Australian Government
Department of Health and Ageing
Office of the Gene Technology Regulator

The Biology of *Musa* L. (banana)

[Photo credit: Janet Gorst, OGTR]

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This document provides an overview of baseline biological information relevant to risk assessment of genetically modified forms of the species that may be released into the Australian environment.

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PREAMBLE

This document describes the biology of *Musa* L. with particular reference to the Australian environment, cultivation and use. Information included relates to the taxonomy and origins of cultivated *Musa* spp., general descriptions of their morphology, reproductive biology, biochemistry, and biotic and abiotic interactions. This document also addresses the potential for gene transfer to occur to closely related species. The purpose of this document is to provide baseline information about the parent organism for use in risk assessments of genetically modified (GM) *Musa* spp. that may be released into the Australian environment.

In this document, the general term 'banana' is used to encompass cultivated varieties of the genus *Musa* that fall into one of two sub-groups (Pillay et al. 2004): the sweet or dessert banana which makes up approximately 43% of world production, and the cooking banana which makes up approximately 57%. The general term 'plantain; is applied to a specific subgroup of cooking bananas (Valmayor et al. 2000). The yellow sweet banana cultivars most commonly found in western greengrocers are the focus of this Biology document. Sweet bananas in general, however, show enormous diversity in terms of plant stature and fruit size, and fruit colour extends from yellow and green to red and orange (Ploetz et al. 2007).

Bananas are a major food crop globally and are grown and consumed in more than 100 countries throughout the tropics and sub-tropics (INIBAP 2000). In developing countries they are the fourth most important food crop after rice, wheat and maize (INIBAP 2000). Worldwide, over 1,000 banana cultivars or landraces are recognized (Heslop-Harrison & Schwarzacher 2007). The banana plant is a tall arborescent monocotyledon with a false stem (pseudostem) consisting of leaf sheaths and an underground true stem (corm) that is able to produce suckers by which the plant can reproduce vegetatively. Each pseudostem produces a single inflorescence the female flowers of which give rise (either parthenocarpically[1] or following fertilization) to the banana fruits.

SECTION 1 TAXONOMY

The genus name *Musa* is thought to be derived from the Arabic name for the plant (*mouz*) which, in turn, may have been applied in honour of Antonius Musa (63 – 14 BC), physician to Octavius Augustus, first emperor of Rome (Hyam & Pankhurst 1995). The name 'banana' is derived from the Arabic *banan* = finger (Boning 2006) and was thought to be used in Guinea (West Africa) concomitant with the introduction of the fruit by the Portuguese. The name then spread to the New World (Cheesman 1948).

The genus *Musa* is a member of the family Musaceae, which includes at least one other genus (*Ensete*) and, depending upon the affiliations of the taxonomist, may also include the monotypic genus *Musella* (Constantine & Rossel 2001). All genera are monocotyledons and, as such, are technically defined as 'herbs' even though some species can grow up to 15 m tall (see Section 3.1).

[1] Parthenocarpy is the development of the ovary of a flower into a fruit without fertilization. Fruits thus formed are typically but not necessarily seedless.

The unresolved taxonomy at the family level continues down to the genus level and there are inconsistencies in the number of sections and number of species proposed for inclusion in the genus *Musa.* This has largely been brought about by the domestication of the fruit-bearing cultivars and the subsequent temporal and genetic separation from the original species, as well as the widespread vegetative reproduction in the genus and natural occurrence of many hybrids (Heslop-Harrison & Schwarzacher 2007). Assigning Linnean binomials[2] to cultivated *Musa* is, in the opinion of some, meaningless and has resulted in such binomials being assigned to taxa that are now known to be well-defined hybrid groups or even cultivars (Constantine & Rossel 2001). For example, the sweet banana was assigned the binomial *Musa sapientum* by Linnaeus but it was shown later that the 'type' plant was, in fact, a cultivar of a complex hybrid (Cheesman 1948). A genome nomenclature was proposed in 1955 (Simmonds & Shepherd 1955) and later revised in 1987 (Silayoi & Chomchalow 1995). This system basically assigns a score for selected morphological features but also requires chromosome counts in order to assign plants to a genome group (Pillay et al. 2004). The system is discussed further on pages 4 and 5 of this Biology document.

The number of sections[3] within *Musa* is between 3 – 5 and the number of species within *Musa* is between 35 – 50 (Constantine & Rossel 2001). Cheesman (1947) first proposed the grouping of the genus *Musa* into four sections, with the grouping being based on morphological characteristics:

> *Eumusa* (now *Musa* (Wong et al. 2002)) and *Rhodochlamys* (both sections containing species with 2n = 2x = 22); and
>
> *Callimusa* and *Australimusa* (both sections containing species with 2n = 2x = 20).

Argent(1976) proposed that one species, *M. ingens* from Papua New Guinea, with an 'anomalous' chromosome number (2n = 2x = 14) should be placed in a new section that was termed *Ingentimusa*. In a further study using principal co-ordinate and clustering techniques Simmonds & Weatherup (1990) found that their results did not support Argent's proposal and that *M. ingens* was more closely allied to several members of the *Musa* section. Some considerations (Daniells et al. 2001) place *M. ingens* in *Incertae sedis*[4].

Recent studies using amplified fragment length polymorphism in an examination of the relationships among the sections *Musa, Rhodochlamys, Callimusa* and *Australimusa* (material from *M. ingens* was not available), determined that the genetic differences between sections grouped in the same chromosome number were actually smaller than the differences found within an individual section (Wong et al. 2002). As a result it was proposed that only two sections, *Callimusa* and *Musa,* based solely on chromosome number, should be recognised but others maintain that further study is required before Cheesman's (1947) four sections are abandoned (Ploetz et al. 2007).

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[2] The eighteenth century Swedish naturalist Carl Linnaeus devised a binomial system, still used today, for naming organisms; the name is formed by the combination of two 'Latinised' words: a) the genus name and b) the descriptive specific epithet (e.g. *Musa acuminata*).

[3] According to the International Code of Botanical Nomenclature, the term 'section' is a secondary rank that is applied below the genus level and above the species level.

[4] *Incertae sedis* is a a general term used to describe species in an uncertain taxonomic position

A Taxonomic Advisory Group for *Musa* was formed by the International Network for Banana and Plantain in 2006 (TAG 2006). Nine action points were considered at the first meeting including a review of the taxonomic status and nomenclature of *Musa*.

A listing of species that may be considered to be a part of the *Musa* genus is given in Table 1 (note that there are more than 50 species but the list contains species that are doubtful). There are two species native to Australia[5] (see Section 8) - *M. acuminata* subsp. *banksii* and *M. jackeyi* - with a third species, *M. fitzalanii* thought to exist only as a herbarium specimen (Ross 1987; Pollefeys et al. 2004).

Table 1. Indicative listing of the possible species in *Musa*.*

Chromosome number	Section	'Minor' Section	Species	Main Distribution
2n=2x=14	*Ingentimusa*		*M. ingens*	Papua New Guinea
2n=2x=20	*Callimusa*	*Callimusa*	*M. angcorensis*[a]	Cambodia
			M. bauensis	Borneo
			M. borneënsis	Bornes
			M. campestris	Indonesia, Borneo
			M. coccinea	China, Indochina, Indonesia, Vietnam
			M. exotica	Vietnam
			M. flavida	Borneo
			M. gracilis	Malaysia
			M. lawitiensis	Borneo
			M. paracoccinea	China, Vietnam
			M. pigmaea	Borneo
			M. salaccensis	Indonesia
			M. splendida[a]	Vietnam
			M. suratii	Borneo
			M. violascens	Malaysia
		Australimusa	*M. alinsanaya*	Philippines
			M. angustigemma[b]	Papua New Guinea
			M. beccarii[c]	Borneo
			M. boman	Papua New Guinea
			M. bukensis	Papua New Guinea
			M. fitzalanii[a]	**Australia**
			M. hirta	Indonesia, Borneo
			M. insularimontana[a]	Taiwan
			M. jackeyi	**Australia**
			M. johnsii	Papua New Guinea
			M. lolodensis	Papua New Guinea
			M. maclayi	Papua New Guinea
			M. monticola	Borneo
			M. muluensis	Borneo
			M. peekelii	Papua New Guinea, Philippines
			M. textilis	Philippines, Brunei, Moluccas
			M. tuberculata	Borneo
			Fe'i cultivars[d]	New Guinea
2n=2x=22	*Musa*	*Musa*	***M. acuminata***[e]	India, Indonesia, Malaysia, Philippines Sri Lanka, Thailand, Vietnam, **Australia**
			M. balbisiana	Philippines, Bhutan, China, India, Vietnam, Papua New Guinea, Sri Lanka
			M. basjoo	Japan, China
			M. cheesmanii	India

[5] The Australian bush food commonly known as 'Bush Banana' (*Leichardtia australis*) is not, in fact, related to *Musa*.

Chromosome number	Section	'Minor' Section	Species	Main Distribution
			M. flaviflora	Bangladesh, Bhutan, India
			M. halabanensis	Indonesia
			M. itinerans	China, India, Thailand, Vietnam
			M. nagensium	China, India, Thailand
			M. ochracea	
			M. schizocarpa	Indonesia, Papua New Guinea
			M. sikkimensis	Bangladesh, Bhutan, India, Thailand
			M. griersonii	Bhutan
		Rhodochlamys	*M. aurantiaca*	India
			M. laterita	India, Burma, Thailand
			M. mannii	India
			M. ornata	Bangladesh, Burma, India, Borneo
			M. rosea	Bangladesh, Burma
			M. rubra	Burma, India
			M sanguinea	Northern India, Burma, China
			M. thomsonii[a]	India
			M. velutina	Northern India

[There is still uncertainty about the taxonomy of *Musa* and this table may overestimate the number of species and the number of sections. The species are grouped into 3 sections although the existence of *Ingentimusa* is arguable. The possible sub-division into 5 sections is indicated by the inclusion of the column headed 'minor' section, although it should be noted that this is not a recognized classification terminology. There is also uncertainty about which section some species belong in]

[a] These species are very poorly known and may not exist (Constantine & Rossel 2001)
[b] These species have been classified as subspecies of *M. peekelii* (Daniells et al. 2001)
[c] *M. beccarii* is placed by some in *Australimusa* (Wong et al. 2002) and others in *Callimusa* (Ploetz et al. 2007)
[d]The Fe'i bananas are widely distributed throughout the Pacific islands, from the Moluccas to Hawaii and Tahiti and their domestication is thought to have occurred independently of other bananas and plantains (Sharrock 2000). Their origin is controversial (Pillay & Tripathi 2007).
[e] *M. acuminata* is regarded by some to comprise a number of subspecies, namely *banksii, burmannica, burmannicoides, errans, malaccensis, macrocarpa, truncata, siamea, zebrina* (Horry et al. 1997; Daniells et al. 2001)

* Information in the table was compiled from a number of sources (Simmonds & Weatherup 1990; INIBAP 2000; Sharrock 2000; Constantine & Rossel 2001; Hakkinen & Sharrock 2001; Pollefeys et al. 2004; Ploetz et al. 2007)

Sections *Callimusa* and *Rhodochlamys* consist of non-parthenocarpic species that have no nutritionally valuable fruits and are important only as ornamentals (Pillay & Tripathi 2007). Most of the cultivated sweet bananas and plantains belong to the Section *Musa* and are triploid varieties that evolved from two wild diploid species, *M. acuminata*, given the genome designation 'AA', and *M. balbisiana*, given the genome designation 'BB' (Simmonds & Shepherd 1955).

The formation of homogenomic triploid (2n=3x) hybrids with the AAA genotype occurred within *M. acuminata* (see Section 2.1) leading to the development of cultivars that mostly comprise the sweet bananas (Daniells et al. 2001). Chloroplast DNA of *Musa* spp. is transmitted maternally, while mitochondrial DNA is transmitted paternally. The use of this feature in phylogenetic studies has suggested that the origin of the edible banana cultivars is linked particularly to two sub-species of *M. acuminata*, namely *M. acuminata* subsp. *banksii* and *M. acuminata* subsp. *errans* (Horry et al. 1997).

Crosses of the diploid and triploid types of *M. acuminata* with *M. balbisiana* led to the formation of heterogenomic triploid hybrids that are mostly plantains (AAB genotype) and other cooking bananas (ABB genotype). Tetraploid (2n=4x) and other

diploid combinations also exist (Pillay et al. 2004). Hybrids of *M. acuminata* and M. *balbisiana* can be referred to as *Musa* x *paradisiaca*[6] [(Espino et al. 1992) see also article H10.2 in ICBN (2000)] as *M. paradisiaca* was the name first given to the 'type' banana by Linnaeus who did not recognise that it was a hybrid. The use of isozymes and molecular markers has confirmed the multi-specific origin of edible bananas (Visser 2000). Studies using restriction polymorphisms of the chloroplast and mitochondrial DNA suggest that species of the section *Rhodochlamys* may constitute a secondary genepool for the improvement of cultivated bananas (Nwakanma et al. 2003).

Simmonds and Shepherd (1955) suggested that genome nomenclature was more appropriate for naming taxa and proposed that the generic name be followed by a letter combination indicating the ploidy and the genome sets, followed by the cultivar/cultivar group[7] name (Table 2). The cultivars in each subgroup show little genetic diversity and are derived from each other through somatic mutations (Horry et al. 1997).

Table 2. Examples of genome nomenclature for some common banana cultivars (with emphasis on cultivars grown in Australia)*

Genome Group	Subgroup	Example of common cultivar name[a]
AA	Sucrier	'Sucrier'; 'Lady's Finger'[b]
AB	Ney Poovan	Lady's Finger[b]
AAA	Cavendish	'Giant Cavendish' (e.g. 'Williams', 'Mons Mari')
		'Grande Naine'
		'Dwarf Cavendish'[c]
		'Extra Dwarf Cavendish' (e.g. 'Dwarf Parfitt')
	Gros Michel	'Gros Michel'
	Red	'Red Dacca'
AAB	Maoli-Popoulu	'Pacific Plantain'
	Mysore	'Mysore'
	Plantain	'French', 'Pisang Ceylan'
	Pome	'Lady's Finger'[b]
	Silk	'Sugar'
ABB	Bluggoe	'Bluggoe', 'Mondolpin'
	Ney Mannan	'Blue Lubin'; 'Blue Java'
	Pisang Awak	'Ducasse'; 'Kluai Namwa Khom'
AAAB		FHIA-01[d] ('Goldfinger'); FHIA-18 ('Bananza')

[a] Common names vary depending on the country
[b] 'Lady ('s) Finger' has been used to name at least four distinct AA, AB and AAB clones; genome group AAB subgroup Pome represents the cultivar that makes up about 4% of Australian production
[c] Dwarf Cavendish is the most widely distributed clone of edible banana worldwide (Ploetz et al. 2007)
[d] FHIA = varieties bred at the Fundación Hondureña de Investigación Agrícola in Honduras
* information taken from (Ploetz et al. 2007)

[6] The prefix 'x' in front of the epithet indicates the hybrid nature of the species
[7] The word 'cultivar' is a contraction of 'cultivated variety' and describes a group of cultivated plants within a species that are significant in agriculture, forestry or horticulture and have clearly distinguished, heritable characteristics. 'Cultivar' is synonymous with the term 'variety'. However it is not analogous with the category 'botanical variety' that is used to refer to naturally occurring variants within a species (Hartmann & Kester 1975). Cultivars/varieties mentioned in this document are indicated in quotation marks eg. 'Cavendish'.

Pillay et al. (2004) point out that there are two other genomes not considered by Simmonds and Shepherd (1955) – the 'S' genome present only in the diploid *M. schizocarpa*, and the 'T' genome characteristic of species found in section *Australimusa.* For this reason Pillay et al. (2004) consider that the classification system of Simmonds and Shepherd (1955), while useful and reliable, has limitations.

The complexity of the composition of genomic groups means that an estimate of the genome size of *Musa* must be given as a range. Pillay et al. (2004) suggest this range lies between 550 and 612 Mbp[8], a relatively small size. An analysis of the organization of the banana genome has been done through sequencing of BAC[9] clones (Aert et al. 2004; Cheung & Town 2007). A comprehensive discussion of *Musa* genomics can be found in Heslop-Harrison & Schwarzacher (2007).

SECTION 2 ORIGIN AND CULTIVATION

2.1 Centre of diversity and domestication

The precise origin of edible bananas is not known but the generally accepted theory is that Malesia, a biogeographical region including the Malay Peninsula, Indonesia, the Philippines and New Guinea, was the primary centre and India was a secondary centre (Simmonds & Shepherd 1955). It is likely that dispersal out of Asia was linked entirely to human movement (Daniells et al. 2001).

The modern day edible bananas are a mix of wild and cultivated, species and hybrids associated with *M. acuminata* and *M. balbisiana*. *M. acuminata* is the most widespread of the species in section *Musa* (Daniells et al. 2001) and the centre of diversity is thought to be either Malaysia (Simmonds 1962) or Indonesia (Horry et al. 1997). Some of the primitive edible seeded diploids of this genus evolved through the development of sterility, parthenocarpy and fleshy seedless fruits (Simmonds 1959a). The genetic basis of parthenocarpy in *M. acuminata* has not been characterized (Heslop-Harrison & Schwarzacher 2007). Clones of the diploids were cultivated in wetter parts of Southeast Asia (Valmayor et al. 2000) and the development of vigorous seedless triploid cultivars was the result of chromosome restitution (Raboin et al. 2005) and/or crosses between edible diploids and wild *M. acuminata* (Daniells et al. 2001).

Edible diploids of *M. balbisiana* underwent a parallel evolution in drier parts of Asia (India, Myanmar, Thailand, Philippines) but there was some geographical overlap with *M. acuminata* (perhaps resulting from human movement of cultivars) and hybrids of the seeded types were produced (Valmayor et al. 2000; Daniells et al. 2001). The Indian subcontinent was a major centre for hybridization (Daniells et al. 2001). The end result of the parallel evolution and subsequent hybridization of the two species was the occurrence of the range of genotypes described in Section 1 (i.e. homogenomic and heterogenomic diploids, triploids and tetraploids). The genomes of the two species contributed different traits, with *M. acuminata* largely contributing parthenocarpy and sterility (Simmonds & Shepherd 1955) and *M. balbisiana*

[8] The amount of DNA in the nucleus of a eukaryotic cell is expressed as the total number of base pairs (bp) in a haploid (1C) chromosome complement.
[9] BAC = bacterial artificial chromosome. BACS can accommodate large quantities of inserted DNA cloned from an organism and a physical map of overlapping BAC clones can span an entire chromosome.

contributing hardiness, drought tolerance, disease resistance and starchiness (Pillay et al. 2002). Most of the cultivars of the edible bananas derive from collections of spontaneous mutants in wild plants that were then brought into cultivation and multiplied vegetatively. The hybridization events and mutations have occurred many hundreds of times over (Heslop-Harrison & Schwarzacher 2007).

