



Why Bananas Matter: An introduction to the history of banana domestication

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Research

Why is the History of Banana Domestication Important?

The multi-disciplinary contributions to this volume are all dedicated to the history of banana (*Musa* spp.) domestication and its significance. Wild bananas of the genus *Musa* have undergone a complex domestication history that has only been partially unravelled and remains to be fully elucidated. This volume is the first attempt to synthesise the latest 'state of the art' research across a range of disciplines (either in combination or separately), including contributions from archaeobotany, genetics, linguistics and phytogeography.

Bananas are a key domesticate of subsistence farmers across the wet tropics and subtropics, including today the Americas, Africa, South Asia, mainland and Island Southeast Asia, Melanesia and the Pacific. Although bananas are one of the most important commercial crops in the world, it is estimated that 87% of banana production is for local food consumption (Bioversity International 2008). Apart from the hundreds of fully domesticated banana varieties, of which many are grown outside their natural range, an uncertain number of varieties cultivated today are still in various stages of domestication, because they are still inter-fertile with wild surrounding populations that continually introduce new genetic material into cultivated stock.

An understanding of the history of banana domestication is important for several reasons.

Firstly, the history of *Musa* spp. domestication is extremely complex, occurred over thousands of years and involved multiple stages, often separated in time and place (Carreel *et al.* 2002, De Langhe & de Maret 1999). The process exhibits the antiquity over which people have affected the natural course of plant evolution in the tropics and subtropics, whether intentionally or unintentionally.

Secondly, the ways people began to use, transplant and cultivate bananas are a window on a broader set of poorly-defined human-environment relationships, namely, how people began to increasingly manage and alter plant resources for food and other uses in tropical rainforests. Plant exploitation practices in tropical rainforests led to the emergence and dispersal of distinctive forms of agriculture in several regions of the world, including the lowland neotropics (Piperno & Pearsall 1998) and New Guinea (Denham *et al.* 2003, Golson 1991). However, the development of plant exploitation practices into agriculture and the attendant social, environmental and morphogenetic transformations are only beginning to be understood for tropical agriculture, particularly for those forms dependent upon vegetative forms of propagation.

Many vegetatively propagated plants – such as most bananas, manioc (*Manihot esculenta* Crantz), potato (*Solanum tuberosum* L.), sweet potato (*Ipomoea batatas* (L.) Lam.), taro (*Colocasia esculenta* (L.) Schott) and yams (*Dioscorea* spp.) - do not yield abundant pollen or har-

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dier plant macrofossils, such as wood, nuts or seeds, that are readily preserved at archaeological sites. The archaeobotany of these soft-tissued plants has awaited the development of several microscopic techniques focused on parenchyma (Hather 1994), phytoliths (Piperno 2006) and starch granules (Torrence & Barton 2005) that survive in certain burial environments following death and decomposition of the plants. Consequently, archaeobotanical investigations of the histories of exploitation and domestication of these food plants, such as bananas, have only been possible following the advent and application of these techniques (e.g., Fullagar *et al.* 2006, Mbida *et al.* 2001, Perry 2004).

Conversely, and this is a third reason why banana domestication is relevant to a wide array of issues, bananas are not only the result of complex genetic modifications and processes, but they also bear unique testimony to the early, long-term and deep impacts of people on rainforests. Just as the long-term occupation of tropical rainforests has made them anthropic environments, so too the long-term manipulation and management of specific plant resources within rainforests, such as bananas, has influenced the evolution of these plants.

Fourthly, multi-disciplinary evidence for the histories of banana domestication and dispersal enables the crop plant to be used as a marker of human processes. For example, archaeobotanical evidence of *Musa* bananas in areas beyond the natural range of the genus, especially Africa, is indicative of introduction, adoption and dispersal by people in the distant or recent past (Neumann & Hildebrand 2009, Vrydaghs & De Langhe 2003, Vrydaghs *et al.* 2003). Additionally, when archaeobotanical evidence is taken in conjunction with plant genetics and historical linguistics, robust chronologies of edible banana generation and dispersal can be established, such as the inferred movement of bananas from New Guinea to eastern Indonesia in the mid-Holocene (Denham & Donohue 2009, Donohue & Denham 2009a, Kennedy 2008).

Lastly, a close examination of a large number of banana cultivars – including the interaction between plant and habitat, human uses and modes of cultivation, as well as the reconstruction of the exact domestication pathway of popular banana varieties – is of crucial importance for breeding programmes (Daniells *et al.* 2001). Through the identification and retention of the entire range of banana domesticates, it is hoped that breeding will be able to generate improved hybrids, while simultaneously retaining the desired fruit and plant qualities.

In equatorial and sub-equatorial regions, bananas will need to continue to meet food demand, which is forecast to dramatically increase in many African and Asian countries. In order to increase plant production, the first target of breeders is to ensure resistance to biotic stresses, such as pests and diseases, which are the major limitations to

banana production in low input systems. Moreover, the quantity of pesticides commonly used in intensive cropping systems is excessive and unsustainable given socio-economic conditions, thereby necessitating the development and diffusion of resistant cultivars. A second target is the promotion of resistance to abiotic stresses, such as drought and cold, in order to extend the cultivated area or, at least, to stabilize production in the face of anthropogenic climate change. In addition to these two sets of targets, there are strong constraints on the improvement of banana varieties; these include the desire for conformity in the fruit crop under subsistence and cash cropping (i.e., in terms of taste, color and culinary properties), as well as the problem of sterility in many diploid and triploid cultivars. These constraints limit breeders to a narrow path for banana improvement that mimics in large part the longer-term domestication process.

Classification and Distribution of Key Species

Primary Diversity: Musaceae

The family Musaceae is composed of the genera *Musa*, *Ensete* and, possibly a third, *Musella*. All edible banana fruits are produced by plants belonging to the genus *Musa*.

The natural distribution of the genus *Musa* stretches in the north from Nepal and southern mountainous China (Simmonds 1956), and in the south to the southern islands of Indonesia and New Guinea, with an outlier in the wet tropical rainforests of Queensland. The western limit is India, with an outlier on Pemba Island near the East African coast. To the east, wild *Musa* were recorded in Melanesia, with an outlier on Samoa. Both these outliers, on Pemba and Samoa, could be anthropogenic (see De Langhe 2009). No wild *Musa* have been recorded on the African continent or in the Americas. These boundaries define the area of primary (natural) diversity of *Musa*.

The genus *Ensete* ($2x = 18$) is sympatric with *Musa* in Asia, but covers most of tropical Africa as well (Simmonds 1962) (note that $2x$ refers to the chromosome number at diploid state of the nucleus). Varieties of the African species *Ensete ventricosum* (Welw.) Cheesman have been domesticated in Ethiopia as a source for starch, which is accumulated in a pseudo-corm at the base of the leaves. The fruits of these cultivars have more pulp than in the wild varieties, but their starch is of relatively minor importance for consumption (Hildebrand 2003, 2007).

The classification of *Musa lasiocarpa* Franch. is currently uncertain, as it could represent a third, monospecific genus, *Musella* (Wu 1976). It is rare and found only in mountainous Southeast Asia.

