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

The Biology of *Ananas comosus* var. *comosus* (Pineapple)

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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.

TABLE OF CONTENTS

PREAMBLE

This document describes the biology of *Ananas comosus* var. *comosus* (pineapple), with particular reference to the Australian environment, cultivation and use. Information included relates to the taxonomy and origins of cultivated *A. comosus* var. *comosus* (*A. comosus*), general descriptions of its morphology, reproductive biology, biochemistry, 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) *A. comosus* that may be released into the Australian environment.

In this document, pineapple is used to refer to *A. comosus* and its cultivars, and to hybrids of *A. comosus* with other varieties.

A. comosus is a tropical, herbaceous, perennial monocot, approximately 1-2 metres tall and wide, with leaves arranged spirally. It bears flowers on a terminal inflorescence, which form a large, edible fruit characterised by a tuft of leaves at its apex. Pineapple is the third most important tropical fruit in world production after bananas and citrus. Pineapple is an introduced crop in Australia and is cultivated almost exclusively in the State of Queensland (Bartholomew et al. 2003).

SECTION 1 TAXONOMY

A. comosus is the most economically important plant in the family *Bromeliaceae,* which is divided into three subfamilies: *Pitcarnioideae*, *Tillandsioideae* and *Bromelioideae*. *A. comosus* belongs to the subfamily *Bromelioideae*, order *Bromeliales*, genus *Ananas* and species *comosus* (Bartholomew et al. 2003).

The family *Bromeliaceae* consists of approximately 2794 species and 56 genera that have adapted to a wide range of habitats ranging from terrestrial to epiphytic, shady to full sun and from hot humid tropics to cold dry subtropics. They can grow in moist to extremely dry situations and at varying altitudes from sea level to alpine conditions. (Bartholomew et al. 2003). Members of this family are characterised by a short stem, narrow stiff leaves arranged in a circular cluster, terminal inflorescences (racemes or panicles), hermaphroditic and actinomorphic trimerous flowers. Fruits are capsules or berries that contain small naked, winged or plumose seeds, with a reduced endosperm and a small embryo (Purseglove 1972; Bartholomew et al. 2003). The subfamily *Bromelioideae*, is the most diverse and consists of the largest number of genera but the lowest number of species. Most members are epiphytes characterised by a rosette like form, with spiny leaves and berry-like fruit containing wet seeds (Coppens d'Eeckenbrugge et al. 1997).

The genus *Ananas* is recognised among *Bromeliaceae* by the characteristic inflorescence, which is fused into a syncarp, a unique dense rosette of scape-wide leaves and medium to large fruits. Pineapple plants are set apart from other monocots by the characteristic star-shaped, scale-like multicellular hairs and unusual coiling stigmas, which fold together lengthwise (Gilmartin & Brown 1987). Cultivated pineapple was first described and named *Karatas* and *Ananas* at the end of the 17th century by Charles Plumier on the island of Hispaniola part of Antilles (West Indies) located between Cuba to the west and Puerto Rico to the east. Later all pineapples were classified in one genus, *Ananas*. Bartholomew et al (2003) stated that in 1892 Mez recognized in the *Flora Brasiliensis* only one species *A. sativus* and five botanical varieties. Pineapple taxonomy underwent further modification several times and it was not until 2003 that the classification developed by Coppens d'Eeckenbrugge and Leal (2003) was internationally adopted.

Based on similarity in floral structure, biology and chromosome number (2n=50), the current classification identifies six botanical varieties of *A. comosus* that intercross successfully with *A. comosus* var. *comosus* to produce fertile offsprings (Coppens d'Eeckenbrugge et al. 1997). The six varieties of *A. comosus* include the former species given below (Coppens d'Eeckenbrugge & Leal 2003):

- *A. comosus* var. *ananassoides* (formerly two species: *A. ananassoides* and *A. nanus*).
- *A. comosus* var. *bracteatus* (formerly two species: *A. bracteatus* and *A. fritzmuelleri*).
- *A. comosus* var. *comosus* (formerly *A. comosus*)
- *A. comosus* var. *erectifolius* (formerly *A. lucidus* (formely *A. erectifolius*)
- *A. comosus* var. *parguazensis* (formerly *A. parguazensis*)
- *A. macrodontes (formerly Pseudananas sagenarius)*

Ananas monstrous has been invalidated because the crownless fruit characteristic is not stable (Coppens d'Eeckenbrugge & Leal 2003). Generally, varieties of pineapple are distributed throughout the tropics and seed production is rare because most varieties of *A. comosus* possess reduced fertility combined with self-incompatibility (Coppens d'Eeckenbrugge et al. 1993).

There are approximately 30 cultivars of *A. comosus* that are grown commercially in tropical and sub tropical countries around the world. However, for convenience in global trade, the numerous pineapple cultivars are grouped in four main classes: 'Smooth Cayenne', 'Red Spanish', 'Queen' and 'Pernambuco' (Abacaxi), despite much variation in the types within each class (Morton 1987; Coppens d'Eeckenbrugge & Leal 2001). The fifth group or class comprising of 'Motilona' or 'Perolera' is commercially important in South America (Sanewski & Scott 2000). In Australia the most dominant cultivar used in commercial plantations for canning purposes is Smooth Cayenne followed by Queen (Bartholomew et al. 2003).

Molecular markers are useful in establishing taxonomic relationships. F1 based genetic maps of DNA markers for *A. comosus* var. *comosus* and *A. comosus* var. *bracteatus* have been published. The map of var. *comosus* consists of 156 markers assembled in 30 linkage groups and covers over 31.6% of the genome; a dominant allele at locus P responsible for morphological traits 'piping', a silvery streak and the absence of spines along the margin of the upper leaf (Cabral et al. 1997) has been included in the latest map (Carlier 2004). The map of var. *bracteatus* gathers 335 DNA markers in 50 linkage groups and covers 57.2% of the genome length. Work is underway to complete the integrated genetic maps of these two varieties (Coppens d'Eeckenbrugge 2006).

SECTION 2 ORIGIN AND CULTIVATION

2.1 Centre of diversity and domestication

It is likely that modern pineapple originated in pre-Columbian times in South America; a mutation for seedlessness and selection for large fruit size, increased sweetness and juiciness and improved flavour occurred over time (Purseglove, 1972). Chronicles of European explorers have described and mentioned pineapple domestication in parts of South America and in the Caribbean. Pineapples were already a part of the diet of the Native Americans before the arrival of Columbus (Collins 1960). Two hypotheses on the possible origin of pineapple have been stated in Bartholomew et al (2003); the first hypothesis by Bertoni in 1919 suggested that pineapples were domesticated by the Tupi-Guarani Indians from *A. comosus* var. *ananassoides* who carried them during their migration northward to the Antilles, northern Andes and Central America. This hypothesis has been quoted in a number of reviews on crop origins (Purseglove 1972; Bartholomew et al. 2003).

The second hypothesis by Leal and Antoni (1981) as stated in Bartholomew et al. (2003), suggested that the genus could have originated and located in an area within 10˚N-10˚S latitude and 55˚-75˚W longitude. They also suggested that south eastern Brazil could have been a secondary centre of origin and distribution (Purseglove 1972; Bartholomew et al. 2003). Purseglove (1972) suggested that modern pineapples could have originated in the Parana-Paraguay river drainage area because of the occurrence of seeded relatives in the wild [*A. bracteatus*, *A. ananassoides* (Bak.) L. B. Smith, *A. erectifolius* L. B. Smith and *Pseudananas sagenarius* (Arudda) Camargo] (Purseglove 1972).

