Breeding Plantation Tree Crops: Tropical Species

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Preface

Tree species are indispensable to support human life. Due to their long life cycle and environmental sensitivity, breeding trees to suit day-to-day human needs is a formidable challenge. Whether they are edible or industrial crops, improving yield under optimal, sub-optimal and marginal areas calls for unified efforts from the scientists around the world. While the uniqueness of coconut as *kalpavriksha* (Sanskrit-meaning tree-of-life) marks its presence in every continent from Far East to South America, tree crops like cocoa, oil palm, rubber, apple, peach, grapes and walnut prove their environmental sensitivity towards tropical, sub-tropical and temperate climates. Desert climate is quintessential for date palm. Thus, from soft drinks to breweries to beverages to oil to tyres, the value addition offers a spectrum of products to human kind, enriched with nutritional, environmental, financial, social and trade related attributes.

Taxonomically, tree crops do not confine to a few families, but spread across a section of genera, an attribute so unique that contributes immensely to genetic biodiversity even while cultivated at the commercial scale. Many of these species influence other flora to nurture in their vicinity, thus ensuring their integrity in preserving the genetic biodiversity. While wheat, rice, maize, barley, soybean, cassava and banana makeup the major food staples, many fruit tree species contribute greatly to nutritional enrichment in human diet. The edible part of these species is the source of several nutrients that makes additives for the daily diet of humans, for example, vitamins, sugars, aromas and flavour compounds, and raw material for food processing industries. Tree crops face an array of agronomic and horticultural problems in propagation, yield, appearance, quality, diseases and pest control, abiotic stresses and poor shelf-life.

Shrinkage of cultivable land and growing demand has enforced these crops to be grown under marginal conditions that call for concerted efforts of plant breeders to go for the genetic improvement of these crops. A lot of research has already been done and is continued to preserve and utilise germplasm for genetic improvement of fruit crops, consumed for nutrition and commercial uses, for growing under environmental stress constraints. The published results are mainly available in the refereed journals and popular magazines. The researchers and scientists have to spend precious time in digging out the desired research references. The compilation of scientific data in the form of a book would certainly help a great deal in

providing information to the scientific community and industry people. There are few books available, which lack recent comprehensive information on a package of conventional breeding, biotechnology and molecular tools in crop improvement. With the use of modern molecular and biotechnological tools, the task of improving yield in tree crops is foremost in the acumen of future global agricultural research for sustainable production. This 2-volume book series deals with both tropical and temperate species, and is a sincere effort towards compiling the available research worldwide and bring them to the reference of scientists, researchers, teachers, students, policy makers and even planters. It is worthwhile to note that in the forthcoming years, tree crops are to be given much importance on par with annual crops due to carbon trading and nutritional up-gradation of the daily diet.

This book volume on tropical species deals with a total of 16 chapters on fruits and nuts (banana, mango, guava, papaya, grape, date palm, litchi, avocado and cashew), oil crops (coconut, oil palm and olive), industrial crops (rubber) and beverages (coffee, tea and cocoa). The second volume will deal with mainly temperate species.

The invited contributory authors are internationally well known specialists in individual crops. We highly appreciate their untiring efforts rendered in ensuring the inclusion of latest research accomplishments and their co-operation in revising their manuscripts timely. A few reviewers spared their valuable time in improving the quality of manuscripts. We are immensely thankful to them for their valuable help. Finally, we thank SPRINGER for bringing out this series to the readers.

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Part I
Fruit and Nut Crops

Chapter 1
Genetic Improvement of Banana

Frédéric Bakry, Françoise Carreel, Christophe Jenny, and Jean-Pierre Horry

1.1 Introduction

World production of bananas, estimated at 106 million tons (Lescot 2006), ranks fourth in agricultural production. Bananas make up the largest production of fruits and the largest international trade, more than apple, orange, grape and melon. Bananas are cultivated in more than 120 countries in tropical and subtropical zones on 5 continents. Banana products represent an essential food resource and have an important socioeconomic and ecological role.

Current varieties are generally seedless triploid clones either of the single genome A from the species *Musa acuminata* (group AAA) or of both genomes A and B from species *M. acuminata* and *Musa balbisiana* (groups AAB and ABB). More rarely, diploid varieties (AA and AB) and tetraploid clones are encountered. There are two major channels of banana production: those cultivated for export and those reserved for local markets. The main banana varieties cultivated for export, known as 'Grande Naine', 'Poyo' and 'Williams', belong to the monospecific triploid bananas (AAA) of the Cavendish sub-group. They differ from each other only in somatic mutations such as plant height or bunch and fruit shape. Their production relies on an intensive monoculture of the agro-industrial type, without rotation, and a high quantity of inputs.

Banana cultivation for local consumption is based on a large number of varieties adapted to different conditions of production as well as the varied uses and tastes of consumers. Diploid bananas, close to the ancestral wild forms, are still cultivated in Southeast Asia. In other regions, triploid clones belonging to different sub-groups – Plantain, Silk, Lujugira, Gros Michel, Pisang Awak – are the most widely distributed.

Bananas have many uses. They are not only consumed as fresh fruits but also cooked, like plantains. They are processed in various ways, into chips, fries, fritters,

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purees, jams, ketchup and alcohol (banana wine and beer have a very significant production in East Africa). The daily per capita consumption of bananas from 30 g to over 500 g in some East African countries. Apart from the fruit, other parts of the plant are also used: the pseudostem is used for its fibres and as floaters (*Musa textilis* or abacá) in the Philippines, and the leaves are used to make shelters or roofs or as wraps for cooking. In Thailand, the floral buds of particular varieties (Pisang Awak) are used in various culinary preparations. Some varieties are also considered to have medicinal properties.

Cultivated throughout the world, bananas are threatened by several diseases and pests (Stover and Simmonds 1987; Jones 1999) that need to be taken into account for banana improvement. Various major fungal diseases are constraints in industrial production and, to a lesser degree, in local production. For example, Sigatoka disease (SD) due to *Mycosphaerella musicola* and black leaf streak disease (BLSD) caused by *M. fijiensis* result in production losses in large industrial plantations and necessitate costly pest control measures to be adopted. In certain production zones, *Fusarium* wilt due to the soil fungus *Fusarium oxysporum* f. sp. *cubense* prevents the cultivation of susceptible varieties like the Gros Michel types. Great constraints are also exerted by the nematodes – *Radopholus similis* and several representatives of the genus *pratylenchus* – and by the black weevil of banana, *Cosmopolites sordidus*. Also, viral diseases are spreading. Those of greatest concern are due to BBTV (banana bunchy top virus), CMV (cucumber mosaic virus), BSV (banana streak virus) and BBMV (banana bract mosaic virus).