Primary Diversity: *Musa*

The genus *Musa* has been classified into four Sections (Figure 1; after Simmonds 1962). These sections, and their distributions, are as follows:

- Section Eumusa (sometimes called 'Musa') (2x = 22) covering the entire primary diversity area, except Eastern Melanesia;
- Section Rhodochlamys (2x = 22) in monsoonal mainland Southeast Asia;
- Section Australimusa (2x = 20) from southeastern Indonesia and southern Philippines to Melanesia;
- Section Callimusa (2x = 20), mainly in the lowlands of the central part (southern Vietnam, Peninsular Malaysia, Borneo, and Sumatra).

Some authors consider 'Rhodochlamys' as a subsection of Eumusa (Shepherd 1999). Rhodochlamys species are closer to *Musa acuminata* Colla than *Musa balbisiana* Colla; specifically the Rhodochlamys species *Musa laterita* Cheesman is very close to *Musa acuminata* ssp. *burmanica* Simmonds and ssp. *siamea* Simmonds.

A recent attempt at merging the Sections Callimusa and Australimusa into one Section under the name 'Callimusa', and based on AFLP analysis (Wong *et al.* 2002), is controversial and is not followed in this introduction. The morphology and habitat of the two sections are very different. Australimusa are giant plants while Callimusa are moderate to small plants which grow in lowland and even marshland areas. In order to avoid confusion, it is for the moment recommended that the two sections are differentiated, until much more comprehensive DNA analysis can be undertaken to investigate the issue. In the present volume, the authors were free to choose which classification system they preferred.

In the Section Eumusa, a striking and significant fact is the contrast in the natural distributions of the two founding species of the common edible bananas, *M. acuminata* and *M. balbisiana* (Figure 2). *Musa acuminata* covers almost the entire Eumusa area except for the northern periphery, whereas *M. balbisiana* is confined to the northern periphery and perhaps the Philippines.

Wild-looking *M. balbisiana* plants in most low altitude regions are considered to be anthropogenic; they were probably introduced by people interested in the utilization of non-fruit parts. Simmonds (1956) demonstrated this for Indonesia and lowland Southeast Asia, and Argent (1976) for Papua New Guinea. The occurrence of the species in

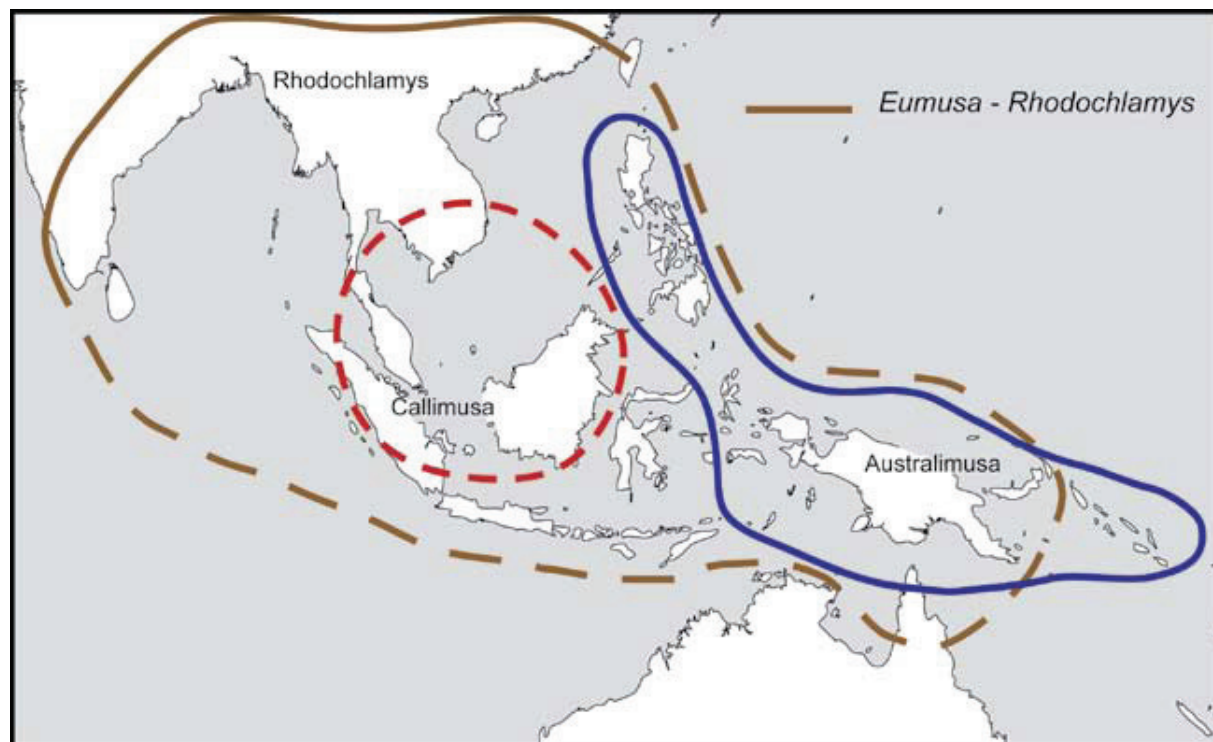


Figure 1. Geographical distribution of the main Sections of the genus *Musa* (Simmonds 1962). Some boundaries of Callimusa and Australimusa (western limit) are uncertain.