Following the discovery of pineapple in South America, it was soon dispersed into other regions of the world by travellers and seafarers. Pineapple was introduced into the Philippines, Hawaii and Guam during the early 16th Century by the Spaniards, and reached India and the east and west coasts of Africa by 1548. In 1594, pineapple plants were reported growing in China and by 1655 in South Africa. Pineapple plants were reported in Europe in 1650 and pineapple fruits were being produced in Holland in 1686. It was not until 1719 that pineapple plants were successfully established in England in greenhouses (Purseglove 1972; Bartholomew et al. 2003).

In 1777, Captain James Cook planted pineapples on the Society Islands, Friendly Islands and elsewhere in the South Pacific. However, it was not until 1885 that the first sizeable plantation of 5 acres (2 ha) was established in Oahu (Purseglove 1972). In 1838, Lutheran missionaries imported pineapple plants from India into Brisbane, Australia. Pineapple was grown on a small scale and in a scattered manner for some time and the fruit was sold locally in Queensland. In Australia, the commercial pineapple industry was established in 1924 and a canning plant was established at Rockhampton and Cairns in 1946. Later cultivation areas increased in size to cater to the fresh market and canning industry. Post war pineapple production increased and replaced some sugarcane cultivation areas in Queensland (Collins 1960; Morton 1987).

The successful dispersion of pineapple on a world-wide basis can be attributed to its ability to tolerate drought and the relative ease with which vegetative propagules can establish under cultivated conditions (Collins 1960; Purseglove 1972). Pineapple is currently grown commercially over a wide range of latitudes from approximately 30ºN to 30ºS (Hayes 1960; Purseglove 1972; Bartholomew & Kadzimin 1977; Medina & Garcia 2005).

2.2 Commercial uses

Pineapple is cultivated predominantly for its fruit that is consumed fresh or canned. The fruit is a good source of manganese and contains significant amounts of vitamins C and B1 (for more information on nutrients refer to Table 4, Section 5.4). Approximately 95% of canned pineapple comes from the cultivar Smooth Cayenne. Pineapple is used as an ingredient in a variety of foods including pizzas, condiments, sweets, savouries, cakes, pastries, yoghurt, punches, ice creams etc (Purseglove 1972; Bartholomew et al. 2003; Rohrbach et al. 2003; Medina & Garcia 2005).

Pineapple contains the proteolytic enzyme bromelain, which is used as a meat-tenderising agent and for medicinal purposes. It has been reported to have valuable biological properties such as interfering with the growth of malignant cells, inhibiting platelet aggregation, fibrinolytic and anti-inflammatory action, enhancing drug absorption and removing skin (debridement) (Gailhofer et al. 1998; Mynott et al. 1999; Hale et al. 2005). Pineapple leaf juice is used as a purgative (agent that cleanses the bowel), emmenagogue (agent that induces menstrual bleeding) and vermifuge (agent that expels intestinal worms) (Leal & Coppens d'Eeckenbrugge 1996; Coppens d'Eeckenbrugge & Leal 2001). Pineapple products have also been marketed as a ‘digestive aid’ in health food stores.

The stems and leaves of the pineapple plant are a source of fibre, which can be processed into paper. Fibres are approximately 60cm in length, white and easily dyed. The cloth made from pineapple fibre is known as ‘pina cloth’ and was in use as early as 1571. Even today in the Philippines small scale cottage industries make high quality clothes from pineapple fibre (Collins 1960; Purseglove 1972; Montinela 1991; Coppens d'Eeckenbrugge & Leal 2001). Pineapple fibre has potential in paper production and the development of low density polyethylene composites (Fujishige et al. 1977; Fujishige & Tsuboi 1978; George et al. 1993). Parts of the pineapple plant are used for silage and hay for cattle feed. Processing wastes in the form of shell, core materials and centrifuged solids from juice production are used as animal feed. Alcoholic beverages can also be made from the juice (Purseglove 1972; Stanley & Ishizaki 1979; Bartholomew et al. 2003). World pineapple production reached 15.5mt in 2004, with Asia contributing 50% and Americas contributing 31.6% (Table 1) (FAO 2005). The international fresh-pineapple market (approximately 670,000 t) is dominated by Costa Rica, the Philippines and the Cote d`Ivoire (FAO 2005).

Table 1. Pineapple production in the top 8 countries in 2004

Country	Area (ha)	Production (t)
Thailand	80,000	1,700,000
Philippines	46,000	1,650,000
China	65,500	1,475,000
Brazil	54,683	1,435,000
India	90,000	1,300,000
Nigeria	116,000	889,000
Costa Rica	17,400	725,224
Mexico	17,906	720,900

*Data compiled from FAO (2005) (FAO 2005).

2.3 Cultivation in Australia

Although all *Ananas* species are found in Australia according to the latest taxonomic classification (Coppens d'Eeckenbrugge & Leal 2003), their distribution is limited except for *A. comosus* var. *comosus* (cultivated pineapple) (Sanewski & Scott 2000):

- *A. ananassoides* (*A. comosus* var. *ananassoides*), *A. parguazensis* (*A. comosus* var. *parguazensis*), *A. fritzmuelleri* (*A. comosus* var. *bracteatus*) and *Pseudananas sagenarius* (*A. macrodontes*) are located only at Maroochy Research Station, Queensland; and
- *A. nanus* (*A. comosus* var. *ananassoides*), and *A. bracteatus* (*A. comosus* var. *bracteatus*) are sometimes found in nurseries or home gardens as ornamental plants mainly in Queensland. A cultigen of *A. comosus* var. *erectifolius* is being assessed by a few pineapple growers in Queensland for the production of cut flowers (Sanewski & Scott 2000).

Various factors like temperature, rainfall, location, soil type, drainage and nutrient requirements influence pineapple plant development and production in managed ecosystems (agricultural). Relative to other pineapple producing areas in the world, Australia (south east Queensland) is unusually far from the equator, with pineapple crops subject to strong seasonal influences. Sinclair (1993) stated that climatic conditions of south east Queensland is less than optimal for pineapple cultivation. Therefore the optimal climatic conditions for pineapple cultivation prescribed by Neild and Boshell (1976) do not apply to Australia.

A temperature range of 18ºC to 32ºC is most favourable for pineapple cultivation (Bartholomew et al. 2003). In Queensland the summers are warm to hot (19ºC to 30.3ºC) and wet, while the winters are cool (6ºC to 20.5ºC) and comparatively dry (Wassman 1990; Bureau of Meteorology 2007). Plant growth decreases rapidly at mean temperatures below 15ºC or above 32ºC (Neild & Boshell 1976). In Queensland, low temperatures occur from May to October and potentially inhibit growth during the mid winter (Glennie 1981; Wassman 1990). Plants do not tolerate frost but temperatures have been reported to drop below 0ºC for short periods in the pineapple growing areas of south east Queensland. Prolonged cold periods (0ºC) will affect plant growth (destroy canopy), delay maturity and cause the fruit to be more acid (Swete Kelly & Bartholomew 1993). In Australia, Smooth Cayenne can initiate reproductive development below 10˚C, however fruit formation is drastically affected and will eventually impact on the harvest dates. High (above 35˚C) and low (below 10˚C) temperatures affect fruit development and retard growth (Purseglove 1972; Bartholomew & Criley 1983; Py et al. 1987; Malezieux et al. 1994).

Pineapple plants are most productive under dry environments where low rainfall is supplemented by irrigation in well-drained soils. Pineapple performs well in relatively low water regimes; it requires as much as 5cm of water per month from rain or irrigation (an annual rainfall of 115cm during spring and autumn) (Black 1962; Purseglove 1972; Py et al. 1987). In Queensland the average rainfall varies from 102-358cm annually. Annual rainfall ranges from 102-165cm in the pineapple growing belt of Queensland (Collins 1960; Black 1962).