East Africa and West Africa represent two main secondary centres of *Musa* diversity as a result of a long history of cultivation in these regions (De Langhe 1995). There are approximately 60 cultivars of African Highland bananas unique to East Africa but it is not known whether these derived from traded plants (maybe 2,000 years ago) or from indigenous edible diploids (De Langhe 1995; Daniells et al. 2001). These Highland bananas have the AAA genotype (Karamura 1998). It is thought that plantains reached West Africa 3,000 years ago and that they may have initially been propagated for their starchy corms and/or fibres rather than for their fruit. Vegetative propagation eventually led to the evolution of fleshy, seedless fruits that were edible (De Langhe 1995).

Another secondary centre of diversity is Polynesia to where the 'Maia Maoli/Popoulu' cultivars (thought to be AAB hybrids) were carried from the Philippines more than 4,000 years ago (De Langhe 1995).

A brief history of the domestication of banana is given by De Langhe (1995). It is claimed that there was written (Sanskrit) reference to bananas as early as 500 BC (De Langhe 1995). It is thought that traders from Arabia, Persia, India and Indonesia distributed banana suckers around coastal regions (except in Australia) of the Indian Ocean between the 5th and 15th centuries. From the 16th to 19th centuries, suckers were traded by the Portuguese and Spanish in tropical America. Further world trade saw the establishment of bananas in Latin America and the Caribbean. Today the cultivation of bananas occurs throughout the tropics and sub-tropics of Asia, America, Africa and Australia.

The most widely distributed banana cultivar is 'Dwarf Cavendish' (Ploetz et al. 2007). It is likely that this was not derived from a single plant but is a group of clones derived by mutation from tall members of the Cavendish subgroup (Constantine & Rossel 2001). Dwarfism is a commonly occurring mutation of Cavendish (see Section 2.3.1). With regard to the 'Dwarf Cavendish' cultivar, which was brought to Australia (see Section 2.3) and became the basis of the Australian industry (see Section 2.3.2), it is thought that the original plants were first obtained in approximately 1826 from southern China by Charles Telfair and taken to Mauritius (Marin et al. 1998). From here, some plants were then taken to England and, several years later, derivatives from these were sold to the Duke of Devonshire (Lord Cavendish) who continued to propagate them in his glasshouses. In 1836, the resulting plants were formally given the varietal name 'Cavendish'. John Williams, a missionary, took suckers from England to Samoa in 1838 and from here the cultivar was spread to Tonga and Fiji in the 1840s (Marin et al. 1998). Plants were probably taken from the Pacific Islands to the eastern coast of Australia in the 1850s (see Section 2.3).

2.2 Commercial uses

The fruit is the main product of the banana plant and bananas are the developing world's fourth most important food crop after rice, wheat and maize (INIBAP 2000). Millions of small-scale farmers in Africa, South Asia and Northern Latin America

grow the fruit for household consumption and/or local markets. The highest consumption of bananas per person is in Uganda, estimated at close to 1 kg per person per day (Edmeades et al. 2006), but few of the bananas are of the sweet type with only 623, 913 tonnes out of 9.68 million tonnes total production in 2005 being attributed to sweet bananas (FAO 2007). The majority of bananas grown in Uganda are East African Highland cultivars used for cooking and brewing (Karamura 1998).

Total world production of bananas (sweet bananas + plantains) in 2005 was over 100 million tonnes (FAO 2007). Current world sweet banana production (latest figure is for 2005) is approximately 67 million tonnes per year (FAO 2007) but only approximately 20% of this enters world trade. The two major sweet banana producing countries are India and Brazil but neither of these exports significant quantities (see Table 3). By comparison Ecuador, the fifth largest producer, exports approximately 67% of its bananas (Table 3) and is the largest supplier of sweet bananas to world trade (Table 4).

The major importers of sweet bananas are the European Community and the USA (Table 5).

Table 3. Major sweet banana producing countries*

Country	Production in 2006 (x1,000 tonnes)	% of bananas exported
India	11,710.3	0.1%
Brazil	7,088.02	3%
Philippines	6,794.56	29%
China	6,708.0	0.6%
Ecuador	6,118.42	67%

* Data taken from FAO (2007)

Table 4. Major sweet banana exporting countries in 2005*

Country	Export (x 1,000 tonnes)
Ecuador	4,085.35
Philippines	1,964.39
Costa Rica	1,597.08
Colombia	1,381.25
Guatemala	1,125.6

* Data taken from FAO (2005)

Table 5. Major sweet banana importing countries in 2005*

Destination	Import (x1,000 tonnes)
European Community (25 countries)	5,842.96
USA	3,917.03
Japan	1,065.89
China	428.702
Canada	415.71

* Data taken from FAO (2005)

In the early 20th century, the principal sweet banana traded was the cultivar 'Gros Michel' (INIBAP 2000). A Panama Disease outbreak (caused by the fungus *Fusarium oxysporum* f. sp. *cubense* (Foc) – see Section 7.2) that occurred in commercial plantations around the world in the early 1940s caused this highly susceptible cultivar to be gradually replaced from 1960 by more disease-resistant cultivars of the Cavendish sub-group (INIBAP 2000). Today these cultivars represent approximately

40 - 50% of the bananas that are grown worldwide and almost all of bananas traded on the world market (Arias et al. 2003). However, a new race of the *Fusarium* fungus (named Tropical Race 4 – abbreviated to FocTR4) to which the Cavendish sub-group is susceptible has now evolved. This has affected plantations in a number of countries in Asia/Oceania including Taiwan, the southern provinces of China, the Northern Territory of Australia, Malaysia and Indonesia (Markham 2006). It is possible that Cavendish cultivars will eventually lose dominance of world trade if resistant varieties from outside the Cavendish subgroup can be found.

The banana fruit can be eaten raw or cooked (e.g. deep fried, dehydrated, baked in the skin, steamed), can be processed into flour and can be fermented for the production of beverages such as banana juice, beer (e.g. *mbege* brewed by the Chagga people in the Kilimanjaro region of Tanzania), vinegar and wine (Morton 1987; Pillay et al. 2002; Nelson et al. 2006; Edmeades et al. 2006; Pillay & Tripathi 2007). The nutritional characteristics of the fruit are discussed in Section 5. Other parts of the banana plant are also eaten (Espino et al. 1992) e.g. the flower is eaten raw or cooked in Southeast Asia; the core of the pseudostem (trunk) is used for cooking in Burma and Bengal; leaf buds are eaten as a vegetable (Nelson et al. 2006); the corm is a source of starch and has been eaten in times of famine in Africa and Asia (De Langhe 1995). All parts of sweet banana/plantain plants, but particularly the fruits, have also been used to feed livestock in those parts of the world where there is excess production (Babatunde 1992). Ashes obtained from burning banana leaves are used as flavouring for curries and a salt substitute in India (Nelson et al. 2006).

Banana leaves have a variety of practical uses including wrapping for food, plates for serving food, polishing floors, thatching (Espino et al. 1992; Nelson et al. 2006). Fibres obtained from the pseudostem are used for making cloth (Espino et al. 1992; Nelson et al. 2006) and leaf fibres are utilised in string, cordage and rope (Nelson et al. 2006). Plants in the section *Australimusa* are an important source of fibres, particularly Abaca/Manila hemp (from *Musa textilis*) (Horry et al. 1997). Manila hemp, until the advent of the first synthetic fibres, was used in the manufacture of marine ropes because of its strength, lightness and water-resistance. Today it is used mainly in the paper making industry where its long staple length, strength and cellulose content, make it useful in specialised papers including tea and coffee bags, sausage casing paper, currency notes, cigarette filter papers, medical/ disposal papers and some high-quality writing paper (Wigglesworth 2007).

The sap of banana plants, particularly the Fe'i cultivars that have a distinctive reddish-violet sap (Sharrock 2000), has been used as a dye and ink (Nelson et al. 2006; Pillay & Tripathi 2007). Various parts of the plant are also used, particularly in Pacific cultures, for medicinal purposes. Root sap can be used to treat mouth thrush in children and skin warts. Banana peel has been found to have antibiotic properties (Nelson et al. 2006).

2.3 Cultivation in Australia

The earliest record of bananas being grown in Australia was in the early to mid 1800's near Carnarvon in Western Australia (ABGC 2007). The plants were thought to have been brought from China by migrants. Bananas had been growing in China since approximately 200 AD (Simmonds 1959a) and the 'Dwarf Cavendish' cultivar that has become the major banana traded globally came from Southern China via

Mauritius, England and Fiji (see Section 2.1). It is likely that introduction of 'Dwarf Cavendish' to Queensland occurred with the drafting of cane cutters from Fiji and other Pacific islands in the 1870's as well as through Chinese migrants (ABGC 2007). 'Lady Finger' and 'Sugar' bananas were also introduced from the Pacific islands (Daniells 1986). These accessions were initially made for ornamental purposes only and the first sweet banana fruits traded commercially were actually imported from Fiji to Sydney. The early Australian banana trade was dominated by Chinese merchants many of whom owned plantations in Fiji (Couchman 2005). When tariffs on imported bananas were raised, these same Chinese merchants promoted the further establishment of banana plantations in northern NSW and by 1919 they owned or managed some 500 acres around the Mullimbimby area (Pearson et al. 2002). This area had originally been planted commercially with bananas after 1891 when Herman Reich introduced the 'Dwarf Cavendish' cultivar to Kororo and the Coffs Harbour area. The growing region was subsequently expanded north to Woolgoolga and the Clarence, Richmond, Brunswick, and Tweed River regions in northern NSW (ABGC 2007). By the 1960s, when NSW was producing 80 per cent of the nation's bananas, the industry in this region had reached its peak (Coffs Harbour City Council 2003). Since then it has declined as major plantings have been developed in northern Queensland (see Section 2.3.2).

Other areas of eastern Australia also became centres for banana production at various times. In the 1880s in northern Queensland, Chinese workers from the Palmer River goldfields established fruit-growing industries, including bananas, around Cooktown, Port Douglas, Cairns and Geraldton (later Innisfail) (Pearson et al. 2002). The Widgee Shire (around Gympie in Queensland) was the largest banana producing area in Australia between 1918 and the early 1930's but then declined with the infestation of rust thrip and the increased commercial competition from other regions, particularly in northern NSW (Cooloola Shire Library Service 2001).

Somatic mutations occur relatively frequently in bananas (see Section 2.3.1) and two cultivars now widely grown in Australia were thought to arise in this way (Daniells 1986). 'Williams', a giant form of the 'Dwarf Cavendish', is thought to have appeared as a mutation in a 'Dwarf Cavendish' plantation in the Clarence Valley of northern New South Wales in the early 1900s. 'Mons Mari' arose as a mutation in a 'Dwarf Cavendish' plantation called Mons Mari (Mountain by the Sea) near Buderim in south east Queensland in about 1910. The two cultivars were traded between NSW and Queensland but, as there is very little difference between them, it has been suggested that the cultivar name is only of academic interest (Daniells 1986). Over the years a number of somatic mutations within 'Williams'/'Mons Mari' and 'Lady Finger' have led to further selections within these cultivars with characters such as pseudostem colour and height, and finger shape being altered (Daniells 1986).

Temperature is an important factor in successful commercial banana production, with the optimum temperature being approximately 27^{o} C and poor fruit production occurring if the temperature drops below 15^{o} C (Espino et al. 1992). Good moisture is required for optimum growth and average weekly rainfall (or equivalent irrigation) should be 50 – 100 mm (DPI&F 2004a). Today, commercial banana plantations are found in the same areas as commercial papaya plantations (OGTR 2008) and Queensland accounts for most of Australia's production. On the east coast of Australia, bananas are grown commercially from the Daintree in far north Queensland to as far south as Nambucca and Yarrahapinni in New South Wales (ABGC 2007). In

Western Australia the main growing areas are Carnarvon and Kununurra, with a minor area in Broome. There are also a small number of plantations in the Northern Territory around Humpty Doo (near Darwin). The commercial growing regions comprise 66 Local Government Areas (LGAs) in Queensland, 14 in New South Wales, 3 in Western Australia and 1 in the Northern Territory (Figure 1) (Biosecurity Australia 2007). Home gardeners as far south as Melbourne can grow fruit-bearing plants under sheltered conditions (Baxter 1997).

Figure 1. Commercial banana growing areas in Australia as defined by Local Government Areas [map taken from Biosecurity Australia (2007)]

2.3.1 Commercial propagation

Most sweet banana cultivars are sterile and hence are propagated vegetatively from sections of the corm (called 'bits') containing unopened buds (or 'eyes'), or from suckers that are young shoots (Morton 1987; Espino et al. 1992). For a detailed description of the morphology of the banana plant see Section 3.

More recently, two tissue culture techniques have been used to propagate banana plants:

Micropropagation is used worldwide and more bananas are micropropagated than any other fruit crop (Smith et al. 2005). However, the cost of micropropagated plants is relatively high and often prohibitive to growers in developing countries (Escalant & Jain 2004). The procedures used for micropropagation of bananas have been extensively reviewed (Vuylsteke 1989; Israeli et al. 1995; Smith et al. 2005). In Australia, in the mid 1990s, the Queensland Department of Primary Industries and Fisheries (QDPI&F) established a banana clean planting scheme based on virus indexed tissue cultured plants. The QDPI&F tissue culture facility

at Nambour (on the Queensland Sunshine Coast) is one of only three globally recognised banana virus indexing centres.

Somatic embryogenesis in cell suspension cultures has now been scaled up to bioreactor stage for some cultivars (Kosky et al. 2002; Kosky et al. 2006). See Section 2.4.2 for further details about somatic embryogenesis.

Bits are usually obtained from plants growing in a designated planting material nursery (Daniells & Williams 2004; Broadley et al. 2004) that has been established in clean ground (ideally, virgin land) from clean planting material (ideally, micropropagated plants). A number of pests and diseases (see Section 7.2) are easily transmitted via infected vegetatively propagated material and planting material nurseries can reduce or eliminate such transmission. In Australia strict controls on the movement and planting of banana plants are imposed to prevent the spread of three of these particularly serious banana diseases, Banana Bunchy Top Virus, Black Sigatoka and Panama Disease (DPI&F 2004a)

The nursery is ready for 'digging' just before plants reach fruiting and hence when there are high carbohydrate reserves in the corm (Morton 1987; Broadley et al. 2004). The pseudostems are removed at approximately 20 cm above ground and the 'butt' (entire corm) is then uprooted. A number of bits, each containing a bud on a cube of corm, are cut out of each butt; formed suckers down to 250 g may also be removed. These parts can then be transported to the plantation 'blocks' for planting. Bits grow slowly at first but eventually catch up to plants grown from suckers (Morton 1987). Preparation of bits and suckers is labour-intensive and also requires specialist skills (Broadley et al. 2004).

In Australia it is common for planting material to be sourced directly from hardened-off micropropagated plants rather than using bits or suckers. Virus indexed micropropagated plants produce high plant yields and uniform crops, and can improve plantation cycle management (Smith et al. 2005). Their use as the preferred planting material is recommended (Lindsay et al. 2000; Broadley et al. 2004; Smith et al. 2005). However, there have been problems with somaclonal variation[10] occurring in micropropagated banana plants with off-type frequencies as high as 100% being reported in tissue culture plantings of 'Lady Finger' (Genome type AAB, Pome subgroup) in north Queensland in 1991 and 1992 (Smith et al. 1999). Most of the off-types in the Cavendish subgroup manifest as either 'dwarf' or 'giant' (Khayat et al. 2004). Dwarfism is the most common off-type (Bairu et al. 2006) and plants not only have short stature but also manifest problems with the fruit including choking (where the bunch fails to emerge fully from the plant), closely packed hands and short finger length (Smith & Drew 1990). In the Australian 'Lady Finger' cultivar the most common off-type has slow growth, poor bunch size and unmarketable fruit (Smith et al. 1999). There is evidence that the rate of somaclonal variation is related to length of time spent in tissue culture and high multiplication rates associated with the use of high concentrations of the cytokinin benzylamino purine in the culture medium (Damasco et al. 1998; Sahijram et al. 2003; Bairu et al. 2006). As a result, there have been recommendations that the number of subculture cycles be limited to eight or that

[10] Somaclonal variation is a term coined (Larkin & Scowcroft 1981) to describe phenotypic variation in tissue cultured plants that would normally not be expected to show any variation. It can be genetic or epigenetic in origin (Sahijram et al. 2003). It is more usually associated with plants regenerated from callus and cell culture than with plants derived from micropropagation (Smith 1988).

the number of plants produced from a primary explant be limited to less than 1,000 (Sahijram et al. 2003). A number of other factors (e.g. genotype, primary explant source, ploidy level, karyotype changes, post-transcriptional events, transposable elements) may also contribute to the rate at which somaclonal variation occurs but the precise mechanism leading to its occurrence in bananas is unknown (Smith 1988; Damasco et al. 1998; Sahijram et al. 2003). Both morphological and molecular screening techniques have been successfully used to identify somaclonal variants at an early stage (Smith & Hamill 1993; Damasco et al. 1996; Smith et al. 1999; Sahijram et al. 2003; Ramage et al. 2004). A major problem with molecular screening has been that off-types are detected by the absence rather than presence of a band; this problem has been overcome by the development of a PCR test containing a positive internal control (Ramage et al. 2004).

Little information is available on the occurrence of somaclonal variation in banana plants derived through somatic embryogenesis although one study suggests that the rate for the cultivar FHIA-18 is very low (Kosky et al. 2006).

The Queensland Banana Accredited Nursery (QBAN) system adopted in both Queensland and New South Wales (NSW) provides both vegetative and tissue cultured planting material acceptable to industry. Tissue cultured sources must be from a QBAN laboratory and be grown-on in a QBAN Nursery, both of which must meet strict hygiene standards (DPI&F 2004c). In Queensland, planting material for any variety, including 'Cavendish', must be obtained only from QDPI&F-approved sources and anyone who moves or plants one or more banana plants needs an *Inspector's Approval to Move and Plant Bananas* (Lindsay et al. 2000; Broadley et al. 2004). Similarly, in NSW, a permit to move or plant must be obtained from NSW Agriculture (Newley 2000). Planting material from interstate can only enter NSW in tissue culture. In northern NSW (north of latitude 29^{o} 7' S – see Section 7.2) where Bunchy Top Virus and Panama Disease have been recorded, non-tissue cultured planting material cannot be moved out of the area. Planting material in southern NSW, which is free of Bunchy Top Virus, can be moved to anywhere in NSW and, in some instances, into Queensland (Newley 2000). Legislation on banana planting is administered in Queensland by the Banana Industry Protection Board and in NSW by Bananas NSW (Broadley et al. 2004).