Chemical control measures used in intensive cultivation are not available to small banana farmers in developing countries. Furthermore, for some diseases, there is no effective chemical control. Genetic improvement has thus been focused mainly on obtaining varieties resistant to principal pests and diseases. Breeding bananas through hybridisation, which began in the 1920s, is currently being pursued at seven research centres. FHIA in Honduras is breeding banana for export as well as the 'cooking' types (Rowe 1984). EMBRAPA-CNPMF in Brazil (Dantas et al. 1993), NRCB and TNAU in India (Sathiamoorthy et al. 2000; Krishnamoorthy and Kumar 2004) aim at breeding local types of dessert and cooking bananas. CARBAP (Jenny et al. 2003) in Cameroon and IITA (Tenkouano and Swennen 2004) in Nigeria are conducting research on plantain and banana breeding in Africa. These six research centres are mainly interested in developing new tetraploid varieties by crossing triploid varieties and wild or improved diploid clones with resistance to diseases. Some secondary triploids derived from crosses between these new tetraploid varieties and other diploid clones were also obtained. In the French West Indies, CIRAD has conceived another crossing strategy aimed at the development of triploid varieties directly from diploid plant material (Bakry et al. 2001).

Since the 1980s, apart from these conventional breeding approaches, other groups have focused on mutagenesis as at IAEA (Roux 2004) in Austria or on the selection of somaclonal variants as at TBRI (Hwang and Ko 1990) in Taiwan. These technologies appeared as a result of the development of in vitro culture techniques designed for rapid industrial multiplication of micro-propagated banana plants.

1.2 Botany and Origin

1.2.1 Morphological Description

Banana is a giant herb whose pseudostem, formed by interlocking leaf sheaths, reaches 1–8 m in height (Fig. 1.1). The leaves emerge from the apical meristem of the underground true stem, small in size, which is a corm or rhizome. The bud at

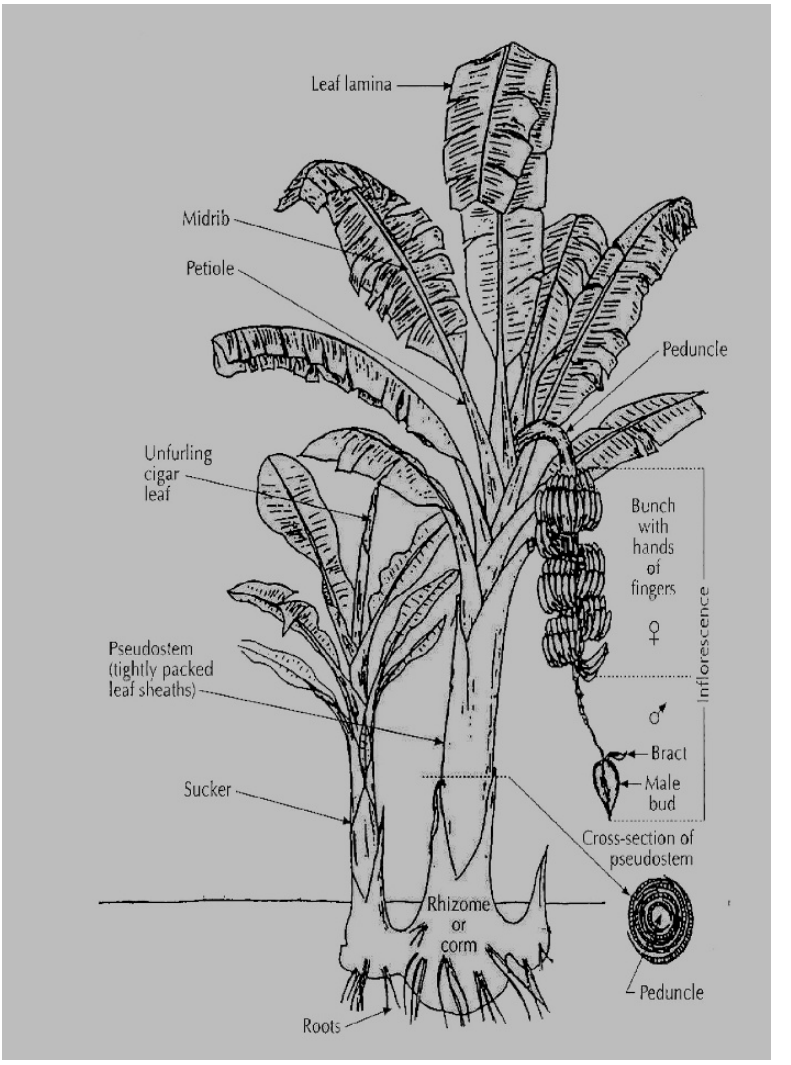

Fig. 1.1 Diagrammatic representation of a fruiting banana plant with suckers (from Champion 1963; Jones 1999)

the axil of each leaf eventually gives rise to a shoot. Shoot production is the natural reproductive mode for cultivated varieties. At the end of the vegetative phase, a quick change in the function of the central meristem induces the 'flower' primordia, followed by the growth and elongation of the true stem within the pseudostem and later by the emergence of the inflorescence.