In the subtropical areas of southern Queensland elevation and aspect are of particular importance in deciding the site for pineapple cultivation (Black 1962). Therefore most pineapple plants are planted on hillsides to escape frost. Pineapples thrive well when planted on a north-easterly aspect where they receive the maximum amount of sunlight and warmth (Bartholomew et al. 2003). Slopes of nearly 40% are farmed with medium sized equipment in Queensland although soil erosion can be an issue (El-Swaify et al. 1993; Ciesiolka et al. 1995).

Pineapple plants require sandy soils and good drainage to prevent water logging and therefore purpose built raised beds on slopes are utilised. Well drained loamy soil with high organic matter and a pH of 4.5-6.5 is best for pineapple cultivation (Morton 1987; Bartholomew et al. 2003). The soils along the coastal regions of Queensland vary from sands, sandy loams, basaltic red loams, clayey loams, gravely loams and gravely clay-loams. The dark brown and reddish-brown basaltic and sandy loams are considered ideal for pineapple production (Collins 1960; Morton 1987).

2.3.1 Commercial propagation

Two cultivars of *A. comosus* are grown commercially in Australia: a spiny leaved small fruit type 'Queen' and smooth-leaved medium fruit type 'Cayenne' (Collins 1960). In Queensland, clonal selection began in 1950 when 100 plants were selected from commercial fields. Four clones of Smooth Cayenne (C8, C10, C13 and C30) along with Hawaiian clone 'Champaka F180' were eventually released into the industry in 1975. Other clones selected by private growers and established include 'Ripley Queen', 'Alexander' and McGregor' obtained from the cultivar 'Queen' (Duke 1997). After 20 years of breeding and testing, the Queensland Department of Primary Industries released a dual purpose cultivar named the 'Queensland Cayenne' in 1975 (Loison-Cabot 1987; Morton 1987; Coppens d'Eeckenbrugge et al. 1997; Sanewski 1998). Other cultivars bred for the fresh fruit market include Mareeba Sweet, Mareeba Gold, Golden circle premium gold and Bethonga Gold which characteristically have low acid levels and true pineapple taste (QMPI&F 2007). 'Aus-Jubilee' is a new variety of pineapple (at its first stage of commercialisation) selected for its high sugar, vitamin C content (twice that of Smooth Cayenne), aromatic flavour, firm flesh and colour (Botella et al. 2000; Medina & Garcia 2005; DAFF 2007a).

2.3.2 Scale of cultivation

Pineapples are grown on a small scale relative to other crops, mainly because only the tropical and sub tropical regions of Queensland provide suitable (though sub optimal) climatic conditions for cultivation. In Queensland, pineapples are grown (up to 40 km inland) over a 1,500 km narrow coastal strip along the eastern seaboard from Cairns in the north to Brisbane in the southeast (Sinclair 1993). The most northerly plantations are at Mossman in Far North Queensland and the most southerly are at Dayboro (just north-west of Brisbane); Rollingstone near Townsville and Atherton tablelands in the north, Yeppoon in central Queensland and Sunshine coast and Caboolture in the south are other important pineapple cultivation areas in Queensland (refer Figure 1 below) (QMPIF 2007). The majority of plantations are in Wamuran and Caboolture approximately 100 km north of Brisbane. Small commercial fields are also located in the Northern Territory, northern New South Wales and central Western Australia (Reid 1990). Pineapple canning centres are located in Yeppoon, Bundaberg, Mary Valley, Gympie, Nambour, the Glasshouse Mountains area and Brisbane (Collins 1960).

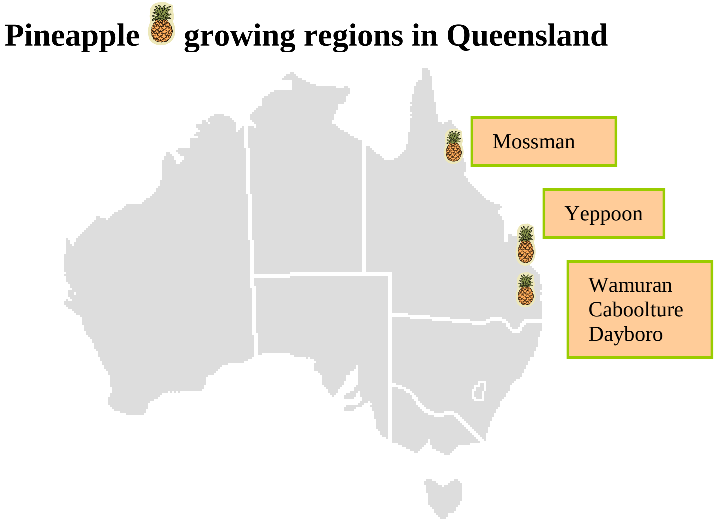

Figure 1. Map taken from Australian, States and Territories Map (2007) (http://www.gov.au/sites/index.html). Location of places on the map is only to give a broad idea of pineapple cultivation areas in Queensland.

Australia exported 1t canned fresh fruit to Hong Kong and East Timor during 2004/05 (Rohrbach et al. 2003; QDPI 2007). Pineapple production reached 139kilo t (kt) worth $44m in 1999/00, while in 2004/05 production decreased to 110kt (worth $37m) and 104kt respectively (DAFF 2007b). Table 2 indicates the pineapple yield in t/ha and the number of hectares under cultivation during 2001-05 in Queensland.

Table 2. Pineapple production, cultivated area and yield in Queensland from 2001-05

Year	Production '000 in t	Bearing area in '000 ha	Yield t/ha
2001	119.6	2.7	43.8
2002	119.3	3.0	40.3
2003	104.7	2.6	40.1
2004	110.4	2.7	41.5
2005	104.0	^ 2.7	37.9

^ data subject to sampling variability between 10% and 25%; *Data compiled from http://www.abs.gov.au/ausstats/abs@.nsf/mf/7113.0Agricultural Commodities, Australia ABS (2007) (ABS 2007)

Details of pineapple production during 2004/05 in Queensland are given in Table 3.

Table 3. Pineapple production in areas of Queensland in 2004-05

Statistical Region	'000 t
Brisbane	^ 27.4
Moreton	^ 28.9
Wide Bay-Burnett	^ 17.6
Darling Downs	-
South West	-
Fitzroy	* 21.7
Central West	-
Mackay	* 0.7
Northern	* 7.6
Far North	0.3
North West	-
Queensland	104.0

- nil or rounded to zero (includes null cells); ^ data subject to sampling variability between 10% and 25%; * data subject to sampling variability between 25% and 50%; Data compiled from ABS (2007) (ABS 2007)

As indicated in Table 3, in 2004-05, most of the pineapples produced in Queensland came from the Moreton, Brisbane and Fitzroy areas (ABS 2007). Since pineapples are not propagated using seeds, there is no seed industry in Australia. There are no commercial plantings of GM pineapples in Australia, however field trials of GM pineapple plants modified to control flowering and ripening (DIR027/2002) and to reduce black heart (DIR028/2002) have been approved.