2.3.2 Scale of cultivation

Almost all of the bananas grown in Australia are for local consumption (FAO 2007). Most of these are consumed as fresh product with sub-group Cavendish bananas accounting for approximately 95% of the Australian market (Broadley et al. 2004; ABGC 2007). There are several Cavendish cultivars but 'Williams' is the most popular with 'Mons Mari' and 'Grande Naine' two other common types (Lindsay et al. 2000; Broadley et al. 2004). About 4% of Australian banana production is represented by the cultivar 'Lady Finger'; other cultivars such as 'Goldfinger', 'Bananza', 'Ducasse', 'FHIA-18', 'Red Dacca', 'Sucrier' and 'Plantain' together represent less than 1% of the total market (ABGC 2007) (see Table 2 for the genome types of these cultivars). The reliance on the Cavendish cultivars makes the industry vulnerable to disease outbreaks.

North Queensland, which now provides most of Australia's bananas, is prone to natural disasters such as cyclones and floods, which greatly influence continuity of

supply. On 20 March 2006, Cyclone Larry crossed the north coast of Queensland near Innisfail causing major damage (approximately 80% of the banana crop was destroyed) in the area between Cairns in the north and Cardwell in the south where 70% of Australia's commercial banana crop is grown (Lindsay et al. 2004). The result was the loss of harvestable fruit for approximately 9 months and the potential for an unwanted degree of synchonization of the crop cycle as plantations came back into production. Staggered plantings partially overcame this (DPI&F 2006b).

Production in Australia in 2005 was 265,570.00 tonnes (FAO 2006). Farm or plantation sizes vary from small family units of less than 5 ha to large plantations growing more than 200 ha of bananas (Lindsay et al. 2004). In 2005, prior to cyclone Larry, Australia had approximately 1,850 banana growers (ABGC 2007). A summary of the major production areas is given in Table 6. Climatic data for representative banana growing areas are given in Appendix 1.

Table 6. Banana production areas in Australia in 2005*

Area	Climatic type[a]	% of Australian production	Number of farms	Average farm size	Predominant soil types	Topography	Irrigation
North Queensland (Babinda to Cardwell)	Tropical rainforest	70%	569	18 ha	Light to medium alluvial clays	Floodplains	Under canopy in dry season
					Basaltic krasnozems	Undulating slopes	
South-east Queensland (Bundaberg to Qld border)	Sub-tropical (no dry season)	20%	1,200	3 ha	Podsolic clays or shales	Wind protected, frost-free slopes	May irrigate in drier periods
Northern NSW (Qld border to Coffs Harbour)	Sub-tropical (no dry season)	7%			Basaltic krasnozems	Plateau	
Humpty Doo (near Darwin, Northern Territory)	Tropical rainforest	1%	4	50 ha	Sandy loams	Tops and slopes of plateaus	May irrigate in drier periods
Kununurra (north-eastern Western Australia)	Grassland (winter drought)	1%	10	14 ha	Sandy loams	Plains and higher land of sandstone ridges	May irrigate in drier periods
					Cracking clays	River banks and levies	
Carnarvon (mid west coast of Western Australia)	Desert (summer drought)	1%	65	2 ha	Sandy loams	Alluvial floodplain	Year round irrigation is essential

[a] Koeppen Classification system taken from Australian Government Bureau of meteorology website (http://www.bom.gov.au/cgi-bin/climate/cgi_bin_scripts/clim_classification.cgi)

* Information compiled from Biosecurity Australia (2007)

2.3.3 Cultivation practices

Practices vary widely across Australia's commercial plantations depending on the climatic conditions, environmental conditions, cultivar and scale of production. Basically the grower has the choice, each season, of replanting from virus indexed material (see Section 2.3.1) or allowing each plant to 'ratoon' - whereby the pseudostem that has just borne fruit is cut down and is replaced by a sucker from the corm (see Section 4.5). Windbreaks are recommended in wind prone areas. Generally slopes of less than 15% are preferred; this reduces the chance of soil erosion and trapping of cold air, improves flexibility in the plantation layout and facilitates

mechanization (Broadley et al. 2004) (see Section 6 for a more detailed discussion of abiotic considerations in the growth of commercial plantations).

Considerable detail about cultivation practices in Australia is covered in a publication produced by the Queensland Department of Primary Industries & Fisheries (Broadley et al. 2004). The more important points are considered below.

Plantations in the tropical north of Australia tend to be cut down and replanted every 2 – 3 years whereas in more southerly areas it is not uncommon for plantations to be ratooned for up to 15 years, with an average of 5 – 7 ratoon cycles (Broadley et al. 2004). A number of factors contribute to the decision on how many ratoons to use, including the extent that mechanization can be utilized (Robinson 1995). In north Queensland, most plantations are on flat land and hence mechanization is high. As ratoon numbers increase, the spatial arrangement of plants becomes less ordered so that machine access can be hampered (Robinson 1995). Continued use of machinery over the same parts of a block can also lead to undesirable soil compaction that can adversely affect yield (Robinson 1995). More southerly plantations have a high frequency of sloped blocks (Broadley et al. 2004) that are too steep to allow machine access and therefore problems of plant spacing and soil compaction caused by machinery are not relevant considerations; the lack of mechanization is an incentive to replant less frequently (Broadley et al. 2004). Other factors that affect the decision about whether to replant or ratoon include the issue of yield decline resulting from a build up of soil nematodes and/or a reduction of soil pH; and marketing issues associated with control over harvest time as maturity of pseudostems developing from suckers tends to become less synchronous (Robinson 1995).

In the Australian tropics, bananas are best planted between June and November (Lindsay et al. 2000). This allows the plant crop and the first one or two ratoon crops to be produced during the winter-spring period when better market prices can be obtained. Also, land preparation and plantation management are easier when plantings are undertaken during these drier months; hot and wet conditions can promote soil erosion and lead to rotting of planting material.

South of Maryborough the planting season can extend from August to the end of January, with planting occurring in September in southern Queensland and usually from October to November in northern New South Wales (Broadley et al. 2004).

The banana crop can be planted in either single rows (leaving either a single or double sucker for the first ratoon) or double rows (leaving a single sucker for the first ratoon), with the plant spacings being adjusted accordingly (Daniells & O'Farrell 2004). In tropical regions, single rows, with a single sucker, are commonly 5 m apart, with plant spacings of 1.2 m. When these are converted to double rows in the first ratoon, with two following suckers, the plant spacings are increased to 2.2 m, with row spacings of 5.5 m. In double rows the plant spacings are 1.7 m, with the centres of double rows spaced 6.5 to 7.0 m apart. The inter-row distance is set on the basis of machinery access (Broadley et al. 2004). Suggested spacings for varieties in the sub-tropics are given in Table 7. A leaf area index for the crop as a whole of approximately 4 (i.e. 4 ha of leaf/ha of land) is optimal and translates to 1,500 – 2,000 plants/ha (Daniells & O'Farrell 2004).

Table 7. Plant spacings of commonly grown varieties in the sub-tropics*

Variety	Spacing between plants (m)	Spacing between rows (m)	Plants per ha
'Cavendish'	1.8-2.1	3-3.5	1362-1852
'Ladyfinger'	3-4	3.2-4	625-1041
'Goldfinger'	2.5-3	3	1111-1333

* Adapted from Broadley et al. (2004)

In some situations wider plant spacings may be beneficial. For example, in the tropics this would allow for air movement between the rows thus reducing the susceptibility to diseases, while in relatively dry, non-irrigated areas wide plant spacings would reduce the competition for water (Broadley et al. 2004).

The banana growth cycle has seven recognised growth stages used by growers to implement farm management practices such as fertilisation and irrigation requirements (Broadley et al. 2004). These stages follow planting or ratooning and can be summarised as follows:

i. 15 leaf stage
ii. 25 leaf stage
iii. bunch emergence
iv. bract fall
v. ½ maturity
vi. mature bunch
vii. postharvest

Weed control is important as weeds can compete vigorously with banana plants as well as harbouring pests. The presence of weeds also makes disease detection in the banana plantation difficult (see Section 7.1 for further discussion).

Management of pests and diseases is also important and it is recommended that an Integrated Pest Management approach be used (Broadley et al. 2004) (pests and diseases are discussed in more detail in Section 7.2). Insecticides can be applied as sprays, dusts or injections into plants parts (the 'bell' and pseudostem). Insect pests are controlled with the use of sulphur dust against mites, chlorpyrifos against caterpillars, thrip and mealy bug and dimethoate against the banana aphid (Broadley et al. 2004). The application rates of fungicides vary depending on where the bananas are grown. For example, in Carnarvon in Western Australia, conditions for leaf diseases are not favourable and no spraying is required; in North Queensland, each year, 20-25 sprays to control leaf disease are required; in South-Eastern Queensland and NSW 4 to 6 sprays per year can be effective to provide control (Kernot 1998; Biosecurity Australia 2007). Fungi such as *Deightoniella* spp. are treated with applications of Mancozeb (tatodust) and chlorpyrifos is used against rust. Mancozeb or propiconazole and tebuconazole with mineral oil are used for the control of Sigatoka disease (Kernot 1998; Vawdrey & Grice 2005).

Banana plants have high nitrogen and potassium requirements in order to produce good fruit yields (Broadley et al. 2004) and 3 – 4 split applications of 10:2:22 N:P:K between August and April are recommended for south Queensland (DPI&F 2004a). Alternatively, nutrients can be applied individually, with nitrogen being supplied every month (except in winter), potassium being applied in January, March, and September, and phosphorus being applied in June (Broadley et al. 2004). 'Cavendish' bananas typically require 240 grams of nitrogen, 400 to 500 grams of potassium and 40 grams of phospohorus per stool per year for optimum growth. The 'Lady Finger' banana requires 10% more nitrogen and potassium than the 'Cavendish' banana (DPI&F 2004b).

Irrigation of plantations may be required during dry periods which, in Carnarvon in Western Australia, is year-round (Biosecurity Australia 2007). In northern NSW, irrigation requirements for bananas are published weekly in the local newspapers. In many instances fertigation (irrigation of plants with water containing fertilizer) may be an efficient way of applying nutrients to the crop (Broadley et al. 2004). While water is important for crop growth, poor drainage may cause yield reduction (Daniells & Evans 2005).

Routine desuckering of banana stools is undertaken at least every 4 months in order to remove suckers (Figure 2) that may compete with the pseudostem for water and nutrients (Broadley et al. 2004).

Figure 2. Banana plant showing the main pseudostem (P) with two suckers. If suckers develop well ahead of fruiting of the pseudostem they should all be removed. However, as the pseudostem matures, one sucker will be left to become the replacement plant. [Photo credit: Janet Gorst, OGTR]

In most commercial operations, the banana bunches are covered in plastic or cloth bags to prevent blemishes from mechanical and bird/flying fox/sugar glider damage (Figure 3). This operation also enhances the effectiveness of insecticides that have been applied to the developing bunch and aids fruit development through provision of a warm environment (Broadley et al. 2004; Daniells & Lindsay 2005). The cover should not be applied until about 21 days after shooting so that the fingers are firm enough to resist frictional damage (Morton 1987). The use of tubular polyvinyl chloride (PVC) and polyethylene was first trialled in Queensland in the late 1950s and became standard practice worldwide (Morton 1987). Different colours of plastic are now available but it is not known if these affect bunch ripening (Daniells & Lindsay 2005). Other tasks performed on developing bunches include bunch trimming, insecticide treatment and removal of the 'male bud' (debelling) at the end of the inflorescence so as to redirect sugars to the developing fruits (Morton 1987; Broadley et al. 2004; Daniells & Lindsay 2005). Pseudostems of some cultivars, particularly those in the Cavendish subgroup, usually require propping to prevent their falling over as the developing bunches become heavier (Figure 3); the props are applied as soon as possible after bunch emergence (Broadley et al. 2004).

Figure 3. Two types of plastic bunch covers. Note propping of pseudostems with wooden stakes to prevent their falling over under the weight of the bunches.

Bananas in Australia are harvested year-round. Bunches from new plantings are usually harvested about 16 to 18 months after planting, but this may be as early as 12 months. Subsequent (ratoon) crops are harvested 6 -12 months after sucker set (Morton 1987). For both the plant crop and ratoon crop this is 3 - 5 months after the bunches appear at the top of the plant, or 90 – 120 days after flowers have opened (Rieger 2006). This may take longer in the cooler part of the year (DPI&F 2004a). Commercially, harvesting takes place when the fruits on the upper hands are just changing to light green (Figure 4). The fruits are generally ripened artificially in storage rooms held at 14.5 – 30^{o} C and with initial high humidity (90 – 95%) that is

reduced to 85% . Ethylene gas is pumped in at a rate that provides the desired speed of ripening (Morton 1987).

Figure 4. Packing shed in a small commercial facility showing cool room (A), harvested bunches hanging on a conveyor system, and turntable (left foreground) for washing individual hands removed from the bunches. [Photo credit: Janet Gorst, OGTR]

Transportation of banana fruit should occur between 13.5°C and 15°C, as lower temperatures can permanently halt the ripening process, and the fruit will develop necrotic flecking and eventually turn grey (Nelson et al. 2006).

Many factors determine yield from a banana plantation including environmental conditions, agronomic practices, the cultivar and ratooning management (Morton 1987). Indicative yields for cultivars grown in Australia are given in Table 8. Cavendish produces approximately 2100 cartons from 1250 plants per hectare. Lady Finger yields about 750 cartons from 750 plants per hectare (DPI&F 2004a). Fruit ripening is particularly affected by the ripening temperatures – see Section 6.1.2.

Table 8. Growth and production of commonly grown varieties

Variety	Number of hands in bunch	Kg/bunch
Giant Cavendish (e.g. Williams)	7-14	20-60 kg (average 22kg) =1.5-2 cartons
Ladyfinger	7-10	10-30 kg (average 13kg) =1 carton
Bonanza and Goldfinger	7-15	25-50 kg
Ducasse	9-12	25-35 kg
Pacific Plantain	10-15	25-40 kg
Red Decca	5-7	20-35 kg

Adapted from Broadley et al. (2004)

Following bunch harvest the practices that are followed are dependent on whether blocks are to be replanted or ratooned. An important aspect of management in commercial plantations that are ratooned is choosing the optimal following sucker (see Section 4.5) to produce the next crop. Sucker development passes through three distinct stages (Pillay & Tripathi 2007):

i) Peeper – where the young sucker possesses scale leaves only

ii) Sword sucker – where the sucker has sword leaves only

iii) Maiden sucker – where the sucker/ratoon has normal foliage leaves but has not reached the fruiting stage (Figure 5).

Figure 5. Maiden sucker developing after the pseudostem (P) has been cut back. Note the circular arrangement of leaf sheaths in the transverse section of the pseudostem (see discussion in Section 3.1). [Photo credit: Janet Gorst, OGTR]

For optimal growth a single, vigorous, sword sucker should be chosen which originates from a deep-seated bud (DPI&F 2005); this will become the maiden sucker and form the next pseudostem. Additionally, one or more 'peepers' may also be

allowed to exist to serve as future replacement plants. All other suckers should be killed to prevent competition with the developing pseudostem. Properly carried out, this practice will lead to higher yields of better quality fruit. It also permits the scheduling of production to coincide with periods of higher prices and increases the evenness of the crop. Choosing uniform healthy followers and maintaining row alignment can extend the life of the plantation (Morton 1987; Broadley et al. 2004).

If delay of production is desired and the grower is prepared to sacrifice bunch weight, the process of nurse suckering can be done. This method actually misses a ratoon cycle (Broadley et al. 2004). It involves allowing a sucker (referred to as the 'nurse sucker') to reach a height of approximately 1.5 m at bunch harvest. The growing point of the sucker is then cut out after bunch harvest and this causes a flush of new suckers to develop from the nurse. From these new suckers a single sucker is allowed to develop into a pseudostem. This technique adds a further 3 months to the harvest time normally expected from a ratoon crop (Broadley et al. 2004).

In blocks that are to be replanted there is usually a 6 – 24 month fallow period (Broadley et al. 2004). The old crop is removed, corms are destroyed and a green manure crop, ideally with a high resistance to burrowing nematode reproduction, is planted. Suitable crops include Bonar rape (*Brassica napus* cv Bonar), Indian mustard (*Brassica juncea*), canola (*Brassica napus*), highland swede (*Brassica napus*), *Paspalum wettsteinii* and rye grass (*Lolium perenne*) (Broadley et al. 2004). The fallow allows an improvement in soil structure, aeration and water holding capacity as well as helping to control nematodes (Robinson 1995; Broadley et al. 2004).

2.4 Crop Improvement

Banana improvement is an expensive, slow and complicated process. There are three major emphases in genetic improvement: conventional breeding, mutation breeding and genetic modification (Vuylsteke 2000; Escalant et al. 2002; Escalant & Jain 2004) but *in vitro* mutation breeding has, so far, delivered the most promising results (Smith et al. 2005). Globally, the problem of banana improvement is tackled through PROMUSA (2007), which was established in 1997 through the efforts of the International Network for the Improvement of Banana and Plantain (now amalgamated in Bioversity International) to foster international cooperation. In 2001, the Global Musa Genomics Consortium was established to apply new technologies to the sustainable improvement of banana (Frison et al. 2004). PROMUSA aims to develop a range of new banana hybrids suitable for production by banana growers worldwide. The programme uses all three approaches for improvement, and research activities are managed within PROMUSA working groups. Pest and disease problems are the main focus of improvement programmes (Pillay et al. 2002).

In addition to the Genomics Consortium, the *Musa* Germplasm Information System (MGIS) was also established in 1997 as a system for the exchange of germplasm data between curators of *ex situ Musa* collections. MGIS is a database containing detailed and standardized information on the accessions stored in different *Musa* genebanks around the world. At the last update of MGIS on 15/12/2006, there were 19 participating institutions as shown in Table 9. MGIS provides a valuable resource for researchers who can use it to identify the most appropriate germplasm to be used in their trials and experiments.

