Section 2.
Bananas and plantains (*Musa* spp.)

1. Taxonomy and genomic groups

1.1. Background

Edible bananas and plantains belong primarily to *Musa* section *Musa* (traditionally *Eumusa*). Within this section, the originally Asian species *Musa acuminata* and *Musa balbisiana* have provided the sources for domestication and development of the great majority of edible fruit. Dessert and cooking bananas and plantains are major foods worldwide, cultivated in over 130 countries throughout tropical regions and in some subtropical regions, in Asia, Africa, Latin America and the Caribbean, and the Pacific. Global production is difficult to determine because the plants are so often grown locally in small plots (*e.g.* household gardens) and consumed locally. The reported area cultivated worldwide in 2006 was 4.2 million hectares of bananas and 5.4 Mha of plantains, with a world production of 70.8 millon metric tonnes of bananas and 34.0 Mmt of plantains (FAO, 2008). The international trade, which involves just a few varieties of fruit, accounts for 15% of production. In addition to the edible species, *Musa textilis* (abacá, Manila hemp) is important for fibre production, and there are several ornamental species (Häkkinen, 2007).

The English word plantain apparently was derived from the Spanish plátano (Simmonds, 1966/1973; Smole, 2002), a name that is used throughout the Spanish-speaking world although its scope changes regionally (and the word's origin is unknown). (Plantain is also employed for the genus *Plantago*, unrelated plants in the Plantaginaceae.) In much of Central America and South America the word plátano is reserved for the starchy fruit and banana is used as in English for the sweet fruit, whereas plátano is used for both fruit types in Mexico and Spain — including the Canary Islands, to which the plants were brought by early Portuguese explorers and from which they were carried to the New World (Ferrão, 1992; Galán Saúco, 1992). The word banana, which probably originated in West Africa and was put into wider use by the Portuguese, also has narrow to broad usages, which frequently can include all the edible *Musa*, or routinely all species of the genus *Musa*. Thus one can speak of a plantain banana and a dessert banana (*e.g.* Tezenas du Montcel, 1985/1987) to maintain the typical distinction between a starchy fruit and a sweet fruit.

In their centres of domestication in Southeast Asia and South Asia there is as well a broad crop concept, with single vernacular names that do not differentiate between dessert and cooking bananas (including plantains): kalpatharu in India, kera in Nepal, chiao in China, chuối in Vietnam, kluai in Thailand, pisang in Malaysia and Indonesia and saging in the Philippines. The numerous cultivated varieties in these regions are typically distinguished by adjectives (*cf.* Table 1) (*e.g.* Valmayor *et al.*, 2000a, 2000b; Uma and Sathiamoorthy, 2002). In Africa, where *Musa* was introduced several thousand years ago (Mbida *et al.*, 2001), the vernacular names also reflect the considerable diversity of cultivated varieties and their uses, and plantain has varied meanings (Swennen and Vuylsteke, 1987; Swennen, 1990a).

Plantains and bananas when distinguised for the respectively starchy and sweet fruits, correspond roughly to two supposed species (but actually hybrids) described by Linnaeus in 1753 and 1759, to which he gave the respective names *Musa paradisiaca* and *Musa sapientum*. *Musa paradisiaca* referred to cultivated plants (similar to the modern 'French Plantain') with bracts and male flowers usually persistent, and horn-shaped fruits that are rather starchy and cooked to become palatable (*cf.* Linnaeus, 1736/1967, 2007). *Musa sapientum* referred to plants (similar to one of the popular dessert bananas of the tropics — 'Silk') with dehiscent bracts and male flowers, and slightly acidic sweet fruits eaten fresh. The distinction was adopted widely, referring to plantain types as *M. paradisiaca* and dessert types as *M. sapientum*; this "species" nomenclature is now outdated, but is still found in use occasionally. Although recognition of the two main types worked fairly well with the commonly cultivated plants from tropical America and West Africa that were then becoming familiar to Europeans, the plants being grown in Southeast Asia (as well as eastern Africa) were much more diverse — for example with dual-purpose plants having fruits consumed either fresh or cooked, and plants with dehiscent bracts and male flowers but starchy fruits used for cooking (Karamura, 1999; Valmayor *et al*., 2000a, 2000b).

Nomenclaturally, as a generality for a limited purpose, the name *Musa ×paradisiaca* L. can be correctly used just to indicate any bispecific hybrid of *M. acuminata* and *M. balbisiana* (*M. ×sapientum* L. is simply a synonym) — as both of the plants Linnaeus described are now considered to be AAB triploids (Figure 1) (Argent, 1984; Karamura, 1999). However, for exact work, a more discriminative advanced classificatory system is required, and the genomic groups of the hybrids and species need to be given (*e.g.* Table 1) (Stover and Simmonds, 1987; Valmayor *et al*., 2000b; Pillay *et al*., 2004).

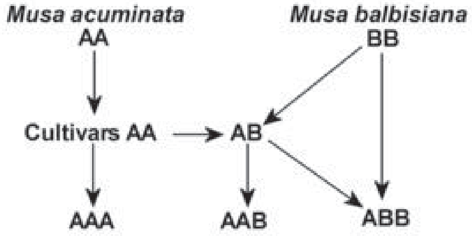
1.2. Taxonomic and genomic classifications

Bananas and plantains are in the genus *Musa* L. of the small family Musaceae (which also includes the genera *Ensete* and *Musella*), in the monocot order Zingiberales (formerly Scitamineae) (Kress *et al*., 2001; Kress and Specht, 2005, 2006). *Musa* has over 60 known wild species (see Appendices 1 & 2), with known diploid (2*n*) chromosome numbers of 22, 20, or rarely 18 or 14 (Simmonds, 1962; Shepherd, 1999). The diploid chromosome number together with phenotypic characteristics of the inflorescence and seeds have been the basis for conventional division of the genus into four, or sometimes five, sections (Appendices 1 & 2): section *Musa* (nomenclaturally correct but often traditionally still called *Eumusa*), *Rhodochlamys*, *Callimusa* and *Australimusa*, and sometimes also *Ingentimusa* (Simmonds, 1962; Stover and Simmonds, 1987; Simmonds and Weatherup, 1990b; Häkkinen, 2004b; De Langhe, 2009). However, researchers are finding some sections ill-defined, and that fewer sections may be more accurate (Jarret and Gawel, 1995; Shepherd, 1999; De Langhe, 2000b; Wong *et al*., 2002, 2003; Nwakanma *et al*., 2003; Bartoš *et al*., 2005; *cf*. Häkkinen *et al*., 2007c; De Langhe *et al*., 2009).

Musa section *Musa* as commonly circumscribed includes over a dozen wild species. Among these are *Musa acuminata* Colla and *Musa balbisiana* Colla, which have provided the great majority of edible bananas and plantains through selection and crossing both intraspecifically (within and between *M. acuminata* subspecies and cultigens), and interspecifically (between these two species) (Figure 1).

Cheesman (1947, 1948a, 1948b) pioneered the modern scientific classification of *Musa* (Simmonds, 1966/1973). Most edible bananas (in the broad sense) derive either from one diploid species, or from its diploid or triploid (or rarely tetraploid) hybrids with one other diploid species. The *Musa acuminata* haploid genome is designated with the letter A, the *M. balbisiana* genome with B. The dessert or sweet bananas often (but not always) are triploids and diploids of *M. acuminata*, and the plantains and other starchy cooking bananas generally (but not always) are triploids derived from hybridisations between *M. acuminata* and *M. balbisiana* (see Figure 1).

Figure 1. Crossing relationships of most cultivated edible *Musa*



A few edible cultigens of interest locally are derived from section *Australimusa* (TT) plants crossed with *Musa acuminata* (resulting in AT or AAT genomes) or also with *M. balbisiana* (resulting in ABBT), and in addition there are a few diploids (AS) from crosses of *M. acuminata* with the section *Musa* species *M. schizocarpa* (SS) (Table 1). Furthermore, the Fe'i bananas, a completely different edible group of cultigens, were domesticated separately from within *Australimusa*; they have not been characterised further genomically (Table 1). *Musa lolodensis* and/or *M. maclayi* may have provided the wild source species for this domestication (Sharrock, 2001).

1.3. Centres of origin of wild Musa species

The genus *Musa*, which is over 50 million years old (Kress and Specht, 2006), has diversified throughout much of the greater Southeast Asian region (*cf.* WWF and IUCN, 1995). *Musa acuminata* and *Musa balbisiana* diverged about 4.6 million years ago (Lescot *et al.*, 2008). Appendices 1 & 2 provide a provisional classification of the wild species of the genus placed in the five sections as conventionally used (*cf.* Daniells *et al.*, 2001; Pollefeys *et al.*, 2004; Häkkinen and Väre, 2008c), and as well their known natural wild distributions. However, the taxonomy of *Musa* is far from settled at the sectional, species, and infraspecific levels, although it has been receiving considerable attention in recent years. The research and explorations are resulting in discovery and description of many distinctive new species as well as many botanical varieties, and in reclassifications of taxa. However some taxa remain little known. The natural geographical range of some taxa is obscure because of limited exploration, and in some cases the difficulty in distinguishing between natural populations and naturalised or adventive (*i.e.* free-living but non-native) plants (*e.g.* De Langhe, 2009). The nomenclature of some taxa is also unsettled (*cf.* Häkkinen and Väre, 2008c; Väre and Häkkinen, 2009a, 2009b). Therefore, Appendices 1 & 2 are a comprehensive sketch of the work actively in progress, but consequently incomplete and not definitive.

The apparently natural range of genuinely wild *Musa acuminata* is the most extensive in the genus, from northeastern India across continental Southeast Asia (including southern China) and the Philippines, and through the Malay Peninsula and Malay Archipelago to northeastern Australia. This species also has the greatest taxonomic diversity. Rigorous taxonomic study of this polymorphic species throughout its range in the wild is needed to evaluate the evolutionary significance of the many named wild subspecies and botanical varieties, some of which are little known. Most of its many subspecies and/or botanical varieties (Appendix 1) are native only west of Wallace's line (between Borneo and Sulawesi), which demarcates the biogeographic discontinuity between Asia and Australasia (Ploetz and Pegg, 1997). In the past 2 million years the region's climate and sea level have undergone considerable fluctuation (Woodruff, 2003; Bird *et al.*, 2005). The climate was drier and more seasonal and the sea 100-120 m lower during glacial maxima 250,000 years ago and again roughly 20,000 years ago (Voris, 2000; Woodruff, 2003). Consequently, a single continental landmass (called Sundaland) then included Indochina, Thailand and the Malay Peninsula integrally with Sumatra, Java and Borneo (and associated smaller islands of the Sunda shelf). The Philippines Archipelago was then largely consolidated. New Guinea and Australia were then part of a separate single landmass, Sahul (which included the nowsubmerged Sahul shelf). The many subspecies and/or botanical varieties of *Musa acuminata* occurring in various areas within this large and diverse region are presented geographically in Appendix 1 to clarify their natural patterns of distribution.

The natural range of *Musa balbisiana* extends from India including the Andaman Archipelago (Sarma *et al*., 1995; Uma and Sathiamoorthy, 2002; Uma *et al*., 2005; Uma and Buddenhagen, 2006; Fuller and Madella, 2009) across northern Myanmar (Burma), Thailand (Swangpol *et al*., 2007; *cf*. De Langhe *et al*., 2000) and Indochina to southern China (Ge *et al*., 2005; Wang *et al*., 2007) and the Philippines (Sotto and Rabara, 2000; Valmayor *et al*., 2002). Farther southward, it may be naturally rare or instead only be introduced and naturalised on the southern Malay Peninsula and in the Malay Archipelago, as well as on New Guinea and New Britain (*cf*. Simmonds, 1962; Argent, 1976; Sharrock, 1990; De Langhe and de Maret, 1999; Häkkinen and Väre, 2008c; De Langhe, 2009). Essentially, *M. balbisiana* may be among the species that originated in the Indochina biogeographic province, which transitions in the mid-portion of the Malay Peninsula to the Sundaland biogeographic province. These two regions are biogeographically distinct (both in floras and faunas) possibly because seaways separated the northern and southern portions of the present-day peninsula (in the Isthmus of Kra area) with the fluctuations in oceanic height at various times in the past (Woodruff, 2003).

2. Domestications, crop difusion, cultigen classification

2.1. Domestications and diversification

There is evidence of utilisation of bananas in the highlands of New Guinea 10,000 years ago and cultivation by 7,000 years ago (Denham *et al*., 2003, 2004; Denham, 2005). Some wild bananas in Southeast Asia were no doubt used for non-food purposes such as shelter, fibre and dyes, and their starchy corms may initially have been the main focus for human food as the wild seedy fruits are not very palatable (De Langhe, 1996; Sharrock, 1997; Kennedy, 2009). Edibility of the fruits of diploid *Musa acuminata* likely developed through selection. The increasing interest in them was probably linked to the occurrence of parthenocarpy (asexual fruit development) and seed decline in the primitive types of *M. acuminata* consequent to their vegetative propagation. Crossing of the seeded edible diploids (AA) — over time involving several of the many subspecies of *M. acuminata* in diverse regions (Appendix 1) — resulted in the formation of generally sterile hybrid progeny with the genome AAA, also propagated vegetatively. Diverse hybridisations with *M. balbisiana* resulted in mostly sterile hybrid progeny mainly with the genomes AB (dessert bananas), AAB (plantains) and ABB (cooking bananas) (Figure 1) (De Langhe and de Maret, 1999; Kagy and Carreel, 2004). Rarely other combinations arose such as bispecific tetraploid AABB cultigens, and quite infrequently a few additional species were involved (subsection 1.2, and Table 1).

The spectrum of starchy and/or sweet fruits found entirely within some of these main genomic groups shows that the A genome itself is quite diverse — several subspecies of *M. acuminata* (Appendix 1) were involved in varied ways (inter-subspecific hybridisations) in the emergence of varying crop lineages (Horry and Jay, 1990; Lebot, 1999; Carreel *et al*., 2002; Kagy and Carreel, 2004; Swangpol *et al*., 2007; Boonruangrod *et al*., 2008, 2009; Perrier *et al*., 2009). The Australasian (Sahul) *Musa acuminata* ssp. *banksii* appears to be the primary source of most of the domesticated plants, which may have arisen first in New Guinea (Lebot, 1999; Denham *et al*., 2003, 2004; Perrier *et al*., 2009). Some bananas and plantains apparently also variously involve the more western (Sundaland) *M. acuminata* ssp. *errans* (a Philippines endemic), *M. acuminata* ssp. *malaccensis* (ranging from Java to Thailand) or *M. acuminata* ssp. *zebrina* (a Java endemic) (Appendix 1) (*cf*. Donohue and Denham, 2009).

Traditional domesticated varieties of diploid and triploid dessert and cooking bananas are still abundant throughout Southeast Asia (Valmayor *et al*., 2000a, 2000b), with their primary areas of diversity in Malaysia and New Guinea. Somaclonal variation, significant because of their vegetative propagation, has increased the genetic diversity (Section VII). Most of the plantain (AAB) types apparently originated in the Philippines and India, the only Asian regions where there is still a great diversity of plantain cultigens (De Langhe, 1996; De Langhe and de Maret, 1999; *cf.* Ball *et al.*, 2006; De Langhe, 2009; Perrier *et al.*, 2009) — the wealth of plantain varieties is found in remote areas of Luzon (Philippines) (Valmayor *et al.*, 2002) and in some parts of South India (Uma and Sathiamoorthy, 2002). West Africa to Central Africa became a secondary centre of diversification, where more than 120 distinct plantain varieties developed (Swennen and Vuylsteke, 1987; Swennen, 1990a; De Langhe *et al.*, 1996; Blench, 2009).