2.3.3 Cultivation practices

Planting

Pineapples are perennials and are cultivated throughout the year mainly by use of vegetative propagules like crowns, slips, hapas or suckers (Purseglove 1972; Bartholomew et al. 2003). These vegetative propagules are desiccation tolerant and can be stored and survive detached from the parent plant for up to 6 months depending on the prevailing conditions. All plant materials designated for vegetative propagation are treated with fungicides and insecticides prior to planting (Coppens d'Eeckenbrugge & Leal 2001). In Queensland, it takes 24 months in the tropics to 36 months in the cool subtropical environment for the propagales to establish into plants and provide fruits (Bartholomew et al. 2003). Soils are cleared of large rocks, and trees, and conventional or minimum tillage is carried out to eliminate weeds before planting. Fertilisers (nitrogen, potassium and phosphorous) are applied to the soil before planting. In pineapple plantations high levels of nutrients are supplemented to maintain good levels of growth (Nightingale 1942a; Morton 1987; Bartholomew et al. 2003).

The type of planting material determines the planting depth; crowns, propagules and plantlets are most sensitive to deep planting and are usually buried at a depth of 5-10cm; slips, hapas and suckers are planted at a depth of 10-15cm. Exposure to sun helps control butt rot in these structures. Drip and overhead irrigation systems are used to apply water and fertilisers. Weeds are controlled to avoid serious damage and impedance to plant growth; in Queensland, special attention is given to clump grasses and vines, which are problematic. Mulches are also used to block weed growth in planting beds (Coppens d'Eeckenbrugge & Leal 2001; Bartholomew et al. 2003). Planting is usually done manually with a traditional short handled narrow bladed hoe (Coppens d'Eeckenbrugge & Leal 2001). Quality of planting is best when hand planted, compared to machines, which damage the growing point of the planting material (Coppens d'Eeckenbrugge & Leal 2001; Bartholomew et al. 2003).

Typical plant densities for Smooth Cayenne range from 29,000 to 86,000 plants per hectare (Bartholomew et al. 2003). Densities are usually based on the intensity of agricultural practices and planned use of the fruit. Plants are planted in single rows or on beds of 2-4 rows with adequate space (80cm) for walking to carry out all field activities. Inter row (between 2 rows) distance is usually approximately 35cm to 40cm (Morton 1987; Coppens d'Eeckenbrugge & Leal 2001; Bartholomew et al. 2003).

Control of flowering

Natural flowering is a major problem and occurs during the months of May and June in plants that are approximately a year old and weigh >500g. In order to avoid uneven natural flowering, artificial induction with chemicals is common in commercial practices, a process called ‘forcing’ (Botella et al. 2000). Application of ethylene and ethylene-releasing chemicals like ethepon or etacelasil are used to induce flowering (Burg & Burg 1966; Kuan et al. 2005). Auxins like naphthalene acetic acid and acetylene are also effective forcing agents (Gowing & Leeper 1959). Ethylene applied as a pressurized spray late in the evening or at night permits uptake through the stomata (Bartholomew & Criley 1983). In Queensland, ethylene is applied either once or twice as a saturated solution in water. Activated charcoal is also added to enhance absorption of ethylene. Personal protective equipment is required to avoid exposure of workers to the highly combustible gas (Bartholomew et al. 2003).

Variation in plant sensitivity was observed in the variety Smooth Cayenne to forcing; plants less than 1.0kg in weight and large plants (above 2 kg) are difficult to force. Therefore plants of optimum size (2kg) are recommended for forcing in order to obtain even flowering (Sinclair 1993; Bartholomew et al. 2003). In Queensland, if plants are induced to flower during June, they are ready to be harvested in the first week of March after a period of 274 days; while plants forced to flower during September are harvested in the fourth week of March after a period of 204 days (Malezieux et al. 1994). In sub tropical parts of Queensland it takes 280-300 days from floral induction to harvest (Dodson 1968; Botella et al. 2000; Bartholomew et al. 2003). In Queensland, the average cost to the pineapple industry for natural flowering is estimated at $900,000/year (Botella et al. 2000). Strategies for increasing pineapple yield and fruit size include application of side dressings of nitrogen, phosphorous and potassium 5 times a year (Py et al. 1987; Morton 1987). Morton also reported increase in fruit size with the application of magnesium (Morton 1987).

Harvest, Storage & Transport

Pineapple is a highly perishable fruit; therefore the stage of maturity of the fruit is important in determining quality of the fruit and harvest times. At the time of fruiting it is crucial to cover the fruits to protect them from sun burn/damage (Coppens d'Eeckenbrugge & Leal 2001; Bartholomew et al. 2003). Fruit colour is a good indicator of fruit maturity; as the fruit matures the outer shell gradually changes from green to yellow (Bartholomew et al. 2003). Other fruit quality indices include size, shape, firmness, absence of decay, sunburn, cracks, bruising, internal breakdown and brown spots, gummosis and insect damage. A reliable way of establishing fruit maturity is by determining the ‘flesh brix’ of the fruit, that is, a measure of total solids at each fruit colour stage. A minimum of 12ºBrix (12% total soluble solids) and 1% maximum acidity was established by CODEX and FAO/WHO in international trade to guarantee consumer acceptance (Coppens d'Eeckenbrugge & Leal 2001).

In Australia harvest is mechanically assisted and usually undertaken before ripening. Pineapples are harvested and placed in bins for cannery processing. Such collected fruits may be accumulated at roadways for transfer to trucks or loaded directly for transportation to canneries or to a central location for trade (Bartholomew et al. 2003). Once harvested, fruits are susceptible to sunburn and therefore should not be placed in direct sunlight for more than an hour. Fruits for the fresh market are harvested without crowns and a short length of peduncle attached. For the best fruit quality it is preferable to harvest fruits when ripe. To help retain fruit quality cut fruits may be waxed and treated with fungicide to reduce black rot (Paul & Rohrbach 1982; Paul & Rohrbach 1985).

The main issues that affect pineapple fruit quality are damage due to bruising during loading, transportation, unloading and conveying. Air and road transportation up to 2 days does not require refrigeration; however fruit quality is retained and improved if refrigerated after picking. Fruits should be refrigerated at temperatures between 7.1ºC to 10ºC if they are to be transported for more than 3 days (Bartholomew et al. 2003). Fresh fruits are transported at 15ºC from Queensland to other states by rail or road with the major markets being Brisbane, Sydney and Melbourne. Significant quantities are also transported to Adelaide, Perth, Hobart and Darwin. Air transportation of pineapples is mainly to neighbouring countries like New Zealand and Hong Kong (Smith 1993).

Crop rotation & Intercropping

Selection of crops to combine with pineapple cultivation can occur in the form of crop rotation or inter row cropping. This practice has been adopted recently in some parts of the world because it permits use of resources more efficiently during the long production cycle of pineapple and in addition reduces the dependency on one crop and spreads income along the cultivation cycle (Lee 1972). The pineapple crop also offers protection against heavy rain and winds to the intercropped species. In turn growth of the pineapple crop is healthier due to frequent weeding, fertilizer and pesticide application to the inter row crops (Uriza-Avila et al. 2005).

Pineapple cultivation is carried out routinely as a monocrop; as a result the crop is susceptible to many fungal diseases. Recent reports recommend crop rotation in pineapple farms as a means of controlling fungal diseases. Crop rotation using legumes like *Canavalia* spp. has decreased the incidence of root disease on pineapple in Mexico. However in Australia, crop rotation is not a common practice. After a crop is harvested the remaining plant material is slashed and ploughed and the field remains fallow for a period of time until new vegetative propagales are planted. Inter row cropping in pineapple plantations is gaining importance and popularity; in Queensland oats are intercropped with pineapple (Garth Sanewski[1] pers comm). This is mainly due to the beneficial effects of chemicals released from oats, which provide protection to the pineapple roots against fungal pathogens (Cruz et al. 2006). Ratooning is an agricultural practice of harvesting a second or additional crop from an original pineapple plant. Generally in Australia, the plant and one ratoon crop are harvested after approximately 3-4 years (Bartholomew et al. 2003). The original plant is called the ‘plant crop’ while the fruit developed from the lateral, axillary branch attached to the axis of the plant crop is called the ‘first ratoon’. A healthy root system is necessary to produce successful ratoon crops. Ratoon crops are fertilized, irrigated, forced, ripened and harvested in a way similar to the plant crop. The amount of fertilizer used however is reduced. In Queensland pineapple farmers avoid the use of ratoon crops to minimise carryover diseases and prefer to plant new vegetative propagules (Purseglove 1972; Bartholomew et al. 2003).