Table 9. List of institutions participating in the Musa Germplasm Information System (information taken from the MGIS website (http://195.220.148.3:8013/mgis_2/homepage.htm).

Country	Institution	MGIS collection code	Collection type	Number of accessions
Australia	Department of Primary Industries, Queensland (QDPI-SOUTH JOHNSTONE)	SJR	*In vivo*	282
Belgium	INIBAP Transit Center (ITC)	ITC	*In vitro*	1245
Cameroon	Centre africain de recherche sur bananes et plantains (CARBAP (NJOMBE))	NYO	*In vivo*	405
China	South China Agricultural University, Tropical and Subtropical Fruit Research Laboratory (SCAU)	SCU	*In vivo*	98
Democratic Republic of Congo	Faculté des Sciences de Kisangani (FSK)	FSK	*?*	46
Guadeloupe (France)	Centre de Coopération Internationale en Recherche Agronomique pour le Développement - Département des Productions Fruitières et Horticoles (CIRAD/FLHOR (GLP))	NEU	*?*	450
Honduras	Fundacíon Hondureña de Investigacíon Agricola (FHIA)	LIM	*?*	458
India	Kerala Agricultural University (KAU)	THR	*?*	133
India	National Research Centre on Banana (ICAR) (NRCB)	TRY	*?*	813
India	Indian Institute of Horticultural Research (IIHR)	IIH	*In vivo*	26
Indonesia	Research Institute for Fruits, Agency for Agricultural Research and Development (RIF-SOLOK)	RIF	*In vivo*	252
Kenya	Kenya Agricultural Research Institute (KARI)	KIS	*In vivo*	172
Malawi	Department of Agricultural Research & Technical Services (DARTS)	BUM	*In vivo*	14
Nigeria	International Institute of Tropical Agriculture (IITA (ONNE))	ONN	*?*	441
Papua New Guinea	National Agricultural Research Institute (NARI-LALOKI)	LAL	*In vivo*	82
Philippines	Bureau of Plant Industry - Davao National Crop Research and Development Center (BPI)	DAV	*?*	292
Philippines	UP Los Baños, Institute of Plant Breeding (NPGRL-UPLB)	MAI	*In vivo*	31
Uganda	National Agricultural Research Organization - Kawanda Agricultural Research Institute (NARO-KARI (KAWANDA))	KAW	*In vivo*	23
Viet Nam	Phu Ho Fruit Crop Research Center (PHU HO FCRC)	PHU	*In vivo*	84

Since 1988, the Queensland Department of Primary Industries and Fisheries (QDPI&F), at its facility in Nambour, has maintained one of the world's largest *in vitro* repositories of banana germplasm, with more than 400 banana accessions collected from around the world. This facility is able to conserve, multiply and distribute pathogen-free germplasm for planting and breeding programmes. The cultures are maintained at approximately 16^{o} C in low light (approximately 13 - 25

µmol m^{-2} s-1) and therefore require infrequent subculturing (once every 6 – 12 months) in comparison with cultures maintained for production that are grown at 26 – 30^{o} C and 40 – 100 µmol m^{-2} s-1 (Vuylsteke 1989). There is, however, a requirement for the occasional re-initiation of cultures as they can deteriorate with prolonged time in tissue culture. The QDPI&F also has a field collection, at South Johnstone in north Queensland, which is a subset of the *in vitro* accessions and provides a valuable source of material for the re-initiation of *in vitro* cultures.

It has been suggested that one of the main problems hampering genetic improvement in *Musa* has been a lack of basic knowledge about the diversity and taxonomic relatedness within the genus (De Langhe 2000). The tools of genomics research such as genetic mapping, identification of quantitative trait loci, marker assisted-breeding/aided introgression, and identification and cloning of (resistance) genes are helping to resolve diversity questions and open up new areas for more efficient breeding of *Musa* (Pillay et al. 2002; Frison et al. 2004; Smith et al. 2005; Pillay & Tripathi 2007; Kahl 2007; Heslop-Harrison & Schwarzacher 2007).

A genome sequencing project is currently being undertaken by the Global Musa Genomics Consortium < http://www.musagenomics.org/index.php?id=50>. To date, consortium members have developed 5 BAC libraries (see Section 1, page 6 for an explanation of BAC), one of *Musa balbisiana* and four of *M. acuminata*. Preliminary work on end-sequencing of large numbers of BACs randomly selected from the *M. acuminata* BAC libraries has helped in the understanding of sequence content and sequence complexity of the *Musa* genome (Cheung & Town 2007).

2.4.1 Breeding

Conventional breeding

The strategy in banana breeding is to incorporate the desired traits often present in wild and cultivated diploids to existing cultivars (Pillay & Tripathi 2007). A major problem with breeding of sweet bananas is that the creation of triploids or tetraploids, rather than diploids, is necessary to maintain the production of parthenocarpic fruits for the commercial sweet banana trade; seedlessness is essential for edibility as seeds are large and hard. Since parthenocarpy is closely linked to male sterility (see Section 4.1.2) this presents a conundrum for the breeder since there is low availability of both female and male parents. Members of the Cavendish subgroup of AAA cultivars, which currently dominate world trade of sweet bananas, set seed so rarely that they can be regarded as female sterile (Shepherd 1987). Members of the Gros Michel subgroup (also AAA genome type) produce an average of 2 seeds per bunch when hand pollinated with diploids (Simmonds 1966). Other banana genome types show a range of seed fertility, which can be influenced by climatic conditions (Ortiz & Vuylsteke 1995).

Notionally, triploids can be produced as a result of crosses of either diploid with diploid (with recombination only from the male parent) or of tetraploid with diploid (with both parents segregating) (Shepherd 1987) where the female parent is the tetraploid, so as to avoid problems associated with pollen derived from a tetraploid (see Section 4.1.2). Both artificial and open pollination are able to generate viable triploid seed (Ortiz & Crouch 1997) and selection for fertility can increase the efficiency of pollination (Ortiz & Vuylsteke 1995).

There are logistical reasons why breeding in *Musa* is less than ideal: the seed-to-seed crop cycle takes about 2 years to complete; and physically, each plant occupies approximately 6 m^2 in the field, thus requiring a large investment in space (Ortiz et al. 1995).

Australia does not have any conventional breeding programmes for banana. However, there are a number of centres worldwide where conventional breeding of *Musa* is undertaken (Vuylsteke 2000; Escalant et al. 2002). The major breeding strategy was developed at the Fundación Hondureña de Investigación Agrícola (FHIA) in Honduras and is based on the development of improved diploids that are then used as male parents in crosses with female-fertile triploids to produce tetraploids (Escalant et al. 2002). While a number of improved tetraploids have been produced and subsequently distributed, progress has been very slow because of the low fertility of the triploid female parents (Escalant et al. 2002). There is also the problem that tetraploid banana plants often show premature senescence, leaf drop, fruit drop, short fruit shelf life, weak pseudostems and undesirable seed production (Shepherd 1987; Ude et al. 2002). The QDPI&F has introduced several FHIA cultivars into Australia and, together with counterparts in New South Wales and the Northern Territory, evaluated them for agronomic performance and pest and disease (especially FocTR4) resistance in a range of environments. The most successful of the sweet banana cultivars obtained to date have been FHIA-01 ('Goldfinger') and FHIA-18 ('Bananza') from the AAAB genome group. 'Goldfinger' is resistant to Panama Disease, highly resistant to Black Sigatoka, tolerant to the burrowing nematode, is cold tolerant and does not lodge (DEST 2003). It also has good fruit quality and postharvest performance (Seberry & Harris 1998).

Other major centres of banana breeding are located in France and Guadeloupe (Centre de Coopération Internationale en Recherche Agronomique pour le Développement – CIRAD-FLHOR); Nigeria and Uganda (International Institute of Tropical Agriculture); Cameroon (Centre de Recherches Régionales sur Bananier et Plantain - CARBAP) and Brazil (Empresa Brasiliera de pesquisa Agropecuaria - EMBRAPA). Because of the lack of effective strategies to control Panama Disease the development of FocTR4-resistant cultivars has been the major priority in genetic improvement programmes in recent time (Moore et al. 2001). Other priorities also relate to pest and disease resistance (Persley & DeLanghe 1986; Horry et al. 1997; Pillay & Tripathi 2007) but commercial attributes such as yield, water use efficiency, fruit dimensions, fruit flavour and ripening characteristics could also benefit from improvement (Pillay & Tripathi 2007; Heslop-Harrison & Schwarzacher 2007). An extensive discussion of banana breeding can be found in Pillay and Tripathi (2007).

A different approach to conventional breeding has been developed by CIRAD-FLHOR and CARBAP and involves the creation of tetraploids from desirable diploids through colchicine doubling; the tetraploids are then used in crosses with superior diploids to produce horticulturally desirable triploids (Hamill et al. 1992; Escalant et al. 2002).

Banana Streak Viruses (BSV) are currently a major constraint to *Musa* genetic improvement and mass propagation. Interspecific hybrids containing the B genome contain integrated sequences for Banana Streak Virus that are readily activated. While a number of promising hybrids have been produced, those containing a B genome

have been found positive for the virus and hence cannot be distributed to growers (Escalant & Jain 2004).

Mutation breeding

Mutation breeding programmes broadly encompass two approaches, namely gamma irradiation and somaclonal variation. However, chemical mutagenesis using ethyl methyl sulphonate (EMS), sodium azide and diethylsulphate has also been used (Smith et al. 2005). The parameters for successful gamma irradiation of shoot tips of *in vitro*-derived plantlets were established in the 1990s and plants of the Gros Michel cultivar 'Highgate', tolerant to *Fusarium oxysporum,* were obtained (Bhagwat & Duncan 1998). In Australia, *in vitro* gamma irradiation of the Cavendish cultivar 'Dwarf Parfitt' yielded a number of putative mutants one of which (DPM25) had good agronomic characteristics as well as field resistance to subtropical race 4 *Foc* although this resistance was not as high as that in the 'Dwarf Parfitt' parent (Smith et al. 2006). Trials are currently underway in the Northern Territory to evaluate DPM25 resistance to FocTR4 (Walduck et al. 2006), a much more virulent race than subtropical race 4.

Somaclonal variation, while presenting a concern to commercial growers (see Section 2.3.1) is a tool that has been used to improve banana germplasm via novel sources of variability (Sahijram et al. 2003). The major centre for development of banana cultivars through somaclonal variation is the Taiwan Banana Research Institute (TBRI) which, in 1984, established a Cavendish breeding programme based on field screening somaclonal variants for resistance to FocTR4 (Tang 2005). Micropropagated banana plantlets are distributed to growers who then screen the plants for superior somaclones. The programme has produced a number of resistant clones although none of these is regarded as a suitable replacement for the existing 'Giant Cavendish' cultivars traded worldwide. In Australia, two somaclone lines (GCTV-119 and GCTV-Formosana) from TBRI are currently being tested in the Northern Territory but results to date suggest that they are varyingly susceptible to FocTR4 (Walduck et al. 2006).

Somaclonal variation is regarded as a convenient strategy for banana improvement for a number of reasons (Vuylsteke 2000): i) a wide range of banana cultivars are already in tissue culture; ii) it is a comparatively cheap strategy that does not involve biosafety issues or regulatory approval; iii) it is not necessary to have undertaken molecular analysis of desirable traits. A problem with the strategy is that the outcome is not predictable and cannot be targetted and, in reality, there have been few commercially useful variants produced (Tang 2005).

2.4.2 Genetic modification

Early experiments with banana established plant tissue culture regeneration systems, a necessary precursor to successful transformation. The main pathway of regeneration is via somatic embryogenesis. As somatic embryos may be of unicellular origin (Escalant et al. 1994), the likelihood of chimeric plants being produced is very low and this therefore makes embryogenic suspension cultures ideal transformation targets (Becker et al. 2000).

Although embryogenic suspension cultures have been induced from various explant types (including the bases of leaf sheaths or rhizome fragments of plants produced *in*

vitro; thin sections of highly proliferating bud cultures placed in liquid medium; and zygotic embryos) the most successful explants are immature male flowers (Cirad 2003). However, a rapid decline in the embryogenic response soon after harvest as well as a seasonal dependence mean that cultures must be induced quickly from harvested flowers (Escalant et al. 1994). There is also the added problem that not all banana cultivars, especially plantains, produce male flowers. The use of other methods for producing embryogenic suspension cultures such as the 'scalp' method can be labour-intensive and protracted (Strosse et al. 2004). Embryogenic suspension cultures have been induced from a wide range of genotypes (Smith et al. 2005).

Transformation protocols involving *Agrobacterium tumefaciens* – mediated transformation (May et al. 1995; Acereto-Escoffie et al. 2005), microprojectile bombardment (Becker et al. 2000; Houllou-Kido et al. 2005) and electroporation of protoplasts (Sagi et al. 1995; Sagi et al. 2000) have been developed. Initially, genetic modification involved the expression of marker genes but as procedures have became more robust the emphasis has shifted to engineering for pest and disease resistance (Atkinson et al. 2003). For a recent review of the transformation of bananas see Smith et al. (2005).

Promoters from both banana and other species have been isolated for use in transformation systems (Smith et al. 2005). In Australia, promoter regions from Banana Bunchy Top Virus (BBTV) satellites S1 and S2 and from the banana vegetative actin gene (*ACT1*) have been used successfully to drive introduced genes in transgenic banana plants (Kahl 2007). Hermann et al. (2001) cloned the *ACT1* gene, which shows strong constitutive expression in the pseudostem, leaves and roots

Transgenic research on resistance to fungal diseases has centred on *Fusarium oxysporum* f. sp. *cubense* (Panama Disease) and *Microsphaerella fijiensis* (Black Sigatoka) (see discussion of these in Section 7.2) with emphasis on the expression of various genes encoding defensin-type antimicrobial peptides and non-specific lipid-transfer proteins (Sagi 2003). There are also several groups worldwide involved in the development of transgenic virus resistance against Banana Bunchy Top Babuvirus, Banana Streak Badnavirus, and Banana Bract Mosaic Potyvirus (Dale & Harding 2003). To date none of the resulting transgenic plants have entered field trials but it is anticipated that trials of plants expressing resistance to *Mycosphaerella fijiensis* may soon be conducted at the Kawanda Agricultural Research Station in Uganda (Dauwers 2007). The research on this genetic modification was undertaken at the Laboratory of Tropical Crop Improvement in Belgium and involved genetic modification of the 'Gros Michel' cultivar with two rice chitinase genes, *rcc2* and *rcg3* (Jacon et al. 2006).

The Israeli company Rahan Meristem has developed genetically modified banana plants showing resistance to nematodes and there have been reports in the press (but not in the scientific literature) of the field testing of these lines (IEICI 2006).

In the mid 1990s the idea of using transgenic plants as edible vaccine-producing systems, especially in underdeveloped countries, saw proposals to genetically modify banana fruit to express antigens of a number of viruses and bacteria such as hepatitis B and cholera (Mason & Arntzen 1995). Despite considerable research, this vision has still not been realized, largely because of regulatory concerns surrounding the entry of

genetically modified staples (such as bananas, potatoes and tomatoes) into the food supply (Arntzen 2005).

SECTION 3 MORPHOLOGY

3.1 Plant morphology

Detailed morphological descriptions of the banana plant can be found in numerous publications (Simmonds 1959a; Barker & Steward 1962; Purseglove 1972; Morton 1987; Ross 1987; Simmonds & Weatherup 1990; Espino et al. 1992; Karamura & Karamura 1995; Rieger 2006; Pillay & Tripathi 2007). Here the description of the morphology of the banana plant is dealt with in more general terms.

The cultivated banana plant is a tall (2 – 9 m) perennial monocotyledon and therefore classed as an arborescent herb. The wild species *Musa ingens* may grow up to 15 m and have a circumference of 2.5 m (INIBAP 2000). The above ground 'trunk' is called a pseudostem and consists of concentric layers of leaf sheaths rolled into a cylinder 20 – 50 cm in diameter (see Figure 5). Variation in pseudostem morphology exists between cultivars, especially its length, disposition and coloration. The pseudostems of Highland and sweet bananas are predominantly green to dark green with black blotches while those of plantains are yellowish green with brown blotches (Pillay & Tripathi 2007). The true stem is a large underground corm (also called a butt) and the meristem of the apical bud initially gives rise to the leaves before it elongates up through the pseudostem and emerges some 10 – 15 months after planting as a large terminal inflorescence (i.e. each pseudostem produces only one inflorescence) (see Figure 7).

The leaves of *Musa* plants emerge, tightly rolled (Figure 6), from the centre of the pseudostem in an anti clockwise spiral manner (Barker & Steward 1962). The leaf sheaths taper on both sides to form the petiole, which can vary in colour between cultivars and even within plants derived from the same corm. The leaf is more or less vertical when it emerges becoming horizontal and eventually drooping. The size of emerging leaves increases until just before flowering and then decreases until the emergence of the last leaf (the flag leaf) immediately before the emergence of the inflorescence. At its maximum size, the leaf of a banana plant is the largest of any plant in the world and the blade (lamina) can grow to 4 m long and 100 cm wide. Each blade has a pronounced midrib and well-marked, pinnately-arranged parallel veins. The leaf margins tear along the veins in windy conditions giving the blades a tattered appearance.

The root system, like that of all monocotyledons, is adventitious spreading out laterally as far as 5.5 m and forming a dense mat mainly in the top 15 cm of soil.

Figure 6. Emergence of a rolled leaf (arrowed) from the top of the pseudostem. The older leaves have unrolled as they have developed and show the characteristic predominant midrib, parallel venation and blade tearing [Photo credit: Janet Gorst, OGTR]

3.2 Reproductive morphology

The shoot meristem transforms into an inflorescence at about the time when the eleventh-last leaf has been produced. There is no evidence of a photoperiodic requirement for flowering (Purseglove 1972). Once it begins to elongate the inflorescence may grow an average of 8 cm per day finally emerging (Figure 7A) after about a month (Simmonds 1959a). The inflorescence is classed as a compound spike and the peduncle (inflorescence stalk) emerges upwards through the centre of the pseudostem before bending down under the weight of the developing spike (Figure 7B).