A completely separate edible group, the Fe‘i bananas, was domesticated and developed from within the *Australimusa* section of the genus. *Musa lolodensis* and/or *M. maclayi* (Appendix 2) may have provided the source(s) for domestication in New Guinea (Jarret *et al.*, 1992; De Langhe and de Maret, 1999; Sharrock, 2001). The Fe‘i group is composed of cultigens characterised by the reddish sap of the plant, shiny bright green bracts, and carotenoid-rich orange-fleshed fruit (Englberger *et al.*, 2003) produced in erect bunches rather than the hanging bunches typical of eumusa types. These crop plants were grown throughout the Pacific region, and notably dominant on Tahiti (Sharrock, 2001; Kennedy, 2008; *e.g.* Englberger and Lorens, 2004).

2.2. Diffusion and migration of crops

Austronesian-speaking people (perhaps from Borneo) may have been the first humans to colonise Madagascar, between 200-500 AD. However much earlier Melanesians apparently reached the East African coast, and brought along several kinds of edible *Musa* for planting (Shigeta, 2002; Perrier *et al.*, 2009). There is suggestive evidence of contact between India and East Africa 4000 years ago, although the earliest definite historical traces of cultural contact date from 2000 years ago (Lejju *et al.*, 2006). Apparent *Musa* leaf phytoliths have recently been found in Uganda dating to 4100-4500 years ago (Lejju *et al.*, 2006; but *cf.* Neumann and Hildebrand, 2009). Based on botanical and ethnographic evidence, De Langhe *et al.* (1996) considered that plantains (AAB) probably reached Africa over 3000 years ago. Apparent *Musa* phytoliths found in Cameroon date to approximately 2500 years ago (Mbida *et al.*, 2001, 2004, 2005, 2006; Vansina, 2003; Vrydaghs *et al.*, 2003; *cf.* Neumann and Hildebrand, 2009). After plantains reached humid forest climates in lowland western Africa, the crop underwent intensive diversification (De Langhe and de Maret, 1999; Karamura, 1999; De Langhe *et al.*, 2005; Blench, 2009).

Edible *Musa* seem to have been distributed throughout Polynesia (remote Oceania) by approximately 200 AD (Kagy and Carreel, 2004; Kennedy, 2008). And between 1000 BC and 500 AD (during Sabean civilisation) possibly some edible *Musa* (ABB cooking bananas, non-plantain AABs) from India reached southwestern Arabia and nearby northeastern Africa through Arab and/or Persian traders, but there is no certain evidence (De Langhe, 2000a). There is inconclusive linguistic speculation on the Arabic words mauz and banana and their association with *Musa* plants (De Langhe, 2000a).

Edible *Musa* probably arrived to the Canary Islands from West Africa during the 15th century (Ferrão, 1992; Galán Saúco, 1992). They were introduced from these islands to the Americas by at least 1516 but likely earlier (the first recorded introduction was to “La Española” island in the Caribbean). *Musa* spread rapidly throughout the tropical regions of the New World (*cf.* Johannessen, 1970). Their considerable distribution soon after Columbus’ first voyage is well documented, leading to speculation on a presence even prior to 1492 (Moreira, 1999; Smole, 2002; *cf.* Perrier *et al.*, 2009). However the usual explanation is that the rapid foothold and spread ran parallel to the slave trade, for which banana and plantain were considered a staple food (Simmonds, 1966/1973). The relative durability of propagation material and the speed with which the plant produces fruit favour this hypothesis (Stover and Simmonds, 1987). By the early 1800s the cultivars ‘Dwarf Cavendish’ and ‘Gros Michel’ had been introduced to the New World from Southeast Asia.

The modern international trade began in the late 19th century, and with improving transportation and storage, banana increasingly became a major food item in temperate-zone markets of the Western World as well as the Far East. Select cultivars were introduced into the Canary Islands by the end of that century and increasingly exported to other European countries (mainly England and France), and are now grown commercially in Portugal, Spain and Turkey.

2.3. Classification of cultivated Musa

The vast majority of plantains, cooking bananas and dessert bananas are sterile seedless triploids (Figure 1) (INIBAP, 1995; Zeller, 2005), but some diploid or rarely tetraploid cultigens are grown, nearly all derived either from *Musa acuminata* or from hybridisation between this diverse species and *M. balbisiana*. Plantains and cooking bananas usually are bispecific triploid hybrids, AAB or ABB respectively, with the exception of the East African Highland bananas, which are starchy AAA triploids used in that region either for beer production or as a cooked vegetable (Karamura, 1999; Karamura and Pickersgill, 1999; Carreel *et al*., 2002).

The dessert bananas are more diverse genomically. The most important to commerce are those of the Cavendish subgroup, which supply 95% of the world export trade. They are AAA triploids, the best known being the cultivars ‘Grande Naine’, ‘Williams’, ‘Valery, ‘Robusta’, Poyo’ and ‘Dwarf Cavendish’; among the other dessert AAA triploids is ‘Gros Michel’, at one time the world’s leading commercial cultivar but now nearly absent due to its high susceptibility to Fusarium wilt disease. Other dessert bananas of smaller economic importance include AA diploids, such as the fruit called ‘Pisang Mas’ in Southeast Asia and ‘Bocadillo’ or ‘Orito’ in parts of Latin America (which is well known due to its excellent taste, and prised by European gourmet fruit retailers); some AB diploids; AAB triploids like ‘Silk’ (*e.g*. ‘Manzano’) and ‘Pome’; and the modern AAAB tetraploid ‘Goldfinger’.

There have been many efforts to inventory and classify the wealth of cultigens and cultivars of bananas and plantains in different *Musa* germplasm collections. Evaluation based on morphology had been the standard (Simmonds and Shepherd, 1955; Simmonds and Weatherup, 1990a; IPGRI-INIBAP and CIRAD, 1996; Ortiz, 1997a). Modern techniques to detect differences have employed isozyme polymorphism (Bhat *et al.*, 1992a, 1992b); and various DNA molecular markers, such as RAPD (Howell *et al.*, 1994; Bhat and Jarret, 1995; Bhat *et al.*, 1995; Damasco *et al.*, 1996); RFLP (Gawel *et al.*, 1992; Jarret *et al.*, 1992; Carreel *et al.*, 1993; Fauré *et al.*, 1993; Bhat *et al.*, 1994); AFLP (Ude *et al.*, 2002a, 2002b; Noyer *et al.*, 2005); and microsatellites (SSRs) (Lagoda *et al.*, 1996; Dussart, 2001; Creste *et al.*, 2004; Buhariwalla *et al*., 2005). Chloroplast DNAs of A and B cytoplasms have been differentiated (Umali and Nakamura, 2003; Boonruangrod *et al.*, 2008), and as well their mitochondrial DNAs (Boonruangrod *et al*., 2008), and the genomic distribution of nuclear ribosomal DNA has been studied in various species (Bartoš *et al*., 2005; Boonruangrod *et al*., 2009).

Table 1 provides a summary of some familiar or otherwise notable cultivated varieties (cultigens, landraces, cultivars) of edible *Musa* species and hybrids classified by cross and the level of ploidy (*cf.* Stover and Simmonds, 1987; Daniells *et al.*, 2001; Carreel *et al.*, 2002; Zeller, 2005). Molecular methods have provided a breakthrough, which is confirming the ploidy and genomic group of most accessions, but also resulting in reclassification of several varieties (*e.g.* Pillay *et al*., 2006).

Table 1. Some cultivated varieties of edible *Musa*

CROSSED SPECIES	GENOME	GROUP/ VARIETY/ CULTIVAR
Section *Musa* (*Eumusa*)		
M. acuminata (AA) × *M. acuminata* (AA)		
	AA	Sucrier: Pisang Mas / Bocadillo Pisang Lilin Pisang Jari Buaya Inarnibal
	AAA	Cavendish: Robusta, Valery Grande Naine (Grand Nain) Pisang Masak Hijau / Lacatan Gros Michel Ambon Putih Red Ibota Mutika/Lujugira (Highland bananas)
	AAAA	Pisang Ustrali Golden Beauty
M. acuminata (AA) × *M. balbisiana* (BB)		
	AB	Ney Poovan: Kisubi Kunnan Kamaramasenge
	AAB (ABA, BAA)	Mysore: Poovan Pisang Raja Silk: Silk Fig, Rasthali, Maçã Pome/Prata Pacovan, Pacha Naadan Nendra Padaththi French Plantain Nendran, Obino l’Ewai False Horn Plantain Agbagba Horn Plantain Three Hand Planty Pisang Nangka Pisang Kelat Laknao (Laknau) Iholena (Pacific plantains) P p ‘ulu / Mai‘a Maoli (Pacific plantains)
	ABB (BAB)	Bluggoe Ney Mannan Monthan Saba

CROSSED SPECIES	GENOME	GROUP/ VARIETY/ CULTIVAR
		Cardaba Kalapua Peyan Pelipita[1] Pisang Awak/Pisang Klutuk[2] Klue Teparod (Kluai Tiparot)[3]
	AAAB	Goldfinger
	AABB	Laknau Der
M. acuminata (AA) × *M. schizocarpa*		
	AS, SA	Ato Ungota Vunamami Kokor Wompa
Section *Australimusa* (TT)		
M. lolodensis, *M. maclayi*		
	Fe'i group[4]	Karat Kole Karat Pako Karat Pwehu Menei Rimina Utafan Utimwas Utin Iap Wain
Section *Musa* (*Eumusa*) (AA & BB) × Section *Australimusa* (TT)		
	AT (TA)	Umbubu
	AAT (TAA)	Karoina Mayalopa Sar
	ABBT	Yawa 2 Giant Kalapua

[1] 8 A chromosomes, 25 B chromosomes (D'Hont *et al*., 2000; Heslop-Harrison and Schwarzacher, 2007)

[2] Pisang Awak was reclassified as AABB by Pillay *et al.* (2006)

[3] Earlier considered to be ABBB (Horry *et al.*, 1998)

[4] Genome not characterised further

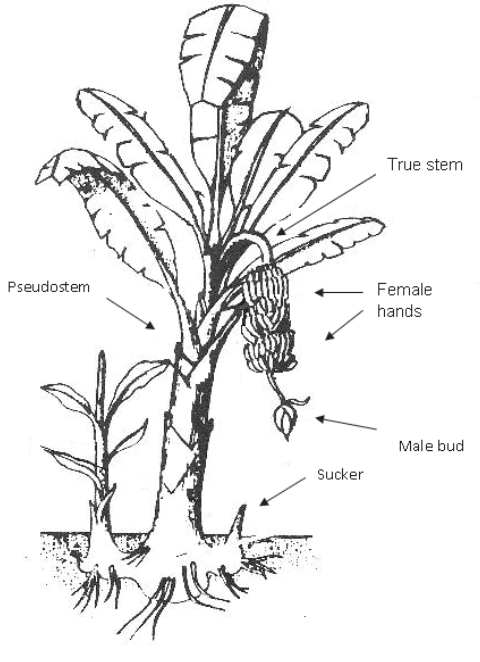
3. Plant cycle and agronomic systems

Bananas and plantains are cultivated in tropical and subtropical regions worldwide within latitudes 30º North and 30º South of the equator and in some additional subtropical regions. In suitable climates, fruits are harvested year-round (Tixier *et al*., 2004; Zeller, 2005).

3.1. Description

Bananas and plantains are large herbaceous plants which can confer the aspect of a tree (Figure 2). One wild species (*Musa ingens*) can reach 16 m tall, although most commercial types grow to between 2 m and 5 m. The main trunk is a pseudostem formed by the concentric assembly of the leaf sheaths (modified petioles), which is crowned by a rosette of very large oblong to elliptic leaves. The leaf blade (up to 2 m^2) normally is transversely split (by wind) between parallel veins, which assists cooling and photosynthesis (Karamura and Karamura, 1995). Leaves are produced successively until the single inflorescence is cast (Allen *et al*., 1988), and are present in variable number (10 to 20 under healthy conditions) depending on the variety, the climate and cultivation practices. Each leaf takes 7-14 days to emerge (Turner *et al*., 2007).

Figure 2. Schematic representation of a cultivated banana plant



The true stem is a subterranean organ (corm) which extends upwards at the core of the pseudostem until culminating in the inflorescence which emerges from the top. The meristem of the true stem produces all other parts of the plant (Swennen and Rosales, 1994). The many main roots emerging from the rootstock are rather straight, adventitious cords (2-10 mm in diameter) that extend up to 2-3 (-5) m outwards, from which (with a density of 8 to 10 per cm of cord root) branch lateral roots (0.3-4 mm in diam) that extend up to 1 m, and from which tertiary rootlets extend for several cm. Under usual commercial growing conditions, most of the root system is within the first 60-100 cm radius from the plant and reaches to 20-40 cm in depth (though roots have been found to 150-180 cm deep in exceptional soils) (Blomme *et al*., 2000; Belalcázar *et al*., 2005; Draye *et al*., 2005; Turner *et al*., 2007).

There are two conspicuous main phases in the development of the banana plant: a vegetative phase characterised by the appearance of leaves, and a reproductive phase during which the inflorescence emerges (Stover and Simmonds, 1987; Swennen and Rosales, 1994; Karamura and Karamura, 1995; Turner *et al*., 2007). This is a simplification of the actual developmental process, as the apical meristem has already differentiated from its vegetative phase into a reproductive meristem before the appearance of the last new leaves. At the transition from the vegetative to the floral stage the plant's growing point shifts mitotic activity, with the whole dome contributing to the aerial stem and inflorescence development. Six months or more after planting, the inflorescence tip first appears at the top of a pseudostem, and the inflorescence continues to elongate and mature, in crop plants typically turning downward. Floral clusterings appear, enlarge, and differentiate into flowers. This elongating aerial stem is totally dependent for its mechanical support upon the surrounding mass of leaf sheaths (the pseudostem).

The large inflorescence is composed of flowering clusters which occur helicoidally along its axis (reproducing the phyllotaxy pattern of the leaf system) and are each covered by a large bract typically ranging from yellow over reddish to purplish. Each nodal cluster has 12-20 flowers, which are aligned in two tightly adjacent rows. The flowers in a cluster usually are either functionally female or male (see Section V), but sometimes are hermaphroditic or neuter (Kwa and Tomekpé, 2000). The first (*i.e.* basal) 3-9 (to 18) clusters, or hands, are female and give rise to the edible fruits — often known as fingers. Subsequent (*i.e.* more distal) clusters are of an intermediate or usually a male character and do not produce edible fruit (in most cultivars, rudimentary fruitlets fall before the edible fingers mature). The distal portion of the inflorescence may continue to elongate and produce many clusters of male flowers from its large terminal bud (which however is absent in some varieties). The group of commonly 5-15 fruiting hands which constitutes the basal portion of the inflorescence is the harvestable unit, called a bunch.

Commercial fruits typically develop by vegetative parthenocarpy (*i.e.* with neither fertilisation nor pollination required), and are completely seedless and sterile. The maturing fruits typically bend upwards in some cultivars, whereas in other cultivars the fruits splay outwards from the inflorescence stalk. Normal commercial bunch weight is 15-30 kg although bunches over 45 kg are not unusual when plants are properly cultivated (and exceptional cases over 125 kg have been recorded). A medium-sized dessert banana finger weighs around 160 g (whereas most wild *Musa* fruits are about 30 g to rarely 80 g).