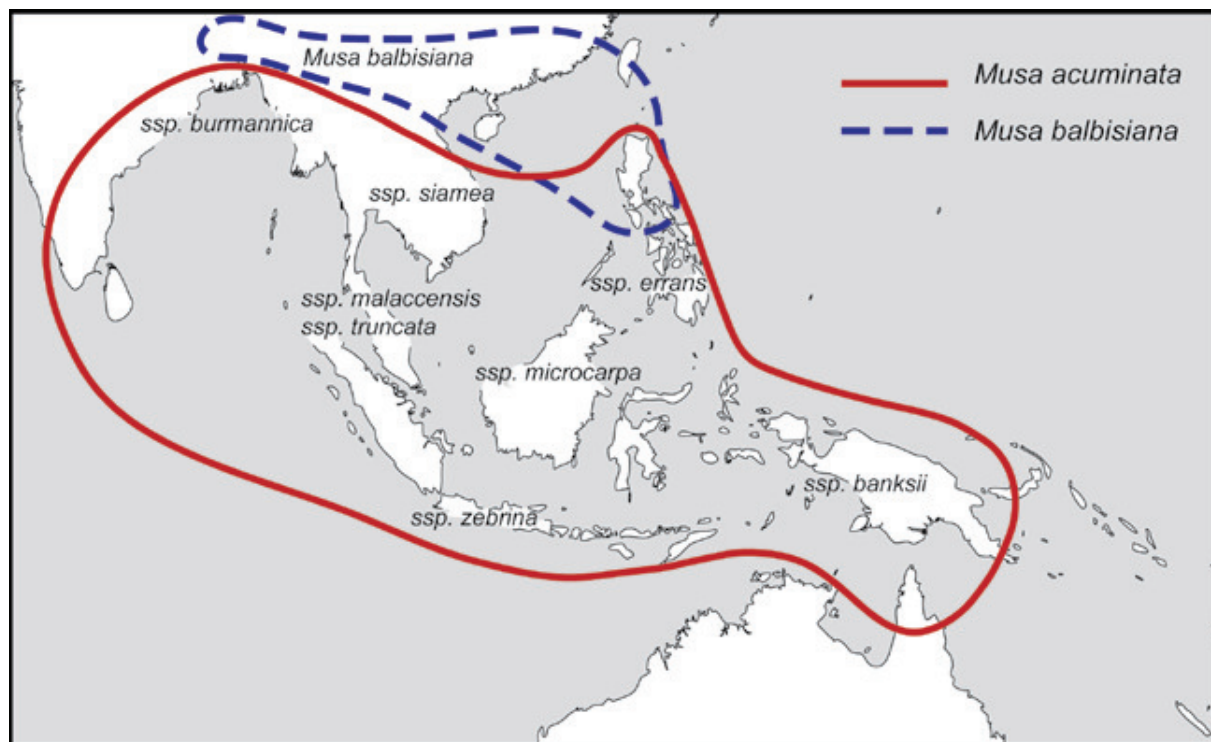


Figure 2. Geographical distribution of the main species and subspecies ancestral to common edible bananas.

several areas of India could be natural or anthropogenic. There are competing hypotheses that the plants had dispersed naturally across southern India during more humid periods (Fuller & Madella 2009) or through human-aided dispersal (De Langhe 2009), with current plant populations being confined to humid refugia separated by drier areas. Of relevance, the occurrence of parthenocarpy in *M. balbisiana* was considered to be unlikely for decades. However, some semi-edible *M. balbisiana* diploids (BB) seem to exist in India, such as the 'Bhimkol', and other examples have been reported in Eastern Indonesia (Valmayor, pers. comm.). The possible role of edible *M. balbisiana* diploids in the generation of edible triploids has been neglected so far, but should be viewed as restricted to a very few regions.

The plants of *M. balbisiana* are vigorous, even at low altitudes, and they can thrive in various natural environments. They are readily crossable with several other *Musa* species, including *M. acuminata*, but the hybrids are generally sterile (Simmonds, 1962). However, such vigorous hybrids can easily be propagated vegetatively, thereby explaining the existence of many edible banana hybrids of *M. balbisiana* and *M. acuminata*. These hybrids combine vigor with various fruit pulp qualities that may have attracted early banana growers.

Morphologic variation within *M. acuminata* is extensive and has been exhaustively studied for breeding purposes because of its close genetic affinity with the commer-

cial bananas, 'Gros Michel' up until the 1940s and 'Cavendish' cultivars since then (Simmonds 1959). Simmonds (1956) found that each of the major variants of *M. acuminata* is confined to a geographical region and proposed the term 'subspecies' for this diversity (see Figure 2). Not all of this diversity has been documented and some ill-described taxa, such as *Musa sumatrana* Becc., probably belong to this species as well. Moreover, the status and genetic signature of some subspecies, such as ssp. *microcarpa* (Becc.) Simmonds and ssp. *errans* (Blanco) R.V.Valmayor, still require further genetic clarification (Perrier *et al.* 2009). For example, one *M. acuminata* form typical of the higher altitudes of Peninsular Malaysia was erroneously considered by Simmonds (1956) to form part of the ssp. *microcarpa* (Shepherd 1990); it has since been considered to be another subspecies with the name *truncata* (Ridl.) Kiew. (Daniells *et al.* 2001) although there is no legitimate botanical description. Moreover, ssp. *errans* was only recently proposed as such (Valmayor 2001); it had previously been considered a variety of ssp. *banksii* (F. Muell.) Simmonds. Since the genetic analysis of ssp. *errans* is restricted to a single specimen of uncertain origin, the genetic basis of the distinction between ssp. *errans* and ssp. *banksii* has yet to be established (Perrier *et al.* 2009).

A few, mostly tetraploid edible banana varieties in the Melanesia-Philippines region show some characteristics of the species *Musa schizocarpa* Simmonds (Section *Eumusa*) and *Musa textilis* Née (Section *Australimusa*) be-

sides those of the major contributing *M. acuminata* and *M. balbisiana*. However, the contribution of *M. schizocarpa* and *M. textilis* to the generation of edible bananas is very minor and probably relatively recent.

Secondary and tertiary diversity: Edible bananas, the basic pattern

It is important to distinguish varieties that are the direct products of domesticated wild species and hybrids, and those that are somatic mutants produced subsequently through clonal propagation over a time-span of centuries or perhaps even millennia. The former group represents a secondary diversity and the latter group is the product of tertiary (somaclonal) diversification. Since almost all diploid and triploid edible bananas are derived from one or two of the species *M. acuminata* (A) and *M. balbisiana* (B), they are classified in the groups AA, AAA, AAB and ABB, according to the relative participation of the respective genomes in the genotype (Simmonds & Shepherd 1955).

New Guinea and surrounding islands, potentially as far north as Mindanao of the Philippines, form the most likely location of earliest banana domestication, with *M. acuminata* ssp. *banksii* and *Musa maclayi* F. Muell. ex Mikl.-Maclay (an *Australimusa* species with several varieties) as the basic taxa.

Domestication of *M. maclayi* led to the generation of the rather unique **Fe'i** bananas in the Pacific, which are traditionally absent anywhere else. The starchy yellow-orange pulp is rich in carotene precursors, but the generally massive pseudostems demand a relatively longer maturation time before bearing fruit. These bananas have been displaced for the most part by bananas derived from the section *Eumusa* and are therefore not considered further.

Domestication of the *M. acuminata* ssp. *banksii* probably generated semi-edible diploid bananas (AA) for a long time. DNA-marking has further indicated that the subspecies must have played a major role in the generation of many common edible diploids and triploids (Perrier *et al.* 2009). It is thus plausible that human contacts in the New Guinea region and across the Sunda area caused natural hybridization of the semi-edible AA with other *acuminata* subspecies, thus eventually generating the current complex edible AA/AAA-pattern typical for Island Southeast Asia (Denham & Donohue 2009). The possibility of a simultaneous early expansion of edible AA cultivars into the Near Pacific should not be overlooked (also see Kennedy 2008).

The first hybridizations of edible AA with *M. balbisiana* may have occurred with the arrival in eastern Indonesia and Melanesia of Austronesian speaking ancestors coming from Taiwan (De Langhe 2009, De Langhe & De Maret 1999), although others propose models which do not invoke such a large-scale mass migration (Donohue & Den-

ham 2009b). These hybridizations would have generated the basic cultivars of two important AAB subgroups: the African Plantains and the **Maia maoli-Popoulu-Iholena** (also called 'Pacific Plantains'). The ubiquitous presence of the latter in Oceania is almost certainly due to colonization and dispersal by Austronesian-speaking voyagers into the Pacific, with tertiary diversification generating numerous cultivars.