The inflorescence, which can be vertical, pendant or sub-horizontal, is complex and made up of an ear of cymes. Cymes are inserted spirally on the floral stem and are composed of one spathe and single or double rows of flowers at its axils. These are the first ranks of flowers, usually called 'hands', from which the fruit bunches develop. The first hand contains flowers (termed female) with an ovary in the inferior position and non-functional stamens reduced to the state of staminodes. Sometimes the stamens develop, however, and these first flowers are hermaphrodite. Wild bananas have fruits filled with seeds but little pulp. In parthenocarpic banana plants usually called cultivars, the ovaries of female flowers are filled with pulp that forms the fruit without pollination or seed formation. As female fertility is quite low (and sometimes null), manual pollination is needed with cultivated varieties to get some seeds and, thus, progenies. After the female flowers, two or three hands of neutral flowers appear with undeveloped floral parts, followed by hands of male flowers (opposite the female flowers) with reduced undeveloped ovaries and well-developed stamens. In some cultivars, growth of the ear meristem is stopped very early (sometimes, immediately after *the* emergence of the first female flowers), but the inflorescence generally continues to grow indefinitely to form the so-called male bud. If it is not cut, this male bud will continue to grow until fruit maturity and stem withering. In addition to wild species, many cultivars have male flowers with some degree of pollen fertility.

1.2.2 Agromorphological Variations

Morphotaxonomy has made it possible to characterise different banana varieties and to establish the basis of the current botanical classification (Table 1.1; Simmonds and Shepherd 1955; Simmonds and Weatherup 1990). A set of 119 agro-morphotaxonomic descriptors has been defined as the norm for description of bananas (IPGRI-INIBAP and CIRAD 1996). These descriptors serve as a basis for a system of information exchange between collections, the MGIS (musa germplasm information system), run by INIBAP. Computerized tools have also been developed to identify the varieties on the basis of these descriptors (Perrier and Tezenas du Montcel 1990).

There is considerable variability regarding the aerial parts. Vegetative parts mainly vary with respect to pseudostem colour, the presence and colour of spots at the petiole base, the shape of the petiolar canal section and the plant height and growth habit. There may also be colour chimeras and variations due to dwarfism – obstruction or deformation of the inflorescences caused by highly compact interlocking of the leaf sheaths, stocky appearance of the leaves and shoot inhibition.

Table 1.1 Deduction of the genomic constitution of a variety based on its ploidy level and score (from Simmonds and Shepherd, 1955); 15 morphological characters were retained for their stability and capacity to discriminate among the different groups of cultivated bananas. Each character has been quantified on a scale of 1 to 5, in which 1 corresponds to a phenotypic expression of wild bananas of the species M. *acuminata*, called A, and 5 corresponds to that of wild bananas of the species M. *balbisiana*, called B. For each cultivar, the level of ploidy and the score obtained by the addition of notes for each of the 15 characters determine its genomic constitution and consequently its position in a given group

	Ploidy Level		
Theoretical score	2x	3x	4x
15	AA (16–23)	AAA (15–21)	AAAA (15–20)
30			AAAB (27–35)
35		AAB (26–46)	
45	AB (46–49)		AABB (45–48)
55			
60		ABB (59–63)	ABBB (63–67)
75	BB (69)		

The most important variations concern the inflorescences and consequently the fruit bunches. Differences between fruits are determined by their size, shape and colour along with the pulp colour. Clones of the plantain sub-group have a very firm cooking orange-yellow flesh, unlike other cooking bananas (sub-groups Laknao, Popoulou, Bluggoe and Monthan). Lujugira, the so-called East African highland bananas, are quite unique and, depending on the clone, used for cooking or brewing beer. Dessert bananas vary in taste and aroma: very sweet in some diploid Pisang Mas cultivars, sweet and acidulous in Silk Banana and bland in the universally appreciated export Cavendish bananas. Morphological variability in the male floral bud involves differences in the shape and colour of the bracts and male flowers.

Depending on the cultural conditions, the duration of the cycle is a varietal characteristic that is subject to wide variations. It ranges from nine to eighteen months, according to the variety, which is relatively critical in terms of the production potential of banana plantations.

1.2.3 Origin and Dissemination

Musa L. (Musaceae) is currently separated into five sections: Australimusa ($2n = 20$), Callimusa ($2n = 20$), Rhodochlamys ($2n = 22$), Eumusa ($2n = 22$) and Ingentimusa (unclassified species). Species usually classified among Callimusa and Rhodochlamys essentially contain plants of floral interest. Among the Australimusa, some accessions are cultivated for their fibre (abacá) and they belong mainly to *M. textilis*. Several other Australimusa accessions have edible fruit on erected bunches. Named Fe'i, they are only cultivated in the Pacific region. All the other *Musa* accessions with edible fruits are bananas.

As first suggested by Kurz (1865), Dodds (1943) and Cheesman (1947) show bananas related to Eumusa and originated mainly from two wild diploid species: *M. acuminata* (genome A) and *M. balbisiana* (genome B). Plants of these two species produce fruit filled with seeds. They reproduce both sexually and by vegetative means from shoots. In Southeast Asia, fruits of some wild accessions are consumed when immature before the seeds become hard and in particular varieties with soft seeded fruits. But real edible bananas are results of a combination of fruit parthenocarpy and sterility. As mentioned by Simmonds and Shepherd (1955), domestication is a succession of non-linear but interdependent stages: selection of parthenocarpic clones, selection for gametic sterility, selection of triploid plant and, finally, enhancement of the phenotypic diversity throughout vegetative propagation.

Parthenocarpy is usually considered as a pure *acuminata* character. It is described by Simmonds (1953) as polygenic. The domestication for starchy fruit was suggested to happen in the area from the Philippines, north of the Moluccas in Indonesia, to Papua New Guinea where some more starchy than usual seed-bearing wild *M. acuminata* subsp. *banksii* were observed by Simmonds (1962) and where wild accessions still have the cytoplasmic genome that is found in almost all cultivated bananas (Carreel et al. 2002). Whether parthenocarpic pure *balbisiana* exists is still being discussed (Valmayor et al. 1991; Jarret and Litz 1986).

Gamete sterility, supposedly with a genetic origin, has been described. Some are independent from parthenocarpy that yields variations in the morphology and physiology of the flowers (Dodds and Simmonds 1948; Dessauw 1988). Other factors have links with parthenocarpy and auxin metabolism that disturb the development of seeds in the fruits. Chromosomal factors also play a major role in banana fertility and, thus, in its evolution. Structural heterozygosity and triploidy are factors known to give meiotic errors that lead to lower fertility (Bakry et al. 1990). Dodds (1943), Dessauw (1988) and Shepherd (1999) showed that more than four chromosome rearrangements exist within the *M. acuminata* complex following the spatial and temporal isolation of the *acuminata* sub-species. Shepherd (1999) structured the species in six groups called 'translocation group' that differentiate by at least one rearrangement and he described the meiotic disturbance of the intergroup hybrids. He also showed that the sterility of inter-specific hybrids may have a genomic origin as the homology between the genome *acuminata* and *balbisiana* is partial.