Up to 2 years are required in a fruiting cycle. Depending on climate, cultivation conditions and the cultivar, vegetative growth lasts 6 to 12 months, and the period between emergence of the inflorescence and harvesting of the bunch can be 2.5 to 10 months (Stover and Simmonds, 1987; *cf.* Turner *et al*., 2007). The time from planting to shooting (inflorescence emergence) generally varies from about 180 to 250 days. Shoot to harvest time in most tropical areas below 500 m elevation varies from about 75 to 125 days, and from about 110 to 250 days in most subtropical areas.

Although the principal plant dies after producing fruit, the whole plant is perennial in as much as suckers successively replace the senescent aerial part without need for replanting. Several suckers emerge consecutively from buds located at leaf axils on the rhizomatous rootstock (Kurien *et al*., 2002). Under commercial cultivation most suckers are regularly eliminated — leaving to replace the mother plant either the firstly emitted vigorous sucker, or the sucker capable of producing a bunch when better prices can be obtained. Sucker growth is in competition with bunch development, so rigorous sucker pruning is needed (Dens *et al*., 2008). During the dependent or juvenile phase, the sucker develops short narrow (lanceolate) leaves that increase in size sequentially until the appearance of the well-developed adult leaves. The subsequent independent phase (easily distinguished in the Cavendish subgroup of cultivars) is signaled by the first adult leaf, which has an orthogonal angle at the base of the blade's left half (as viewed from beneath) (Galán Saúco, 1992).

3.2. Abiotic environment

3.2.1. Edaphic adaptation

Bananas can be cultivated in soils of varied textures, from very sandy to very clayey, although the former soil extreme may require more frequent watering or a mulching system to maintain water content, and the latter soil extreme causes problems of aeration. Good soil drainage is necessary to cultivate the crop efficiently (Simmonds, 1966/1973). Soil depth should be at least 80 cm and preferably reach 120 cm, but can be as shallow as 40-60 cm for single-cycle high-density plantations from *in vitro* plant material (Stover and Simmonds, 1987).

A high content of organic material (> 2.5%) and pH range between 6 and 7 are optimal, but values between 4.2 and 8.1 are found in established plantations (Soto, 1985). A good soil must have large amounts of potassium (K) and magnesium (Mg). Generally 200-350 mg of potassium per kg of soil is considered enough (unless the soil has large quantities of calcium). The K/Mg ratio must be around 0.25 in sandy soils and close to 0.50 in heavier soils. Soils with a high content of soluble potassium render banana plants more tolerant to salts. Under these conditions the development of the plant is not affected in soils with conductivity up to 7 dS/m (Stover and Simmonds, 1987). Average annual fertiliser applications to the commercial crop are often in the range of 200-450 kg/ha nitrogen (N_2); 400-1200 kg/ha potassium (K_2O); and 40-96 kg/ha phosphorus (P_2O_5) (Lahav and Turner, 1983; Soto, 1985). Banana plants are accumulators of silicon (Henriet *et al.*, 2006).

3.2.2. Light

Light intensity under normal plantation densities and crop conditions is not a serious concern. But a lack of light, for example from excessive plantation density, can cause a prolonged plant cycle, and mild sun exposure together with excess water reduce growth and development. Photosynthetic activity increases rapidly at light intensities between 2,000 and 10,000 lux, and increases further between 10,000 and 30,000 lux. Except under extreme conditions, day-length variations do not have a substantial influence (Champion, 1963/1968; *cf.* Turner *et al.*, 2007). Exposure to high light intensities combined with high temperatures causes scorching in the plant.

3.2.3. Temperature

The rate of plant growth and time to fruit maturity are chiefly determined by temperature. Optimum temperature for foliar growth is 26-28ºC (Ganry, 1980), and for fruit development is slightly higher at 29-30ºC. Temperatures of 37ºC or more cause leaf scorch, and growth stops at 38-40ºC. As for low temperatures, foliar emergence for the tallest Cavendish clones stops below 16ºC and all growth stops at about 10ºC (Aubert, 1971; Stover and Simmonds, 1987). Flower development is strongly affected by temperature (Turner *et al.*, 2007). If low temperatures (10-15ºC) occur prior to flowering, the emergence of the inflorescence must overcome the pressure imposed by leaves that remain blocked. Consequently, the true stem can be twisted and the pseudostem broken (Stover and Simmonds, 1987). When emergence of the inflorescence is difficult, it is necessary to help by making a “caesarean” cut. Even in cases free of blockage, floral differentiation during subtropical winter may result in the generation of bunch malformations (typically in May in the northern hemisphere, November in the southern hemisphere). Low temperatures — even close to the normal of 12ºC for fruit transport — cause fruit damage, such as uneven softening of the pulp during ripening and shortening of shelf life. Below 9ºC, latex coagulation occurs in the pericarp and the fruit’s ripening capacity is lost (Stover and Simmonds, 1987).

3.2.4. Water requirements, humidity and wind

The banana plant’s hydric state is generally considered the second main factor responsible for growth and development and fruit production, being particularly important above 20ºC. The plant has high water requirements due to its fast development and large foliar area, but it has some tolerance to drought apparently by closing stomata and maintaining strong root pressure (Turner *et al*., 2007). A plant's typical daily water transpiration has been estimated to vary between 5.6 mm under direct sun exposure and 1.9 mm when totally cloudy (Champion, 1963/1968; Turner *et al*., 2007). The amount needed increases as the temperature rises, and above 30ºC the water consumption can double. Between 60% and 80% relative humidity is ideal (*cf*. Lu *et al*., 2002).

In regions of limited rainfall intensive modern plantations are equipped with drip irrigation systems, but sprinkling or flood irrigation systems are still frequent in many plantations. Bananas can sometimes tolerate up to 48 hrs of flooding with flowing water (*e.g.* after a storm), but stagnant water with full sunshine kills adult plants.

In general, cultivars better adapted to subtropical conditions also better tolerate wind speeds up to 40 km/h. But at the higher speeds severe crop damages occur, and wind above 55 km/h can cause total destruction of the plant.

3.3. Cultivation practices

The main commercially important *Musa* cultivars are grown alone, commonly in open-air plantations in the tropics. Cultivar selection, planting design and culture practices play important roles in the plant's development. The most frequent designs in commercial plantations have 2000 to 2400 plants per hectare, with one plant per planting hole, aligned in rows that are separated by wide aisles. Particular cultivars can be difficult to manage depending on the planting distances. Cutting off several leaves after flowering is often recommended to favour light penetration for plant development. Modern planting designs use drip irrigation and mulching, which facilitates mechanical and chemical weed control. Lists of weeds commonly associated with banana cultivation, and herbicides commonly employed, are provided by Belalcázar *et al*. (1991).

In subtropical regions where climatic requirements may not be sufficiently fulfilled, greenhouse cultivation offers the possibility of increasing fruit quality and yields. Spain (Canary Islands) and Morocco are the major countries producing banana under greenhouse, both with about 3000 ha. Commercial greenhouse cultivation is also carried out in Greece (Crete) (400 ha) (Galán Saúco, 1992), South Africa (3 ha) (Eckstein *et al.*, 1998), and several other countries including Portugal, Tunisia, Turkey, Korea and Argentina. Israel has been interested in increasing greenhouse plantation (beyond about 50 ha) mainly due to the reduction in water consumption.

In many parts of the humid tropics *Musa* is grown traditionally with other crops (Swennen, 1990b; Rodrigo *et al*., 1997; Norgrove and Hauser, 2002; Achard *et al*., 2004). As the *Musa* plants require a large interrow, other crops may be successfully grown in between. For example *Dioscorea* (yams), *Alocasia macrorrhizos* (giant taro) and *Piper methysticum* (kava) are intercropped in Micronesia, and *Colocasia esculenta* (taro, cocoyam) in Papua New Guinea. In southern Nigeria intercropping with *Manihot esculenta* (cassava) was found to reduce yield but also the incidence of black Sigatoka disease. In southern Cameroon the fields are prepared by clearing secondary forest manually and intercropping plantain with *M. esculenta*, *Cucumeropsis mannii* (white-seed melon, egusi-itoo) and *Xanthosoma sagittifolium* (yautia, tannia). *Musa* is also grown as an intercrop in the early stage of establishing plantations of coconut (*Cocos nucifera*), betelnut (*Areca catechu*), coffee (*Coffea* spp.), black pepper (*Piper nigrum*), cocoa (*Theobroma cacao*) and rubber (*Hevea brasiliensis*). *Musa* is sometimes grown in combination with timber production, for example under *Casuarina* trees in the Papua New Guinea highlands and *Ficus natalensis* (Natal fig) in southwestern Uganda.

3.3.1. Propagation

Most edible bananas and plantains are vegetatively parthenocarpic, producing fruits without needing any stimulus from pollination or seed development. Because the fruits of most cultivars are either always or normally seedless, agricultural propagation is principally asexual by means of suckers and other vegetative multiplication techniques, including micropropagation. Plants are generally propagated from traditional planting material (which may be obtained from commercial plantations), either emerged suckers (of different sizes) or sucker corms originating from axillary buds, or from the lateral buds of corms or rhizomes of decapitated grandmother plants (which may have or lack suckers). Modern plantations are being established with plants propagated through *in vitro* culture (Section VII), which provides a large quantity of uniform, disease-free (including virus-free) plants. This approach however can generate somaclonal variants that result in off-type plants if not properly managed.

3.3.2. Sucker selection and desuckering

As a general rule, the more advanced the development of the mother plant, the taller must be the sucker selected to replace it in the plant's following cycle. In the tropics it is generally recommended to preserve the axial sucker, which is normally the most vigorous and was first emerging from the mother plant (Champion, 1963/1968; Simmonds, 1966/1973). In South Africa and Israel deep-emerging suckers are preferable (particularly the axial sucker). However, given these subtropical climates, the period of flower differentiation is also matched with the warmest months in summer. This is done to achieve better yields and direct the harvest period to wintertime when prices are traditionally higher. In the Canary Islands the usual desuckering practice is elimination of new shoots emerging during wintertime (before April). The sucker that will replace the mother plant is chosen in June or July from among those that emerged in the springtime.

Desuckering by mechanical or chemical means eliminates undesired suckers and so enhances the plant's yield (*cf.* Kurien *et al.*, 2006; Dens *et al.,* 2008); only those suckers that will support continuity of the plantation are kept. Desuckering can be accomplished by repeatedly cutting off the emerging plant at ground level, the mechanical removal of the apical meristem, or application of 2-5 ml of kerosene; 2.5 ml per plant can be injected directly through the leaf bases of intact, 10-40 cm high suckers. For plants started from *in vitro* culture, which have high sucker proliferation during their first cycle, desuckering must be done before new shoots are over 40 cm high to avoid competition and toppling of the mother plant.

3.3.3. Practices enhancing fruit development

The developing commercial fruit is protected by carrying out several operations to prevent the bunch from falling to the ground and appearance of skin blemishes. The first practice is deleafing — leaves that may be touching the newly developed hands are cut off, and collapsed and leaf-spot infected leaves are removed. Next are bagging, debudding, and dehanding. This operation consists of bagging the bunch, removal of the male-flowers bud (the distal portion of the inflorescence), and breaking off the false hand plus one or two of the smallest apical hands. Bunch-bagging is a common practice to reduce the time between flowering and harvest, and improve fruit yield and quality. The bags are cylindrical (open-ended), perforated, and made of transparent or blue polyethylene; the ends are left open but secured to avoid wind damage. Bags are normally placed after bunch deflowering and application of insecticide, about 3 weeks after bunch emergence.

3.4. Harvest and storage

Most of the fruit's pulp develops from the outer part of the trilocular ovary (Stover and Simmonds, 1987). Fruit is age-graded in order to prevent the occurrence of ripe fruits during storage and transport. Determination of the ripening stage is normally done by observation of the bunch-filling degree (which varies depending on the time after emergence of the inflorescence or flowering and the month of bunch formation), the size of the fruit and fruit angularity, its specific gravity, and pulp-to-skin ratio. Quality rules have establishd that the minimal finger thickness must reach 27 mm.

Bunch cut-off at harvest time must be done with extreme care. One worker partially cuts the pseudostem halfway up its length (not necessary for Dwarf Cavendish) while the other puts the bunch on his shoulders and holds it firmly until the first worker cuts the rachis across just above the first hand.

Banana is a highly perishable fruit, with post-harvest losses of 30-40% (Salunkhe and Desai, 1984). Methods for extending the shelf life of fruits include the harvesting of bunches a few days before they reach full maturity, storage at reduced temperatures (about 15ºC), storage in a modified atmosphere of enriched CO_2 with low O_2 (3-4%), packing in film bags to prevent weight loss, pre-treatment with fungicides, and skin coating (Waskar and Roy, 1996). For cultivars susceptible to high levels of CO_2 an alternative storage method is vacuum packing (Mary and Sathiamoorthy, 2003).

4. Diseases and pests

The most relevant interactions between cultivated bananas and plantains and other organisms are the effects of agricultural diseases and pests, and as well weeds. Bananas and plantains are affected by many diseases and pests, some of which are of profound importance for these major food crops. The main diseases have been summarised by Jones (2002a) and Ploetz *et al.* (2003), the main pests by Gold *et al.* (2002) and Jones (2002a). Some commonly serious or critical diseases and pests (Jones, 2002b) are discussed below (also note Table 2, in Section VI).

4.1. Fungi

Musa plants are known to provide substrate for over 200 species of fungi (a zygomycete, 60 ascomycetes, 23 basidiomycetes, and 120 mitosporic fungi) (Photita *et al.*, 2002).

Sigatoka leaf spot diseases of banana involve two related ascomycetous fungi: ***Mycosphaerella*** *fijiensis*, which causes black leaf streak disease, commonly known as **black Sigatoka**; and *M. musicola*, which causes Sigatoka disease, now usually known as **yellow Sigatoka** (Mourichon *et al.*, 1997; Marín *et al.*, 2003). Symptoms include respectively dark brown or pale yellow streaks on lower leaf surfaces and large areas of leaf destruction, which causes premature fruit ripening and reduces yields. Black Sigatoka is the more serious because younger leaves show symptoms and more damage is caused to photosynthetic tissue, and it affects many cultivars such as plantains and cooking bananas that have resistance to yellow Sigatoka (Mobambo *et al.*, 1993, 1996; Manzo-Sánchez *et al.*, 2005). **Eumusae leaf spot disease** (formerly Septoria leaf spot disease), caused by *M. eumusae*, has been recognised relatively recently, occurring in several countries across eastern Asia as well as Mauritius and Nigeria (Carlier *et al.*, 2000; Crous and Mourichon, 2002).

Black Sigatoka has been reported throughout the Pacific, Asia, Africa, Latin America and the Caribbean. Yield losses from 30-50% have been reported (Mobambo *et al.*, 1993). As much as 27% of production costs in tropical America can go to its control (Stover and Simmonds, 1987), and the disease can be responsible for 15-20% of exported fruit's retail price. Yellow Sigatoka is one of the classic global plant epidemics from the first half of the 20th century, and has now been reported in most banana-growing areas. Devastation of commercially grown bananas by the Sigatoka diseases and the danger to a major food staple led to creation in 1984 of the International Network for the Improvement of Banana and Plantain (INIBAP). Perhaps no other diseases or pests have so seriously jeopardised banana production throughout the world (Marín *et al.*, 2003).

In commercial plantations systemic fungicides are used to control black Sigatoka, but resistance to some fungicides has developed in strains of both *M. fijiensis* and *M. musicola*. Incorporating genetic resistance into the crops has become the long-term goal (see Section VI).