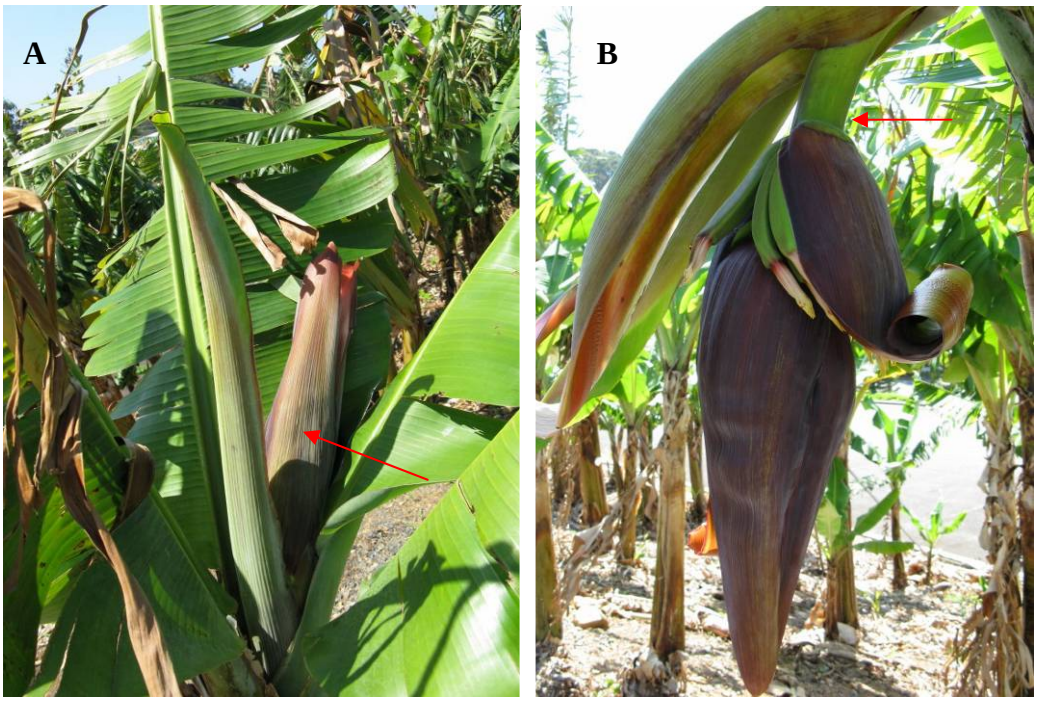

Figure 7. A) Inflorescence (arrowed) eme ging through the top of the pseudostem, and B) Developing inflorescence, wh ch has bent down, showing the bell shape, peduncle (arrowed) purple bracts, and fruits developing on the female flowers inside the bract at the proximal end of the inflorescence (see Figure 8 for a close-up). [Photo credit: Janet Gorst, OGTR]

The immature inflorescence is encased inside purple bracts (Figure 7B) that give the appearance of a large bud; it is often referred to as the 'bell'. Inside the bracts are 5-15 double whorls of floral parts comprising female flowers at the proximal end (closest to the base of the peduncle), male flowers at the distal end (closest to the tip of the peduncle), and neuter or hermaphrodite flowers sometimes present in between. Each node is covered by a purple bract. These bracts open in sequence (1 per day) from base to tip, becoming reflexed before being shed. As the hands of fruits start to develop from the female flowers (Figure 8A), the male flowers are usually shed leaving the peduncle bare except for the very tip, which consists of a 'male bud' (also referred to as the bell) containing the last-formed of the male bracts and flowers (Figure 8B). In some cultivars, this male part is shed quickly, and this character may be a useful distinguishing characteristic.

Figure 8. A) Close-up of female flowers showing the remains of the white, tubular tepals (arrowed) and the fruits (*) developing from the ovaries in a hand and,
B) maturing inflorescence showing the fruits developing from the female flowers and starting to reflex (turn upwards), and the 'bell' containing the male flowers [Photo credit: Janet Gorst, OGTR]

The tepals[11] are white, tubular and toothed (Figure 8A). The flowers secrete nectar at the tip of the ovary and this then collects at the base of the tepals. They are negatively geotropic and turn upwards as they develop (Figure 8B). Male and female flowers are morphologically indistinguishable until the inflorescence is about 12 cm long; at this point the ovary in the male flower fails to develop any further (Simmonds 1959a). Flowers have a 3-lobed stigma and style and an inferior ovary fused from 3 loculi. Each loculus of a female flower contains two rows of ovules embedded in a strip of mucilage (Simmonds 1953). There are 5 stamens in male flowers; these are reduced to staminodes in female flowers. Pollen, if produced, is sticky (Simmonds 1959a).

Each fruit is a berry and is known as a 'finger'. Each cluster of fruits at a node is known as a 'hand' and the entire collection of hands is known as a 'bunch'. The number of hands varies with species and cultivar. The outer protective layer of each fruit, known as the 'skin' or 'peel', is a fusion of the hypanthium (floral receptacle) and outer layer (exocarp) of the pericarp (fruit wall derived from the ovary wall). This peel is easily removed from the fleshy pulp that originates mainly from the endocarp (innermost layer of the pericarp) (Simmonds 1953). During the development of the fruit from the ovary, the tepals, style and staminodes abscise leaving a characteristic calloused scar at the tip of the fruit. Colour, size, texture and flavour of common

[11] In flowers such as those of banana where there may not be a clear distinction between sepals and petals, the resulting structures may be referred to as 'tepals' (Simmonds 1959a). Other authors (Ross 1987) consider that there is a distinction between petals and sepals but refer to these collectively as the 'perianth'.

cultivated *Musa* fruits vary with cultivar. Edible *Musa* cultivars have fleshy, seedless fruits while wild bananas may have little flesh and be filled with black seeds 3 – 16 mm wide (Morton 1987). The seeds have linear embryos, large amounts of endosperm and a thick, hard testa (Ellis et al. 1985).

SECTION 4 DEVELOPMENT

4.1 Reproduction

4.1.1 Asexual reproduction

All *Musa* spp. can propagate asexually; in the triploid sweet bananas this is, effectively, the only form of reproduction. Information on asexual reproduction in commercial plantings and unmanaged plantings is contained in Section 2.3.1 and Section 4.5, respectively.

4.1.2 Sexual reproduction

Pollen viability and total pollen counts vary between cultivars but, generally, diploid *Musa* species produce more viable pollen than tetraploids which, in turn produce more viable pollen than triploids. In one study the pollen of the diploid cultivars had 88% viability, the pollen of tetraploids had 29% viability and the pollen of triploids had less than 10% viability (Fortescue & Turner 2004). Viability is, however, only measured in terms of the presence of vital features such as an intact plasma membrane or positive esterase activity (Fortescue & Turner 2004). This does not take into account the fact that while the pollen produced by tetraploids may be viable, it is essentially 'impotent' because it is diploid (Shepherd 1987). The germination of such pollen *in vivo* if it occurs is very slow; however, it is possible to achieve fertilization by using pollen from tetraploid plants (Ortiz 2000).

The sweet banana cultivars traded globally are inherently female sterile and seed set is low (Simmonds 1959a; Ortiz & Vuylsteke 1995). Male sterility and parthenocarpy are closely linked although the reasons for their occurrence may be different (Fortescue & Turner 2005). While the occurrence of male sterility in edible triploid banana cultivars is caused mainly by chromosome irregularities at meiosis, the female sterility that also occurs is widespread across all ploidy levels and is often due more to morphological defects such as multiple archesporia, failure of embryo sac development, failure of fertilisation and derangement of post-fertilization events (Simmonds 1962). Triploid females without such functional abnormalities can successfully produce diploid progeny when crossed with diploid pollen (Fortescue & Turner 2004). A recent study suggested that the ovules of both triploid and diploid plants contain embryo sacs but that in triploids the embryo sacs are often incorrectly positioned and this may be a significant contributor to the sterility of triploids (Fortescue & Turner 2005). It has also been determined that the presence of the *M. balbisiana* B genome increases the likelihood of embryo sacs being correctly positioned and that this may be a reason for the increased fertility of triploid cultivars containing the B genome (e.g. AAB and ABB) over those with the AAA genome (Fortescue & Turner 2005).

Evidence suggests that wild bananas are moderately outbred (though self-pollination may be a frequent event) and that they tolerate an occasional generation of inbreeding without suffering significant inbreeding depression (Simmonds 1962).

4.2 Pollination and pollen dispersal

As already discussed, pollination is not a common occurrence in cultivated sweet bananas and there are few seeded cultivars in Australia (see Section 8 and Section 9 for further consideration of opportunities for crossing of cultivated with wild species in Australia). Pollination is essential for fruit development in the seeded cultivars (Simmonds 1959a).

Both male and female flowers are nectiferous. The abundant nectar and sticky pollen suggest animal pollination in the wild species. While a variety of insects have been observed visiting flowers, the characteristics of the inflorescences of many banana types suggest adaptation to bat pollination. These characteristics include nocturnal opening of flowers, characteristic odour, strong, often pendent inflorescences, accessible nectar, dull flower colour, and flowers exposed freely below the foliage (Simmonds 1962; Nur 1976; Liu et al. 2002). The pollen of flowers visited by bats is also high in protein and the nectar-feeders are able to supplement their nitrogen intake by also feeding on the pollen (Howell 1974) .In commercial bananas that do not produce pollen the flowers would not present a complete food source (Law 2001).

The Database of Neotropical Bat/Plant Intercations (Geiselman et al. 2002) lists a number of species of new world tropical bats pollinating *Musa* spp. (see Appendix 2a). None of these occurs in Australia. Old world bats such as *Macroglossus minimus*, *Macroglossus sobrinus* and *Eonycteris spelaea* are implicated in long distance pollination of wild banana species (Nur 1976; Fujita & Tuttle 1991; Liu et al. 2002) and have been attributed with the maintenance of genetic diversity both between and within populations (Ge et al. 2005); again, these do not occur in Australia. Australia does, however, have a number of *Pteropus* (flying fox) species (see Section 4.3) and while there is no specific record of their pollinating seeded banana types it is possible that they may do so; the hair on the heads of the flying foxes is modified with hooks which can entrap pollen. The majority of these flying foxes feed during the night within a radius of 30 km from their camp, however, they may commute up to 50 km and thus are regarded as long distance pollinators (Eby 1995).

Syconycteris australis (Common blossom bat) is a nectar feeder that occurs in northern Queensland. It is known to feed on the blossoms of the native species *M. acuminata* subsp. *banksii* (Law 2001) and its range also coincides with the native *M. jackeyi* (see Section 8). As such, it could have a role in the pollination of these two species. *S. australis* is often forced to forage on the nectar of cultivated bananas because of fragmentation of its native habitat. For the reason given above concerning the lack of pollen (and hence protein) in commercial bananas, this reliance on commercial banana nectar has been offered as an explanation for the atypically male-biased sex ratio of *S. australis* on the Atherton Tableland in northern Queensland (Law & Lean 1999).

Honeybees and birds are also regarded as pollinators of *Musa* in other parts of the world (Ortiz & Crouch 1997). These visit flowers during the day and, hence alternate with the nocturnal bat pollinators. The sunbird *Arachnothera longirostris* (family Nectariniidae) pollinates *Musa itinerans* in southwestern China (Liu et al. 2002). *Nectarinia jugularis*, known as the yellow-bellied sunbird in Australia, is the only member of the Nectariniidae in Australia.(Maher 1992). It occurs in northern Queensland and its range coincides with the two native *Musa* species (Slater et al. 1986). It has been observed pollinating *Musa acuminata* subsp. *banksii* (Armstrong

1979). Nectar-feeding marsupials such as the sugar glider (*Petaurus breviceps*) may also play a role in pollination of the native *Musa* species in Australia. Sugar gliders are troublesome in commercial plantations in Australia because they may damage developing fruit as they forage for nectar (Broadley et al. 2004).

4.3 Fruit/seed development and seed dispersal

The fruits of triploid sweet banana cultivars are parthenocarpic (develop without fertilization) and, while the ovules initially are larger than those of seeded banana cultivars, these ovules usually shrivel within 9 – 14 days of anthesis (Simmonds 1953; Fortescue & Turner 2005) leaving only vestiges that may be visible as brown specks in the centre of the fruit (Simmonds 1959a; Morton 1987). It is possible, however, for cultivars of some parthenocarpic triploid bananas (e.g. 'Awak Legor') to be pollinated and some seeds may develop; the presence of seeds has a stimulatory effect on pulp production (Simmonds 1953). If there is no pollination in the seeded cultivars, the ovaries of the female flowers will swell slightly but they then shrivel after a few weeks (Simmonds 1959a).

The maximum number of fruit that may potentially develop in a bunch is correlated with the climatic conditions occurring during the very early formation of the flowers at the time when the last 3 – 4 leaves are developing (Simmonds 1959a). Whether this number is realized depends upon conditions during the time when functional differences arise between male and female flowers.

Fruit development in parthenocarpic fruit appears to be mediated by autonomous production of auxin in the ovary (Simmonds 1959a); this stimulus replaces the stimulus in seeded fruits that derives from the developing seeds. Development may follow a concave volume curve (⌣) in some parthenocarpic cultivars (e.g. 'Gros Michel') or a convex curve (⌢) in others (e.g. 'Bluggoe') (Simmonds 1953). The immature fruit contains a high amount of starch that is rapidly degraded into sugars during ripening. Genes producing enzymes such as starch phosphorylase (da Mota et al. 2002), sucrose-phosphate synthase (Oliveira do Nascimento et al. 1997) and starch synthase (Clendennen & May 1997) are up- or down-regulated. These, along with other proteins, are activated in response to the burst of ethylene production that signals the beginning of the climacteric[12] (Clendennen & May 1997; Peumans et al. 2002). The unripened fruit of bananas also contains bitter tasting latex; this is broken down during ripening.

Banana fruits left on the plant ripen much slower than those that are removed (Purgatto et al. 2001; Peumans et al. 2002) and this is thought to be due to the transport of metabolites from the plant that inhibit the conversion of starch to sucrose. At least two candidates for this inhibition are indole-3-acetic acid (Purgatto et al. 2001) and gibberellic acid (Rossetto et al. 2003). However, the protein composition of the pulp and peel of detached fruits is similar to that of fruits left to ripen on the plant (Peumans et al. 2002).

[12] The climacteric is an increase in cellular respiration that occurs during the ripening of many fruits including banana. Increased ethylene synthesis precedes, and is responsible for, many of the ripening processes in climacteric fruits

The main external sign of a ripe fruit is the change to yellow of the skin. Continued ripening eventually results in blackening of the skin, emission of a disagreeable aroma and a change of the pulp to a gelatinous texture.

Wild *Musa* types are fully seeded and their fruits develop only after pollination. Fruit size depends on the number of seeds and a parenchymatous pulp develops around each seed. The growth volume curve is sigmoidal (Simmonds 1953).

The Database of Neotropical Bat/Plant Intercations (Geiselman et al. 2002) lists a number of species of new world tropical bats dispersing seed of *Musa* spp. (see Appendix 2b). None of these occurs in Australia.

In Australia flying-foxes (sometimes referred to as fruit bats) have been considered a pest species by fruit growers since the beginning of European settlement because they eat a wide range of commercial and backyard fruit including bananas (Tidemann et al. 1997), although their main diet is assumed to come from native plants (Birt et al. 1997). Grey-headed flying-foxes (*Pteropus poliocephalus*), Little Red Flying-fox (*Pteropus scapulatus*) and Black Flying-fox (*Pteropus alecto*) all occur in banana growing regions and have been observed in NSW feeding on cultivated banana fruits (Eby 1995). Other species that also occur in banana growing areas include the Spectacled Flying-fox (*Pteropus conspicillatus*), Tube-nosed flying fox (*Nyctimene robinsoni*), and Common blossom bat (*Syconycteris australis*). There is no scientific literature detailing the eating of seeded banana cultivars by flying foxes. However, it is pertinent to note that flying foxes (Megachiropterans) have a very short digestive tract and food will pass through the gut within 12 – 30 min (Birt et al. 1997). This suggests that seeds are unlikely to be digested and could germinate after being passed in the faeces. Animals may also hold seeds in cheek pouches for extended periods and then deposit them beneath trees in which they are feeding or camping (Eby 1995). However, it is noted that seeds larger than 9 mm (such as may occur in banana) are not carried in this way (Eby 1995). The long distances that *Pteropus* spp. can travel, and thus potentially disperse seed, has already been discussed in Section 4.2.

4.4 Seed dormancy and germination

Simmonds (1959b) has detailed the results of a number of experiments on the germination of banana seeds and described the early growth of the seedling.

Seeds, if produced, have a thick, hard testa (seed coat) that can prevent the oxygen and water that are essential for germination from entering the seed. Simmonds (1959b) determined that the highest germination is obtained from mature seeds extracted from ripe fruits, cleaned and sown immediately. Use of immature seed or seed extracted from rotting fruits had lower viability. Studies using seeds of *Musa balbisiana* (Stotzky et al. 1962; Stotzky & Cox 1962) have shown that, under artificial germination conditions, chipping of the testa to expose the endosperm and at least 9 cycles of exposure to an alternating temperature regime with a large amplitude (e.g. 12-18 h at 12^{o} – 18^{o} C/6 – 12 h at 27^{o} - 35^{o} C) improved germination. Normally, the seeds of *M. balbisiana* do not begin germination for 3 – 6 weeks and germination may then proceed in a flush or be spread over a 3 – 15 week period; the percentage germination is highly variable and depends on factors such as the maturity of the fruit at seed harvest, the post-harvest age of the seed and the method of storage (Stotzky et al. 1962).

While the actual seed viability of triploids, tetraploids and hybrid diploids may be poor (Karamura & Karamura 1995) banana seed has the potential to remain dormant in the soil for at least a year and seeds of the related species *Ensete* may survive for up to 25 years (Ellis et al. 1985). This is despite the fact that the seeds may be exposed to the warmth and moisture that causes rapid loss of viability in artificially stored seed. Relatively high carbon dioxide levels in the soil may contribute to this longevity and Simmonds (1959b) determined that 2% - 10% CO_2 levels were favourable for preservation of viability.

In general, germination of widely grown cultivars of *Musa* in soil may be less than 1% (Pillay et al. 2002). However, seeds that remain in the soil in a viable state can germinate *en masse* when the site is disturbed. Fire, landslip, and land clearing stimulate germination (Simmonds 1959b; Stotzky & Cox 1962). This has been observed in several species including *M. acuminata* subsp. *banksii* in forest in Queensland (Simmonds 1959b). A striking example is also the wild species *M. balbisiana* that produces approximately 10,000 seeds, which become distributed around the base of the plant after the fruit has fallen to the ground and decayed. Following disturbance a dense mat of seedlings germinate. Such prolific germination does not, however, lead to a dense stand of mature plants as most seedlings die due to competition (Simmonds 1962).