Polyploidy in banana can be diploid, triploid or tetraploid. The 3*x* and 4*x* bananas are often more vigorous and give larger fruits than diploids. Most banana productions in the world rely on triploids while tetraploidy is considered as the maximum ploidy level giving usually viable plants with overall higher water content (personal observation), poor fruit post-harvest qualities and dropped leaves. Thus, triploidy is generally considered as the optimum ploidy level to have good agronomic behaviour as it guarantees the highest gamete sterility in production conditions. In natural conditions, triploid varieties have resulted from cross-pollinations between diploid clones producing 2*n* gametes and diploid clone producing *n* gamete (Fig. 1.2). The appearance of some tetraploids must have followed the same process ensuing the production of 2n gametes by triploid clones.

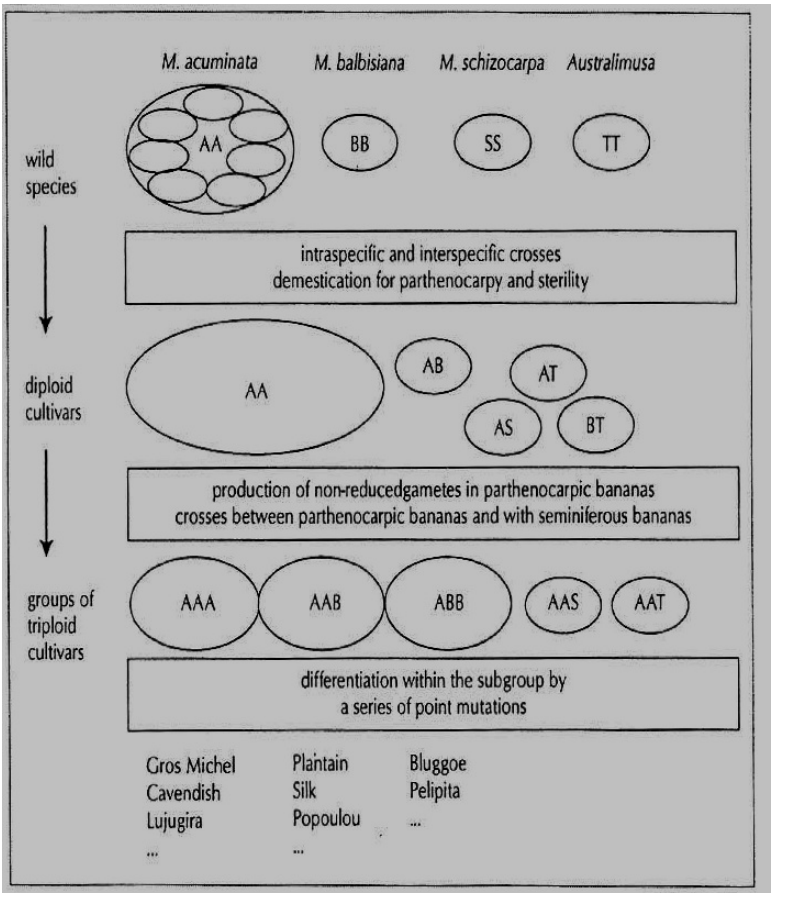

Fig. 1.2 Domestication of bananas

1.2.4 Enlargement of Phenotypic Diversity

The mode of reproduction of the triploid ancestral cultivars, characterised by a low degree of fertility, prompted natural somatic mutations, which contributed in the second phase, to the enlargement of phenotypic diversity. Thus, the global phenotypic diversity of the current triploid varieties resulted from two distinct phases: a first stage of fixation by the sexuality of ancestral triploid plants followed by a second stage of diversification due to the vegetative propagation of these proto-varieties by humans. In the *Musa* complex, varieties derived from each other by vegetative propagation are related to the same sub-groups.

Musa structuration, origin and migration of cultivars have been drawn by Champion (1967) and De Langhe (1995). These data are being clarified by linguistic (Rossel 1999) and phytoliths approach (Lentfer and Boyd 2004; Lejju et al. 2006; Ball et al. 2006). In the previous era, bananas were cultivated from India to the

Pacific region, from north of Australia to Taiwan and even in southern Japan. They were introduced at various times in Africa. More than 3000 years ago, plantains and probably a few diploids (still found in Comoro Islands today – personal data) were the first to reach East Africa through Pemba and Zanzibar, from Southeast Asia (De Langhe 1995). Bantu-speaking peoples took them to West Africa. Today, plantains have almost disappeared from the east coast of Africa, but are found in all the humid zones of Central and West Africa. In the fifth century, there was a second wave of introductions of so-called East African highland bananas: Mutika-Lujugira which are beer and cooking bananas originally from Indonesia that probably arrived via Madagascar.

On the American continent, the appearance of dessert-type banana plants is linked with the discovery of the New World in the fifteenth century. However, some authors have hypothesised that cooking types – plantains and popoulous – may have arrived earlier from the Philippines on the west coast of South America, in Peru and Ecuador, about 200 years before the current era (Langdon 1993). This early colonisation could explain the spread of banana in the eastern Pacific region, but these hypotheses remain controversial.

The evolution involved species existing within a given biotope. It gave rise to monospecific *M. acuminata* cultivars or to inter-specific hybrids derived from crosses between *M. acuminata* and *M. balbisiana* and even between sections Eumusa and Australimusa (Jenny et al. 1999).

1.3 Structuration of Genetic Ressources

1.3.1 Diversity of Diploids

The diploid bananas, wild and cultivated, are presently much less widespread than the cultivated triploids. However, they are still found in the endemic state throughout Southeast Asia. The plants are generally weaker and have smaller yields than the triploids. The diploid clones are nevertheless indispensable for genetic improvement programmes, especially because of the low fertility of the triploids. Deforestation and loss of traditional gardens endanger these precious genetic resources.

1.3.2 Wild Bananas

The seminiferous wild bananas of the genus *Musa* are found in the humid but well-drained valleys and glades of forests in the tropical zone, in south and Southeast Asia and in the Pacific, from the Indian peninsula to the Samoan islands. More than 25 species have been described and included within the genus *Musa*. Only those that have contributed to the genome of parthenocarpic bananas are discussed here.