Fusarium wilt or Panama disease of banana is caused by several soil-inhabiting fungi called ***Fusarium*** *oxysporum* f. sp. *cubense* (Ploetz, 2006). The disease has been reported from all banana-growing regions except Melanesia, some South Pacific islands and some countries bordering the Mediterranean; it is regarded as one of the most destructive plant diseases of modern times (Moore *et al*., 1995; Ploetz, 2000, 2005a, 2005b). Some clones in the AAA Cavendish subgroup are susceptible, including 'Valery', 'Grande Naine' and 'Williams', as well as some clones in the AAB group (*e.g*. 'Silk', 'Pome') and the ABB Bluggoe subgroup. The decline of commercial plantations of 'Gros Michel' resulted in a shift in the mid-20th century to cultivars in the Cavendish subgroup as the main export banana types (Ploetz, 2000, 2005a, 2005b). However, in the early 1990s Cavendish plantations in Southeast Asia and northern Australia began to experience significant losses (Hwang and Ko, 2004).

External symptoms include yellowing of leaf margins which spreads from the oldest to youngest leaves, and lengthwise splitting of the lower portion of the outer leaf sheaths. The leaves gradually collapse and die (forming a skirt around the pseudostem), and new leaves are pale and small. Many infected suckers may be produced before the clump dies.

Several factors influence the development of this disease — the fungus strain and crop cultivar, drainage, environmental conditions and soil type. Four races of *Fusarium oxysporum* f. sp. *cubense* are typically recognised. Three races are pathogenic to particular sets of *Musa* cultivars. Race 1 caused the collapse of the 'Gros Michel' export trade. The now-emerging tropical race 4 affects cultivars that produce 80% of the world's bananas and plantains (Ploetz, 2005b, 2006). These pathogens also colonise alternative hosts, such as relatives of banana and several weed species. The fungi can survive in the soil for up to 30 years as chlamydospores, in infested plant debris, and in the roots of alternative hosts. Spread is most commonly by infected rhizomes or suckers and adherent soil. The disease can spread very rapidly if spores are carried in surface runoff water or contaminate an irrigation reservoir.

Soils in which microbial populations suppress the pathogens are found in Central America, the Canary Islands, South Africa and Australia. Chemical control, flood-fallowing, crop rotation and use of organic amendments have not been very effective. The best means of control is host resistance (*cf*. Javed *et al*., 2004). Useful AAB and ABB hybrids have been bred (Table 2), but no Cavendish replacement. Biotechnology, mutation breeding and somaclonal variation are being employed to produce resistant genotypes (Ploetz, 2005b).

4.2. Unknown agents

False Panama disorder (de Beer *et al*., 2001), which can easily be confused with Fusarium wilt, was first described by Deacon *et al.* (1985). Cavendish bananas in South Africa and the Canary Islands are affected, but other dessert bananas and plantains are affected in Panama, Colombia, Surinam and Grenada. The incidence is usually low, but as much as 60% (perhaps more) of a plantation can be impacted.

External symptoms include yellowing of leaves, necrosis, leaf death, and small bunches. The discoloured vascular strands are usually discontinuous. Examination of a rhizome that has been split open characteristically shows brown spots and white strands.

False Panama disorder seems not to appear in old plantations, nor to be transmitted from one plant to another. Although it has not been possible to isolate a pathogen from affected plants, it is accepted that a fungal pathogen is not the primary cause. Factors influencing the appearance of the disorder may include low temperatures, nematodes, drought, nutritional imbalances and waterlogging (Rabie, 1991; de Beer *et al.*, 2001). The incidence of the disorder can be kept down or prevented by reducing stress to newly planted material.

Another serious disorder that can be confused with Fusarium wilt has been called **matooke wilt**, although it is of unknown aetiology. At first thought to be limited to East African Highland bananas (in Uganda matooke refers to traditional bananas), it was later found in Uganda on more recently introduced types as well (Kangire and Rutherford, 2001). Leaves may appear healthy or be smaller with marginal necrosis. Pseudostems are thin, dry and weaker, and fruits small and less developed. Internally the pseudostem has conspicuous brown to purple vascular strands. Affected plants are found in areas where household or animal wastes have been discarded.

4.3. Bacteria

Moko disease is a vascular wilt of bananas and plantains caused by strains of phylotype II ("race 2") in the ***Ralstonia*** *solanacearum* (*Pseudomonas solanacearum*) complex (Eyres *et al.*, 2005; Fegan and Prior, 2006); it was first reported in the 1890s in Trinidad. In the Caribbean, Central America and South America this bacterial wilt has caused severe losses in smallholder plantations; it is nearly absent in the eastern hemisphere, but has been found in the Philippines. The Cavendish subgroup (AAA) and some ABB cultivars (*e.g.* 'Bluggoe') are susceptible, whereas 'Pelipita' (ABB) is highly resistant, and the Horn plantain (AAB) is seldom infected. **Bugtok disease**, widespread on cooking bananas (*e.g.* 'Saba', 'Cardaba') in the Philippines, is similar and apparently caused by the same bacterium complex (Soguilon *et al.*, 1995; Hayward, 2006).

Another bacterial vascular wilt, **banana blood disease**, is caused by strains of phylotype IV ("race 4") of the species complex (Eden-Green, 1994; Fegan and Prior, 2006). This disease was first reported in about 1914 from South Sulawesi in central Indonesia, causing the abandonment of dessert banana plantations being developed on a nearby island. Although its distribution was very limited, it has recently been spreading in Java and elsewhere in Indonesia and poses a serious threat.

Its symptoms are similar to those of Moko disease, and vary according to the growth stage of the plant and route of infection. They include a conspicuous transient yellowing, loss of turgor, desiccation and necrosis. The youngest leaves cease emerging and develop whitish and then necrotic panels in the lamina. Blackening and shrivelling of male flowers is frequently found in mature plants. Daughter suckers may show general wilting, but sometimes healthy suckers are produced. Internally, vascular bundles exhibit a reddish-brown discolouration, and the fruits are usually uniformly discoloured reddish-brown and rotten.

Infection occurs *via* inflorescences, and the disease is transmitted by insects or infected planting material; the pathogen can probably persist in soil or plant debris. Fruits from infected plants may be a source of infection, as affected bunches can appear normal. Sanitation measures include disinfection of cutting tools, field sanitation and selection of disease-free planting materials.

Banana Xanthomonas wilt (or banana bacterial wilt) is a devastating disease emerging in East Africa to which most cultivars appear vulnerable; it is caused by ***Xanthomonas*** *vasicola* pv. *musacearum* (Biruma *et al.*, 2007; Aritua *et al.*, 2008). Symptoms are somewhat cultivar-specific and determined by route and stage of infection. Foliar symptoms often resemble those of Fusarium wilt, but excretion of a yellowish bacterial ooze from cut tissues is characteristic of this new disease. Yield losses, which can reach 100%, vary with cultivar susceptibility, crop growth stage at infection and prevailing climatic conditions, with effects being worse during seasons of high rainfall. Disease transmission and sanitation measures appear similar to those given above for banana blood disease.

4.4. Viruses

Banana bunchy top disease, the most important widespread viral disease of banana, is caused by a babuvirus (Nanoviridae) transmitted by the banana aphid *Pentalonia nigronervosa* (Thomas *et al*., 1994; Ferreira *et al*., 1997; Su *et al*., 2003). The disease is native to Southeast Asia, and occurs in many countries of the eastern hemisphere (including Pacific islands); in Africa it has been found in Gabon, D.R. Congo (formerly Zaire) and Burundi. It has also been detected in the southern Caribbean on the island of Curaçao. The disease can cause devastating plantation losses, which have reached 100% in some districts of Pakistan (Pietersen and Thomas, 2003). Infected plants have a rosetted appearance with narrow, upright and progressively shorter leaves. Leaf edges roll upwards and show marginal yellowing. Dark green streaks are found on midrib and petiole, extending downward into the pseudostem. The symptoms only appear on the leaves forming after infection — most diagnostic are short dark green dots and dashes along the minor leaf veins, which form hooks as they enter the edge of the midrib.

All tested *Musa* species and cultivars appear susceptible to the banana bunchy top virus (BBTV), but the incubation period may vary. BBTV is controlled by eradication of diseased plants, and use of virus-free planting material. Severe attacks may require strict programmes with the goal of regional eradication.

Banana streak disease was first recognised in Côte d’Ivoire in the mid-20th century and later reported in Morocco, where the incidence of infection exceeded 50% in many ‘Dwarf Cavendish’ plantations. Banana streak badnaviruses (BSVs) (Caulimoviridae) have been found worldwide, infecting a wide range of Musa genotypes, with yield losses of 7-90% (Lockhart, 1995; Lockhart and Jones, 1999; Agindotan *et al*., 2006). Co-infection with banana mild mosaic virus (BanMMV) (Flexiviridae) can increase the disease’s severity (Pietersen and Thomas, 2003). Although some clones are asymptomatic or tolerant of field infection, the broad range of cultivars susceptible to BSVs include the Cavendish subgroup, ‘Gros Michel’, Highland bananas, plantains and cooking bananas. The modern increase and movement of Musa germplasm, including the tissue cultures of improved hybrids, have been significantly affected by the risk of spreading these badnaviruses.

Several *Badnavirus* species are recognised to be involved in this disease complex (Lheureux *et al*., 2007; Gayral *et al*., 2008). Disease can result from a BSV species transmitted exogenously, but can arise endogenously as well. Varied DNA sequences from BSVs have integrated into both the B and A genomes. Viral sequences (integrant virus species) in the B genome can become activated and cause disease, for example as a result of stress from tissue-culturing plants (micropropagation), sexually creating interspecific hybrids for breeding purposes, or temperature shifts (Ndowora *et al*., 1999a, 1999b; Geering *et al*., 2005; Fargette *et al*., 2006; Gayral *et al*., 2008). Practical molecular methods are being devised to detect the DNA of episomal BSV infecting *Musa* separately from concomitant BSV endogenous pararetroviral sequences (Agindotan *et al*., 2006; Le Provost *et al*., 2006).

Symptoms of banana streak disease vary considerably — depending on the pathogen species and strain, host cultivar, environment and season — from inconspicuous chlorotic flecking to lethal chlorosis. The most common symptoms are chlorotic streaks and blotched leaves. Other symptoms include streaks in the pseudostem, narrow leaves, constriction and reduction of the bunch, fruit-peel streaks and peel splitting. Transmission by citrus mealybugs (especially *Planococcus citri*) occurs, but spread is primarily by multiplication and dissemination of infected planting material. Control consists mainly in use of starting materials (in the lab and the field) free of both non-integrant BSVs and B-genome integrated virus sequences, and the prompt elimination of infected plants.

Banana bract mosaic disease is widespread in the Philippines and has been found as well in Vietnam, Thailand, India, Sri Lanka and Western Samoa. A potyvirus, banana bract mosaic virus (BBrMV), has been isolated from infected plants (Thomas and Magnaye, 1996; Thomas *et al*., 1999). BBrMV occurs in a wide range of edible banana genotypes. It is common in the ABB cultivars ‘Cardaba’ and ‘Saba’ popular in the Philippines — up to 40% yield losses have been recorded there in ‘Cardaba’ and the also-popular ‘Lakatan’. BBrMV and another potyvirus, abacá mosaic virus (AbaMV), also infect *Musa textilis* in the Philippines (Pietersen and Thomas, 2003).

The diagnostic symptom of BBrMV disease is a dark reddish-brown mosaic pattern on the bracts subtending male flowers in the inflorescence. Initial symptoms (depending on cultivar) include green or reddish-brown streaks or spindle-shaped lesions on the petioles and a congested leaf arrangement. Lamina symptoms, spindle-shaped chlorotic streaks parallel to the veins, are most prominent on young leaves in recent infections. When dead leaf sheaths are pulled away from the pseudostem, distinctive dark-coloured mosaic patterns, stripes or spindle-shaped streaks are visible. There are no reports of mechanical transmission, but BBrMV is transmitted by several species of aphids. The virus is also transmitted in vegetative planting material including “bits”, suckers and tissue-cultured plantlets.

Strains (in subgroup I but as well II) of **cucumber mosaic cucumovirus** (CMV) (Bromoviridae) are increasingly being found on bananas, and may cause no symptoms or mild to in some cases severe disease — chlorosis, mosaic and heart rot (Pietersen and Thomas, 2003). CMV occurs worldwide, has the largest host range of any plant virus, and is transmitted by many species of aphids. It is particularly important to use CMV-free source material for *in vitro* mass propagation. Agronomic practices include co-operation regionally to avoid growing other host crops nearby and eliminate weed hosts.

4.5. Insects

The **banana weevil or banana borer *Cosmopolites*** *sordidus* (Coleoptera: Curculionoidea, Dryophthoridae) generally is the most important insect pest of banana and plantain and also impacts the related Musaceae crop enset (genus *Ensete*) (Gold and Messiaen, 2000; Gold *et al*., 2001). Losses of more than 40% to even 100% of the planting have been recorded, as the weevil populations increase in successive cropping cycles. Problems are most severe in plantains and Highland cooking bananas, contributing to disappearance of the latter crop in parts of East Africa (Kiggundu *et al*., 2007). In commercial Cavendish plantations, this weevil has been reported to be relatively unimportant.

The species evolved in Southeast Asia (Malaysia-Indonesia) and has been spread to all banana and plantain production regions. Adults are attracted by volatiles emanating from the host plants. Cut corms and young suckers are especially susceptible. Larvae bore into the corm and interfere with root initiation, kill existing roots, limit nutrient uptake, reduce plant vigour, delay flowering, and increase susceptibility to diseases and other pests, and to toppling by wind.

Control in commercial banana plantations is mainly chemical, using nematicides with insecticidal activity and specific insecticides. However, the banana weevil has shown the ability to develop resistance to most classes of chemicals. Botanical compounds may serve as deterents. Hot-water treatment has been widely promoted for control. Significant biological control may sometimes be achieved *via* foraging ants (*e.g. Pheidole* and *Tetramorium*, Myrmicinae), some species of which will even forage in the weevil’s tunnels (Abera-Kalibata *et al*., 2007).

Primary sources of resistance are found in some wild accessions or clones, such as Calcutta 4 (group AA), ‘Yangambi-Km 5’ (AAA), FHIA-03 (AABB) (or its parents), Kayinja (ABB) and the IITA diploid hybrids TMB2x 7197-2 and TMB2x 8075-7 (Pavis and Lemaire, 1996; Kiggundu *et al*., 2003, 2007).

The **banana stem weevil or banana pseudostem borer *Odoiporus*** *longicollis* (Coleoptera: Curculionoidea, Dryophthoridae) is among the most important pests of banana and plantain (Padmanaban and Sathiamoorthy, 2001). The species is believed to have originated in the region of South Asia and Southeast Asia. It is a key pest in India, China, Thailand, Malaysia and Indonesia (Valmayor *et al*., 1994). Plantains and Highland bananas are preferred. The weevil can cause 10-90% yield loss depending on crop growth stage and management efficiency.

Adults are attracted by volatiles released by the host plants. Infestation normally starts in 5-month-old plants, retarding growth and development, and increases susceptibility to wind lodging. Early symptoms include pinhead-sized holes in the pseudostem, exudation of a gummy substance, and fibrous extrusions from the base of petioles. The pseudostem shows extensive tunnelling in the leaf sheaths. Rotting occurs due to secondary infection. The fruits are dehydrated, with premature ripening.