4.5 Vegetative growth

Banana leaves can unfurl at the rate of one per week in summer but only one per month may be produced in the sub-tropics in winter (Morton 1987; Espino et al. 1992) Most banana plants produce 30 – 40 leaves in a lifetime (Pillay & Tripathi 2007) but as older leaves are pushed outwards they eventually die leaving 5 – 15 fully functional leaves on a mature plant. A minimum of 8 -10 functional leaves are required to allow proper maturation of a bunch of fruit (DPI&F 2004a; Rieger 2006).

The pseudostem dies back after flowering but axillary buds of the corm are able to elongate into rhizomes (underground stems) from which suckers (or offsets) are produced, forming a clump called a 'stool' or 'mat'. Once the bunch has ripened and is removed the mother stem dies and the remaining suckers develop into mature plants (Broadley et al. 2004). In unmanaged plants, the oldest sucker generally develops into the next pseudostem and this process of succession can continue indefinitely although, as successive generations of suckers tend to be borne closer to the soil surface, plants become more weakly anchored and may eventually fall over (Espino et al. 1992). Also, if too many pseudostems develop at one time, as can happen, the entire mat is weakened (Boning 2006) because of competition for light and space. The successive development of pseudostems where extension growth is from lateral axes rather than the original tip is termed 'sympodial' growth.

Cultivars vary in the rate and time of suckering (Espino et al. 1992). There are two types of suckers that can be produced (Espino et al. 1992; DPI&F 2005) and their occurrence has implications for management of commercial crops that are ratooned (see Section 2.3.3):

> *'Sword leaf' suckers* develop on the corm of a current bearing plant. The growth of the suckers is held back by correlative inhibition from the 'parent' (on which the suckers rely for nutrition) and normal leaves are unable to develop until after flower initiation. The leaves that do develop prior to flowering of the parent are

very narrow and hence are referred to as sword leaves. Plants derived from sword leaf suckers can progress to inflorescence emergence as soon as 6 months after development of the first normal leaf, under optimal environmental conditions (Espino et al. 1992).

'Water' suckers often form on the corm of an already harvested plant and develop normal leaves early. Plants derived from water suckers are not nourished by a parent plant and therefore mature early and show early nutritional deficiency with the result that small, uneconomical bunches of fruit are produced (Espino et al. 1992; Broadley et al. 2004).

Roots are produced continuously until flowering (Price 1995). Extension rates can reach up to 2-4 cm per day in the lowland humid tropics and daylight growth is up to 30% higher than night time growth (Price 1995). [For abiotic factors influencing root growth see also Section 6]. Studies have shown that root system development during vegetative growth can be estimated from the above ground shoot growth characteristics and that diseases such as Black Sigatoka adversely affect root development due to the reduction in functional leaf area (Blomme et al. 2001).

SECTION 5 BIOCHEMISTRY

The biochemical composition of banana fruits depends on the cultivar, abiotic factors such as climate, cultivation method and nature of the soil (del Mar Verde Mendez et al. 2003). Table 10 shows representative levels of nutrients and minerals that can be found in the sweet banana. The banana fruit contains relatively high levels of potassium. Vitamin A content is generally low in the commercially grown 'Cavendish' and 'Lady Finger' varieties but some of the Fe'i banana cultivars grown in Micronesia contain high levels of vitamin A (Englberger et al. 2003).

Table 10. Nutrient values of banana fruit without peel /100g

Component	Recorded level/concentration
energy	350(84) kJ (kcal)
starch, total	4.8 g
water	73.5 %
ash	0.8 %
sugars total	13.5 g
sucrose	6.4 g
glucose	4.4 g
fibre total	1.8 g
fibre water insoluble	1.0 g
fat total	0.4 g
linoleic acid	26 mg
α-linolenic acid	20 mg
Sterols total	11.6 mg
protein total	1.1 g

Component	Recorded level/concentration
potassium	360 mg
magnesium	33 mg
calcium	7 mg
zinc	0.2 mg
iron	0.5 mg
iodine	1μg
selenium	1μg
vitamin A retinol activity equivalents	1.7μg
vitamin D	0
vitamin E	0.2 mg
vitamin K	0.5 μg
vitamin C	12.0 mg
folate	12.5 μg
riboflavin	0.05 mg
vitamin B1	0.05 mg
vitamin B12	0
carotenoids	29.7μg

* data compiled from NUTTAB 2006 (FSANZ 2006) and KTL (2007)

5.1 Toxins

There are no known significant toxic properties of the banana. Bananas contain high levels of biogenic amines such as dopamine and serotonin. High level intake of banana has previously been implicated in the occurrence of endomyocardial fibrosis (EMF) (Foy & Parratt 1960). Another study determined that serotonin is rapidly removed from circulating plasma and does thus not contribute to elevated levels of biogenic amines in healthy individuals (Ojo 1969). Subsequent studies by Shaper (1967) also determined that there is no evidence for implicating the banana/plantain as a factor in the cause of EMF.

5.2 Allergens

Allergic reactions to banana fruit occur and can take two different forms. One type of allergic reaction is related to an allergy to tree pollen such as birch (Informall 2007) and results in the oral allergy syndrome; symptoms include itching and swelling of the mouth and throat usually within one hour of ingestion. The allergic reactions are due to the allergen Mus xp 1, a profilin, which is an actin-binding protein of the cytoskeleton. The profilins are moderately stable proteins belonging to the pathogenesis related proteins, PRPs (Informall 2007), that are thought to be produced by the plant in response to infections or adverse environmental conditions (Breiteneder 2004). The profilins are more stable than Betv 1, a major birch-pollen related allergen, which also belongs to the PRP group of proteins. Profilin is an important mediator of IgE cross reactivity of antigens from different sources; cross reactivity between the banana profilin and birch profilin, Bet v 2 and the latex profilin

Heb b 8 have been demonstrated (Grob et al. 2002). As a result of the widespread IgE cross-reactivity, this has led to the description of profilins as pan-allergens (Wagner & Breiteneder 2002).

A second type of allergic reaction to banana fruit is associated with a latex allergy. This type of allergy causes urticaria (severely itchy skin) and gastrointestinal symptoms. Anaphylaxis and recurrent loss of consciousness have been reported in severe cases (Cinquetti et al. 1995; Woltsche-Kahr & Kranke 1997). Anaphylaxis can also occur in people who are not allergic to latex (Reindl et al. 2002). People with latex allergy often also show an allergy to other fruits such as avocado, mango and kiwi fruit, and common IgE epitopes in latex, banana and avocado extract have been identified (Moller et al. 1998). Two of the major allergens of banana involved in the fruit-latex syndrome are the 32-33 and 34-37 kD class I chitinases known as Ba 1 and Ba 2, respectively. These are thermolabile proteins and cross react with hevein (Sanchez-Monge et al. 1999). Hevein-like, chitin-binding domains are highly conserved in many plant defence proteins. These proteins also belong to the PRP family PR3 and may have anti-plant pathogen activity.

Leone et al (2006) isolated a thaumatin like protein (TLP) from banana, Ban-TLP, which has a similar tertiary structure to the thaumatin like PR5 proteins. Some PR5 proteins have anti fungal properties but the banana TLP is devoid of anti fungal activity (Barre et al. 2000). X-ray crystallography has indicated that conserved residues of exposed epitopic determinants are likely to be responsible for the allergenic properties of this protein. It shares some structurally conserved IgE-binding epitopes with similar proteins from other fruits and pollen such as that of the mountain cedar (*Juniperus ashei*) (Leone et al. 2006).

5.3 Other undesirable phytochemicals

Several lectins have been isolated from banana fruit, including BanLec, which belongs to the mannose-specific jacalin-related lectins (Peumans et al. 2000). This lectin is an important murine T-cell mitogen and can induce human T-cell proliferation (Koshte et al. 1990). It is thought that the lectins in banana form a carbohydrate-protein complex in the pulp, since relatively low amounts of free lectin are present in the pulp prior to the addition of glucose or methyl-mannoside (Koshte et al. 1990; Mo et al. 2001). Jacalin-like lectins also have insecticidal properties and may play a possible role in plant defence (Peumans et al. 2000).

5.4 Beneficial phytochemicals

Banana fruits contain high levels of potassium, which has been shown to be important as a blood pressure regulating chemical. The banana is thus a food potentially beneficial to people with medical conditions associated with high blood pressure and hypertension (Whelton et al. 1997). The sweet banana contains a variety of beneficial chemicals; high levels of the biogenic amines such as dopamine and serotonin, and other antioxidants like vitamin C, vitamin E, beta carotene and flavonoids such as catechins, indole alkaloids and vitamin K. Banana pulp contains high levels dopamine and vitamin C (Kanazawa & Sakakibara 2000). The peel contains even higher levels of dopamine; it is thought that the production of high levels of antioxidants may minimise the damage from the oxidative stress resulting from intense sunlight. Dopamine has been determined to protect against intestinal mucosal injury through

modulation of eicosanoid (signalling molecules) synthesis (MacNaughton & Wallace 1989; Alanko et al. 1992). Antiscorbitic (anti-scurvy) properties of the banana have also been demonstrated (Lewis 1919). The common sweet banana is relatively low in vitamin A. However two Fe'i banana cultivars, 'Uht en Yap' and 'Karat', which originate from regions in Asia, have up to 10 -275 times more β-carotene (a type of provitamin A carotenoid) than conventional Cavendish bananas (Englberger et al. 2003).

Green bananas have been reported to reduce the severity and duration of persistent diarrhoea (Rabbani et al. 2001; Rabbani et al. 2004). It is thought that the high levels of amylase resistant starch aids in this process through the stimulation of colonic salt and water absorption (Binder & Mehta 1989; Binder & Mehta 1990; Rabbani et al. 1999). It also protects against damage of the mucosal lining and improves peptic ulcers (Rabbani et al. 2001).

SECTION 6 ABIOTIC INTERACTIONS

Musa species have limited ranges of temperature tolerances within their natural habitats, which occur in warm or hot climates. No species is frost tolerant (Simmonds 1962). Sweet bananas are restricted to subtropical or tropical areas between 30^{o}N and 30^{o}S, with mean air temperature of 26.7^{o}C and a mean rain fall of 100 mm per month with no more than a 3 month dry season. Generally bananas require 50-100 mm per week as rainfall or supplied through irrigation (DPI&F 2004a). Optimal root growth occurs between 22-25^{o}C; lower temperatures will slow root growth. Bananas can be grown in a wide range of soil types but perform best in well drained, clay-loam soil, preferably to a top soil depth of 50 cm. A north-easterly, north-westerly aspect, frost free and protected from cold, strong winds is preferred, with a slope of less than 15% (Broadley et al. 2004; Pattison & Lindsay 2006).

6.1 Abiotic stresses

6.1.1 Nutrient stress

Soils with a low pH solubilise elements such as aluminium and manganese that can be toxic and result in reduced root growth. Macronutrients required by banana plants include nitrogen, potassium, phosphorus, calcium, magnesium and sulphur. They require particularly large amounts of nitrogen and potassium. A lack of potassium can result in reduced buoyancy, which can interfere with post harvest production line processes; the fruit sinks when the fruit is dipped in hot water for the treatment against certain diseases (Morton 1987). Supplementation of the soil with extra potassium can restore the buoyancy of the fruit. Other micronutrients required by bananas include boron, iron, manganese, copper, zinc, molybdenum, chlorine and cobalt. Deficiencies in these elements can lead, for example, to morphological malformation of the leaves, reduced growth and yield and poor fruit quality (Nelson et al. 2006). Boron deficiency can result in fruit that does not 'fill'(Broadley et al. 2004).

Bananas do not thrive in areas of high salinity, although some varieties are more tolerant than others. High levels of sodium result in reduced crop growth due to a reduction in osmotic pressure of the soil, which leads to an increase in ions that are toxic to the plant (Richards 1992; Bohra & Doerffling 1993; Gomes et al. 2002).

6.1.2 Temperature stress

Cool temperatures retard growth although susceptibility to the cold varies among cultivars (Broadley et al. 2004). Some examples of impact of cold on plant growth include: if low temperatures occur at the time of flowering the bud may not emerge from the stem; root growth will cease at temperatures below 13^{o}C; frosts kill the plant although the corm normally remains viable (Broadley et al. 2004). Planting on sunny hills of elevations of 60m to 300m assists in preventing cold air from reaching the plantation.

The fruit is also adversely affected by the cold and bunches may not fill (Broadley et al. 2004). November Bunch, associated with temperatures of less than about 6^{o}C at the time of bunch initiation, results in abnormal flowers, a reduction of hands of fruit and irregular sized, twisted fruit (Daniells 2004b). Choke Throat occurs when the bunch becomes trapped in the pseudostem at various stages of emergence. Less severe cases result in bunches that only partially emerge from the pseudostem and are thus susceptible to disease because they are difficult to cover (Daniells 2004a). Choke Throat can be caused by a number of factors, with cold temperatures in winter and early spring in southern Queensland and northern New South Wales exacerbating the condition (Daniells 2004a).

6.1.3 Water stress

Bananas have high water requirements, however waterlogging of the soil can result in oxygen starvation of the roots, causing shutdown of the plant (Daniells & Evans 2005). Oxygen deficiency for more than 6 hours results in root tip death, which in turn leads to branching of the roots (Pattison & Lindsay 2006).

No species is highly drought resistant but there is a considerable range of drought tolerance. Very broadly, response to drought is correlated with natural habitat and ranges from natives of non-seasonal climates (*Australimusa* and *Callimusa*) being intolerant, to those from extreme monsoonal areas that have severe drought seasons (*Rhodochlamys*) showing drought evasion by dying down to the corm in dry weather and sprouting again with rain. Members of section *Musa* tend to show variable tolerance with *M. balbisiana* able to withstand weeks of dry weather while the Australian native species *M. acuminata* subsp. *banksii* has a much greater requirement for water (Simmonds 1962).

Periods of drought can lead to a reduction of root growth and root tip death. When sufficient water becomes available and roots recommence growing, it may result in multiple branching giving a 'witches broom' appearance (Pattison & Lindsay 2006). Plants can tolerate short periods of drought because of their water-filled energy reserves but may only produce small bunches of bananas (Nelson et al. 2006). Lack of water may also result in bunches that don't 'fill' (Broadley et al. 2004). Periodic water stress is also associated with 'maturity bronzing' manifested by discolouration of mature bananas and cracking of the skin (Nelson et al. 2006).

6.1.4 Other stresses

A soil pH of 5.5-7.5 is suitable for growing bananas, with a pH of 5.5 considered optimal (Broadley et al. 2004). Most soils in north Queensland are naturally acidic. A low pH however solubilises elements like iron, aluminium and manganese; these can be toxic and have negative effects on the plant such as reduced root growth. This is

exacerbated when the soil becomes waterlogged or has low carbon levels. A low pH also reduces the availability of other nutrients such as calcium. Careful fertilizer management reduces soil acidification. A pH higher than 6.5, can reduce the availability of trace elements such as boron, zinc, copper and iron (Broadley et al. 2004).

All *Musa* species grow best in the open sun providing moisture is not limiting (Simmonds 1962). While, they can withstand shade of up to 80%, a maximum of 50% shade is recommended. If they are shaded, plants have thinner pseudostems, reduced leaf production and suckering, delayed fruiting and production of smaller bunches. Deep shade causes stools to die (Simmonds 1962; Nelson et al. 2006).

Fire will generally not kill the banana plant; they recover by regrowing from the corm (Nelson et al. 2006).

High humidity, >95%, during the final stages of ripening can lead to 'splitting' of the fingers (Nelson et al. 2006).

Bananas are also susceptible to strong winds, which can twist and distort the crown, and, in extremes, uproot whole plantations especially after heavy rains. In areas prone to windy conditions, dwarf varieties are often grown (Nelson et al. 2006). The leaves can also be shredded by winds thus interfering with metabolism. Note, however that because of the large dimensions of the banana leaf, some tearing is believed to be beneficial as it effectively causes the leaf to be split into many smaller segments that lead to a more favourable photosynthesis to transpiration ratio during times of environmental stress (Taylor & Sexton 1972).

6.2 Abiotic tolerances

Musa species are tolerant of a wide range of soil types. The plants will grow and produce fruit in very poor soil conditions but will not flourish or be economically productive (Simmonds 1962; Morton 1987).

SECTION 7 BIOTIC INTERACTIONS

The most conspicuous biotic factor in banana ecology is competition with other plants and all species are quickly killed by deep shade, are intolerant of root competition and are particularly sensitive to the presence of grasses. This has important implications for plantation management (Simmonds 1962).

7.1 Weeds

Weeds compete with the banana plants for nutrients, especially nitrogen (Morton 1987; DPI&F 2004a). They can also be a refuge for pests and act as intermediates for diseases. Weeds are more of a problem in planted crops, as crops that are ratooned tend to shade out weeds (Broadley et al. 2004).

Effective control of weeds in banana plantations is a requirement in accordance with the *Diseases in Plants Act* (DPI&F 2006a). The height of vegetation within a 2 m radius of banana plants must be kept to less than 60 cm in Queensland and less than 30 cm in NSW so as to facilitate inspections and allow ease of identification of disease symptoms.

Weeds are best controlled through herbicide sprays (glyphosate, glufosinate-ammonium, paraquat, diuron) combined with mulching and use of ground covers (Broadley et al. 2004)

7.2 Pests and diseases

7.2.1 Pests

Vertebrate pests, including nectar feeding birds, flying-foxes (also referred to as fruit bats) and sugar gliders can cause considerable damage to the banana fruit. Feral pigs have been known to cause damage to the banana plant and can also facilitate the spread of Panama Disease (Broadley et al. 2004). The common blossom bat (*Syconycteris australis*) is also known to feed on the blossoms of the native banana *Musa acuminata* subsp*. banksii* and commercial banana cultivars.

Major invertebrate pests of banana in Australia are given in Table 11. The Banana scab moth (*Nacoleia octasema*) is a frequent and severe pest of bananas (Pinese & Elder 2004c). *Heliconia* and *Pandanus* are the alternate host for this insect. The larvae feed on the young fruit causing superficial scarring which later forms a black callous in the curve of the finger adjacent to the bunch stalk, making the fruit unmarketable. The infestations are most severe in hot weather.

The weevil borer can have a large impact in southern areas. The larvae inflict damage on the plant by tunnelling within the corm just below the soil surface and large infestations can result in tunnelling a short distance up the pseudostem. This tunnelling weakens the plant and it may become susceptible to wind damage. Impact on the plant tends to be greater on slow growing and neglected plants.