Species belonging to the section Australimusa (giving the T genome) and *M. schizocarpa* (S genome) of the section Eumusa are present east of the range

of *Musa*: in the eastern area of Indonesia, Papua New Guinea and the Pacific. The Australimusa are identified by their erect inflorescence. The various species of this section were described by Cheesman (1947) and Argent (1976) as related and morphologically very close. Molecular analyses show little variability and structuration compared to the Eumusa section. *M. schizocarpa* is characterised by water-green stem colour and a green colour of the bracts of the male bud. Up-to-date little variability has been found at the morphological as well as at the molecular level compared to *M. acuminata* (Argent 1976; Carreel et al. 1994).

M. balbisiana, of the section Eumusa, is found from India to the Philippines, Papua New Guinea and occasionally in the Indochina peninsula. Up to the 1990s, accessions available in ex situ collections were showing a low variability and a structuration in four main types (Horry 1989). During the previous decade, new interest for this species resulted in the identification of more polymorphism (Uma et al. 2005; Ge et al. 2005). Even so, more plant prospection and molecular characterisation are still needed.

The extension of *M. acuminata*, section Eumusa, covers most of the area of distribution of the genus *Musa*, from west to east, from Myanmar to Papua New Guinea. The topography of its area of origin has led to geographic and, thus, reproductive isolation, which is a source of differentiation. Chromosome rearrangements (inversions and translocations) observed by Shepherd (1999) between different accessions of *M. acuminata* can be associated with this process of reproductive isolation.

The high level of morphological variation associated to its geographic distribution led to the description of nine *acuminata* sub-species (Fig. 1.3). This

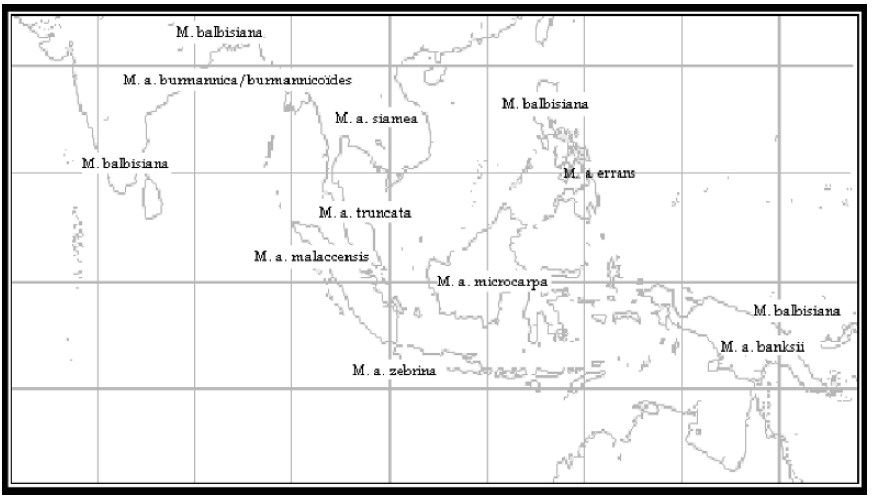

Fig. 1.3 Geographic distribution of Musa acuminata and Musa balbisiana in Asia

structuration has been described by cytogenetic, nuclear and cytoplasmic molecular analyses with the available accessions. It allowed to differentiate homozygote accessions from heterozygotes. Among the homozygotes, five pools can be defined. The first pool relates the *M. a. banksii* (Mueller) accessions from Papua New Guinea, the *M. a. errans* (Blanco) from Philippines and the *M. a. microcarpa* (Beccari) from Borneo area. It can be associated with the 'Standard structure' karyotype defined by Shepherd (1999) as what must have been the primordial chromosome structure. The second pool groups the *M. a. zebrina* (Van Houtte) from the western part of Indonesia and can be associated to the 'Javanese' karyotype of Shepherd. The third pool groups the *M. a. malaccensis* (Ridley) mainly from Malaysia and south of Thailand. The fourth pool relates to *M. a. burmannica* (Simmonds) and *M. a. burmannicoides* (De Langhe) from Bangladesh and eastern India to Myanmar, with *M. a. siamea* that originated in north Thailand and north Laos. This pool recognized by Shepherd as the Northern karyotype can be split in to two: Northern 1 and 2 that differ by only one translocation. Even if little prospected, the *M. a. truncata* is very distinct from all other sub-species (Carreel et al. 1994; Wong et al. 2001). This fifth pool must be associated to the 'Malayan Highland' karyotype of Shepherd though, unfortunately, no common accessions could be studied. From five pools to nine sub-species, it

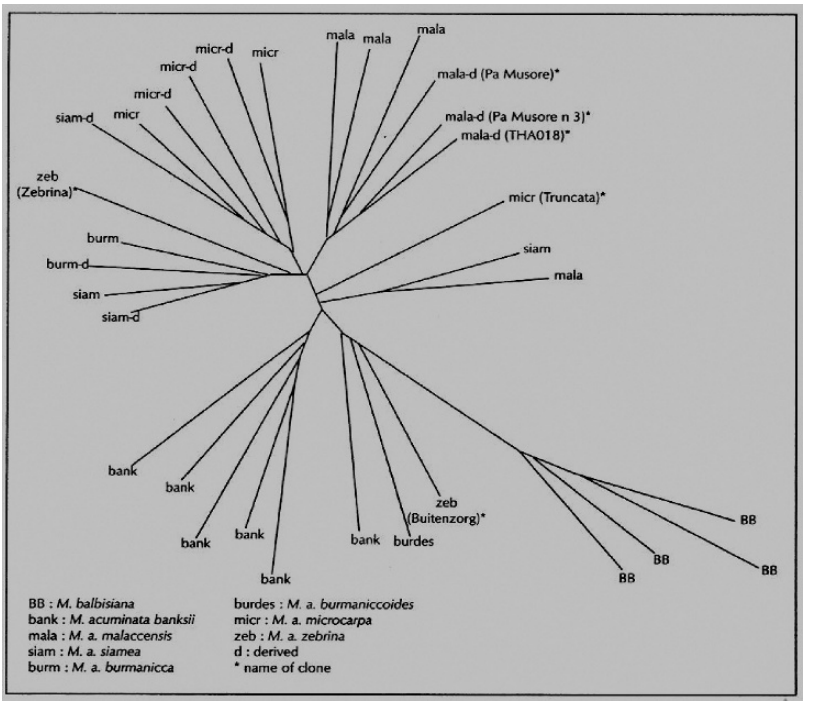

Fig. 1.4 Morphological diversity of seedy bananas (Guadeloupe collection): tree representation according to the NJ tree method, realized on the basis of dissimilarity between 32 accessions on the basis of 99 morphological descriptors (from Jenny et al. 1999)

shows how *M. acuminata* is variable and best-structured among the *Musa* species (Fig. 1.4).