The African Plantains apparently underwent a sustained tertiary diversification in Africa over a long time, judging from the large number of cultivars that have never been recorded elsewhere (Blench 2009, De Langhe 2007). The movement of these plantains from Southeast Asia to Africa, which is necessarily due to human intervention, remains a matter of much speculation. Southern India is probably another region of secondary and tertiary diversification, judging from the variety in edible AB diploids which have not been recorded elsewhere, and the typical AAB triploids of Indian origin, with somaclonal variants (Fuller & Madella 2009).

A special case in terms of banana cultivars are the many 'Highland AAA' cultivars in East Africa which have not been recorded elsewhere. Some edible AA, and even AAA, in New Guinea show similar morphologies. However, rather than necessarily being an introduction, it is possible that secondary diversification took place in Africa through the inter-crossing of semi-edible AA that were introduced in a distant period. Again, an understanding of these botanical processes requires a more precise (pre)history of the responsible people in order that we can more fully reconstruct how this particular genome-type was generated.

The generation of ABB cultivars is also not self-evident. The logical pathway 'AB x BB → ABB' looks plausible for South Asia with the edible ABs in southern India. The absence of edible ABs in mainland Southeast Asia and the Philippines calls for more complex ABB formation processes via crosses and back crosses. Although the existence of BBB was excluded by Simmonds (1962), at least one subgroup of cultivars in the Philippines, the '**Saba**' subgroup, may express a BBB genome constitution (Valmayor *et al.* 1981), and its generation may have occurred along the pathway 'BB x B → BBB'.

Secondary and tertiary diversifications have produced the following geographical distributions of high cultivar density (Figure 3):

1. most of the edible AA and AAA: the triangle 'Indonesia-Philippines-Melanesia', with exceptional AA-density in New Guinea and around;
2. the altitude-adapted Highland AAA: the Great Lakes region in East Africa;
3. the AAB Plantains: the rainforest zone in Africa;
4. the AAB **Maia maoli-Popoulu-Iholena**: Oceania;
5. the AB and other AAB: South India;

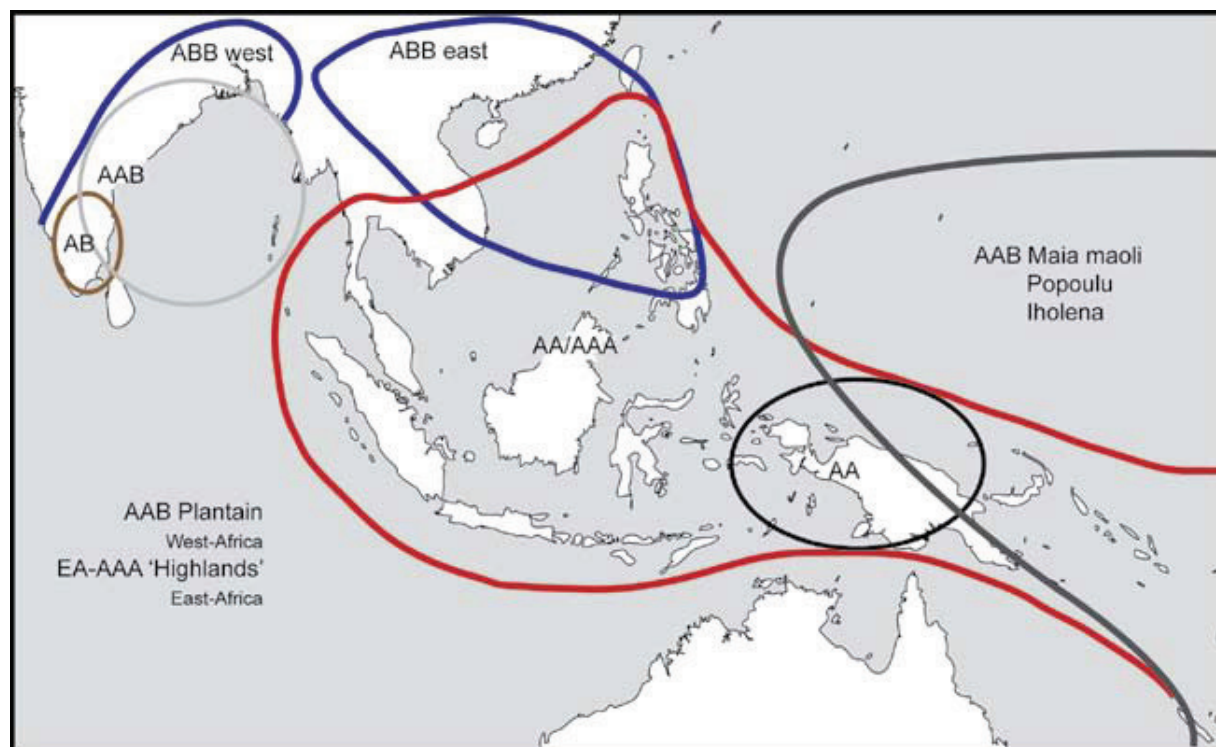


Figure 3. Geographical distribution of the main banana cultivar groups.

6. an eastern ABB subgroup (a part of this subgroup is considered by some specialists to be the BBB genome-type; Valmayor *et al.*, 1981): Philippines and Vietnam; and,
7. a western ABB subgroup: Northeast India and South India.

The cultivar groupings (3) to (5) indicate that while all plantains are AABs, not all AABs are 'plantains'. The misconception that 'all AABs are plantains' is rather persistent in literature and creates much confusion. Equally confusing is the concept of the B genome being solely responsible for starchy bananas. Numerous AA and AAA bananas in New Guinea produce starchy fruits like most of the East-African Highland AAA bananas. Even some ABB subgroups, generally with starchy bananas, contain mutants with 'dessert' quality, for example, among the '**Pisang awak**' cultivars of Thailand.

Edible Bananas. The confusing current pattern

The basic pattern explained above has been obscured in many regions during the last two millennia due to various colonizations, diffusionary processes and population movements.

The presence of several Indian AAB and ABB cultivars in mainland and Island Southeast Asia may be linked to the eastern expansion of Indian civilizations, such as that of the Palava Dynasty from the first centuries AD. For ex-

ample, the Malaysian name **Pisang radjah** is applied to more than one cultivar. It is likely that Rajas at different places had their own preference, and that their subjects began to name each cultivar '**Pisang radjah**' (the banana of the Raja). This aspect of cultivar nomenclature is potentially a very important subject of investigation for linguists, in collaboration with banana taxonomists, in order to reconstruct the likely processes of 'cultivar expansion' (e.g., Blench 2009, Donohue & Denham 2009b).

In later times, Arabic civilizations dominated trade across the Indian Ocean and could have been responsible for the first introduction in East Africa of Indian-derived, and potentially some Island Southeast Asian-derived, cultivars in East Africa. Still later, Portuguese traders seem to have been instrumental in the introduction of some AAB/ABB cultivars to West Africa (Blench 2009).

The remarkably rapid post-Columbian dispersal of plantains and other bananas in Latin America, originally from Africa via the slave trade, is supposed to be well known. Yet, the precise origin of generic terms for bananas in South America, such as **platano** and **bacova**, are still a matter of conjecture, showing that the articulated history of the banana odyssey in America remains vague. Consequently, speculation regarding the possible pre-Columbian existence of bananas in South America can still not be efficiently addressed, although an earlier introduction of at least a few cultivars by Polynesians voyaging across the Pacific remains a possibility (Koeppel 2008, Langdon

1993). For example, the AAB cultivar 'Pompo', rather popular in Colombia, is a Pacific Plantain of the **Maia Maoli-Popoulu** subgroup, although its origin is obscure.