Chemical control involves injection of a systemic organophosphorus compound into the pseudostem or swabbing with either surfactants or mud slurry containing an insecticide, or fumigation. After harvest the banana stumps must be removed and destroyed. Natural enemies, including arthropods, entomopathogenic nematodes and entomopathogens have great potential as biological control agents to reduce the weevil population in severely infested home gardens.

Host plant resistance may offer a long-term solution. Charles *et al.* (1996) identified 27 *Musa* accessions that exhibited tolerance to the pest. A high degree of resistance can be found in some *Musa balbisiana* clones.

4.6. Nematodes

The **burrowing nematode *Radopholus*** *similis* is one of the most important root pathogens attacking bananas in the tropical zone (Sarah *et al*., 1996), especially in Cavendish types. Vegetative propagation using infested corms or suckers has disseminated this pest worldwide (Marín *et al*., 1998). It is common on plantains and cooking bananas, except in Central America, West Africa, the highlands of central-eastern Africa and subtropical zones of production. The distribution is mainly due to the species' preference for a temperature range from 32º to 24ºC.

Radopholus similis is a migratory endoparasite, completing its life cycle in 20-25 days in root and corm tissues. Their destruction results in reduction of host growth and development, even to uprooting and toppling. Yield losses can be reduced through propping or guying pseudostems. There can be severe losses in bunch weight, and a longer time between harvests. Crop losses depend on soil fertility, drainage and nematode pathogenicity, and vary from 15 to 30 to 75% in three cycles of production.

Nematode populations may be reduced to an undetectable level by a 1-year fallow with non-host plants, 6-7 weeks of complete flooding, or soil fumigation. Recontamination of soil is avoided through use of nematode-free plants and treated corms or suckers.

Some physical and chemical barriers to infection have been detected in roots (Wuyts *et al*., 2006, 2007). Sources of resistance are found in several genome groups in *Musa acuminata* and *M. balbisiana* wild and cultivated diploids (Moens *et al*., 2005; Dochez *et al*., 2006). Pisang Jari Buaya (AA) cultivar types are the source of resistance in the modern AAAB cultivar 'Goldfinger'. 'Yangambi-Km 5' (AAA) also shows resistance. Endophytes of *Fusarium oxysporum* can induce systemic resistance to *R. similis* (Vu *et al*., 2006).

The **root-lesion nematodes *Pratylenchus*** *coffeae* and *P. goodeyi* are major pests of *Musa* wherever they occur (Bridge *et al*., 1997). *Pratylenchus coffeae* is probably a native of the Pacific and Pacific Rim countries but now has a worldwide distribution, especially affecting Southeast Asia. In Central America and South America it is the most important nematode species affecting Cavendish cultivars, whereas in Africa it affects plantains. This species has an extremely wide host range and is a major pest on other crops. In contrast, *Pratylenchus goodeyi* has a much more restricted distribution. It is considered indigenous to Africa, and is an important pest of Highland bananas and plantains. It is the main nematode affecting Cavendish bananas in the Canary Islands and has the potential to become an important pest where bananas are grown in cooler climatic zones of the Mediterranean and Middle East.

Pratylenchus coffeae and *P. goodeyi* are both migratory endoparasites of the root cortex and corm of banana, plantain and abacá (*Musa textilis*). Their presence in banana root lesions is generally highly correlated with infection by fungi. Nematode populations are reduced by a bush fallow period exceeding one year, removal of roots, paring of corms to remove the lesions and exposure to direct sunlight. Hot water treatment eradicates almost all nematodes from planting material. The nematicides for control of *Radopholus similis* are expected to be equally effective for the root-lesion nematodes.

Root-knot nematodes, especially ***Meloidogyne*** *incognita* and *M. javanica,* occur on banana and plantain roots wherever the crops are grown (De Waele and Davide, 1998). These nematodes are often found with *Radopholus similis* and *Pratylenchus* spp. (Moens *et al*., 2006), which tend to outnumber and eventually replace the root-knot nematode populations but provide feeding sites for *Meloidogyne*. *Meloidogyne* spp. can become abundant in areas where *R. similis* has not been introduced or the climate is too cold for it, or *P. goodeyi* is not present. In Asia, especially Southeast Asia, *Meloidogyne* spp. are often the most common and abundant nematode species on cooking and dessert bananas.

Root-knot nematodes often occur together with soil-borne fungi; there are indications that synergistic effects exist between these groups of pathogens, but they have not been documented. In roots of ‘Grande Naine’ infected with *M. incognita*, the endomycorrhiza *Glomus mosseae* isolates suppressed root galling and nematode build-up. *Glomus intraradices* increases plant growth by enhancing nutrition.

Meloidogyne spp. are sedentary endoparasites with a wide host range, especially on dicots. On banana and plantain the most obvious symptoms of infection are swollen, galled primary and secondary roots. Root-tip growth ceases and new roots proliferate just above the infected tissues, giving rise to a lower number of secondary and tertiary roots. Aboveground symptoms include yellowing and narrowing of leaves, stunted plants and reduced fruit production. Losses may range from 25 to 60%.

Meloidogyne spp. may spread with infected planting material. Corms can be disinfected by peeling followed by treatment with hot water, a nematicide, or 5-10 min of 1% sodium hypochlorite. Restraining methods include maintenance of weed-free fallows and cover crops or rotation systems. Limited fallowing may be ineffective, however, since *Meloidogyne* spp. can persist in the soil in the absence of bananas for up to 29 months.

Root extracts from the plants Tagetes erecta, Leucaena leucocephala, Cynodon dactylon and Mimosa pudica, bulb extracts from Allium sativa and A. alia, and leaf extracts from Anthocephalus chinensis and Eichhornia crassipes are highly effective against M. incognita egg hatching and infestation. Purified extracts of several Penicillium spp. (P. oxalicum, P. anatolicum), Aspergillus niger and liquid and powder formulations containing Paecilomyces lilacinus and Penicillium oxalicum have shown high nematicidal activity.

5. Reproductive biology and ecology

The male and female flowers of edible *Musa* differ in several respects (Simmonds, 1966/1973; Stover and Simmonds, 1987). The female flowers are larger (*e.g.* 10 cm long), with a well-developed inferior trilocular ovary that exceeds the somewhat tube-like toothed perianth in length, a stout style and stigma, but stamens reduced to staminodes. In male flowers the exserted stamens have well-developed anthers, but the ovary is rudimentary, with a slender style and small stigma. Beginning at the base of the inflorescence (Section III), each hand of female flowers is exposed by the opening of its large bract; as pollination is not necessitated in the crop plants, the ovaries continue to develop parthenocarpically into the persistent fruits (which lack an abscission layer). The male flowers of a cluster, after being exposed by its large bract for about 24 hrs from dusk to the subsequent night, abscise from the abortive ovary in most cultivars and are shed whole.

5.1. Pollination

Pollination is essential for development of fruits in wild species of *Musa*. Bats and sunbirds (Nectariniidae) as well as honeybees play main roles in the pollination ecology of *Musa*. The sticky pollen is transported by bats and/or birds seeking the copious nectar (in some cases also pollen), and/or by insects (Nur, 1976; Start and Marshall, 1976; Gould, 1978). In regions where suitable bats or sunbirds are not present, insects (*e.g.* honeybees) may play the key role in pollination — which then tends to be more local. *Musa* species with pendulous inflorescences are considered to be especially pollinated by bats, those with erect inflorescences by sunbirds (Itino *et al*., 1991). *Musa itinerans* flowers produce nectar in two peaks, attracting both bats and birds, each at their respective time period during the night or morning, with both groups having similar pollination effectiveness (Liu *et al*., 2002a). Production of scent and nectar by bananas and plantains suggests that pollination may occur from dusk to nearly mid-morning (Gould, 1978; Mutsaers, 1993). In South India, the production of nectar by *Musa* ×*paradisiaca* peaked at 20:00 hr (Elangovan *et al*., 2000).

In wild populations of *Musa balbisiana* within its natural range in China, populations were pollinated by the long-tongued fruit bat *Macroglossus sobrinus* and insects as well as the sunbird *Arachnothera longirostris* (little spiderhunter); no gene flow was detected without animal vectors (Ge *et al*., 2005). Throughout Southeast Asia the least blossom bat *Macroglossus minimus* is an important *Musa* pollinator. In lowland Papua New Guinea these bats are ubiquitous; in a study there the bats regularly visited both wild and cultivated *Musa* and had home ranges of 0.6-15.1 ha (averaging 5.8 ha) (Winkelmann *et al*., 2003). In northeastern Papua New Guinea's Bismarck Archipelago, black-bellied fruit bats *Melonycteris melanops* are common (and endemic). Their home ranges of 0.5-9.2 ha (averaging 2.3 ha with a long axis of 371 m) had a core area that was based on one to six flowering cultivated banana plants, which were utilised for nighttime nectar feeding as well as daytime roosting (Bonaccorso *et al*., 2005).

Populations of the pollinating long-tongued fruit bat (*M. sobrinus*) are diminishing in parts of southern China because of increasing forest use, thus genetically isolating wild populations of *Musa balbisiana* (Ge *et al*., 2005). In northeastern Australia where the tropical forest is reduced and fragmented, southern blossom bats *Syconycteris australis* now utilise the floral resources provided by cultivated bananas (Law and Lean, 1999). In Papua New Guinea these common bats can have a home range of 2.7-13.6 ha, with a long axis of 263-725 m (Winkelmann *et al*., 2000).

In the most primitive edible *Musa* cultivars in Southeast Asia seeds are of frequent occurrence (Stover and Simmonds, 1987). However, among cultivated bananas and plantains generally, pollination never or seldom results in seeds (*e.g.* Ortiz and Crouch, 1997; Ssebuliba *et al*., 2006a). Seedlessness is due to a complex of causes involving sterility genes, polyploidy, and chromosomal structural changes in varying degrees depending on the cultivar or particular clone (Section VI). Most of the edible *Musa* are triploids and almost completely sterile (Vuylsteke *et al*., 1993d). Much of the characteristic sterility in commercial clones for the export trade (*i.e.* the AAA Cavendish subgroup) is due to high inherent female sterility. Male gametic sterility does not always occur along with female sterility. Fertility can depend not only on maternal conditions (*cf*. Fortescue and Turner, 2005) but also pollen availability and viability. The 'Gros Michel' dessert banana can produce many seeds if planted in areas where suitable pollen and pollinators are around. In screening germplasm of the International Institute of Tropical Agriculture (IITA) for viable pollen, nearly 40% of the *Musa* accessions (67 of 168) were sufficiently fertile for use as the male parent in breeding (Dumpe and Ortiz, 1996).

In a study of pollen viability in the anthers just before anthesis along with a detailed review (Fortescue and Turner, 2004), some viable pollen was reported even in "male-sterile" triploids. Viability was calculated from the total quantity of pollen produced — between 11 and 1495 grains. Pollen of seeded diploid species was three times more viable than pollen of edible fertile tetraploids, which had three to four times more viable pollen than edible triploids. Among triploids cultivated in Australia, 'Gros Michel' had 13% viable pollen, and triploids from India could reach 29% viable pollen. Triploids used in the genetic improvement programme in Cuba had 40-43% fertile pollen (Landa *et al*., 1999). The size of the spherical pollen grain increases with the ploidy level; in diploids the diameter is about 100 µ, in triploids 112 µ and in tetraploids 135 µ (Tenkouano *et al*., 1998).

5.2. Seeds

Although the production of seeds in most cultivated varieties is either not possible or difficult and rare, in specialised breeding work some varieties can be forced to produce seeds (Section VI) (Stover and Simmonds, 1987; Tomekpé *et al*., 2004; Ssebuliba *et al*., 2006b). For example, 0-183 and 0-219 seeds per bunch have resulted from pollinating triploid plantains (AAB) with the pollen from diploid bananas (AA) (respectively Tomekpé *et al*., 2000, and Swennen and Vuylsteke, 1993). Furthermore seed set can fluctuate substantially within the year (Swennen and Vuylsteke, 1990). Pollen viability in plantains and cooking bananas is increased by high relative humidity, low temperature and low solar irradiance (Ortiz and Vuylsteke, 1995; Ortiz *et al*., 1998a). These researchers found that seed set was highest in ABB cooking bananas, followed by AAB French Plantains, and lowest in AAA dessert bananas. Cultivars with two rather than three sets of homologous chromosomes thus had an increased frequency of viable eggs.

Musa fruits are consumed by many species such as bats, birds, rodents and primates, which in some cases can be considered pests of the crop (*e.g.* Naughton-Treves *et al*., 1998; Duncan and Chapman, 1999; Liu *et al*., 2002a; Tang *et al*., 2005). Mature fruits of wild *Musa* have many seeds (*e.g.* 30-400). In the wild, utilisation of fruits by such mammals and birds can result in seed dispersal (*e.g.* Liu *et al*.2002a; Tang *et al*., 2005; Meng *et al*., 2008). *Musa balbisiana* was introduced and has now become naturalised in Taiwan (Chiu *et al*., 2007). In Belize (Central America), this seedy species has become invasive locally in several relatively open disturbed areas (Meerman, 2003; Meerman *et al*., 2003).

6. Genetics and hybridisation

6.1. Genetic diversity and genomic architecture

There is quite limited information about most wild *Musa* species' ranges and habitats (De Langhe, 2000b). Wild populations apparently tend to be isolated, maintaining significant genetic diversity among the dispersed populations rather than within each population (Asif Javed *et al*., 2002; Ge *et al*., 2005; Wang *et al*., 2007). In Southeast Asia where wild bananas occur naturally, they are often in open disturbed areas such as on steep slopes, and they are often among the first colonisers when natural regeneration follows forest clearance (*e.g.* Tang *et al*., 2003) — thus showing pioneer characteristics. Semi-wild or free-living populations occur in human-made habitats such as the edges of cleared land and on roadsides. *Musa* genetic resources are now found in an array of habitats such as forest edges and openings, fallow land, and home gardens and farms. The human communities living around such habitats maintain variability through cultivation of traditional cultigens and landraces, and by conservation of natural areas and ecosystems (Sharrock and Engels, 1997; Uma and Buddenhagen, 2006). Both of the wild diploid progenitor species are still valuable genetic resources for banana improvement (De Langhe, 2000b). Their populations contain important traits such as resistance to various diseases, and the ability to thrive in relatively dry and cool environments (Ude *et al*., 2002b; Häkkinen and Wang, 2007; Wang *et al*., 2007).

Knowledge of *Musa* had been limited due to the complex and varied genomes between sections, but with modern molecular methods great progress is being made. For example the traditional cooking bananas 'Kluai Ngoen' and 'Pisang Awak' have been reclassified and considered to have the genome AABB (Horry *et al*., 1998; Pillay *et al*., 2006). In recent years there have been studies on genome identification (Pillay *et al*., 2000, 2006) and genome structure (D'Hont *et al*., 2000). Genomic *in situ* hybridisation (GISH) can differentiate the chromosomes of the four designated genomes of the diploid species — A (*M. acuminata*), B (*M. balbisiana*), S (*M. schizocarpa*) and T (section *Australimusa* spp.)

— and determine the genome constitution of interspecific cultivated clones (D'Hont *et al.*, 2000). The molecular characterisation of genomes in *Musa* and applications have been reviewed by Pillay *et al.* (2004).

The cytogenetics of the nuclear genome has been reviewed by Doležel (2004). The karyotypes of the *Musa* A and B chromosome sets appear similar (Osuji *et al.*, 2006). The diploid genome is rather small — Kamaté *et al.* (2001) measured the 2C nuclear DNA content of *M. balbisiana* as 1.16 pg, and *M. acuminata* averaged 1.27 pg with a variation of 11% between subspecies, whereas triploid 2C values ranged from 1.61 to 2.23 pg (*cf.* Bartoš *et al.*, 2005). These diploids therefore have some 560 to 610 million bp of DNA (Kamaté *et al.*, 2001), of which about half has been estimated to be non-coding DNA (H ibová *et al.*, 2007).