Table 11. Major invertebrate pests affecting commercial bananas in Australia

Common and Scientific name	Occurrence	Damage	Prevention/Control	References
The banana aphid (*Pentalonia nigronervosa*)	Southern and northern Queensland	The vector for the Banana Bunchy Top Virus (BBTV)	Biological control through ladybird beetles, earwigs and lace or chemically through dimehoate	(Pinese & Elder 2004a).
The spider mite (*Tetranychus lambi*)	Frequent and widespread in banana growing regions	Reduction of plant growth damage to fruit	Reduction of dust on road and good farming practices	(Pinese & Elder 2004d; Biosecurity Australia 2007).
Silvering thrip and rust thrip (*Hercinothrips bicinctus* and *Chaetanophothrips signipennis*)	Queensland and the North coast of NSW	Infects fruit	Fipronil or chlorpyrfos sprays for rust thrip. Normally no chemical intervention is required for silvering thrip	(Pinese & Elder 2000; Treverrow 2002; Broadley et al. 2004)
The banana fruit caterpillar (*Tiracola plagiata*)	Southern Queensland especially plantings close to nearby scrub or rainforest	Attacks the foliage and fruit of the banana plant	Fipronil or chlorpyrfos sprays	(Pinese & Elder 2004b).
The banana fruit fly (*Bactrocera musae*)	Coastal regions north of Townsville	Destruction of fruit flesh	Minor infestations controlled naturally by several parasitoids that attack the maggot stage. Spot spraying selected areas using dimethoate is used if chemical treatment is required and the areas bordering the plantation should be targeted.	(Pinese & Elder 2004a; Biosecurity Australia 2007)
Queensland fruit fly (*Bactrocera tryoni*)	Western districts of Queensland occasionally further south	Destruction of fruit flesh		
The sugarcane bud moth (*Opogona glycyphaga*)	Queensland, NSW and Carnarvon in Western Australia	Superficial scarring of fruit	Spiders aid in the biological control of the moth. Severe infestations can be combated with chloryfos	(Pinese & Elder 2004e).

Common and Scientific name	Occurrence	Damage	Prevention/Control	References
Banana scab moth (*Nacoleia octasema*)	Only found north of Ingham in north Queensland	causing superficial scarring which later forms a black callous in the curve of the finger	Biological control by spiders and natural predators, synchronised bunch cycle can aid control. Chemical control through bunch injections using chlorpyrifos, bifenthrin, acephate or bendiocarb	(Pinese & Elder 2004c)
The root lesion nematodes (*Pratylenchus coffeae* and *Pratylechus goodeyi*)	*Pratylenchus coffeae* in Northern Queensland and *Pratylechus goodeyi* in NSW	Damage to the root system can lead to stunted growth, low bunch weight and longer ripening times, toppling in high winds	Immersing of the corm in either hot water-55 degrees for 20 minutes or in solutions of non-volatile Nemacur or Mocap Injecting the corms with glyphosate. Sugarcane ash has been shown to suppress nematodes. Chemical control using cadusafos, fenamiphos, oxamyl and terbufos	(Bridge et al. 1997) (Biosecurity Australia 2007) (Hodda 2003) (Stirling et al. 2002) (Morton 1987) (Lindsay et al. 2003). (Broadley et al. 2004)
The root burrowing nematode (*Radopholus similis*)**, the spiral nematode** *Helicotylenchus multicinctus* and t**he root-knot nematode** (*Meloidogyne* spp.),	All banana growing regions	Not deemed very important		
The weevil borer (*Cosmopolites sordidus*)	Queensland especially southern regions The potential threat of the weevil has increased in recent time due to the development of resistance to cyclodienes and organophosphates	Tunnelling within the corm just below the soil surface, large infestations can result in tunnelling a short distance up the pseudostem, weakening the plant making it susceptible to wind damage	Good plantation hygiene practices, cane-toads ants and beetles can provide a level biological control. Injection of old stems with insecticides, use of bait systems; gouge bait, axe baits and wedge baits. Butt spraying with chlorpyrifos, cadusafos, bifenthrin, fipronil, oxamyl, prothiofos or terbufos is the most effective method of control	(Treverrow 2003; Pinese & Elder 2004e)

7.2.2 Diseases

Bananas can be affected by a variety of diseases. Currently three diseases, Black Sigatoka, Panama Disease and Banana Bunchy Top Virus (BBTV) are the major threats to the banana industry in Australia (DPI&F 2004a). Several disease including Moko, Blood Disease and Banana Bract Mosaic Virus are currently not a problem in Australia. Plant Health Australia (2004) has produced a summary of diseases affecting bananas and their establishment and potential to spread.

As a result of the diseases that affect bananas in Australia quarantine areas have been established in Queensland to restrict the movement of potentially infected material[13] (Queensland Government 1999). Each of the areas has a list of approved varieties that may be cultivated within these areas. NSW also restricts the movement of banana material within the state based on a pest and disease quarantine zone (Newley 2000). There are two zones in NSW a northern and a southern zone. The southern zone is currently free of BBTV and has only had a few cases of Panama Disease. The southern zone extends south from Grafton; movement of plant material out of this zone is unrestricted. Material may not be moved out of the northern zone and movement within the zone is strongly discouraged (Newley 2000).

For the Queensland special pest quarantine area and southern pest quarantine area permitted banana cultivars for commercial planting include; 'Blue Java', 'Bluggoe', 'Ducasse', FHIA 01 ('Goldfinger'), 'Kluai Namwa Khom', 'Lady Finger', and 'Pisang Ceylan' (Mysore type) (DPI&F 2007). For more details see Lindsay et al (1999) and DPI&F (2007). Movement of plant material into and out of these zones is restricted; this is especially applicable in relation to Panama disease, a severe and untreatable fungus disease caused by *Fusarium oxysporum*.

There are a number of approved cultivars for residential growers. In southern Queensland individuals may plant a maximum of 10 plants (total) of one or more of several cultivars, but only after obtaining an inspector's written approval. Residential plantings are defined as those bananas not grown for commercial purposes. In addition to the cultivars permitted for commercial use, approved cultivars for residential planting for the Far northern and northern buffer pest quarantine areas, Northern pest quarantine area, and Southern buffer pest quarantine area; include 'FHIA 02, 'Goly Goly Pot Pot', 'Sh 3436', 'Simoi', 'Tu-8', 'War War', 'Yangambi Km5'. In the Special pest quarantine area and Southern pest quarantine area the only permitted cultivars for residential planting are the commercial cultivars (DPI&F 2007).

Table 12 summarises the major banana diseases in Australia. These are discussed in more detail following the table.

[13] The Queensland Department of Primary Industries & Fisheries has produced maps of 4 quarantine areas relating to banana.: i) Far northern and northern buffer pest quarantine areas; ii) Northern pest quarantine area; iii) Southern buffer and special pest quarantine area; iv) Southern pest quarantine area.These can be viewed at the following website: http://www2.dpi.qld.gov.au/health/3988.html

Table 12. Major diseases affecting commercial bananas in Australia

Disease + causal organism	Occurrence	Damage	Prevention/Control	References
Panama disease: the fungus *Fusarium oxysporum* f. sp. *cubense* (Foc)	Race 1: Queensland and NSW Race 2 :contained in north Queensland Race 3: not considered a problem Race 4 : currently only found in the Northern Territory	Spreading of infection in the plant causing death	Eradicating infections, weed control within the banana plantations and strict quarantine practices have restricted the spread. The development of resistant varieties is considered to be the long term solution	((DPIFM 2006) (Stansbury et al. 2000b) (Hennessy et al. 2005)
Yellow Sigatoka (leaf spot): the fungus *Mycosphaerella musicola*.	Serious in tropical growing regions	Delay in bunch filling, resulting in mixed ripened bunched and ultimately reduced marketability		(Peterson 2007).
Black Sigatoka (black leaf disease): the fungus *Mycosphaerella fijiensis*	Cape York, Weipa and Daintree (not in commercial mainland plantations)	Fruit losses occur due to the reduction in functional leaf surface area resulting in loss of photosynthetic capabilities	Deleafing	(Stansbury et al. 2000b; Biosecurity Australia 2007) (Murad 2005b)
Banana bunchy top virus (BBTV)	South eastern Queensland, south of Cooloobin and the Tweed and Brunswick River valleys of northern NSW but has not been detected in Western Australian, the Northern Territory, North Queensland or the Coffs Harbour region of NSW	Yellowing of the leaf with subsequent withering and death	There is no treatment for the disease, and affected plants must be destroyed. There are also strict quarantine restrictions to prevent movement of contaminated planting material	(Stansbury et al. 2000a) (Stansbury et al. 2000b; Biosecurity Australia 2007)
Banana freckle: the fungi *Phyllosticta* and *Guignardia musae*	It does not occur in the Northern Territory but has been in NSW, Queensland and more recently in Cavendish in remote areas of WA	Severe infections result in yellowing of the leaf with subsequent withering and death		(Meredith 1968)(Biosecurity Australia 2007) (Murad 2005a)
Banana Streak Disease: the virus banana streak virus **(BSV)**		Symptoms ultimately lead to choking and the production of small bunches with short fruit	Plantings of BSV free material	(Daniells et al. 2004)

The relative susceptibility of bananas to disease differs between cultivars (see Table 13).

Table 13. Relative susceptibility of different banana cultivars to diseases*

Variety	Yellow Sigatoka	Black Sigatoka	Panama Disease Race 1	Panama Disease Subtropical Race 4
Williams and other Cavendish	susceptible	susceptible	resistant	Susceptible
Ladyfinger	susceptible	susceptible	susceptible	Susceptible
Ducasse	resistant	resistant	susceptible	Susceptible
Pacific Plantain	moderately susceptible	moderately susceptible	susceptible	Susceptible
Goldfinger	moderately resistant	moderately resistant	resistant	Resistant
Red Decca group	moderately susceptible	moderately susceptible	susceptible	Susceptible
Bananza	moderately resistant	resistant	resistant	Resistant

* Adapted from Broadley et al 2004

Panama disease initially manifests itself as reddish-brown discolouration of the xylem of the root followed by the rhizome. This is followed by above ground symptoms and eventually the leaves turn bright yellow and wilt. With progression of the disease, younger and younger leaves are affected and the plant usually dies after a few months. Plants that are less than 1.5 m tall and younger than 4 months old do not develop symptoms (Stansbury et al. 2000b). There are 4 'physiological' races of Panama Disease based on their difference in pathogenicity, Races 1, 2, 3 and 4. Race 4 has been subdivided further into another 2 sub races, Sub tropical race 4 and Tropical race 4 (FocTR4). Sub tropical race has not been detected in Western Australia but has been recorded in properties near Darwin, in southern Queensland and northern NSW. This race tends to attack stressed plants only (Stansbury et al. 2000b). Tropical race 4 has been particularly destructive in that it attacks unstressed plants and has to date been found in the Northern Territory only (DPIFM 2006). The disease is spread through water and may persist in the soil for many decades (Stansbury et al. 2000b). Primary hosts of this disease include cultivated banana, *Musa acuminata* (wild banana) and *Musa textilis* (Manila hemp). Wild hosts such as *Heliconia caribaea* and some grass species such as *Paspalum fasciculatum* may serve as alternative hosts (Stansbury et al. 2000b). Strict quarantine practices have helped in restricting the spread of this disease. Weeds collected within banana plantations have been shown to be infested with FocTR4 in northern Australia, illustrating the importance of weed control within banana plantations (Hennessy et al. 2005).

Yellow Sigatoka infection develops through five distinct stages from tiny yellowish-green specks through to mature grey-dark brown/black spots sometimes with a yellowish halo (Peterson 2007). The fungus produces two types of spores, sexual ascospores and asexual conidia. The former are produced within the plant tissue and forcibly ejected into surrounding air currents and can be carried over long distances. These spores are produced in warm, moist conditions and absent during the cooler and

drier winter and spring periods. The conidia are produced on the top of the leaf surface and disperse in water droplets and thus tend to spread over shorter distances within the plantation (DPIFM 2006; Peterson 2007; Leutton et al. 2007).

Farmers are required by legislation to control the disease. There are different levels of 'infestation' allowed inside and outside the quarantine areas in Queensland; in the Northern Pest Quarantine Area (NPQA, Appendix 3, map 2), the maximum allowable level of leaf disease on a banana plant is 5%, of any one banana leaf in either a commercial or backyard banana plating. Other production areas outside the NPQA have a seasonal 'acceptable' level of 15% during the wet season, from November to May, and 30% during the dry season, from June to October (DPIFM 2006; Leutton et al. 2007). Control of the infection includes a deleafing program and spraying with protectant and systemic fungicides such as benomyl, trifloxystrobin, propianazole and pyrimethanil where appropriate (Broadley et al. 2004). The development of resistance of *Mycosphaerella musicola* to the fungicides is a major concern of the banana industry (Leutton et al. 2007).

Black Sigatoka is more virulent and devastating than yellow Sigatoka. The development to spot stage is faster and it can produce up to eight times more ascospores than yellow Sigatoka (Stansbury et al. 2000b). Infection occurs mainly in the younger leaves. It manifests itself as small choriotic flecks on the under surface of the third and fourth expanded leaves. The colour of the streaks intensifies to red, brown or black. Fruit losses ultimately occur due to the reduction in functional leaf surface area resulting in loss of photosynthetic capabilities (Stansbury et al. 2000b). Symptoms are usually visible 15-20 days after infection. The disease to date has not established in commercial mainland plantations. Outbreaks of the infection have been recorded in several regions including Cape York, Weipa and Daintree. However, it has been eradicated each time it was encountered and has not spread outside Cape York. Western Australia has not been affected by the disease, and remains officially under control (Stansbury et al. 2000b; Biosecurity Australia 2007). Like Yellow Sigatoka, the disease develops spores in the humid high-rainfall summers in tropical and sub-tropical regions. Deleafing has been a practice used to reduce the spread of the disease, reducing the development of the number necrotic patches thus limiting the number of ascospores that can be spread by the diseased plant (Murad 2005b).

BBTV infection is transmitted through an aphid vector *Pentalonia nigronervosa.* Transmission can occur through propagation material including tissue culture. Symptoms of infection occur at the apex of the leaves, which become marginally choriotic, narrower, dwarfed and upright. The edges of the leaves often curl upwards and develop yellowing. Dark green streaks on the midribs, petioles and leaf veins are the first signs of infection. The length of the streaks varies giving a characteristic 'morse code' appearance (Stansbury et al. 2000b). To date the disease has occurred in south eastern Queensland, south of Cooloobin and the Tweed and Brunswick River valleys of northern NSW but has not been detected in Western Australian, the Northern Territory, North Queensland or the Coffs Harbour region of NSW (Biosecurity Australia 2007). The impact of the disease on production can vary from minimal, at infestations of less than 5%, to major, such as that observed in the earlier part of the 20th century when over 90% of the area in northern NSW and southern Queensland had ceased production as a result of infection by the virus. The native species *M. acuminata* subsp.*banksii* is susceptible. Plants such as *Colocasia esculenta*, carrier of the host aphid vector, may be a symptomless carrier of the virus

(Stansbury et al. 2000a). There is no treatment for the disease, and affected plants must be destroyed. Control of the virus depends on prompt detection and subsequent destruction of infected stools. There are also strict quarantine restrictions to prevent movement of contaminated planting material (Stansbury et al. 2000a).

Banana freckle is caused by the fungi *Phyllosticta* and *Guignardia musae* and affects the fruit and leaves. Symptoms include dark brown/black spots that can run together to form streaks on the leaves and fruit. Severe infections result in yellowing of the leaf with subsequent withering and death. The disease spreads through transport of infected plant material or through spores; conidia and ascospores. Spread through conidia occurs in the wetter months, while ascospore-mediated spread occurs in the drier cooler months (Meredith 1968; Biosecurity Australia 2007). Banana freckle has tended to be more a disease of the cooking banana, but has in the past been detected on 'Cavendish' bananas in the Ord River area. Freckle has not been detected in commercial banana plantations (Biosecurity Australia 2007). It does not occur in the Northern Territory but their are several records of the disease in NSW, Queensland and more recently it has been reported in Cavendish bananas in remote areas of Western Australia (Murad 2005a; Biosecurity Australia 2007). The native banana *M. acuminata* subsp. *banksii* is susceptible to the disease (Biosecurity Australia 2007). The fungus is controlled through the removal of diseased leaf tissue and fungicide application (Biosecurity Australia 2007).

SECTION 8 WEEDINESS

Weeds are plants that spread and persist outside their natural geographic range or intended growing areas such as farms or gardens. Weediness in Australia is often correlated with weediness of the plant, or a close relative, elsewhere in the world (Panetta 1993; Pheloung et al. 1999). The likelihood of weediness is increased by repeated intentional introductions of plants outside their natural geographic range that increase the opportunity for plants to establish and spread into new environments, e.g. escapes of commonly used garden plants (Groves et al. 2005).

Characteristics in plants that are generally associated with weediness include prolonged seed dormancy, long persistence of seeds in the soil, germination under a broad range of environmental conditions, rapid vegetative growth, short lifecycle, very high seed output, high seed dispersal and long-distance seed dispersal (Keeler 1989; Keeler et al. 1996).

8.1 Weediness status on a global scale

Although plants in the genus *Musa* are generally persistent and compete well with other plants in an agricultural setting, they are not considered to be invasive. The seeds of some varieties have the potential to spread and become pests through being eaten by birds, bats and other vertebrates (Nelson et al. 2006). As described in Section 4.3, the vast majority of cultivated sweet bananas are seedless and generally do not reproduce sexually.

In the wet tropics, wild banana plants tend to briefly occupy a site during the process of ecological succession and their existence is quickly terminated by competition. Wild species rarely propagate vegetatively although it is possible for suckers to be broken off a parent plant and carried away by water or landslip. Seed propagation and

a short life-span appear to be the normal life cycle. This is in contrast to cultivated bananas where vegetative propagation is so significant (Simmonds 1962).

8.2 Weediness status in Australia

There are two recognised *Musa* species that are native to Australia, *Musa acuminata* subsp. *banksii* (section *Musa*) and *Musa jackeyi* (section *Australimusa*) (Ross 1987). *M. acuminata* subsp. *banksii* is the most common and can be found along the tip of Cape York and northern Queensland. It produces large viable seed. *M. jackeyi* has been reportedly found in Bellenden Ker and Cooktown and is considered rare by the World Conservation Monitoring Center (WCMC). Neither of these species is classed as a weed.