Finally, and during the nineteenth century, several sweet banana cultivars, such as 'Gros Michel' and the 'Cavendish' subgroup, were introduced 'from east to west' in the former British and French empires. Once again, however, the exact place of origin and dispersal routes are not firmly established (Champion 1967:65,70), although the colonial history of at least one Cavendish cultivar has been elucidated (Koeppel 2008). Research focused on 'the banana' in historical documents and, perhaps, during excavations would clarify a situation in which the basic pattern of banana history is currently blurred.

Domestication Terminology for Bananas

While banana domestication has been a relatively continuous process, distinct stages in the alteration of utilized plants can be distinguished from the botanical and genetic data. Although these stages are not always clearly demarcated in space and time, current and future discussions of the domestication process for bananas, and potentially other plants, would greatly benefit from an agreed upon set of terms reflecting each of the major stages.

Wild: Any fully sexually fertile *Musa* individual or population growing naturally within the natural habitat, or range, of the species to which it belongs. These wild species and populations represent the primary diversity of *Musa*.

Foragers regularly visited and exploited the population for various uses (medicinal, fibre and even food). At this stage, there is no botanical or genetic means to distinguish *Musa* populations utilized by people from those that were not. Although natural sexual propagation is likely to be the dominant form of reproduction, accidental vegetative propagation by people, animals and geomorphological processes should not be excluded, for example, suckers partly consumed by animals and abandoned elsewhere with intact meristem tip.

Cultiwild: Any member of a wild population, or its direct fertile derivatives, whether cloned or not, growing outside the natural habitat, or range, of the species to which it belongs. The concept embraces a continuum of human intervention involving increasing transformation through selection and propagation.

People may have transplanted around settlements suckers from preferred wild plants. Clones may have been preferentially selected for fruit quality or other beneficial or sought attributes. Through vegetative propagation, each originally selected plant became a clone. However, people may also have carried bunches for pulp-consump-

tion in a settlement. Chewing the fruit and spitting out the seeds leaves the latter in good condition (largely due to the remaining pulp enzymes) for germination. As a result of these processes, the cultiwild population in and around a settlement would become a mixture of seedlings and clones.

If people grew cultiwilds from different origins in their area of subsistence, the cultiwild population would be heterogeneous. Spontaneous hybridization could have led to hybrids and back-crosses, and the generation of new plants. If people moved to other areas or regions, and carried with them the propagules of favoured cultiwilds, they may have augmented the resource base in their new environment and considerably widened the overall cultiwild germ plasm.

The specific uses of each cultiwild may have been quite diverse, and food may have remained a minor use. Sustained clonal propagation of cultiwild diploids would eventually have changed fruit morphology and provided a basis for reproducing parthenocarpic individuals; such human selection could also have lowered seed fertility to a variable degree. If sustained cloning over centuries of banana plants of the genus *Musa* triggers the same mechanisms as in *Ensete ventricosum* (Welw.) Cheesman clones in Africa (Hildebrandt 2003), decreases in sterility are very likely. With continued human selection, the clones would progressively dominate local banana populations and the term cultiwild would no longer be appropriate.

Naturalized: Any member of a cultiwild population that was abandoned by humans, but survived in the area through sexual propagation.

Non-cloned cultiwilds would morphologically be indistinguishable from the original wild specimen. Cloned 'cultiwilds' would either have died out (if sterility was severe) or progressively have returned to the fertile and non-parthenocarpic 'wild' stage, as has been noted for naturalized *E. ventricosum* plants (Hildebrandt 2003). It is also possible that some translocated plants became naturalized and may have reverted back quite quickly to some sort of natural fertility.

Basic Cultivar (clone): A selected clone from a cultiwild population, which became popular in and beyond its original area of existence as a result of diffusion, migration and so on.

During the probably millennia-long evolution from a pure cultiwild population to a set of selected clones, many other clones may have existed for a while but were abandoned. In regions where the diffusion of plants occurred, either through exchange or accompanying human migration, hybridization between cultiwild populations and still partly fertile clones from different origins led to the generation of (a) more sterile intersubspecific AA diploids, and (b) the

more vigorous and nearly sterile triploids (AAA first, then AAB and later on ABB). Selection among these new diploids and the triploids produced a new set of basic cultivars. Different regions would thus have generated and become characterized by different sets of basic cultivars (as witnessed in chapters through this volume).

Derived Cultivar: A clone with a slightly different morphology and presumed to stem vegetatively from somatic mutation of the basic cultivar.

The most popular and widespread form of cultivated bananas is supposed to be the basic cultivar. But the distinction between a basic and a derived cultivar is not always clear. In some places, derived cultivars may have become more popular than basic cultivars. The application of genetic techniques may hopefully clarify these distinctions in different regions. In any case, these phases in the domestication process are part of a continuum and plants may have interacted at various stages. Semi-wild and vegetative species have probably coexisted and interacted for a long time.

'Groups' are the different genome assemblies: AA, AAA, AAB and ABB that constitute the entire spectrum of edible bananas. The term 'Subgroup' refers to the total set of a basic cultivar and its derived clones. Some subgroups appear to have been generated in regions distant from the primary (natural) distribution of *Musa*. These distant regions are equally referred to as secondary and tertiary diversity centres and for bananas include the following subgroups: African Plantains, Pacific Plantains and East African Highland AAA bananas.

Derived cultivars can undergo somatic mutation, thus leading to new derived cultivars. Such processes account for the observed complex ramification in several popular subgroups of cultivated bananas today.

Rainforests, Biodiversity, Long-time Depths and the Impact of People

If edible bananas and their amazing diversity are an artefact, their history is closely linked to another artefact, the rainforest. Although the rainforest has become a symbol of unspoiled nature, there is no 'virgin' or 'primeval' tropical forest, devoid of human footprint (Willis *et al.* 2004). Even if it does not exist anymore, the concept of a tropical forest without people is necessary to understand how tropical ecosystems function, and thus how they have been impacted and gradually managed. In doing so, we will shed light on the early history of the bananas.

Of course, there were rainforests long before people. The majority of the species, as well as the interactions that produced and perpetuated them, that created the rainforest had nothing to do with our ancestors. Today, in one

way or another, rainforests have been transformed by human actions, but the effects of these transformations can only be understood if we know what was there initially to be transformed (Hladik *et al.* 1993, McKey 2000).

Furthermore in order to protect the present day rainforest, and to predict the future evolution of communities and ecosystems in this time of climatic change, an evolutionary approach to ecology provides a useful source of insights needed for long term resource management (Janzen 1998). However, our understanding of the early human occupation of the rainforests of the world is still very much in its infancy (Froment & Guffroy 2003, Mercader 2003).