6.2. Natural or spontaneous hybridisation, genetic behaviour and genetic mapping

There are reports of probable natural hybridisation between wild species of *Musa* in their native ranges, and between wild subspecies of *Musa acuminata*, and of probable introgression in the wild. The following are representative observations (not a complete review, given the extent of incomplete botanical and genetic knowledge). For example, the native range of *Musa balbisiana* likely does not go as far south as Java (*cf.* Häkkinen and Väre, 2008c) so the hybrid with *M. acuminata* found there (Simmonds, 1962) would be a spontaneous cross instead of a truly natural cross between indigenous species.

- *Musa acuminata* ssp. *halabanensis* × *Musa acuminata* var. *sumatrana*
Indonesia (Sumatra) (Nasution, 1991)
- *Musa acuminata* ssp. *malaccensis* × *Musa acuminata* ssp. *truncata*, including introgression
Peninsular Malaysia (Simmonds, 1962, but *cf.* Wong *et al.*, 2001a; Asif Javed *et al.*, 2002)
- *Musa acuminata* ssp. *malaccensis* × *Musa acuminata* ssp. *siamea*
Thailand (De Langhe *et al.*, 2000)
- *Musa acuminata* ssp. *banksii* × *Musa schizocarpa*
Papua New Guinea (Argent, 1976; Arnaud and Horry, 1997; Shepherd, 1999; Carreel *et al.*, 2002)
- *Musa acuminata* ssp. *siamea* × *Musa laterita*
Thailand (*cf.* Simmonds, 1962; De Langhe *et al.*, 2000)
- *Musa acuminata* × *Musa balbisiana*
Indonesia (Java) (Simmonds, 1962) — spontaneous
- *Musa balbisiana* × *Musa nagensium*
Myanmar (Simmonds, 1962)
- *Musa balbisiana* × *Musa sikkimensis*
Northeast India (Sikkim) (Simmonds, 1962)
- *Musa balbisiana* × *Musa textilis*
Philippines (Simmonds, 1962; Carreel *et al.*, 2002)
- *Musa borneensis* × *Musa textilis*
Borneo (Wong *et al.*, 2002; Häkkinen and Meekiong, 2005)— spontaneous (rather than natural), as *M. textilis* was introduced to Borneo and has naturalised
- *Musa boman* × *Musa lolodensis*
Papua New Guinea (Argent, 1976; Nasution, 1993)

- *Musa flaviflora* × *Musa velutina*, including introgression
  Northeast India (Simmonds, 1962)

The great majority of domesticated bananas are products of an array of prehistoric crosses between diploid *Musa acuminata* plants of several subspecies (A genomes) and further crosses of such cultigens with the less diverse *Musa balbisiana* (B genome), which has resulted in several ploidy levels (diploids, triploids, a few tetraploids) and an array of varying progeny (*e.g.* Table 1). A spontaneous doubling of gamete chromosomes from *n* to 2*n* apparently facilitated such crossings (Ortiz, 1997b; Raboin *et al.*, 2005; Ssebuliba *et al.*, 2008; Perrier *et al.*, 2009). Experimental crosses in early cytogenetic studies also made hybrids between *M. acuminata* and *M. balbisiana*. Experimental interspecific crosses have been carried out between various species within section *Musa* ("*Eumusa*"), between eumusa species and species in other sections, and between non-eumusa species in the other sections (Dodds, 1943, 1945; Dodds and Pittendrigh, 1946; Dodds and Simmonds, 1946, 1948a, 1948b; Simmonds, 1962; Shepherd, 1999; Choy and Teoh, 2001).

Relatively little research on inheritance has been undertaken in *Musa* spp. due to the several characteristics of domesticated bananas and plantain that make inheritance analysis difficult. Since the first studies on inheritance of fruit parthenocarpy (Cheesman, 1932; Dodds, 1943, 1945), half a century passed to the next such study, on inheritance of whole-plant albinism (Ortiz and Vuylsteke, 1994a). A number of studies followed (*cf.* Ortiz and Vuylsteke, 1996, 1998b; Ortiz, 2000), for example on inheritance of black Sigatoka resistance by the wild diploid Calcutta 4 (Ortiz and Vuylsteke, 1994b).

Some genetic maps have been developed that help to further understand the genetics of traits of interest. Fauré *et al.* (1993) developed the first map by using isozymes and RFLPs. A global programme for *Musa* improvement, PRO*MUSA*, was formed in 1997. Research that includes a large consortium for genomics and genetic improvement of *Musa* is making available useful information for breeding (GMGC, 2002; Roux *et al.*, 2008). A genetic map developed through a joint effort characterised more than 300 markers (Lagoda *et al.*, 1998a). Another map was based on single sequence repeats (SSRs) (Lagoda *et al.*, 1996). CIRAD published 45 sequence-tagged microsatellite site (STMS) markers in the EMBL database (Lagoda *et al.*, 1998b). Fluorescent *in situ* hybridisation (FISH) has been used to determine the number and distribution of the 18S-25S and 5S rDNA sites on mitotic chromosomes of edible diploid bananas (Doleželová *et al.*, 1998). Bacterial artificial chromosome (BAC) libraries have been constructed of *Musa acuminata* composed of 55,152 clones (Vilarinhos *et al.*, 2003), and *Musa balbisiana* composed of 36,864 clones (Šafá *et al.*, 2004), as well as a BIBAC (binary BAC) library of a diploid *M. acuminata* cultivar (Ortiz-Vázquez *et al.*, 2005).

6.3. Experimental breeding

Breeding improvement for crops in which most of the accessions and the cultivated varieties are highly sterile is challenging. Most cultigens that are commercially acceptable are parthenocarpic triploids producing few seeds if any — and yet seedlessness is a characteristic that the breeder must retain in the crop (Hamill *et al.*, 1992). Experimental crossing of banana and plantain is hampered by polyploidy, the differences between their sets of subgenomes, and the plants being generally sterile, with seedless fruit. Banana improvement programmes rely on development of new hybrid genotypes obtained from the fertilisation of female-fertile plants with pollen of male-fertile plants. Even when viable hybrids can be obtained experimentally, most are sterile. In plantain some crosses have yielded a very few seeds, with great variability. Asexual *in vitro* multiplication and other biotechnological methods have been developed to obtain viable progeny (see Section VII).

6.4. Breeding schemes

Different breeding schemes are based on crosses between plants of different ploidy, from which improved tetraploids or triploids can be selected (Bakry *et al.*, 2001; Escalant *et al.*, 2002; Tenkouano and Swennen, 2004; Oselebe *et al*., 2006). The breeding approach produces tetraploid progeny *via* crosses of triploid females and diploid males, choosing the female parents from the few triploids that show some female fertility. This strategy also includes producing secondary triploid hybrids from tetraploid × diploid crosses, achieved by hybridisation of African plantain landraces with wild or cultigen Asian diploid banana accessions (Vuylsteke *et al*., 1993d). The key intermediate step is to obtain improved diploids with novel traits of interest (Tenkouano *et al*., 2003).

Crossing to generate new hybrids has proven efficient in plantain improvement when genetic variability can be included through use of female-fertile parents (Swennen and Vuylsteke, 1993; Ortiz, 1997c), but obtaining new commercial cultivars is difficult because most clones lack female fertility (Rosales and Pocasangre, 2002). Ortiz *et al.* (1998a) suggested optimising apparent male fertility by higher solar irradiation and temperature. Often the level of fertility of accessions available to a breeding programme still needs to be determined.

Table 2. Some important *Musa* hybrids produced by agricultural breeding programmes

HYBRID NAME	PLOIDY	CHARACTERISTICS & COMMENTS	REFERENCE
DESSERT BANANAS:			
FHIA-01, Goldfinger	tetraploid	black Sigatoka resistant, Fusarium wilt races 1 and 4 resistant Grown in Latin America, Africa and Australia	Rowe and Rosales, 1993; Orjeda and Moore, 2001; Gallez *et al.*, 2004
FHIA-02	tetraploid	black Sigatoka resistant	Ortiz and Vuylsteke, 1996
FHIA-17	tetraploid	Fusarium wilt race 1 resistant	Orjeda and Moore, 2001
FHIA-18	tetraploid	black Sigatoka resistant, Fusarium wilt resistant Grown in Latin America and Australia	Rowe and Rosales, 1993
BITA-3	tetraploid	black Sigatoka resistant	Ortiz *et al.*, 1995b
IRFA 909	aneuploid	yellow and black Sigatoka resistant, Fusarium wilt resistant	Ortiz and Vuylsteke, 1996
TM3x series	secondary triploids	black Sigatoka resistant	Ortiz *et al.*, 1998b
PLANTAINS:			
TMPx series	tetraploids	black Sigatoka resistant	Vuylsteke *et al.*, 1993c
TMP2x series	diploids	black Sigatoka resistant	Vuylsteke and Ortiz, 1995
PITA-9	tetraploid	black Sigatoka resistant	Vuylsteke *et al.*, 1995
FHIA-21	tetraploid	black Sigatoka resistant	Ortiz and Vuylsteke, 1996
PITA-14	tetraploid	black Sigatoka resistant, BSV tolerant	Ortiz and Vuylsteke, 1998a
TM3x series	secondary triploids	black Sigatoka resistant	Ortiz *et al.*, 1998b
PITA-15	secondary triploid	best fruit quality amongst TM3x series	Ortiz and Vuylsteke, 1998a
PITA-16	secondary triploid	BSV and CMV tolerant	Ortiz and Vuylsteke, 1998a
PITA-20	secondary triploid	higher yield	Ortiz and Vuylsteke, 1998a
COOKING BANANAS/			
TMBx series	tetraploids	black Sigatoka resistant	Vuylsteke *et al.*, 1993a
FHIA-03	tetraploid	black Sigatoka resistant Grown in Latin America and Africa	Ortiz and Vuylsteke, 1996; Gallez *et al.*, 2004

The different general breeding schemes of the major *Musa* research centres, and their main achievements, have been reviewed by Ortiz *et al.* (1995a) and Rosales and Pocasangre (2002). Modern breeding started with a banana improvement programme active from 1922 to 1980 in the Caribbean region (Trinidad and Jamaica). The programme's strategy was based on crosses between the triploid (AAA) cultivar 'Gros Michel' and its mutants with a range of resistant male diploid parents. The programme did not produce any commercially acceptable hybrid, but set the basis for future breeding strategies by using improved male diploids (Cheesman, 1948b; Simmonds, 1966/1973; Shepherd, 1974; Ortiz *et al.*, 1995a). In 1959 an intensive breeding programme was established in Honduras, initially supported by the United Fruit Company. The programme was later donated to the Fundación Hondureña de Investigación Agrícola (FHIA) which started its activities (with international support) in 1984. This research focused on developing a superior diploid population to be used for production of primary tetraploids. Selected accessions were crossed to 'Gros Michel' and its dwarf mutants to produce tetraploids combining specific resistances and good agronomic characteristics (Stover and Buddenhagen, 1986). In 1989 FHIA released the tetraploid (AAAB) FHIA-01 or 'Goldfinger', the first multi-resistant dessert hybrid that is grown commercially (Rowe and Rosales, 1993; Ortiz and Vuylsteke, 1996). Other variously broad improvement programmes are carried out in Brazil, Nigeria, Cameroon, Uganda, India, Australia and the French West Indies.

6.5. Targets and results

The main targets in breeding are resistance to major diseases and pests (Section IV) caused by (1) the Sigatoka complex (*Mycosphaerella* spp.) and the different races of the Fusarium wilt pathogen; (2) Moko disease; (3) viruses; (4) nematodes; and (5) the weevil borer. Among agronomic and quality traits of primary breeding attention are (1) yield; (2) fruit quality regarding finger shape, fruit tastes for local consumption and for export, culinary traits, and ripening and shipping characteristics; and (3) traits such as dwarfism, toppling resistance, short ratoon cycles, regular suckering, and foliage and bunch peduncle strengths (Persley and De Langhe, 1987; Ortiz *et al.*, 1995a).

Sources of resistance to the Sigatoka leaf spot diseases are available in subspecies of *Musa acuminata* such as ssp. *malaccensis*, ssp. *burmannica* and ssp. *truncata* (Appendix 1) (Vuylsteke *et al.*, 1993c). Resistance to Fusarium wilt has been detected in *M. acuminata* ssp. *burmannica* and ssp. *malaccensis*, and the fertile diploid hybrid SH-3142 (Rowe and Rosales, 1989; Javed *et al.*, 2004). The AA diploid Pisang Jari Buaya group of accessions is resistant to the burrowing nematode, but the parent has given problems with sterility and inviability of seeds. Nonetheless the hybrid SH-3142 has such resistance and is being utilised in further development (Rowe and Rosales, 1989; Viaene *et al.*, 2003).

In spite of difficulty in breeding and the few commercially acceptable improved cultivars, significant advances are being made. Several tetraploid plantain hybrids with potential for use in disease-devastated areas of tropical Africa have been bred by the International Institute of Tropical Agriculture (IITA) (Vuylsteke *et al.*, 1993b, 1993c). Ortiz *et al.* (1998b) developed triploid black Sigatoka-resistant banana and plantain germplasm (designated TM3x) by crosses between resistant diploids and triploids. Orjeda and Moore (2001) have reported on the performance of various cultivars resistant to *Fusarium*.

A selection of important hybrids obtained in several breeding programmes follows in Table 2.

7. Genetic improvement and biotechnology

Genetic improvement of *Musa* is difficult for a variety of reasons (Section VI) (Ortiz *et al.*, 1995a; Ortiz and Vuylsteke, 1996). Breeding is hampered because so few viable seeds and seedlings are obtained, but as well because up to 2 years are required in a seed-to-seed crop cycle. The different approaches to improve banana and plantain are mainly *via* crossing, mutation, somatic embryogenesis, somaclonal variation, and genetic engineering (genetic modification, genetic transformation) (Jain and

Swennen, 2004). Colchicine and oryzalin are used to induce chromosome duplication as a step in *Musa* breeding schemes (Hamill *et al.*, 1992; Tezenas du Montcel *et al.*, 1994; Van Duren *et al.*, 1996; Ganga and Chezhiyan, 2002; Bakry *et al*., 2007). Vegetative propagation techniques are widely used, because of the low levels particularly of female fertility, and the relative lack of useful genetic variability and the limited number of landraces and accessions selected from natural germplasm. Breeding schemes utilise *in vitro* culture extensively, and in some cases employ mutagenesis and genetic engineering.

7.1. Mutagenesis

The appearance of spontaneous mutants at a higher rate than in many other crops makes physical mutagenesis an attractive technique for banana and plantain improvement (Novak *et al*., 1993; Domingues *et al*., 1994; Roux, 2004; Kulkarni *et al*., 2007). For example, with FAO/IAEA (Food and Agriculture Organization of the United Nations / International Atomic Energy Agency) co-operation, by irradiation researchers were able to obtain aluminium-tolerant mutants of the AAA banana cv. Nanicão (Matsumoto and Yamaguchi, 1990, 1991); early-flowering mutants GN-60 Gy/A (Novak *et al*., 1990) and FATOM-1 (GN-60/A) (Tan *et al*., 1993) from cv. Grande Naine; and improved agronomic characteristics of cv. Dwarf Parfitt, a Cavendish cultivar resistant to *Fusarium oxysporum* f. sp. *cubense* race 4 (Smith *et al*., 1993; OGTR, 2008).