1.3.3 Cultivated Diploids

Cultivated diploids are still mainly restricted to their area of origin in Southeast Asia. Nevertheless, some particular AA diploids have also been reported from the east side of Africa in Comoros (personal data) and Tanzania (De Langhe 2001). Only AA varieties of the Pisang mas (= sucrier) type, which have small, very sweet fruits, are cultivated on a large scale outside their zone of origin. Diploid edible bananas or cultivars are classified according to their genome in groups AA, AB, AS or AT, of which more than 90% are AA. For example, out of 135 diploid clones of the CIRAD collection in Guadeloupe (F.W.I.), only 10 accessions have been identified as inter-specific.

Among the AA, morphotaxonomic and molecular analyses revealed a nearly continuous cloud. Small sub-grouping only emerges for few accessions that are the most cultivated. Variability among those accessions belonging to the Pisang Mas type or Pisang Jari Buaya type is described as of somatic origin. The general cloud structuration can be explained, through the analysis of cytoplasmic and nuclear genomes, as originated from a gene flow between the *M. acuminata* sub-species. Carreel et al. (2002) showed that the AA cultivars are separated into four classes of chloroplastic profiles and five classes of mitochondrial profiles, each related to a specific sub-species. In banana, information on the chloroplast and mitochondrial genomes indicated a paternal heredity (Fauré et al. 1994) (Table 1.2). The AA cultivars can thus be divided into nine cytoplasmic types or cytotypes, but most of them correspond to three cytotypes. Each cytotype can be assigned either to distinct sub-species or to an inter-subspecific origin. That relatedness between cultivars and origin of the diploid cultivars has also been observed through the analysis of nuclear genome. From this classification, CIRAD has defined the base populations for its breeding programme (Bakry et al. 2001).

1.3.4 Triploid Bananas

The use of more complete morpho-descriptors or molecular markers and their analysis by multivariate statistical methods led to organisation in genomic groups: AAA, AAB and ABB with few AAT/ATT/AAS (Table 1.3). The RFLP molecular data do not indicate as clear a distinction between AAB and ABB as morphological markers. *M. balbisiana* is less polymorphic with the molecular markers and the two genomes B of ABB are rarely differentiated. Several AAB cultivars also have their two A genomes nearly identical. In these two cases, the AAB and ABB clones have molecular profiles of the AB type, and only a reading of the relative intensity of RFLP bands – which is possible only for some probe—enzymes combinations – allows us to clearly differentiate the AAB from the ABB (Carreel et al. 2002).

Table 1.2 Structuration of bananas according to their cytotype

Chloroplast profile	Mitochondrial profile								
	α	B	χ	δ	ε	φ	γ	η	τ
I									
II	*M. a. errans* AA cv (36)* AAA cv (Orotava, Red, Cavendish, Gros Michel) ABA cv (Mysore, Nadan, Pome)	AA cv (1)*	*M. a. burmannica* *M. a. burmannicoïdes* *M. a. siamea*	*M. a. malac-censis* AA cv (2)* AB cv ABA cv (Silk)	AA cv (1)*	AA cv (3)* AAA cv (3)**	*M. a. micro-carpa*		ABB cv (Saba 1, Bluggoe, Ney Mannan)
III	AA cv (4)* AAA cv (1)**				*M. a malac-censis*				
IV	AA cv (1)*		*M. a. siamea*						
V	AA cv (49)* AAA cv (4)** ABA cv (Laknao, Maia Maoli) ABB (1)*				AAA cv (Lujugira-Mutika)	*M. a. banksi* AA cv (18)* ABA cv (Plantain, Popoulou, Laknao)		AS w (2)*	ABB cv (Pelipita, Saba 2)
VI	AS cv (1)*					AS w (1)* AS cv (2)*		*M. schizo-carpa*	
VII									*M. balbisiana* Type 2
VIII	BAA cv (P. Rajah Bulu)				BAA cv (P. Kelat)				*M. balbisiana* Type 1, 3, 4 BAB cv (Peyan, Bendetta, P. Awack)
IX									BAB cv (P. Kepok)

* Number of clones having this cytotype.

** Number of clones of indeterminate sub-groups. In italics: seedy bananas. W: wild; cv: cultivated.

Table 1.3 Classification and geographic distribution of the principal banana cultivars