On most maps, tropical forest appears as a large uniformly green area. But in reality, the rainforest is a mosaic, a complex, diverse and dynamic reality. It is less a green desert than a biodiversity paradise with a patchwork of biotopes. Biodiversity is at all levels higher than in most other ecosystems, and there is evidence that human disturbance if not too intense or frequent, can enhance that diversity (e.g., Denham & Barton 2006).

Rainforests are also fragile and they keep lasting traces of climatic changes and of human impacts (Maley 2002, Vincens *et al.* 1999). During the Late Pleistocene, dry phases repeatedly reduced considerably the size of the tropical forest around the globe, around 60 kya, 40 kya, 25-11 kya (Dupont *et al.* 2000, Maley 2004, Sémah & Renault-Miskovsky 2004, Sultan *et al.* 2001, Van der Hammen & Hooghiemstra 2000). During the Last Glacial Maximum in Central Africa, for example, the rainforest at ~20 kya had almost disappeared except for a few crucial refugia that are still biodiversity hotspots, from where rainforest species expanded once climatic conditions improved and stabilized during the Holocene. Climatic changes also influenced sea levels during the Pleistocene and Holocene (Lambeck & Chappell 2001). All these environmental transformations must have had impacts on the long term evolution of bananas primarily through their effects on gene flow or isolation.

Wild *Musa* species attracted human interest in such a way that initially unconscious and subsequently conscious selection took place. We do not know when this domestication process started and we are unsure which characteristics of wild *Musa* species prompted human care. However, we know that early crops may not have always been grown for food. Many parts of the banana plant, like leaves, are used for practical purposes (Kennedy 2009), or potentially for ritual. Indeed, ritual use has often been the engine for change. Clay, for example, was used to shape statuettes more than 10,000 years before pottery (Vandiver *et al.* 1989). The same seems to be the case with the development of architecture or metallurgy. The earliest forms of plant and animal domestication were not aimed at food production (Cauvin 1994), e.g., bottle gourd

(Erickson *et al.* 2005) and dog (Vila *et al.* 1997). In any case, domesticated plants result from a long coevolutionary process between human cultural practices and plant biology.

The domesticated segment of biodiversity has attracted much less attention than 'wild' biodiversity. The processes that create and maintain this diversity are poorly understood at the population level. This is particularly true for vegetatively propagated crops that dominate many tropical forest agroecosystems, such as cassava, bananas, sweet potatoes, yam and taro (McKey 2000).

In traditional agroecosystems in the rainforests of the world, each plot of land is home to high biodiversity, with often several dozen different plant species and distinct varieties of the same crop. Farmers, like the Makushi Amerindians in Guyana with cassava, promote this genetic diversity by using the 'sexual reproduction of the plant, without managing it, to generate a diversity of genotype, and then "freeze" selected combinations by clonal propagation' (Elias *et al.* 2000, McKey 2000:25, Pujol *et al.* 2002). The possibility that similarly early banana cultivators kept experimenting with new varieties resulting from spontaneous hybridization in the wild should not be overlooked and may explain some of the present day genetic diversity of *Musa*. The adoption of a multi-disciplinary approach to unravel this complex domestication history may serve as a model for understanding the dynamics of genetic diversity in other vegetatively propagated crops. It may also lead to a "deeper appreciation of agroecosystems as arenas for ecological and evolutionary interactions, not only as habitats but also at the landscape level" (McKey 2000:25).

Documenting Domestication

The contributions to this volume provide a comprehensive and state of the art overview of the multiple lines of evidence pertaining to the history of banana domestication. Jean Kennedy (2009) provides an ethnobotanical overview of the use of bananas within traditional societies to show that *Musa* bananas have not been used, or presumably domesticated, solely for food. Following this, Xavier Perrier and colleagues (CIRAD, France)(2009) present a synthesis of previous and new studies of molecular investigations of wild and cultivated bananas.

Several papers present innovative developments in the techniques applied to materials and samples collected at archaeological sites. Developments in microfossil applications focus on the ability, or not, to discriminate the leaf phytoliths (Vrydaghs *et al.* 2009), seed phytoliths (Lentfer 2009a) and starch granules (Lentfer 2009b) of subspecies (principally among *M. acuminata* ssp.), species and sections (different *Musa* spp.) and genera (*Musa* versus *Ensete*), as well as potential problems (Neumann & Hildebrand 2009). More systematic approaches to plant macrofossils comprise a key for the classification of seeds

(De Langhe 2009) and the identification of pseudostem impressions in slag (Iles 2009). Three papers draw on historical linguistics, to varying degrees in concert with archaeobotany, genetics and phytogeography, to illuminate regional histories of banana dispersal for Melanesia and Island Southeast Asia (Donohue & Denham 2009b), India (Fuller & Madella 2009) and West Africa (Blench 2009).

Although much remains to be revealed regarding the history of banana domestication and dispersal, this synthetic and multi-disciplinary volume marks a major step forward in current understanding.

An Agenda for the Future

In advocating the conservation of what is left of the world's tropical rainforest, one usually emphasizes their role as a major reservoir of biodiversity and as a crucial carbon store. In so doing, one overlooks their significance in the history of humankind and the very early role of these ecosystems in the domestication process. At this stage, it is the history of banana domestication which provides us a first glimpse of the various processes involved in this emerging and complex topic.

Vegetatively propagated crops often have a critical role in the subsistence base of people inhabiting rainforests. Among them, bananas and their (pre)history have received more attention than other plants. Bananas are thus the best available indicator to understand the early stages of plant domestication within tropical rainforests.

How did natural selection, human selection and gene flow, due to both natural processes and exchanges of plant material by people, interact over millennia to generate today's varietal diversity? With recent progress in biomolecular and archaeological research, it is obvious that the early stages of the process of bananas domestication were complex and remain far from clear. In order to move forward, we should focus on three crucial themes.

1. The natural dispersal of bananas

We need from biogeography a much more detailed picture of the original wild distribution of bananas and their dispersal mechanisms:

- seeds and pollen
- role of birds, bats, mammals
- role of climate variation and sea level changes
- role of human disturbance and *Musa* as a pioneering species
- habitat preferences, i.e., to what extent are bananas pioneering species?

2. The early stage of the domestication process

In many ways, to phrase the issue in archaeological terms, the key question is: How to distinguish banana as ecofact

from banana as artefact? Did it happen in one place, or was it multicentric?

3. The human dispersal of bananas

At what stage in the domestication process did humans start to propagate bananas and how did they begin to move them around? Then, after the initial steps, how and when did the long distance, transoceanic and transcontinental dispersals occur?

As this volume illustrates, significant progress has been made in the last decade regarding the history of banana. If we want to keep the present momentum we need to take a multi-disciplinary approach much further.

- We need from biomolecular studies more fine sequencing, as this changes our perspective on the very early stages of domestication.
- We need from archaeobotany improved, and the more widespread application of, macrofossil and microfossil methods in order to distinguish subspecies, species, sections and genera of bananas.
- We need from ethnobotany more research documenting the various uses and cultivation practices for bananas.
- We need from linguistics a much greater understanding of comparative terms for banana plants and plant parts.
- From archaeology, we need more excavations in crucial areas, starting in the vast area between China, the Philippines, Indonesia and New Guinea.