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2.4 Crop Improvement

2.4.1 Breeding

Pineapple is largely vegetatively propagated. Sexual reproduction is rare in nature because pineapple is self sterile; seeds if produced by self fertilization germinate slowly with low vigour and young seedlings are fragile due to inbreeding depression (Purseglove 1972; Daniela 1999; Bartholomew et al. 2003). However, since pineapple is heterozygous, hybridisation is possible between *A. comosus* var. *comosus* and other varieties as mentioned in Section 1. Hybrids are valuable material in pineapple breeding and breeders can generate a wide variety of genotypes. Many important fruit characteristics such as high ascorbic acid and carotene content, low acidity, increase in total soluble solids, size increase and high translucency were obtained by clonal selection (Chan 2006). Small scale hybridization programs aimed at clonal selection of Smooth Cayenne were also carried out during 1970s in Australia (Loison-Cabot 1987; Sanewski 1998; Coppens d'Eeckenbrugge et al. 1997). For more details refer Section 2.3.1.

Conventional breeding has disadvantages due largely to the domination of a single variety Smooth Cayenne in the markets and the low level of molecular diversity between varieties of *A. comosus* (Duval et al. 2001). This has resulted in poor success in varietal improvements. In addition, hybridization programs are resource intensive; an estimated 15 years is required to produce hybrid varieties (Loison-Cabot 1987; Sanewski 1998).

2.4.2 Genetic modification

A range of useful traits *viz* improved fruit quality, flowering control, pathogen resistance and herbicide tolerance are being developed using genetic techniques. Attempts have been made by scientists in Australia to inactivate the *Polyphenol Oxidase* (PPO) gene to reduce or eliminate discolouration (black heart) of the pineapple fruits. The inactivation is expected to reduce or eliminate the discoloration of the fruit pulp (Graham et al. 2000). Fields trials of this GMO have been successfully conducted in Queensland in which the PPO gene expression was reduced. Sripaoraya and co workers (2001, 2006) have successfully transformed the ‘Phuket’ cultivar of pineapple by introducing the herbicide (bialophos) tolerance *bar* gene (Sripaoraya et al. 2001; Sripaoraya et al. 2006) that are tolerant to commercial herbicide basta and could potentially reduce residual herbicides in the plant and environment.

Flowering control to achieve synchronous natural flowering is another important aim pursued by the Hawaiian Pineapple Genetic Engineering Consortium in collaboration with Queensland Department of Primary Industries (Botella et al 2000). Rohrbach and co workers (2000) and Botella and co workers (2000) have successfully transformed pineapple by down regulating the *1-aminocyclopropane-1-carboxylate* (*ACC) synthase* gene (Botella et al 2000) or over expressing the *ACACS2* in pineapple to achieve suppression due to methylation of the same endogenous gene (Trusov & Botella 2006). *ACC synthase* is a key enzyme responsible for the biosynthesis of ethylene (which can cause early flowering). Preliminary results of field trials conducted in Queensland indicate a low incidence of natural flowering in the both types of GM pineapple (Rohrbach et al. 2000; Botella & Fairbairn 2005; Trusov & Botella 2006).

Nematode types like root knot and reniform and mealby wilt virus are significant pathogens of pineapple. The ban on use of nematicides such as methyl bromide has encouraged scientists to develop transgenic nematode resistant pineapple. Bakhetia's group at the University of Leeds have successfully developed nematode resistant pineapple plants using anti-feeding defence strategy (Bakhetia et al. 2007). Two *Ampeloviruses*, *Pineapple mealybug wilt associated virus-1 & 2* (PMWaV1 & 2) have been identified in pineapples grown in Hawaii. The coat protein gene PMWaV-2 was introduced into pineapple as an inverted repeat; glass house testing of such modified pineapple produced five putative transgenic lines resistance to the virus (Perez et al. 2006).

SECTION 3 MORPHOLOGY

3.1 Plant morphology

Pineapple is an herbaceous plant approximately 1-2 metres tall and wide (refer Figure 2 for morphological details). The plant has a spiral morphology due to the arrangement of the leaves. The stem is a distinct central cylinder, erect and club-shaped approximately 25-50cm long, 2-5cm wide at the base, 5-8cm wide at the top and contains nodes and internodes (Collins 1960; Purseglove 1972; Bartholomew et al. 2003; Medina & Garcia 2005).

A fully grown pineapple plant has many (68-82) leaves arranged in the form of a dense compact rosette. The older leaves are located at the base of the plant and the younger ones in the centre. Leaves are usually sword shaped (except for the ones at the tip) and taper toward the tip (approximately 5-20cm in length). The margins may or may not contain spines (cultivar Smooth Cayenne contains spines at the tip of the leaf only). The upper and lower surfaces of the leaf are covered with hairs that are more pronounced on the lower surface (Purseglove 1972; Morton 1987; Coppens d'Eeckenbrugge & Leal 2001; Bartholomew et al. 2003).

Parts of a pineapple plant

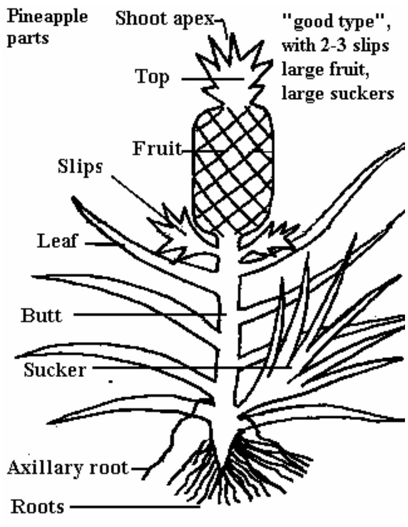

Figure 2. Picture taken from Elfick (2007) (Elfick 2007)

The leaves enclose the stem up to two thirds of its circumference, are wide at the base and form a sheath around the stem. Due to the tendency to collect water at the base, the leaves are semi rigid; this feature may also provide aerial roots with water and nutrients (Bartholomew et al. 2003). The plant can flower after producing 70-80 leaves (Purseglove 1972; Coppens d'Eeckenbrugge & Leal 2001; Medina & Garcia 2005).

The root system is primarily adventitious, typical of monocots, and may spread up to 1-2 m laterally and 0.85 m in depth under optimal conditions (Purseglove 1972). The shoot weight determines the number of roots produced. Adventitious roots are present on the stem and grow in a distorted manner around the stem between the leaves, forming a tuft of fibrous roots near the base of the stem. Crowns present as leafy parts on the top of fruits produce more roots than shoots (Purseglove 1972; Bartholomew et al. 2003). The crown, suckers, slips, butt and stumps are parts of the plant used in vegetative reproduction and are discussed in Section 4.1.1.

3.2 Reproductive morphology

The pineapple flower is an inflorescence that usually develops from the apical meristem in an acropetal (ascending or youngest at the apex) succession and lasts for up to 15 days. The inflorescence consists of 50 to 200 individual flowers borne spirally and capped by a crown made of approximately 150 short leaves on a short stem. The stage of inflorescence emergence is called ‘red heart’ due to the reddish peduncle bracts (usually five to seven) that are produced at its base and are shorter and narrower than the ordinary leaves (refer Figure 3 below) (Purseglove 1972; Coppens d'Eeckenbrugge & Leal 2001; Bartholomew et al. 2003).