Sub-group	Cultivar	Type of fruit	Distribution
Group AA			
Sucrier	Pisang Mas, Frayssinette, Kirun	Dessert, Sweet	All continents
Pisang Lilin	–	Dessert	Indonesia, Malaysia
Samba	Samba, Chicame, Nzumoheli	Dessert, Acid	Comoros
Tjau Lagada	Tjau Lagada, IDN 110, Gu Nin Chiao, Sa	Dessert, Sweet	Indonesia
Sub-group AAA			
Cavendish	Lacatan, Poyo, Williams, Grande Naine, Dwarf Cavendish	Dessert	All continents (tropical and subtropical areas)
Gros Michel	Gros Michel, Highgate, Cocos	Dessert	All continents
Red	Red, Green Red, Pisang Glintong	Dessert	All continents
Lujugira-Mutika	Intuntu, Mujuba, Bwara, Nakitembe, Mukite	Beer and Cooking	East Africa (Uganda), Colombia
Ibota	Yangambi km5, Khom Bao, Pisang Saripipi, Lagun Vunalir	Dessert	Indonesia, Thailand, Africa
Group AB			
Ney Poovan	Ney Poovan, Safet Velchi, Lal Kelat	Dessert, Sweet Acid	India, Africa
Kunnan	Kunnan	Dessert, Sweet Acid	India
Group AAB			
Silk banana	Silk, Maçá, Malbhog, Supari	Dessert, Sweet Acid	All continents
Pome	Prata, Foconah, Dahomey, Pacovan, Pachanadan	Dessert, Sweet Acid	India, Malaysia, Australia, Brazil, West Africa
Mysore	Pisang Ceylan, Poovan, Zabi, Gorolo, Embul	Dessert, Sweet Acid	India, Sri Lanka, Malaysia, Comoros, West Indies, Zanzibar
Pisang Kelat	Pisang Kelat, Pisang Pulut	Dessert	India, Malaysia
Pisang Rajah	Pisang Rajah Bulu	Dessert, Cooking	Malaysia, Indonesia
Plantains	Dominico, Bobby Tannap, Batard, Orishele, Cuerno, Tanduk	Cooking	all continents
Popoulou/Maia Maoli	Iho U Maohi, Poingo, Popoulou, Maia Maoli	Cooking	Pacific (French Polynesia, Hawaii), Australia, Ecuador,
Laknau	Laknau, Adimoo, Bagatow, Mugus, Pisang Kastroli	Cooking	Philippines, Malaysia, Papua New Guinea
Pisang Nangka	Pisang Nangka	Cooking	Malaysia
Group ABB			
Pisang Awack	Fougamou, Bom, Pisang Kepok, Ducasse, Gia Hui, Muisa Tia	Dessert	Thailand, India, East Africa, Philippines

Table 1.3 (continued)

Sub-group	Cultivar	Type of fruit	Distribution
Bluggoe	Bluggoe, Matavia, Cacambou, Monthan, Barabay, Burro	Cooking	All continents (tropical and subtropical areas)
Pelipita	Pelipita	Cooking	Philippines, Latin America
Saba	Saba	Cooking	Philippines, Indonesia, Malaysia
Peyan	Peyan	Cooking	India
Group AAAA			
Champa Nasik	Champa Nasik	Dessert	- - -

The classification of triploid bananas is much easier to establish than that of the diploid clones because of the mode of evolution of the triploid clones. At this stage, there is almost no fertility and propagation is exclusively vegetative. By vegetative propagation, the clones are differentiated among each other only through small mutations that lead rapidly to the identification of true sub-groups. Thus, structuration of each group in sub-groups emerges from morphological analysis and the identification of morphotypes. This was confirmed by molecular markers: varieties belonging to the same sub-groups have identical or very similar nuclear and cytoplasmic profiles, these results expressing a very restricted genetic variability within each sub-group (Noyer et al. 2005). On the other hand, it is not true at the phenotypic level. The degree of variability within each sub-group is correlated to the intensity with which each type of clone was used and thus multiplied. The greatest phenotypic variability has been found in two sub-groups particularly exploited in Africa: plantains throughout the Central African zone and West Africa and Lujugira, also called the Highland East African Banana.

Molecular analysis also highlights few differences of classification usually due to homonymy. One of the most glaring examples is probably the Mnalouki cultivar, AAB of the Comoro Islands, the appearance of which causes it to be mistaken for a plantain of the French type: molecular markers and just the taste of the fruit, however, prove that it has nothing to do with the plantain. Differences between morphotaxonomy and molecular analysis also show that limits of sub-group are not always as clear as in the best known plantain or Cavendish sub-groups. D'Hont et al. (2000) checked with GISH the exact genome structure of some inter-specific cultivated clones. In most cases, the results were consistent with the chromosome constitution estimated by means of phenotypic descriptors (e.g. 11 A and 22 B for the ABB). It also shows exception may exist as for the clone 'Pelipita' that has 8 A and 25 B chromosomes instead of the predicted 11 A and 22 B.

Within each group, it is also possible to distinguish clones of the dessert type from clones of the cooking type within the AAB on a morphological basis, and within the three groups AAA, AAB and ABB by means of molecular markers (Fig. 1.5). Thus, among the AAB, dessert bananas of the sub-groups Silk, Mysore, Pome-Prata and Pisang Kelat are differentiated from the typical cooking bananas: Plantain, Popoulou, Maia Maoli and Laknao. It is to be noted that the clone Pisang

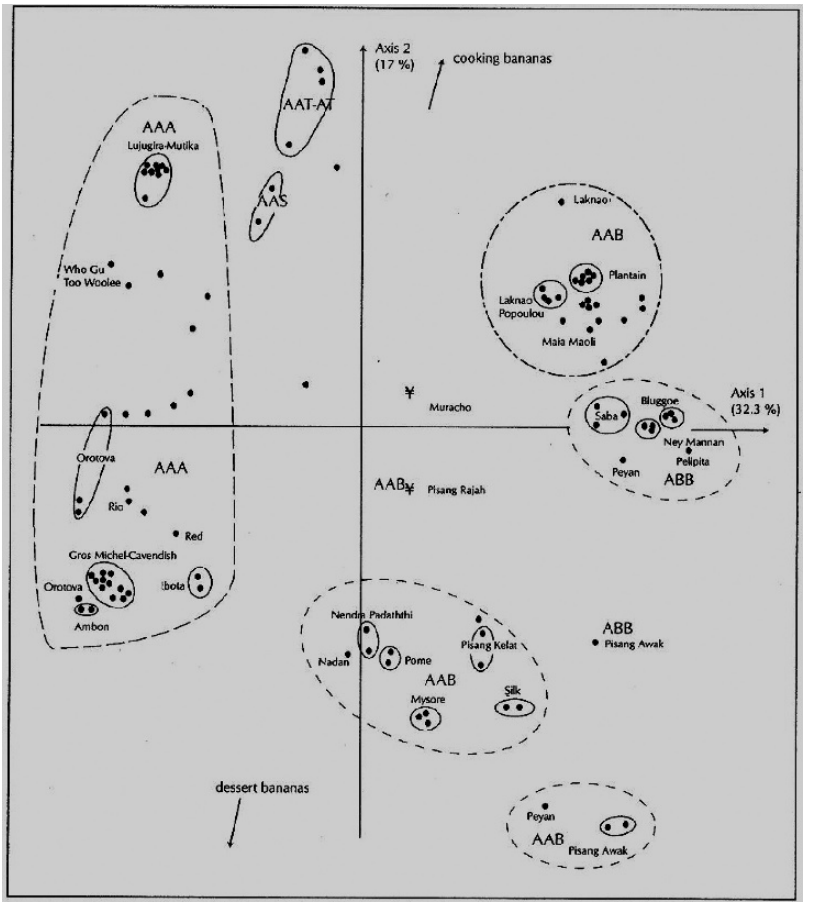

Fig. 1.5 Nuclear molecular diversity of triploid bananas according to their genomic group and sub-group. First plane of a factorial analysis on a Jaccard dissimilarity between 109 cultivars on the basis of 267 variables (from Jenny et al. 1999)

Raja Bulu of the sub-group Pisang Rajah has a profile intermediate between the dessert and cooking types This dessert/cooking classification can be ascribed to the genome A of each of these sub-groups.