7.2. **In vitro** *culture, somatic embryogenesis and somaclonal variation*

In vitro culture of meristems, embryos, and cell suspensions has been used for micropropagation, including major *Musa* germplasm conservation (Van den houwe *et al*., 1995, 2003) and exchange (Krikorian *et al*., 1995; Van den houwe *et al*., 2006). Micropropagation is extensively used for the commercial production of planting material, and for germplasm conservation in the International *Musa* Germplasm Collection at the INIBAP Transit Centre in Belgium, which is under the auspices of FAO. At this global banana collection facility, all banana accessions are kept either as meristem cultures under low light and temperature conditions (*i.e.* medium-term conditions) (Van den houwe *et al.*, 2006) or as cryopreserved meristems (Agrawal *et al.*, 2004; Panis *et al.*, 2005a, 2005b, 2007).

Meristem culture of *Musa* began in 1959 (Baker, 1959; Baker and Steward, 1962), and much of the development work was accomplished in the 1980s. Micropropagation was achieved using several tissues: apical meristems (Álvarez *et al.*, 1982; Mante and Tepper, 1983; Tulmann Neto *et al.*, 1989), shoot tips (Ma and Shii, 1972; Cronauer Mitra and Krikorian, 1984b; Stover, 1987; Vuylsteke, 1989; Vuylsteke *et al.*, 1991; Bhagwat and Duncan, 1998), and floral explants (Balakrishnamurthy and Sree Rangaswamy, 1988; Cronauer Mitra and Krikorian, 1988; Dore Swamy and Sahijram, 1989).

Cronauer Mitra and Krikorian (1984a) first reported accomplishing somatic embryogenesis in *Musa*. Subsequently regeneration *via* somatic embryogenesis in diploid and triploid bananas has been reported by various researchers (*e.g.* Banerjee *et al.*, 1987), using for explants rhizome tissues (Novak *et al.*, 1989; Sannasgala *et al.*, 1995; Mendes *et al.*, 1996; Lee *et al.*, 1997); meristematic buds (Schoofs *et al.*, 1998; Sales *et al.*, 2001; Strosse *et al.*, 2003); leaf bases (Novak *et al.*, 1989; Shchukin *et al.*, 1997; Conceição *et al.*, 1998); immature zygotic embryos (Escalant and Teisson, 1989); and young male flowers (Escalant *et al.*, 1994; Grapin *et al.*, 1996, 2000; Ganapathi *et al.*, 1999; Gómez Kosky *et al.*, 2002; Jalil *et al.*, 2003). Gómez Kosky *et al.* (2002) report having achieved 89% regeneration of plantlets from somatic embryos of the AAAB cultivar FHIA-18. Somatic embryogenesis is only successful in some cultivars, and has different varietal responses (Strosse *et al.*, 2006).

Although somaclonal variation can be a problem in micropropagation (Vuylsteke *et al.*, 1988, 1991, 1996; Sahijram *et al.*, 2003; Oh *et al.*, 2007), some researchers have focused on using it as a source of genetic variability (Reuveni *et al.*, 1986; Stover, 1987; Israeli *et al.*, 1991) where not enough is otherwise available, as may be the case for Cavendish cultivars (Hwang *et al.*, 1996). For example, a dwarf somaclonal mutant of the Cavendish banana ‘Thai Chiao No. 1’ resistant to *Fusarium oxysporum* f. sp.

cubense has been found (Tang and Hwang, 1998). The frequency of off-types from shoot-tip culture has varied from 0 to 70%, depending upon the originating genotype (Vuylsteke *et al*., 1991).

Embryogenic cell suspension cultures can be obtained from a great variety of source materials, such as leaf sheaths or rhizome fragments of plants produced *in vitro* (Novak *et al*., 1989); thin sections of a highly proliferating bud culture (Gómez Kosky *et al*., 2002); immature zygotic embryos (Escalant and Teisson, 1993; Marroquin *et al*., 1993); triploid somatic embryos (Escalant and Teisson, 1993); scalps (Dhed'a, 1992; Schoofs *et al*., 1998, 1999; Strosse *et al*., 2003, 2006); and male flower buds (Escalant *et al*., 1994; Côte *et al*., 1996). Plant regeneration in cell suspension cultures has been achieved in the cooking banana cv. Bluggoe (ABB group) (Dhed'a *et al*., 1991) and in cv. Pisang Mas (AA group) (Jalil *et al*., 2003).

Protoplasts can easily be isolated but callus formation has only been obtained when starting material was established under quite specific conditions (Novak *et al*., 1989; Megia *et al*., 1992, 1993). The production of protoplasts and plant regeneration from them is straightforward when embryogenic cell suspensions are used as the starting material (Panis *et al*., 1993). Somatic hybridisation has been obtained through electrofusion of banana protoplasts (Matsumoto *et al*., 2002b; Haïcour *et al*., 2004).

7.3. Genetic engineering

Direct genetic transformation (*i.e.* genetic engineering) of *Musa* is likely to have a major impact on banana and plantain improvement (Sági *et al*., 1998; Rout *et al*., 2000; Escalant and Panis, 2002; Viljoen *et al*., 2004). The first genetic modification by microprojectile bombardment was achieved using embryogenic cell suspensions from meristematic buds of the ABB cooking banana 'Bluggoe' (Sági *et al*., 1995c). The efficiency of one to four transgenic plants regenerated per bombardment plate made this technique practical (Remy *et al*., 1998b; Dale, 1999). The first *Agrobacterium tumefaciens*-mediated transformation was achieved using meristems from tissue-cultured plants of the AAA Cavendish clone 'Grande Naine' (May *et al*., 1995). Transformation by electroporation has been achieved using protoplasts of the ABB 'Bluggoe' and meristems from the AAB plantain 'Harton' (Sági *et al*., 1994, 1995a, 1995b; de García and Villarroel, 2002).

Thus plants in the three most economically important genomic groups have been genetically engineered, and by a variety of techniques. 'Grande Naine' has been stably transformed and regenerated *via* microprojectile bombardment of embryogenic suspension cells derived from immature male flowers (Becker *et al*., 2000). Stable transformation and regeneration have been achieved in the cultivars 'Williams' (AAA), 'Three Hand Planty' and 'Maçã' (AAB), and 'Bluggoe' (ABB) (Remy *et al*., 1998a, 1998b; Swennen *et al*., 1998, 2003; Sági *et al*., 2000; Matsumoto *et al*., 2002a), and in the tetraploid cultivar FHIA-21 (AAAB) (Daniels *et al*., 2002).

Research *via* genetic engineering of banana and plantain is focused on fungal, insect, nematode, and virus resistances, as well as gene discovery. The three main strategies employ non-specific non-banana genes such as those encoding antimicrobial proteins (AMPs) (Broekaert *et al*., 1995, 1997; Sági *et al*., 1998; Remy *et al*., 1999; Chakrabarti *et al*., 2003; Pei *et al*., 2005); systemic acquired resistance (Malek and Dietrich, 1999); and specific resistance genes (R genes) (Hammond Kosack and Jones, 1997). Enhanced *in vitro* resistance in transgenic bananas to both Fusarium wilt and black Sigatoka has been reported (Remy *et al*., 1998b). Genetic engineering has also lead to the identification of novel banana promoter sequences (Santos *et al*., 2007).

In the case of nematodes, other strategies include use of anti-feeding proteins (Von Mende *et al*., 1993) or other proteins that interfere in the nematode-plant interaction. A Cavendish banana has been transformed (using *Agrobacterium tumefaciens*) to express a bioengineered rice cystatin that confers resistance to the burrowing nematode (Atkinson *et al*., 2004).

The major antiviral strategies are coat protein-mediated resistance (Dale *et al.*, 1993; Fauquet and Beachy, 1993) and RNA-mediated resistance. A large number of Cavendish and Bluggoe lines have been transformed with BBrMV-derived sequences designed to trigger RNA-mediated resistance (Dale, 1999). Banana streak viruses are a special case that may prove most difficult to control because BSV dsDNA has integrated into the *Musa* genome (see Section IV). The badnaviral sequences in the A genome are incomplete and have not caused infection, but the complete BSV genome has been found in the B genome — in fact four badnavirus species have been found as separate integrants (Geering *et al.*, 2005; Gayral *et al.*, 2008). *Musa balbisiana* (BB) harbouring integrated BSVs are still resistant, but when the haploid B subgenome occurs in an AAB triploid or AAAB tetraploid, stress can trigger BSV activation, infection and disease (Gayral *et al.*, 2008).

The present aim in *Musa* breeding is to develop a wide range of improved varieties, bringing together conventional breeding and biotechnology, including the rapidly developing genomics and proteomics technologies (Crouch *et al.*, 1998; Dale, 1999; Rout *et al.*, 2000; Escalant and Panis, 2002; Escalant *et al.*, 2002; Carpentier *et al.*, 2005, 2007, 2008a, 2008b; Heslop-Harrison and Schwarzacher, 2007; Samyn *et al.*, 2007). The development of molecular markers and marked-assisted selection methods is improving the efficiency of selection of improved cultivars. The Global *Musa* Genomics Consortium was created in 2001 to support such endeavours (GMGC, 2002; Frison *et al.*, 2004).

8. Human health and biosafety

People are the main consumers of banana and plantain fruits and derived products. The fruits are utilised in a multitude of ways in the human diet. They are also used in animal feed, and for starch and alcohol production. The plants can be a source of fertiliser, fibre, wrapping for food, plates and umbrellas, and for making clothes, shoes, furniture and paper (Morton, 1987; Sharrock, 1997). Bananas and plantains constitute a major food staple for many millions of people, and a main source of carbohydrates, vitamins and minerals. The vast majority of producers are small-scale farmers growing these diverse tropical crops either for home consumption, or local markets. Bananas and plantains are often the cheapest food to produce, as well as providing a valued source of income *via* local trade and international trade. Through increasing sales the plants sometimes become an important cash crop, in some cases providing the sole source of income for rural populations.

8.1. Medicinal and therapeutic value

Easy digestibility and good nutritional content make ripe banana an excellent food, particularly suitable for young children and the elderly. In the green stage, the liquified fruit is used in Brazil to treat dehydration in infants, as its tannins tend to protect the lining of the intestinal tract against further loss of liquids (Moreira, 1999). In general banana is appropriate for consumption when a low-fat, low-sodium and/or cholesterol-free diet is required, making banana recommended particularly for people with cardiovascular or kidney problems, arthritis, gout or gastrointestinal ulcers (Robinson, 1996).

As the fruit is easy to carry and peel, it is a quick healthy method of replenishing energy, due to its high energetic value of 75-115 kcal/100 mg of pulp (lower for banana, higher for plantain). Both bananas and plantains contain complex carbohydrates capable of replacing glycogen (*cf.* Nascimento *et al.*, 1999), and important vitamins (particularly B_6 and C) and minerals (potassium, calcium, magnesium, iron). Some varieties are very rich in provitamin A (Davey *et al.*, 2009). Ripe fruit has been used to treat asthma and bronchitis and control diarrhoea. Boiled and mashed ripe fruit (especially mixed with other plant substances) is cited as a good remedy against constipation.

Many purported remedies are not well documented and would require further investigation (*cf.* Orhan, 2001). The banana pseudostem is cooked in India as the dish khich khach, taken monthly to prevent constipation (Gopinath, 1995). The juice extracted from the male bud is considered good for stomach problems. Fresh leaves have been used medicinally for a range of disorders from headaches to urinary tract infections, and stem juice was considered a remedy for gonorrhoea. The peel of ripe bananas has antiseptic properties and can be used to prepare a poultice for wounds or applied directly in an emergency (Frison and Sharrock, 1999).

Bananas are considered an ideal vehicle for edible vaccines as the dessert fruits are widely appealing, palatable and can be eaten raw (Mor *et al.*, 1998). There is extensive research aiming to express different vaccines in the fruit (*e.g.* Brown, 1996; Bapat *et al.*, 2000; Sala *et al.*, 2003; Arntzen *et al.*, 2004; Sunil Kumar *et al.*, 2005).

8.2. Allergenicity

Allergy to banana and plantain is increasingly identified, especially in some people adversely affected by latex, but as well in some people allergic to some tree or weed pollens (Magera *et al.*, 1997; Mikkola *et al.*, 1998; Grob *et al.*, 2002). Allergens are present in fresh fruit and refrigerated bananas, and in extracts — where the allergens may be concentrated (Magera *et al.*, 1997).

Appendix 1. Provisional classification of the wild species of *Musa* L. section *Musa*

Taxa (sections, species, subspecies, botanical varieties) (in some cases, a taxon's recognition or placement is tentative)	Natural distribution (approximate, sometimes incomplete)	References
♦ **Section *Musa* (*Eumusa*) (2*n* = 22)**		
Musa acuminata Colla [1]	Sri Lanka?, India to China, Indochina, Malesia (*i.e.* Malay Archipelago) and Northeast Australia	Cheesman, 1948b; De Langhe and Devreux, 1960; Nasution, 1991; Silva, 2000; Nasution and Yamada, 2001; Wong *et al*., 2001a; Wattanachaiyingcharoen *et al*., 2004; Boonruangrod *et al*., 2008, 2009
●● *M. acuminata* ssp. *burmannica* N.W. Simmonds synonym *M. acuminata* ssp. *burmannicoides* De Langhe [2]	India, Myanmar (formerly Burma), Thailand	De Langhe and Devreux, 1960; Horry and Jay, 1990; Shepherd, 1990; Carreel *et al*., 1994, 2002; Ude *et al*., 2002b; Uma and Buddenhagen, 2006; Boonruangrod *et al*., 2008; De Langhe, 2009
M. acuminata var. *chinensis* Häkkinen & H. Wang	China	Häkkinen and Wang, 2007; Häkkinen, 2008
● *M. acuminata* ssp. *siamea* N.W. Simmonds	China (Yunnan, Guangxi)?, Indochina, Thailand; Peninsular Malaysia?	Shepherd, 1990, 1999; Carreel *et al*., 1994, 2002; De Langhe *et al*., 2000; Asif Javed *et al*., 2001b, 2002; Wong *et al*., 2002
●● *M. acuminata* ssp. *malaccensis* (Ridley) N.W. Simmonds	Thailand, Peninsular Malaysia (lowlands), Indonesia (Sumatra, Java)	Shepherd, 1990; Nasution, 1991; De Langhe *et al*., 2000; Wong *et al*., 2001a; Asif Javed *et al*., 2002 Wattanachaiyingcharoen *et al*., 2004
M. acuminata var. *flava* (Ridley) Nasution	Peninsular Malaysia, Borneo (Kalimantan)	Simmonds, 1956; Nasution, 1991; Asif Javed *et al*., 2001b; Häkkinen and Väre, 2008c
● *M. acuminata* ssp. *truncata* (Ridley) Kiew	Peninsular Malaysia (highlands)	Shepherd, 1990; Asif Javed *et al*., 2001a, 2001b, 2002; Häkkinen and De Langhe, 2001; Wong *et al*., 2001a; Carreel *et al*., 2002; Ude *et al*., 2002b
M. acuminata var. *alasensis* Nasution	Indonesia (Sumatra)	Nasution, 1991
M. acuminata ssp. *halabanensis* (Meijer) M. Hotta	Indonesia (Sumatra)	Meijer, 1961; Nasution, 1991
M. acuminata var. *sumatrana* (Beccari ex André) Nasution	Indonesia (Sumatra)	Meijer, 1961; Nasution, 1991; Häkkinen and Väre, 2008c
M. acuminata var. *longepetiolata* Nasution	Indonesia (Sumatra)	Nasution, 1991
M. acuminata var. *bantamensis* Nasution	Indonesia (Java)	Nasution, 1991
M. acuminata var. *breviformis*	Indonesia (Java)	Nasution, 1991