Flowers contain both the male and female reproductive organs (Purseglove 1972). The individual flowers are typical of monocots, trimerous with three sepals and petals, six stamens (approximately half the length of petals) in two whorls and one pistil, which contains three carpels (Bartholomew et al. 2003). The flower petals are white at their base, to violet-blue at their tip and tongue-shaped (refer Figure 3). Each flower is surrounded by a thick bract, which is covered by trichomes and pointed at its tip. The sepals are more or less triangular in shape and are comparable to the bracts in colour and texture. The flowers are arranged in a narrow compact tubular manner that only insects or specialised birds can access (Purseglove 1972; Coppens d'Eeckenbrugge & Leal 2001)

Anthers are bilobed turned inwards and contain numerous pollen grains that are sticky, spheroidal in shape, bilaterally symmetrical and contain two apertures (Bartholomew et al. 2003). Large variations have been reported in the size of the pollen grains of varieties Smooth Cayenne and Queen (from 35 to 81 microns [µ] and from 36 to 68µs, respectively). Reports also indicate differences in pollen size (44.62µ to 62.49µ) and fertility (2.16% to 54.92%) between clones and cultivars (Nayar & Lyla 1980). Pollen grains produced by genotypes that are triploid are mostly sterile because of irregular meiosis, while those produced by tetraploids are 90% uniform and relatively larger than the ones produced by diploids.

The style is trifid and longer than the stamens. The ovary contains three trilocular carpels, with the ovules present in two single or double rows. Depending on the cultivar, the number of ovules can vary from 16-71. The stigma is made up of three lobes and is borne within the petals (Bartholomew et al. 2003). Three nectar-secreting glands are located on the ovaries, which open into the flower cup at the bottom of the style (Collins 1960; Purseglove 1972).

Flowering in pineapple

Figure 3. Photographs courtesy of Mike Smith, Principal Research Scientist, Queensland Department of Primary Industries & Fisheries, Maroochy Research Station, Nambour, Queensland

Pineapple flowers do not abscise; the petals, stamens and style wither and the entire flower develops parthenocarpically into a berry-like fruitlet. The fruit of pineapple is a seedless syncarp and polygonal in shape. A syncarp is derived from the fusion of many individual flowers/fruitlets into one fruit. The fruit consists of the fused ovaries, bases of sepals and bracts, and cortex of the central core. In the mature fruit, the bract, sepal and ovary tissues are prominent (Medina & Garcia 2005). A 20-fold increase in weight occurs during the growth from flower to fruit.

The fruit may weigh approximately 2.3 kg or more (Bartholomew et al. 2003). The ripe fruit has a yellow peel and pleasant aroma. The pulp is yellow to golden yellow, sweet and juicy. Seeds are produced rarely and appear flat on one side and curved on the other, with a pointed end. They are approximately 3-5 mm in length and 1-2 mm in width, with a hard seed coat. The fruit usually contain a tuft of small leaves at the top known as the crown that may be used for vegetative propagation (Collins 1960; Purseglove 1972; Bartholomew et al. 2003; Medina & Garcia 2005).

SECTION 4 DEVELOPMENT

4.1 Reproduction

4.1.1 Asexual reproduction

Asexual reproduction by vegetative propagation is the predominant form of reproduction. The different vegetative parts of the pineapple plant (refer Figure 1 in Section 3.1) include:

- *slips*: leafy branches attached below the fruit on the peduncle, grouped near the base of the fruit; sometimes produced from basal eye of the fruit.
- *collars*: these structures are commonly preferred; may produce fruit within 14-16 months after planting
- *ground suckers* (ratoon): shoots produced from the stem just above the ground; will produce fruit in 12-14 months after planting
- *side shoots or suckers/stem shoots*: shoots produced from the above ground portion of the stem; will produce fruit in 18-20 months after planting
- *crown*: the short stem and leaves growing from the apex of the fruit; not commonly used; may take up to 24 months after planting to produce fruit (Purseglove 1972; Duke 1997; Bartholomew et al. 2003).

Butts or stumps have also been used for propagation in Australia (Purseglove 1972). In Queensland, tops and slips from the summer crop of Smooth Cayenne are stored upside down, close together, in semi-shade for planting during autumn (Duke 1997). Some farmers use crowns from the best fruits to obtain high quality planting material. Some plants may lack a crown or may produce multiple crowns. Crownlets can also grow at the base of the main crown or from some of the upper fruitlets (Bartholomew et al. 2003; Coppens d'Eeckenbrugge & Leal 2003).

The time taken from planting to harvest depends on the type of planting material used and is 15 to18 months for shoots, approximately 20 months for slips and 22-24 months for crowns. Crowns produce more uniform crops when compared to shoots. Large planting material produces large plants, earlier fruiting and higher yields. The average rate of production of propagules in Cayenne is approximately two per year. When planting material is limited, cutting the dormant axillary bud at the axil of the leaf on the stem induces the formation of new plants (Purseglove 1972; Duke 1997).

4.1.2 Sexual reproduction

With the onset of reproductive stage, new leaves stop developing and leaves that were previously initiated fail to grow to their full size. The bract is the first structure to appear in the axis of the fruitlet followed by the sepal, petal and stamen primordia. The carpels are the last to be formed (Bartholomew et al. 2003). As the first flower begins to appear the peduncle starts to elongate. Flower primordia develop in an ascending order as a new bract is produced above. The number of florets produced in an inflorescence is highly variable and is based on the variety, size of the plant at induction and plant population density (Purseglove 1972).

In Smooth Cayenne, the inflorescence develops between 30 and 40 days after reproductive induction. This is the 'open heart' stage when the bracts are bright reddish to reddish orange in colour. After this stage, within a week to ten days the inflorescence is observable and is called the 'early cone' stage. The 'midcone' and 'late cones' stages follow at approximately weekly intervals. The stage of inflorescence emergence is called 'red heart' because of the reddish peduncle bracts (5-7 in number) at its base (Bartholomew 1977).

The flowers open in the sequence of their origin, starting with the whorl of flowers at the base of the inflorescence. Approximately 5-10 flowers open daily and flowering lasts for 10-30 days. The flowers open in the night; the anthers dehisce during late morning or shortly after midday and begin to wither late in the afternoon, closing at sunset. Anthers contain abundant pollen grains. Anthesis is completed within 15 to 25 days, depending on the number of florets and the prevailing average temperature (Collins 1949; Purseglove 1972; Bartholomew et al. 2003).

Ovule numbers reportedly vary from 16 to 71 per flower in *A. comosus* var. *comosus*, while var. *bracteatus* contains 40-70 per flower. There are also variations reported in the number of normal embryo sacs and relative fertility (Coppens d'Eeckenbrugge et al. 1993). Fertility rates in *A. comosus* var. *ananassoides* were reported to be 6% (0.85 seeds per flower) and 35% (18.4 seeds per flower) in var. *bracteatus*. In *A. comosus* var. *comosus*, cultivars with piping leaves exhibited higher fertility (4 to 11%, with 2 to 5 seeds per flower) when compared to common cultivars like Smooth Cayenne, which exhibited less than 5% fertility i.e. (0 to 2 seeds per flower) (Bartholomew et al. 2003).