Other species such as *Musa acuminata* and *Musa* x *paradisiaca* are classified as a 'class 1' weed in Queensland (i.e. they may be naturalised and a minor problem but do not warrant control at any location) (Groves et al. 2003). Some diploid banana species have been found in northern NSW and these have the capacity to spread through seeds being eaten by vertebrates, such as bats, and birds (Bevan 2006). In the Northern Australia feral bananas tend not to be a significant problem because they die during the dry season, unless irrigated (DPIFM 2006). Banana seed has the potential to be dormant in the soil for at least a year (Ellis et al. 1985).

Any banana plants that belong to the *Musa* or *Ensete* genus, other than those that produce edible fruit (e.g. commercial cultivars), or are a non-volunteer indigenous plant, are considered to be potential weeds. This is especially the case in isolated areas where control would be difficult (Lindsay et al. 1999). The fruits of these plants often contain viable seeds that can be spread by animals that feed on them. In addition these plants can harbour pests and diseases that affect edible bananas. *Musa* plants that have potential to become weeds in Australia are ornamentals that may 'escape' from domestic gardens and include *Musa basjoo* (Japanese banana), *M. ensete*, M. *ornata*, *M. paradisiaca royalii*, *M. velutina* and *M.violacea*.

Commercial banana cultivars do not pose a weed problem in Australia, mainly because of their low fertility (see Section 4.1.2). Compared with the diploid *M. acuminata* with 71% pollen viability, commercial triploid cultivars have low viability, [e.g. 'Ducasse' (20%), 'Gros Michel' (13.5%) and 'Dwarf Cavendish' (9%) (Fortescue & Turner 2004)]. Extreme erosion as a result of heavy rains or cyclone associated weather can result in exposure of the roots and suckers of banana plants, especially those that are planted on slopes. In such cases the suckers of the banana plant could be dislodged and become part of the run off thus allowing the plant to be spread outside of the plantation setting. However, there are no reports of this occurring. Furthermore, State Legislation to prevent the spread of disease is also effective in ensuring that any volunteers must be destroyed (Queensland Government 1999).

8.3 Weediness in agricultural ecosystems

Commercially grown bananas in Australia reproduce vegetatively only. They are not known to be a weed, except if previous crops have not been removed properly prior to the planting of subsequent 'crops'. Removal of unwanted corms prior to cultivation of the subsequent crop is achieved using the methods outlined in Section 8.5.

8.4 Weediness in natural ecosystems

Near Tumbulgum in northern NSW individual plants of seeded bananas are an ongoing problem. These bananas are similar to the 'Ducasse' variety, but distinctly different from varieties such as 'Cavendish', 'Lady Finger' and 'Goldfinger' and can contain up to 50 small pebble sized seeds. More recently a weedy diploid species has also been found in several locations in and around Lismore, NSW. Seed from illegally obtained varieties, such as *M. ornata, M. velutin*a and *Ensete ventricosum*, may exist in natural ecosystems, along creek beds and forests, and other inaccessible areas, even though authorities target these plants for removal and control (Biosecurity Australia 2007). These plants have the capacity to spread through seeds being eaten by vertebrates, such as bats, and birds (Bevan 2006). Feral plants can also be spread when the rhizomes of ornamental varieties are discarded by householders.

Spread of bananas through seeds in a natural environment is dependant on a variety of factors. *Musa acuminata* and *M. balbsiana* seeds that are released into the environment in ripe fruit that has fallen to the ground in general do not have a high survival rate or viability. Seeds that become buried in the soil may have their viability somewhat preserved, with carbon dioxide concentration implicated as an important factor in preserving seed viability (Simmonds 1959b).

Normally wild bananas that grow in natural environments rely on the dispersal of their seeds by vertebrates such as bats and birds. Seeds of *M acuminata* that fall to the ground may, under optimal conditions remain dormant for up to a year (Simmonds 1959b). In general, seeds that have fallen to the ground and survive may germinate but then die. Seeds are known to germinate after disturbance of the site after for example, a landslide. Simmonds (1959b) observed a number of germinated, small seedlings of *M. acuminata* subsp. *banksii* in Queensland in the last century.

8.5 Control measures

Bananas can be killed through either chemical or non-chemical means. Non-chemical destruction involves digging out the pseudostem, suckers, corms or rhizomes, using a modified crowbar or special desuckering shovel, and chopping them up. This is very laborious and all remaining eyes need to be destroyed so as to avoid re-shooting.

The chemical destruction method uses an application of a solution of 2,4-dichlorophenoxyacetic acid (2,4-D) amine, glyphosate or diesel to the cut stumps, or injection into the stem close to the growing point (Lindsay et al. 2003). Destruction or removal of unwanted suckers involves application of mixtures of 2,4-D, diesel distillate and kerosene. Good management practices including the killing and removal of unwanted corms is an essential component of integrated pest management (Lindsay et al. 2003). Injecting the corms with glyphosate is an also effective method in pest management; the corms die faster thus removing any live plant material available as a breeding ground for pests and pathogens (Lindsay et al. 2003).

SECTION 9 POTENTIAL FOR VERTICAL GENE TRANSFER

9.1 Intraspecific crossing

The commercial sweet banana cultivars are effectively sterile and therefore the chances of natural intraspecific hybridisation are remote (see also Sections 2.4.1. and

4.1.2.). In addition, the agricultural practices of covering bunches (see Section 2.3.5), would prevent any seeds that may develop being eaten for example, by bats and birds (Fortescue & Turner 2005; Bevan 2006).

Introgression (backcrossing of hybrids of two plant populations to introduce new genes into a wild population) between subspecies of *M.acuminata* can theoretically occur in nature providing that the parents are sympatric (share the same geographical range). There is genetic evidence of spontaneous hybridization of *M. acuminata* with wild relatives (Ellstrand 2003). In cultivation, hybrids produced from crosses within subspecies of *M. acuminata* tend to be vigorous and fairly fertile (Simmonds 1962). *M.acuminata* subsp. *banksii* is a native diploid banana found in northern Queensland and has the potential to cross with cultivated triploid and tetraploid cultivars with a *M. acuminata* background. However, the commercial varieties grown in Australia are both male and female sterile and as such rarely produce viable pollen or viable seed.

9.2 Natural interspecific crossing

Generally, species within the genus *Musa* are regarded as being reproductively isolated (Simmonds 1962). It is, however, relevant to consider the possibility of hybridisation in terms of species with the same chromosome number. As noted in Section 9.1, the realization of natural hybridisation can only occur when species are sympatric. Species within the sections *Musa* and *Rhodochlamys* both have 2n = 2x = 22. Although the composition of the sections has changed somewhat since Simmonds (1962) wrote about reproductive isolation within and between the sections, his comments provide a useful background. He suggests that species within *Musa* are highly differentiated and thus reproductively isolated, while those in *Rhodochlamys* are less differentiated and introgression between wild populations is likely providing the species are sympatric. Interestingly, crosses between *M. acuminata* (*Musa*) and species within *Rhodochlamys* can produce hybrids albeit with low fertility.

Species within *Australimusa* and *Callimusa* both have 2n = 2x = 20. Those within *Australimusa* generally cross readily and yield vigorous hybrids. The crossing relationships within *Callimusa* have not been widely studied.

Simmonds (1962) noted that the following natural interspecific crosses had been observed:

M. balbisiana x *M. acuminata* (*Musa* x *Musa*)

M. nagensium x *M. balbisiana* (*Musa* x *Musa*)

M. balbisiana x *M. sikkimensis* (*Musa* x *Musa*)

M. balbisiana x *M. textilis* (*Musa* x *Australimusa*)

M. flaviflora x *M. velutina* (*Musa* x *Rhodochlamys*)

There are a number of factors that should be considered in relation to interspecific crosses within the genus (Simmonds 1962):

Pollen tube growth and fertilization. Even in very distant crosses, which differ in basic chromosome numbers, ovule swelling occurs after pollination. This indicates that isolation occurs at or before fertilization.

Seed yields from interspecific crosses. Results are highly variable but suggest that wide natural crosses (e.g. *M. balbisiana* x *M. textilis*) can still yield some viable seed.

Hybrid viability. Results from a range of wide crosses indicate that resulting hybrids may show a spectrum of viability ranging from zygote inviability through to weak young plants to vigorous, flowering mature plants.

Hybrid meiosis and fertility. The pairing of chromosomes at first metaphase of meiosis in a hybrid varies from normal to extremely low and can contribute significantly to reproductive isolation. Irrespective of the degree of pairing, fertility tends to be much lower than in the parents. In wild species, there is usually seed fertility of 200 – 700 seeds/1,000 ovules whereas in hybrids, even in those between parents with the same chromosome number, fertility may be 0 – 180 seeds /1,000 ovules.

Meiotic breakdown. This occurs frequently in interspecific hybrids and may lead to female flowers that produce giant embryo sacs and undesirable pentaploid progeny following pollination, and male flowers that are sterile.

The above discussion, while relevant to a consideration of crosses between wild species of *Musa*, is not particularly relevant to crosses involving a cultivated variety that may carry a varying incidence of sterility factors superimposed on parthenocarpy (see Section 4.1.2 for a more detailed discussion). The outcome of this is to render the likelihood of successful natural crossing close to zero where a cultivated variety is one of the parents.

9.3 Crossing under experimental conditions

Hybridisation is possible with judicious selection of male and female parents (Simmonds 1962). With regard to crosses involving a cultivated parent: *M. balbisiana* is an ineffective male parent in crosses with AAA genome types (e.g. 'Cavendish', 'Williams', 'Mons Mari') but is better with AAB (e.g. Lady Finger') and ABB (e.g. 'Bluggoe') genomes. *M. acuminata*, on the other hand, is a less effective pollen parent than *balbisiana* for the AAB and ABB genomes. Female fertility in the resulting hybrid, however, increases with increasing *balbisiana* contribution (see Section 4.1). Edible AA diploids have been used both as female and male parents. The AA cultivar 'Pisang Lilin' is a particularly good male parent (50% male fertile) and has produced many viable diploids when crossed to other edible diploids but it is a poor female parent (Simmonds 1962).

Simmonds (1962) listed the viability of hybrids of a number of crosses made within and between wild species of the *Musa* and *Rhodochlamys* sections (Table 14).

Table 14. The viability of hybrids obtained from crosses between species from *Musa* and *Rhodochlamys*

Male parent / Female parent	*ac*	*ba*	*bj*	*it*	*la*	*or*	*sa*	*Ve*
Musa acuminata (ac)		weak	weak - inviable	fairly vigorous	vigorous	vigorous	barely viable	seedlings weak, but vigorous if plants reach maturity
balbisiana (ba)	vigorous		fairly vigorous	inviable	vigorous	weak - inviable	v. weak seedlings but vigorous if plants survive	Weak
basjoo (bj)	weak - inviable	inviable		fairly vigorous	weak	inviable	v poor germination	crossing difficult
itinerans (it)	fairly vigorous	inviable	weak - inviable		weak	inviable	inviable	weak – inviable
Rhodochlamys laterita (la)	vigorous	moderately vigorous	weak	weak		inviable	v. poor germination	fairly vigorous
ornata (or)	vigorous	weak - inviable	inviable	inviable	seedlings weak but vigorous if plants survive		inviable	Vigorous
sanguinea (sa)	barely viable	weak - inviable	v. poor germination	inviable	v. poor germination	inviable		Weak
velutina (ve)	seedlings weak	fairly vigorous	crossing difficult	weak - inviable	poorly vigorous	weak - inviable	vigorous	

Information adapted from Simmonds (1962)

Even if seed is obtained the seed yield of hybrids in breeding programs is usually low and germination is extremely variable and relatively difficult (Stotzky et al. 1962). This often means that germination with a large number of seeds has to be attempted in order for a few viable seedlings to be produced. *In vitro* embryo culture has been proposed as a method for obtaining seedlings although it is a painstaking task to remove the 0.7 – 1 mm diameter embryo from inside the hard seed coat. The technique has been applied successfully to non-hybrid embryos from seeds of *Musa velutina* (Pancholi et al. 1995) and *Musa balbisiana* (Afele & De Langhe 1991).

The recent finding that it may be the incorrect positioning of embryo sacs in ovules that leads to the lack of fertility in many triploids (see also Section 4.1.2) would suggest that breeding potential could be more effectively exploited by removing the ovules from the flowers of triploids and pollinating them *in vitro* (Fortescue & Turner 2005).

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APPENDICES

Appendix 1. Comparison of monthly temperature and rainfall statistics in areas where bananas are grown commercially in Australia*

1. Carnarvon – Western Australia (Desert, summer drought)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	31.2	32.5	31.5	29.0	26.1	23.3	22.2	22.9	24.3	25.8	27.4	29.2	27.1
Mean min temp (°C)	22.4	23.3	22.0	19.1	15.0	12.3	11.0	11.6	13.9	16.3	18.6	20.6	17.2
Mean rainfall (mm)	11.8	19.4	15.0	13.2	37.4	47.9	47.0	18.2	5.9	5.6	4.1	1.9	228.4

2. Broome – Western Australia (Grassland, winter drought)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	33.3	32.9	33.9	34.3	31.5	29.1	28.8	30.2	31.7	32.8	33.5	33.8	32.2
Mean min temp (°C)	26.3	26.0	25.4	22.6	18.3	15.2	13.6	14.9	18.5	22.3	25.0	26.4	21.2
Mean rainfall (mm)	176.6	178.3	103.4	26.9	27.5	18.7	6.0	1.8	1.4	1.3	8.0	52.6	601.1

3. Kununurra – Western Australia (Grassland, winter drought)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	36.4	35.5	35.3	35.5	32.9	30.5	30.2	33.6	36.4	38.3	38.8	38.1	35.1
Mean min temp (°C)	25.1	24.9	24.1	21.3	19.1	15.9	15.0	17.5	20.8	23.7	25.4	25.7	21.5
Mean rainfall (mm)	196.6	213.0	140.1	21.2	10.0	1.3	3.9	0.1	2.8	25.5	70.9	105.3	727.7

4. Darwin (Humpty Doo) – Northern Territory (Tropical rainforest)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	31.8	31.4	31.9	32.7	32.0	30.6	30.5	31.3	32.5	33.2	33.2	32.6	32.0
Mean min temp (°C)	24.8	24.7	24.5	24.0	22.1	19.9	19.3	20.5	23.0	25.0	25.3	25.3	23.2
Mean rainfall (mm)	419.0	358.1	319.1	102.9	21.0	2.0	1.3	5.4	14.9	69.3	140.4	246.1	1685.9

5. Innisfail – Northern Queensland (Tropical rainforest)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	30.8	30.6	29.8	28.3	26.4	24.5	24.1	25.1	26.7	28.4	29.7	30.8	27.9
Mean min temp (°C)	22.8	22.8	22.0	20.4	18.3	16.1	15.1	15.4	16.8	18.9	20.7	22.0	19.3
Mean rainfall (mm)	505.1	595.5	661.5	463.5	300.7	190.4	134.8	119.0	85.1	83.0	154.5	263.7	3558.8

6. Bundaberg – Southern Queensland (Sub-tropical, no dry season)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	30.1	29.9	29.1	27.3	24.7	22.5	22.0	23.2	25.3	26.8	28.2	29.3	26.5
Mean min temp (°C)	21.3	21.3	19.9	17.5	14.2	11.5	10.2	10.8	13.6	16.5	18.8	20.4	16.3
Mean rainfall (mm)	171.9	153.0	102.7	58.9	69.1	50.5	41.1	34.5	36.1	73.8	88.6	123.2	998.0

7. Coffs Harbour – Northern New South Wales (Sub-tropical, no dry season)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	26.9	26.8	25.9	24.1	21.4	19.3	18.7	19.7	21.9	23.6	24.9	26.3	23.3
Mean min temp (°C)	19.4	19.5	18.1	15.2	11.7	9.0	7.5	8.2	10.9	13.8	16.1	18.1	14.0
Mean rainfall (mm)	183.8	212.5	243.6	173.0	163.2	114.4	72.9	81.4	61.6	92.1	129.2	142.4	1668.2

* data taken from the Australian Government Bureau of Meteorology website, September 2007: http://www.bom.gov.au/climate/averages/

Appendix 2a. Species of new world tropical bats pollinating *Musa* spp.*

Musa Species	Bat Species
M. acuminata	*Carollia perspicillata*
M. acuminata	*Glossophaga soricina*
M. acuminata	*Platyrrhinus lineatus*
M. paradisiaca	*Anoura caudifer*
M. paradisiaca	*Phyllostomus hastatus*
Musa (unspecified)	*Artibeus jamaicensis*
Musa (unspecified)	*Carollia perspicillata*
Musa (unspecified)	*Choeronycteris harrisoni*
Musa (unspecified)	*Choeronycteris mexicana*
Musa (unspecified)	*Glossophaga commissarisi*
Musa (unspecified)	*Glossophaga soricina*
Musa (unspecified)	*Hylonycteris underwoodi*
Musa (unspecified)	*Leptonycteris curasoae*
Musa (unspecified)	*Leptonycteris nivalis*
Musa (unspecified)	*Leptonycteris sanborni*
Musa (unspecified)	*Leptonycteris yerbabuenae*
Musa (unspecified)	*Lonchophylla concava*
Musa (unspecified)	*Lonchophylla mordax*
Musa (unspecified)	*Lonchophylla robusta*
Musa (unspecified)	*Lonchophylla thomasi*
Musa (unspecified)	*Musonycteris harrisoni*
Musa (unspecified)	*Phyllostomus discolor*
Musa (unspecified)	*Vampyrops lineatus*

Appendix 2a. Species of new world tropical bats dispersing seed of *Musa* spp.*

Musa Species	Bat Species
M. paradisiaca	*Anoura caudifer*
M. paradisiaca	*Artibeus jamaicensis*
M. paradisiaca	*Artibeus lituratus*
M. paradisiaca	*Glossophaga soricina*
M. paradisiaca	*Micronycteris megalotis*
Musa (unspecified)	*Phyllostomus hastatus*
Musa (unspecified)	*Carollia brevicauda*
Musa (unspecified)	*Carollia perspicillata*
Musa (unspecified)	*Glossophaga soricina*
Musa (unspecified)	*Phyllostomus discolor*
Musa (unspecified)	*Phyllostomus hastatus*
Musa (unspecified)	*Sturnira lilium*
Musa (unspecified)	*Sturnira mordax*
Musa (unspecified)	*Uroderma bilobatum*

* Data for both Appendices derived from the Database of Neotropical Bat/Plant Interactions (Geiselman et al. 2002). The plant and bat names are as reported in the original publication and are not necessarily currently accepted names.