as large as those of the cultivated species. Archaeological proof of domestication comes with the appearance of pale white seeds, contrasting starkly with the dark brown wild type; the mutation producing this change has never been recorded historically. Associated with the change in colour are improved popping quality and flavour. A small proportion of dark seeds is generally present in the grain crops. Where selection for pale seed colour is relaxed, as when the plants are grown as ornamentals, the dark seeds become predominant.

The earliest record of the pale-seeded crop is from Tehuacan, Puebla, Mexico, where *A. cruentus* appeared about 4000 B.C. and was joined by *A. hypochondriacus* about A.D. 500 (Sauer, 1969). By the fourteenth century A.D., pale-seeded *A. hypochondriacus* was also cultivated by Arizona cliff-dwellers (Bohrer, 1962). The earliest record of *A. caudatus* is from 2,000-year-old tombs in north-western Argentina, where its pale seeds were found mixed with those of *Chenopodium quinoa* and with dark seeds of weed amaranths and chenopods (Hunziker and Planchuelo, 1971).

The three crop species may have been indepen-

dently domesticated but there is an alternative possibility, namely that there was a single primary domestication of *A. cruentus* from *A. hybridus*, with the other two domesticates evolving secondarily by repeated crossing of *A. cruentus* with weedy *A. powellii* and *A. quitensis* as the crop spread into their respective territories. Pal and Khoshoo (1974) discount the role of hybridization in evolution of the grain amaranths because of low fertility in their experimental hybrids; however, few of their hybrids were totally sterile and the particular combinations involving *A. cruentus* that are pertinent here were not actually tried.

Evolution of all three domesticates has involved increased size of the whole plant and particularly of the inflorescence, resulting in greatly increased seed yield. All three domesticates also display the effects of selection for striking anthocyanin pigmentation of leaves, stems and inflorescences. Presumably, the intense red colour had ceremonial meaning. At the time of the Spanish Conquest, grain amaranths were important in rituals of the Aztecs and other Mexican peoples. Judging by later ethnographic evidence, ceremonial use of red Amaranths extended from the Pueblo region of the southwestern United States to the Andes and was more widespread than use as a grain crop. The ceremonial dye Amaranths are generally extremely deep red forms of *A. cruentus* with dark seeds; in the Andes some may be *A. cruentus* × *A. quitensis* hybrids.

4 Recent history

In Spanish America after the sixteenth century, grain Amaranth cultivation was regarded as a symbol of paganism and repressed; thus the crop nearly disappeared from history. However, by the early nineteenth century, grain Amaranths had appeared as a staple food crop in the Nilgiri Hills of south India and in the Himalaya; they have since been noted over an increasingly wide area of India as well as across the interior of China to Manchuria and eastern Siberia. Pale-seeded *A. hypochondriacus* constitutes the bulk of the Asiatic crop; dark-seeded *A. hypochondriacus* and pale-seeded *A. caudatus* are minor components. In the 1940s, cultivation of *A. hypochondriacus* was begun in East Africa to supply grain to the local Indian population. The wide latitudinal spread of these species in the Old World presumably required evolutionary changes, because their flowering is controlled by photoperiod.

Amaranthus cruentus has not become established as a grain crop in the Old World. However, dark-seeded, deep red forms of this species have been widely planted in tropical Africa and Asia for over a century as ornamentals, dye plants, fetishes and potherbs.

All three of the domesticated species may have been introduced to the Old World via Europe; they have been grown in European gardens as ornamentals and curiosities for at least 250 years. Only dark-seeded forms of *A. hypochondriacus* were known to have been present in Europe until Hanelt (1968) found a pale-seeded specimen in a sixteenth century German herbarium collection.

5 Prospects

At least some of the grain Amaranths possess the unusual and highly efficient 4-carbon photosynthetic pathway (Tregunna and Downton, 1967; El-Sharkawy, Loomis and Williams, 1968), which may account for the excellent yields claimed. However, at present India seems to offer the only signs of significant expansion of the crop and sustained scientific breeding.

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