1.3.5 Relationships Between Diploid and Triploid Varieties

Several morphological resemblances are known between diploid and triploid clones. Bunches of several AA cultivars – ‘Pongani’ and ‘Kekiau’, for example – that come from collections in Papua New Guinea are similar to those varieties of the plantain sub-group. The taste and type of consumption of other AA cultivars, such as ‘IDN110’, relate them to triploids of the Silk sub-group. These relationships have

Table 1.4 Identification of the putative diploid parents of cultivars from Cavendish and Gros Michel sub-groups

Attributes	Cultivars	Origin	Ploidy	Total number of bands	Bands in common with targeted triploid	Bands of targeted triploid not in 2*n* gamete	Pole 1 specific bands[a]	Pole 2 specific bands[a]	Pole 3 specific bands[a]
Targeted triploid	Gros Michel		3x	73	73	13	3	2	1
sub-group	Akondro Mainty	Madagascar	2x	60	60	–	3	1	0
Putative	Samba	Comoros	2x	60	60	–	3	1	0
unreduced	Chicame	Comoros	2x	60	60	–	3	1	0
gamete donor (2n gamete)									
Normal haploid	Sa	Thailand	2x	59	49	13	2	1	1
gamete donor	Khaï Naï On	Thailand	2x	59	50	13	2	1	1
(best matching	Fako Fako	Papuasy	2x	55	49	11	1	2	1
candidates)	Hom	Thailand	2x	52	39	11	0	0	5
Targeted triploid	Cavendish		3x	72	72	12	3	3	1
sub-group	Akondro Mainty	Madagascar	2x	60	60	–	3	1	0
Putative	Samba	Comoros	2x	60	60	–	3	1	0
unreduced	Chicame	Comoros	2x	60	60	–	3	1	0
gamete donor (2n gamete)									
Normal haploid	Sa	Thailand	2x	59	45	10	2	1	1
gamete donor	Khaï Naï On	Thailand	2x	59	46	10	2	1	1
(best matching	Pisang Rojo Uter	Indonesia	2x	54	48	9	1	3	1
candidates)	Pisang Bangkahulu	Indonesia	2x	59	45	9	1	2	0

[a] *M. acuminata nuclear RFLP genetic pole 1 assembles M. a. banksii and M. errans sub-species, pole 2 M. a. zebrina and M. a. microcarpa, pole 3 M. a. burmannica, M. a. burmannicoïdes and M. a. siamea, pole 4 M. a. malaccensis (Carreel 1994; Carreel et al. 1994). Specific bands are from one pole of wild diploid Musa acuminata germplasm that are not present in any of the other three poles.*

been confirmed by molecular analysis of cytoplasmic and nuclear genomes, and other relationships have been brought to the fore.

The emergence of triploids in *Musa* may be explained by the hybridisation between cultivars producing non-reduced gametes (Simmonds and Shepherd 1955) and diploids producing normal haploid gametes. For example, to trace the diploid ancestors of Cavendish and Gros Michel sub-groups, the nuclear RFLP patterns of 178 diploid clones representing the worldwide variability of the species were compared with that of the triploid varieties. This analysis led to the identification of mainly three AA clones (namely 'Akondro Mainty', 'Chicame' and 'Samba') as the common putative diploid ancestor of Cavendish and Gros Michel varieties that contributed to triploid formation through the production of 2*n* gametes. A sub-group of two Thai AA clones ('Sa' and 'Khai Nai On' suspected to be mutants of each other) was also identified as putative donor ancestor of the haploid gamete that may have brought the complementary alleles (Table 1.4; Raboin et al. 2005). This method can be applied to any mono- or inter-specific triploid clones.

Over 300 accessions, wild and cultivated clones, diploid or triploid, were studied with the same markers for its cytoplasmic and nuclear genome (Carreel et al. 1994, 2002). As for the Gros Michel and Cavendish sub-groups, it revealed relatedness between diploid and triploid accessions and highlighted putative ancestors of triploids. It allowed breeders to target the diploid progenitors that are more closely related to the triploids, which needs improvement.

1.4 Genetic Resources Utilization

For banana cultivation, a distinction can be made between production for export and for domestic markets, which are very important in areas such as India, Brazil and Africa where a subsistence food-crop system prevails.

Cultivation of bananas for export has passed through several stages in the last 100 years (Maillard 1986). It really began at the end of the last century, from 1870 in Jamaica where Baker organised the first exports of Gros Michel bananas to the North American markets and, in 1880, from Costa Rica where Keith set up a similar commodity chain. Two years later, Fyffe began to supply the English market with another variety, 'Dwarf Cavendish' from the Cavendish sub-group, which had flourished in the Canary Islands since the beginning of the fifteenth century. Fruits were first refrigerated for transport in 1903.

Techniques for commercial cultivation and large-scale exports were developed during this early period. Gros Michel, which is characterised by the natural robustness of its fruit, permitted shipment of entire packed bunches. Because of its tall height, only low-density plantations were possible – 800 plants per h – and treatment of plants against leaf diseases (carried out by spraying underneath the foliage) was difficult. This variety was perfectly amenable to the low-intensity agricultural practices of the time and areas cropped with banana continued to increase in Central America. Concomitantly, productivity decreased progressively in plantations due to plant wilt as the variety proved susceptible to a soil fungus, *Fusarium oxysporum*