A. comosus produces functional germ cells that are self-sterile through gametophytic incompatibility (Brewbaker & Gorez 1967). This incompatibility is generally stronger in *A. comosus* var. *comosus* than in other varieties. Gametes from other plants of the same cultivar are also incompatible. However, some cultivars exhibit pseudo-self-incompatibility, expressed in the variable production of self-seeds, although the resulting self-fertility is always lower than cross fertility (Coppens d'Eeckenbrugge & Leal 2003). As mentioned in Section 1, *A. comosus* var. *comosus* is naturally compatible with other sub species, varieties and cultivars of *A. comosus* var. *comosus*.

In *A. comosus,* self-incompatibility occurs due to the inhibition of pollen tube growth in the upper third of the style, generally in the stigmatic lobes (Kerns et al. 1936; Majumdar et al. 1964). This feature is controlled gametophytically by a single locus with multiple alleles (Brewbaker & Gorez 1967). Self incompatibility is characteristic of the cultivated *A. comosus* that prevents or reduces self-fertilization rates. Flowers of *A. comosus* var. *comosus* are normally self-sterile and fruit development is parthenocarpic (does not require fertilisation) (Py et al. 1987).

4.2 Pollination and pollen dispersal

Pineapple flowers are elongated and tubular in shape. Although nectar is secreted inside the blossom cup, it seeps on to the sepal and bract surfaces at the base of the flower (Okimoto 1948). In Australia, honey bees (*Apis mellifera*), native bees, pineapple beetles (*Nitidulid spp.*), ants and honey eaters are occasional visitors that feed on the nectar and play a relatively minor role in pollen dispersal and cross pollination (Wee & Rao 1979) compared to Humming birds, which are the major pollinators in Hawaii but are not present in Australia (Purseglove 1972). Therefore, in Queensland, long distance pollen dispersal is unlikely because of the absence of major pollinators. Occasionally collected pollen has been reported on unprotected fruits, but this is not due to direct pollination (Garth Sanewski see[1] pers comm).

Pineapple pollen is relatively sticky, travels very short distances and remains viable for short periods of time (Kerns 1931 &1936; Purseglove 1987). Pollen in excised flowers remains viable for longer periods of time and dehydrates less rapidly. Kerns (1931) and Kerns and co workers (1936) reported that pollen grains could be stored in cool, dry air for 15 days with minimal loss of viability (Kerns 1931; Kerns et al. 1936). For more information on the shape and size of pollen grains refer to Section 3.2.

4.3 Fruit/seed development and seed dispersal

The pineapple blossom develops parthenocarpically into a large fruit formed by the complete fusion of 100-200 berry-like fruitlets. The edible part of the fruit consists mainly of the ovaries, the bases of sepals and bracts, and the cortex of the axis (Purseglove 1972; Bartholomew et al. 2003). The fruit shell is primarily composed of sepal and bract tissues and the apices of the ovaries (Okimoto 1948).

As individual fruits develop from the flowers they fuse together forming a cone-shaped compound, juicy, fleshy fruit approximately 30cm or more in length, with the stem serving as the fibrous but fairly succulent core. The tough, waxy/glossy rind, made up of hexagonal units or eyes become flattened and the colour of the fruit changes from dark-green to yellow or orange-yellow or reddish when the fruit ripens. Colour development usually starts from the base and moves toward the top of the fruit. The flesh of the fruit ranges from white to yellow depending on the stage of maturity (Purseglove 1972). Biochemical changes such as accumulation of sugars and carotenoids occurs mainly in the last week of fruit maturation (Okimoto 1948).

Generally, pineapple fruits take a long time from flowering to maturity; in south-east Queensland it normally takes at least 5 months (Sanewski & Scott 2000). It is difficult to judge when the pineapple is ready to be harvested as size and colour are not reliable indicators. In general, for the fresh fruit market, the summer crop is harvested when the eye shows a light pale green colour. The winter crop on the other hand matures slowly and the fruits are picked when there is a slight yellowing around the base. The winter fruit tends to be more acidic and has a lower sugar level when compared to summer fruit. Fruits for canning can be harvested at a latter stage of maturity. Overripe fruits lack flavour and are highly perishable (Purseglove 1972; Bartholomew et al. 2003).

Depending on whether the flowers have been pollinated or not, small hard seeds or traces of undeveloped seeds may be present (Purseglove 1972; Bartholomew et al. 2003). Fruits are not normally dispersed and in commercial plantations seeds are not produced. Seeds are desired only in breeding programs and are usually the result of hand pollination. Seeds when produced naturally or by artificial pollination remain within the fruit and do not get dispersed naturally. Such seeds are ready for harvest 5-6 months after cross pollination (Purseglove 1972). They are usually obtained by slitting the fruit in longitudinal sections and removing the fruit flesh around the carpel cavities and then washing and drying them. Under natural conditions since the fruit develops parthenocarpically, undeveloped, whitish transparent seeds may be present. Seeds are small, approximately 3-5x1-2mm in size with a rough and tough brown testa, hard and firm endosperm and a tiny embryo (Purseglove 1972).

4.4 Seed dormancy and germination

Pineapple seeds exhibit significant dormancy due to an impermeable seed coat. They are usually treated with a fungicide and concentrated sulphuric acid to reduce seed dormancy and improve the uniformity of germination. This process is called chemical scarification. Untreated seeds can take up to 10 days to initiate germination (Purseglove 1972; Filho et al. 1995). Temperatures from 24ºC to 35ºC are used to germinate seeds. Under artificial conditions a seed germination rate of 80-90% can be achieved. Longevity of hybrid seeds has been estimated to be less than six months in storage in Cote d'Ivoire (Loison-Cabot 1990). However, seeds can be stored for up to 2 years when placed in sealed plastic bags with silica gel at 4-5ºC (Loison-Cabot 1987).

After 3 months of growth at the 6-8 leaf stage the seedlings are transferred to nurseries. Seedlings are transferred from the nursery to the field when 15-18 months old and require 16-30 months to reach the mature fruiting stage; in comparison vegetatively propagated plants fruit within 15-22 months (Purseglove 1972; Morton 1987). Given that seeds are produced rarely in the fruit with no natural means of dispersal, there is only a remote chance of seed persistence in the environment during commercial cultivation.

4.5 Vegetative growth

Soon after planting when conditions of growth like sunlight, temperature, nutrients and water are available, root initiation begins followed by the formation of new leaves. Theoretically, roots of Smooth Cayenne can reach a length of 1.8m and grow to a depth of 85cm (Sideris & Krauss 1934). Root growth decreases after flower induction and maximum root mass is achieved at anthesis. Growth continues in the root, stem and leaf meristem (Bartholomew et al. 2003).

Smooth Cayenne exhibits strong apical dominance. Stem weight gradually and progressively increases from the time of planting. Plants accumulate starch reserves in the stem and the amount of starch varies with plant age, size and environment. Climatic conditions determine active growth of the plant (Bartholomew et al. 2003). Leaf length, mass and numbers differ depending upon the propagules (sucker, crown etc) used to produce the plant. Leaves grow from the base and attain maximum length several months after initiation. Under equatorial conditions the pineapple plant takes approximately 4 months to attain full growth (temperature of approximately 30 ºC) (Sideris & Krauss 1936). The maximum length and width of an individual leaf is approximately 100cm and 7cm, respectively (Py et al. 1987). Leaves constitute nearly 90% of the plant fresh weight (Purseglove 1972; Bartholomew et al. 2003).