Nasution		
●● *M. acuminata* ssp. *zebrina* (Van Houtte ex Planchon), comb. nov. ined.? synonym *M. acuminata* var. *zebrina* (Van Houtte ex Planchon) Nasution	Indonesia (Java)	Horry and Jay, 1990; Nasution, 1991; Carreel *et al*., 2002
M. acuminata var. *nakaii* Nasution	Indonesia (Java)	Nasution, 1991
M. acuminata var. *cerifera* (Backer) Nasution	Indonesia (Java)	Nasution, 1991
M. acuminata var. *rutilipes* (Backer) Nasution	Indonesia (Java, Bali)	Nasution, 1991; Häkkinen and Väre, 2008c
● *M. acuminata* ssp. *microcarpa* (Beccari) N.W. Simmonds	Borneo	Shepherd, 1990; Nasution, 1991; Häkkinen and De Langhe, 2001; Wong *et al*., 2001a; Carreel *et al*., 2002; Perrier *et al*., 2009
● *M. acuminata* ssp. *errans* (Blanco) R.V. Valmayor	Philippines	Shepherd, 1990; Valmayor, 2001; Carreel *et al*., 2002; Valmayor *et al*., 2004
M. acuminata var. *tomentosa* (Warburg ex K. Schumann) Nasution	Indonesia (Sulawesi)	Nasution, 1991; Häkkinen and Väre, 2008c
M. acuminata ssp. *acuminata*	Indonesia (Moluccas, New Guinea: Papua [formerly Irian Jaya])	Nasution, 1991
●● *M. acuminata* ssp. *banksii* (F. Mueller) N.W. Simmonds synonym *M. banksii* F. Mueller	New Guinea, Australia (Queensland)	Argent, 1976; Ross, 1987; Shepherd, 1990; Tezenas du Montcel, 1990; Wong *et al*., 2003; *cf.* Häkkinen and Väre, 2008c
Musa balbisiana Colla [3]	Sri Lanka?, India, Nepal, Myanmar, Thailand, Indochina, China, Philippines	Argent, 1976; Sharrock, 1990; Silva, 2000; Sotto and Rabara, 2000; Wu and Kress, 2000; Ge *et al*., 2005; Uma *et al*., 2005, 2006b; Uma and Buddenhagen, 2006; Wang *et al*., 2007; Boonruangrod *et al*., 2008; De Langhe, 2009; Väre and Häkkinen, 2009a; *cf.* Häkkinen and Väre, 2008c; Fuller and Madella, 2009
M. balbisiana var. *andamanica* D.B. Singh, Sreekumar, T.V.R.S. Sharma & A.K. Bandyopadhyay	India (Andaman Islands)	Singh *et al*., 1998; Uma and Buddenhagen, 2006
M. balbisiana var. *balbisiana*	(see distribution of species)	
Musa basjoo Siebold ex Iinuma	China [4]	Liu *et al*., 2002b; Turner *et al*., 2002; Häkkinen and Väre, 2008c, 2009
Musa cheesmanii N.W. Simmonds	India (Northeast); Nepal?	Simmonds, 1956; Häkkinen, 2008

Musa formosana (Warburg) Hayata synonym *M. basjoo* var. *formosana* (Warburg) S.S. Ying	Taiwan	Wu and Kress, 2000; Ying, 2000; Chiu *et al.*, 2004; *cf.* Häkkinen and Väre, 2008c
Musa griersonii Noltie	Bhutan	Noltie, 1994a, 1994b
Musa itinerans Cheesman — with 6+ varieties	India (Northeast), Myanmar, Thailand, Indochina, China	Wu and Kress, 2000; Liu *et al.*, 2002b; Valmayor *et al.*, 2005; Uma and Buddenhagen, 2006; Häkkinen *et al.*, 2008
Musa nagensium Prain — with 2 varieties	India (Northeast), Myanmar, China (Yunnan), Thailand	Liu *et al.*, 2002b; Uma and Buddenhagen, 2006; Häkkinen, 2008
Musa ochracea Shepherd	India (Northeast?)	Shepherd, 1999; Häkkinen and Väre, 2008c
Musa schizocarpa N.W. Simmonds	New Guinea	Argent, 1976; Tezenas du Montcel, 1990
Musa sikkimensis Kurz	India (Northeast), Bhutan; Myanmar, Thailand?	Simmonds, 1956; Noltie, 1994a; De Langhe *et al.*, 2000
Musa thomsonii (King ex Baker) A.M. Cowan & J.M. Cowan synonym *M. flaviflora* N.W. Simmonds	India (Northeast), Bhutan	Noltie, 1994a; Häkkinen and Wang, 2007; Häkkinen and Väre, 2008c
Musa yunnanensis Häkkinen & H. Wang — with 4 varieties	China (Yunnan)	Häkkinen and Wang, 2007, 2009; Häkkinen, 2008

[1] No comprehensive, modern study of *Musa acuminata* taxonomic diversity in the wild has been done. The listed botanical subspecies and varieties thus do not represent different degrees of evolutionary divergence (as has been discerned for example in *M. maclayi* — see Appendix 2), but simply reflect the unintegrated recognition of biological entities (taxa) by different researchers. The agronomically most well-known subspecies (noted with the symbol ● or ●●) and relatively more accepted subspecies (noted with the symbol ●●) (*cf.* Boonruangrod *et al.*, 2008, 2009; Perrier *et al.*, 2009) have been studied the most extensively, although primarily from a limited sample of germplasm accessions.

[2] *Musa acuminata* ssp. *burmannicoides*, which was presented by De Langhe and Devreux (1960), is not considered distinct from *M. acuminata* ssp. *burmannica* (Shepherd, 1990; Carreel *et al.*, 1994, 2002; Ude *et al.*, 2002b; Boonruangrod *et al.*, 2008, 2009). The name is based on accession Calcutta 4 from the Calcutta Botanic Garden, and considered to be a wild-type plant of unknown provenance in India or Myanmar; this germplasm has been propagated and utilised extensively in breeding and research.

[3] Two additional botanical taxa have been recognised by Häkkinen and Väre (2008c): *Musa balbisiana* var. *brachycarpa* (Backer) Häkkinen (Indonesia: Java); and *M. balbisiana* var. *liukiuensis* (Matsumura) Häkkinen (Japan: Ryukyu Islands: Okinawa). The genuinely natural range of *M. balbisiana* is unclear (*e.g.* De Langhe, 2009).

[4] Erroneously considered native in Japan (Liu *et al.*, 2002b; *cf.* Turner *et al.*, 2002).

Appendix 2. Provisional classification of the wild species of *Musa* L. sections *Ingentimusa*, *Rhodochlamys*, *Callimusa* and *Australimusa*, as well as *Incertae sedis* (section unknown)

Taxa (sections, species, subspecies, botanical varieties) (in some cases, a taxon's recognition or placement is tentative)	Natural distribution (approximate, sometimes incomplete)	References
♦ **Section *Ingentimusa* Argent (2*n* = 14)**		Argent, 1976; Wong *et al.*, 2003
Musa ingens N.W. Simmonds (2*n* = 14)	Papua New Guinea	Argent, 1976
♦ **Section *Rhodochlamys* Baker (2*n* = 22)**		Häkkinen and Sharrock, 2002; Häkkinen, 2003b, 2005b, 2007, 2009a; Uma *et al.*, 2006a; Häkkinen *et al.*, 2007c
Musa aurantiaca G. Mann ex Baker	India (Northeast), Myanmar, China (Tibet)	Uma *et al.*, 2006a; Häkkinen, 2007; Häkkinen and Väre, 2008a
Musa chunii Häkkinen	Myanmar, China (Yunnan)	Häkkinen, 2009b
Musa laterita Cheesman	India (Northeast), Myanmar, Thailand	Häkkinen, 2001, 2003b, 2007; Uma *et al.*, 2006a
Musa mannii H. Wendland ex Baker	India (Assam)	Häkkinen, 2007; Häkkinen and Teo, 2008
Musa ornata Roxburgh synonym *M. rosacea* Hort., non Jacquin	India, Bangladesh; Myanmar?	Sundararaj and Balasubramanyam, 1971; Argent, 1984; Alquini, 1987, 1988; Hore *et al.*, 1992; Uma and Buddenhagen, 2006; Uma *et al.*, 2006a; Häkkinen, 2007; Väre and Häkkinen, 2009a
Musa rosea Baker synonym *M. angcorensis* Gagnepain	Cambodia, Vietnam	Häkkinen, 2006c, 2007
Musa rubinea Häkkinen & Teo	China (Yunnan)	Häkkinen and Teo, 2008
Musa rubra Wallich ex Kurz	India (Mizoram), Myanmar	Häkkinen, 2003b, 2007, 2009b
Musa sanguinea Hooker f.	India (Northeast), China (Yunnan)	Liu *et al.*, 2002b; Uma *et al.*, 2006a; Häkkinen, 2007
Musa siamensis Häkkinen & R. H. Wallace	Thailand, Cambodia	Häkkinen, 2007; Häkkinen and Wallace, 2007, Häkkinen *et al.*, 2007c
Musa velutina H. Wendland & Drude or *Musa dasycarpa* Kurz [1]	India (Northeast), Myanmar	Uma *et al.*, 2006a; Häkkinen, 2007; Häkkinen and Väre, 2008b; Väre and Häkkinen, 2009b
Musa zaifui Häkkinen & H. Wang	China (Yunnan)	Häkkinen and Wang, 2008
♦ **Section *Callimusa* Cheesman (usually 2*n* = 20)**		Wong *et al.*, 2002; Häkkinen, 2004b, 2009a; Häkkinen *et al.*, 2007b
Musa azizii Häkkinen	Borneo (East Malaysia)	Häkkinen, 2005a

Musa barioensis Häkkinen	Borneo (East Malaysia)	Häkkinen, 2006a
Musa bauensis Häkkinen & Meekiong	Borneo (East Malaysia)	Häkkinen and Meekiong, 2004
Musa beccarii N.W. Simmonds ($2n = 18$) — with 2 varieties	Borneo (East Malaysia)	Wong *et al.*, 2001b; Häkkinen, 2004b; Häkkinen *et al.*, 2005, 2007a, 2007b
Musa borneensis Beccari — with 6 varieties; includes *M. flavida* M. Hotta	Borneo (East Malaysia, Brunei, Kalimantan)	Häkkinen and Meekiong, 2005
Musa campestris Beccari — with *ca.* 6 varieties	Borneo (East Malaysia, Brunei, Kalimantan)	Häkkinen, 2003a, 2004a, 2004c
Musa coccinea Andrews synonym *M. uranoscopos* sensu Loureiro, non Rumphius ?	China, Indochina	Wu and Kress, 2000; Argent and Kiew, 2002; Liu *et al.*, 2002b; Häkkinen and Väre, 2008c
Musa exotica R.V. Valmayor	Vietnam	Danh *et al.*, 1998; Valmayor, 2001; Valmayor *et al.*, 2004
Musa gracilis Holttum ex Cheesman	Peninsular Malaysia	Kiew, 1987
Musa hirta Beccari	Borneo (East Malaysia)	Häkkinen, 2004b
Musa lawitiensis Nasution & Supardiyono — with 4 varieties; includes *M. suratii* Argent	Borneo (East Malaysia, Brunei, Kalimantan)	Wong *et al.*, 2001b; Häkkinen, 2006b
Musa lokok Geri & Ng	Borneo (East Malaysia)	Geri and Ng, 2005
Musa monticola M. Hotta ex Argent	Borneo (East Malaysia)	Wong *et al.*, 2001b
Musa muluensis M. Hotta	Borneo (East Malaysia)	Häkkinen, 2004b
Musa paracoccinea A.Z. Liu & D.Z. Li	China, Vietnam	Liu *et al.*, 2002b
Musa pigmaea M. Hotta, nom. nud.	Borneo (East Malaysia, Kalimantan)	Häkkinen, 2004b; Häkkinen *et al.*, 2005
Musa salaccensis Zollinger ex Backer	Indonesia (Sumatra, Java)	Meijer, 1961; Nasution, 1993; Häkkinen and Väre, 2008c, 2009
Musa splendida A. Chevalier	Vietnam	Valmayor *et al.*, 2004
Musa tuberculata M. Hotta	Borneo (Brunei)	Häkkinen, 2004b
Musa violascens Ridley	Peninsular Malaysia	Kiew, 1987
Musa voonii Häkkinen	Borneo (East Malaysia)	Häkkinen, 2004b
♦ Section *Australimusa* Cheesman ($2n = 20$)		Sharrock, 2001; Wong *et al.*, 2002, 2003
Musa alinsanaya R.V. Valmayor	Philippines	Valmayor, 2001; Valmayor *et al.*, 2004

Musa angustigemma N.W. Simmonds synonym *M. peekelii* ssp. *angustigemma* (N.W. Simmonds) Argent	Papua New Guinea	Jarret *et al*., 1992
Musa boman Argent	Papua New Guinea	Argent, 1976
Musa bukensis Argent	Papua New Guinea	Argent, 1976
Musa fitzalanii F. Mueller	Australia (Queensland)	Ross, 1987
Musa insularimontana Hayata	Taiwan	Wu and Kress, 2000; Ying, 2000; Chiu *et al*., 2007
Musa jackeyi W. Hill	Australia (Queensland)	Ross, 1987
Musa johnsii Argent	Indonesia (New Guinea: Papua [formerly Irian Jaya])	Argent, 2001
Musa lolodensis Cheesman	Indonesia (Moluccas), New Guinea	Argent, 1976; Nasution, 1993
Musa maclayi F. Mueller ***ex*** Miklouho-Maclay	Papua New Guinea	Argent, 1976
M. maclayi ssp. *ailuluai* Argent		
M. maclayi ssp. *maclayi*		
M. maclayi ssp. *maclayi* var. *erecta* (N.W. Simmonds) Argent		
M. maclayi ssp. *maclayi* var. *maclayi*		
M. maclayi ssp. *maclayi* var. *namatani* Argent		
Musa peekelii Lauterbach	Papua New Guinea	Argent, 1976
Musa textilis Née	Philippines	Valmayor *et al*., 2002
♦ ***Incertae sedis***		
Musa lutea R.V. Valmayor, L.D. Danh & Häkkinen	Vietnam	Valmayor *et al*., 2004
Musa sakaiana Meekiong, Ipor & Tawan	Borneo (East Malaysia)	Meekiong *et al*., 2006
Musa tonkinensis R.V. Valmayor, L.D. Danh & Häkkinen	Vietnam	Valmayor *et al*., 2005
Musa viridis R.V. Valmayor, L.D. Danh & Häkkinen	Vietnam	Valmayor *et al*., 2004

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[1] *Musa velutina* is not the earliest name for this species, but the earlier name *Musa dasycarpa* has seldom been used, and there is a recent formal nomenclatural proposal to conserve *Musa velutina* as the accepted name (Väre and Häkkinen, 2009b).

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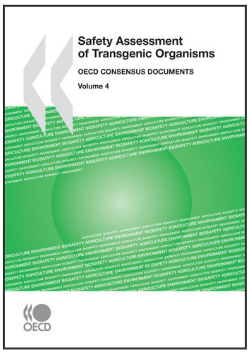

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