Literature Cited

Argent, G.C.G. 1976. The wild bananas of Papua New-Guinea. *Notes of the Royal Botanical Gardens of Edinburgh* 35:77-114.

Bioversity International 2008. *Not a funny fruit*. <http://bananas.bioversityinternational.org/content/view/52/77/lang,en/>.

Blench, R. 2009. Bananas and plantains in Africa: Re-interpreting the linguistic evidence. *Ethnobotany Research and Applications* 7:363-380.

Carreel, F., D. Gonzalez de Leon, P. Lagoda, C. Lanaud, C. Jenny, J.-P. Horry & H. Tezenas du Montcel. 2002. Ascertaining maternal and paternal lineage within *Musa* chloroplast and mitochondrial DNA RFLP analyses. *Genome* 45:679-692.

Cauvin, J. 1994. *Naissance des divinités, naissance de l'agriculture*. CNRS Editions, Paris.

Champion J. 1967. *Les bananiers et leur culture*. Tome I. Botanique et génétique des bananiers. Institut Français

de Recherches Fruitières Outre-Mer (I.F.A.C.). Editions SETCO, Paris.

Daniells J., C. Jenny, D. Karamura & K. Tomekpe. 2001. *Musalogue: A catalogue of Musa germplasm. Diversity in the Genus Musa*. Compiled and edited by E. Arnaud & S. Sharock. International Network for the Improvement of Banana and Plantain, Montpellier.

De Langhe, E. 2007. The establishment of traditional plantain cultivation in the African rain forest: a working hypothesis. Pp. 361-70 in *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*. edited by T.P. Denham, J. Iriarte & L. Vrydaghs. Left Coast Press, Walnut Creek.

De Langhe, E. 2009. Relevance of banana seeds in archaeology. *Ethnobotany Research and Applications* 7:271-281.

De Langhe, E. & P. de Maret. 1999. Tracking the banana: Its significance in early agriculture. Pp. 377-96 in *The Prehistory of Food: Appetites for Change*. Edited by C. Gosden & J. Hather. Routledge, London.

Denham, T.P. & H. Barton 2006. The emergence of agriculture in New Guinea: Continuity from pre-existing foraging practices. Pp. 237-64 in *Behavioral Ecology and the Transition to Agriculture*. Edited by D.J. Kennett & B. Winterhalder. University of California Press, California.

Denham, T.P. & M. Donohue. 2009. Pre-Austronesian dispersal of banana cultivars west from New Guinea: Linguistic relics from eastern Indonesia. *Archaeology in Oceania* 44:18-28.

Denham, T.P., S.G. Haberle, C. Lentfer, R. Fullagar, J. Field, M. Therin, N. Porch & B. Winsborough. 2003. Origins of agriculture at Kuk Swamp in the Highlands of New Guinea. *Science* 301:189-193.

Donohue, M. & T.P. Denham. 2009a. Island Southeast Asia during the mid-Holocene: Reframing Austronesian history. *Current Anthropology*. In Press.

Donohue, M. & T.P. Denham. 2009b. Banana (*Musa* spp.) domestication in the Asia-Pacific region: Linguistic and archaeobotanical perspectives. *Ethnobotany Research and Applications* 7:293-332.

Dupont, L.M., S. Jahns, F. Marret & S. Ning. 2000. Vegetation change in equatorial West Africa: Time-slices for the last 150 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology* 155:95-122.

Elias, MA., L. Rival & D. McKey. 2000. Perception and management of cassava (*Manihot esculenta* Crantz) di-

De Langhe et al. - Why Bananas Matter: An introduction to the history of banana domestication 175

- versity among Makushi Amerindians of Guyana (South America). *Journal of Ethnobotany* 20:239-265.
- Erickson, D.L., B.D. Smith, A.C. Clarke, D.H. Sandweiss & N. Tuross. 2005. An Asian origin for a 10,000 year-old domesticated plant in the Americas. *Proceedings of the National Academy of Sciences USA* 102:18315-18320.
- Froment, A. & J. Guffroy. 2003. Editors of *Peuplements anciens et actuels des forêts tropicales*. IRD Editions, Paris.
- Fullagar, R., J. Field, T.P. Denham & C. Lentfer. 2006. Early and mid Holocene tool-use and processing of taro (*Colocasia esculenta*), yam (*Dioscorea* sp.) and other plants at Kuk Swamp in the highlands of Papua New Guinea. *Journal of Archaeological Science* 33:595-614.
- Fuller, D. & M. Madella. 2009. Banana cultivation in South Asia and East Asia: A review of the evidence from archaeology and linguistics. *Ethnobotany Research and Applications* 7:333-351.
- Golson, J. 1991. The New Guinea Highlands on the eve of agriculture. *Bulletin of the Indo-Pacific Prehistory Association* 11:82-91.
- Hather, J. 1994. Editor of *Tropical Archaeobotany*. Routledge, London.
- Hildebrand, E. 2003. *Enset, Yams, and Honey: Ethnoarchaeological approaches to the origins of horticulture in southwest Ethiopia*. PhD dissertation, Department of Anthropology, Washington University in St. Louis.
- Hildebrand, E. 2007. A tale of two tuber crops: How attributes of Enset and Yams may have shaped prehistoric human-plant interactions in Southwest Ethiopia. Pp. 273-298 in *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*. Edited by T.P. Denham, J. Iriarte & L. Vrydaghs,. One World Archaeology 51. Left Coast Press, Walnut Creek
- Hladik, C.M., A. Hladik, O.F. Linares, H. Pagezy, A. Semple & M. Hadley. 1993. Editors of *Tropical Forests, People and Food. Biocultural Interactions and Applications to Development*. Man and the Biosphere Series 13. Parthenon Publishing Group, Paris: UNESCO and Pearl River, New York.
- Iles, L. 2009. Impressions of banana pseudostem in iron slag from eastern Africa. *Ethnobotany Research and Applications* 7:283-291.
- Janzen, D. 1998. The gardenification of the wildland nature and the human footprint. *Science* 279:1312-1313.
- Kennedy, J. 2008. Pacific bananas: Complex origins, multiple dispersals? *Asian Perspectives* 47:75-94.
- Kennedy, J. 2009. Bananas and people in the homeland of genus *Musa*: Not just pretty fruit. *Ethnobotany Research and Applications* 7:179-197.
- Koeppel D. 2008. *Banana. The Fate of the Fruit that Changed the World*. Hudson Street (Penguin), New York.
- Lambeck, K. & J. Chappell. 2001. Sea level change through the last glacial cycle. *Science* 292:679-686.
- Langdon, R. 1993. The banana as a key to early American and Polynesian history. *Journal of Pacific History* 28:15-35.
- Lentfer, C.J. 2009a. Tracing domestication and cultivation of bananas from phytoliths: An update from Papua New Guinea. *Ethnobotany Research and Applications* 7:247-270.
- Lentfer, C.J. 2009b. Going bananas in Papua New Guinea: A preliminary study of starch granule morphotypes in Musaceae fruit. *Ethnobotany Research and Applications* 7:217-238.
- Maley, J. 2002. A catastrophic destruction of African forests about 2,500 years ago still exerts a major influence on present vegetation formations. *IDS Bulletin* 33:13-30.
- Maley, J. 2004. Les variations de la végétation et des paléoenvironnements du domaine forestier africain au cours du Quaternaire récent. Pp. 143-176 in *L'évolution de la végétation depuis deux millions d'années*. Edited by A.-M. Semah & J. Renault-Miskovsky. Editions Artcom, Paris.
- Mbida, C.M., H. Doutrelepont, L. Vrydaghs, R.L. Swennen, R.J. Swennen, H. Beeckman, E. de Langhe & P. de Maret. 2001. First archaeological evidence of banana cultivation in central Africa during the third millennium before present. *Vegetation History and Archaeobotany* 10:1-6.
- McKey, D. 2000. Tropical forest peoples and biodiversity. Pp. 12-32 in *Les peuples des forêts tropicales aujourd'hui, vol. II Une approche thématique*. Edited by S. Bahuchet. Final Report Avenir des Peuples des Forêts Tropicales. Université Libre de Bruxelles, Brussels.
- Mercader, J. 2003. Editor of *Under the Canopy. The Archaeology of the Tropical Rain Forests*. Rutgers University Press, New Brunswick, New Jersey and London.
- Neumann, K. & E. Hildebrand. 2009. Early bananas in Africa: The state of the art. *Ethnobotany Research and Applications* 7:353-362.
- Perrier, X., F. Bakry, F. Carreel, Ch. Jenny, J.P. Horry, V. Lebot & I. Hippolyte. 2009. Combining biological ap-

- proaches to shed light on evolution of edible bananas. *Ethnobotany Research and Applications* 7:199-216.
- Perry, L. 2004. Starch analyses reveal the relationship between tool type and function: An example from the Orinoco valley of Venezuela. *Journal of Archaeological Science* 31:1069-1081.
- Piperno, D.R. 2006. *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists*. AltaMira, Lanham, Maryland.
- Piperno, D.R. & D.M. Pearsall. 1998. *The Origins of Agriculture in the Lowland Neotropics*. Academic Press, San Diego.
- Pujol, B., G. Gigot, G. Laurent, M. Pinheiro-Kluppel, M. Elias, M. Hossaert-McKey & D. McKey. 2002. Germination ecology of cassava (*Manihot esculenta* Crantz, Euphorbiaceae) in traditional agroecosystems: Seed and seedling biology of a vegetatively propagated domestic plant. *Economic Botany* 56:366-379.
- Sémah, A.-M. & J. Renault-Miskovsky. 2004. Editors of *L'évolution de la végétation depuis deux millions d'années*. Editions Artcom-Errance, Paris.
- Shepherd, K. 1990. Observations on *Musa* taxonomy. Pp. 158-165 in *Identification of Genetic Diversity in the Genus Musa: Proceedings of an International Workshop held at Los Baños, Philippines 1988*. Edited by R.L. Jarred. International Network for the Improvement of Banana and Plantain, Montpellier, France.
- Shepherd, K. 1999. *Cytogenetics of the Genus Musa*. International Network for the Improvement of banana and plantain, Montpellier.
- Simmonds N.W. 1956. Botanical results of the banana collecting expedition, 1954-5. *Kew Bulletin* 11:463-490.
- Simmonds N.W. 1959. *Bananas*. Longmans, London.
- Simmonds N.W. 1962. *The Evolution of the Bananas*. Tropical Science Series. Longmans, London.
- Simmonds, N.W. & K. Shepherd. 1955. The taxonomy and origins of the cultivated bananas. *Journal of the Linnean Society (Botany)* 55:302-312.
- Sultan, B., E. Servat, J. Maley & G. Mahé. 2001. Interrelations entre les forêts tropicales et la variabilité climatique: Une synthèse des études récentes. *Sécheresse* 14:221-229.
- Torrence, R. & H. Barton. 2005. Editors of *Ancient Starch Research*. Left Coast Press, Walnut Creek.
- Valmayor R.V., F.N. Rivera & F.M. Lomoljo. 1981. *Philippine Banana Cultivar Names and Synonyms*. NPGRL, Institute of Plant Breeding Bulletin No. 3. University of the Philippines at Los Bânos, Los Bânos.
- Valmayor, R.V. 2001. Classification and characterization of *Musa exotica*, *M. alinsanaya* and *M. acuminata* ssp. *errans*. *The Philippine Agricultural Scientist* 84:325-331.
- Van Der Hammen, T. & H. Hooghiemstra. 2000. Neogene and Quaternary history of vegetation, climate and plant diversity in Amazonia. *Quaternary Sciences Reviews* 19:725-742.
- Vandiver, P.B., O. Soffer, B. Klima & J. Svoboda. 1989. The origins of ceramic technology at Dolni Vestonice, Czechoslovakia. *Science* 246:1002-1008.
- Vila, C., P. Savolainen, J.E. Maldonado, I.R. Amorim, J.E. Rice, R.L. Honeycutt, R.L. Crandall, J. Lundeberg & R.K. Wayne. 1997. Multiple and ancient origins of the domestic dog. *Science* 276:1687-1689.
- Vincens, A., D. Schwartz, H. Elenga, I. Reynaud-Farrera, A. Alexandre, J. Bertaux, A. Mariotti, L. Martin, J.-D. Meunier, F. Nguetop, M. Servat, S. Servat-Vildary & D. Wirrmann. 1999. Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes. *Journal of Biogeography* 26:879-885.
- Vrydaghs, L. & E. De Langhe. 2003. Phytoliths: An opportunity to rewrite history. Pp. 14-17 in *INIBAP Annual Report 2002*. International Network for the Improvement of Banana and Plantain, Montpellier.
- Vrydaghs, L., R.R. Swennen, C. Mbida, H. Doutrelepont, E. De Langhe & P. de Maret. 2003. The banana phytolith as a direct marker of early agriculture: A review of the evidence. Pp. 177-85 in *Phytolith and Starch Research in the Australia - Pacific - Asian Regions: The State of the Art. Terra Australis* 19. Edited by D.M. Hart & L.A. Wallis. Pandanus Books, Research School of Pacific and Asian Studies, Australian National University, Canberra.
- Vrydaghs, L., T. Ball, H. Volkaeart, I. van den Houwe, J. Manwaring & E. De Langhe. 2009. Differentiating the volcaniform phytoliths of bananas: *Musa acuminata*. *Ethnobotany Research and Applications* 7:239-246.
- Willis, K.J., L. Gillson & T.M. Brncic. 2004. How 'virgin' is virgin rainforest? *Science* 304:402-403.
- Wong, S., R. Kiew, G. Argent, O. Set, S.K. Lee & Y.Y. Gan. 2002. Assessment of the validity of the Sections in *Musa* (Musaceae) using ALFP. *Annals of Botany* 90:231-238.

De Langhe et al. - Why Bananas Matter: An introduction to the history of banana domestication 177

Wu C.Y. 1976. *Musella lasiocarpa*. Pp. 580-582 in *Iconographia Cormophytorum Sinicorum. Tomus V*. Science Press, Beijing.