SECTION 5 BIOCHEMISTRY

5.1 Toxins

The pineapple plant does not contain any known toxins. However, when eaten raw and in large quantities pineapple produces a burning sensation of the lips and mouth (Watt & Breyer-Brandwijk 1962) and can also produce angular stomatitis (inflammation of the mucous membranes of the mouth, cheeks, gums, lips, tongue and mouth) (Fasal 1945). Excessive consumption of pineapple cores can cause the formation of fibre balls (benzoars) in the digestive tract (Morton 1987). Pineapple cutters experience partial or complete obliteration of the fingerprints by removal of the *stratum corneum* (outer layer of the skin) due to the effects of pressure together with the keratolytic (softening and shedding of the outer layer of skin) effects of the substance bromelain (more details in Section 5.4) present in the fruit (Baur & Fruhmann 1979). However, their nails were unaffected unlike the nail damage that occurs in workers exposed to proteases of animal origin (Polunin 1951).

5.2 Allergens

Pineapple pollen is relatively sticky and is not known to be wind dispersed and therefore not a wind borne allergen. There are a few reports of allergic reactions in people who consumed or worked with pineapples or pineapple products (Baur & Fruhmann 1979; Kabir et al. 1993; Tanabe et al. 1997; Gailhofer et al. 1998; Reindl et al. 2002). A study conducted in 356 allergic patients concluded that 4 (1.2%) subjects were allergic to apples/pineapples (Ortega et al. 2004). Case histories of 380 food-allergic patients were evaluated in a study that revealed 19 subjects had immediate reactions to fresh pineapples. Most patients suffered from oral allergy syndrome and exhibited reaction in the oral cavity as well as on the lips. Other effects included itching, rash, vomiting, diarrhoea, asthma, rhinitis and bronchial obstruction (Galleguillos & Rodriguez 1978; Baur & Fruhmann 1979; Kabir et al. 1993; Tanabe et al. 1997; Gailhofer et al. 1998; Reindl et al. 2002). However most studies concluded that minor allergies may occur in exotic fruits like pineapple but they are a rare clinical phenomenon. (Baur & Fruhmann 1979; Kabir et al. 1993; Tanabe et al. 1997; Gailhofer et al. 1998; Reindl et al. 2002).

Profilin is a protein found in pineapple fruit which is reportedly an important mediator of IgE cross-reactivity. It consists of 131 amino acid sequence residues with high amino acid sequence identity to known allergenic pollen and food profilins (71-84%) (Reindl et al. 2002). Pineapple fruits also contain ethyl acrylate, which (when applied in 4% petrolatum) produced sensitisation in 10 of 24 subjects in a skin sensitisation test. However it is important to note that ethyl acrylate is used in creams, detergents, food, lotions, perfumes and soaps (Opdyke 1975). Safety assessments on pineapple concluded that they are not commonly allergenic fruits. This is mainly because they are not known to contain measurable amounts of goitrogens, oxalates, or purines. In fact pineapple is often used as a fruit in allergy avoidance diets partly for the reasons mentioned above and due to the useful properties of bromelain (refer to Section 5.4) (Mateljan 2007).

5.3 Undesirable phytochemicals

Pineapple does not contain any harmful phytochemicals (Mateljan 2007).

5.4 Beneficial phytochemicals

The presence of proteolytic enzymes like bromelain in pineapple juice was demonstrated in 1891 as stated in Lotz-Winter (1989). The highest concentration of bromelain is found in ripe pineapple fruit pulp and in the stems. Bromelain is commonly used in food production, in pharmaceutical industries and in diagnostic laboratories. Primary production centres of bromelain are located in Japan and Taiwan (Gailhofer et al. 1998).

Bromelain consists mainly of cysteine proteases, with small amounts of other proteases that include peroxidase, acid phosphatase, amylase and cellulose. Cysteine proteases present in pineapple stems include Ananain, Comosain and Stem bromelain, while the cysteine protease present in the pineapple fruit is known as fruit bromelain (Maurer 2001). Although these proteases differ in their substrate specificity, molecular mass, isoelectric point and pH optimum, bromelain is internationally classified as a single entity/enzyme (Lotz-Winter 1990). Lotz-Winter (1990) and Maurer (2001) have reviewed the biochemical, pharmacological and medical uses of pineapple bromelain.

Bromelain has been demonstrated to affect immune responses *viz* stimulatory effect on leukocyte populations particularly increase in T cell activation (Mynott et al. 1999; Hale et al. 2005; Secor Jr et al. 2005). Bromelain present in pineapple fruit is a non-toxic inhibitor of cell signalling and cytokine production that helps in blocking IL-2 production but does not affect cell proliferation. These properties are useful in therapeutic treatment of inflammation, trauma and hypersensitivity disorders (Mynott et al. 1999). Bromelain also has anti-inflammatory and analgesic properties and could potentially be used as a safe alternative treatment in osteoarthritis (Brien et al. 2004). In addition it has been reported to reduce clinical and histologic severity of colonic anti inflammation in inflammatory bowel disease (Hale et al. 2005). Bromelain attenuated development of allergic airway disease (AAD) and alterated lymphocyte populations. The reduction in AAD outcomes suggests that bromelain may have similar effects in treatment of human asthma and hypersensitivity disorders (Mynott et al. 1999; Secor Jr et al. 2005).

The edible part of the pineapple fruit (60% of the fresh fruit), is made up of 85% water, 0.4% protein, 14% sugar, 0.1% fat and 0.5% fibre (Purseglove 1972). The sugar content varies considerably during the ripening process and is cultivar dependent. Pineapple fruit is a good source of vitamins A, B1, B6 and C, copper, manganese and dietary fibre. (refer Table 4) (Purseglove 1972; Morton 1987; Mateljan 2007).

Table 4. Nutritional information of pineapple: Pineapple: 1 cup =155.00 grams = 75.95 calories

Nutrients	Amount milligrams (mg)
Manganese	2.56
Vitamin C	23.87
Vitamin B1(thiamine)	0.14
Copper	0.17
Dietary Fibre	1860.0
Vitamin B6 (pyridoxine)	0.13
Calcium	6.2-37.2
Nitrogen	38.0-98.0
Phosphorous	6.6-11.9
Iron	0.27-1.05
Ascorbic acid	27.0-165.2
Carotene	0.003-0.055
Thiamine	0.048-0.138
Riboflavin	0.011-0.04
Niacin	0.013-0.267

Data compiled from Morton (1987) and Mateljan (2007) (Morton 1987; Mateljan 2007)

SECTION 6 ABIOTIC INTERACTIONS

6.1 Abiotic stresses

Abiotic stresses significantly affect the growth and development of the pineapple plant. Major stress factors include nutrients, temperature and water, while minor stresses like solar radiation and wind can also influence plant growth and development.

6.1.1 Nutrient stress

Abiotic stress due to the lack of major nutrients like Nitrogen (N), Potassium (K), Phosphorous (P), Calcium (Ca) and Magnesium (Mg) or lack of minor nutrients like Iron (Fe), Sulphur (S), Zinc (Zn), Boron (B), Manganese (Mn), Copper (Cu), Molybdenum (Mo) and Chlorine (Cl) can affect pineapple plant growth. Table 5 summarises the nutrient requirements of pineapple plants and the symptoms associated with their deficiency.

In Queensland deficiencies of Fe, Zn, B, Cu and Mo commonly occur in pineapple-growing soils and is usually managed by timely applications of fertilisers containing these elements (Bartholomew et al. 2003).

Table 5. Nutrient deficiency symptoms of pineapples.

Essential nutrients	Levels required	Deficiency symptoms
N	High requirement Optimal soil levels 120 parts per million (ppm) Deficiency 50ppm or below	▪Reduced leaf size, leaf number and crown mass ▪Crowns absent ▪Leaves turn green to greenish yellow and yellow ▪Reduced fruit quality
K	High requirement Optimum soil levels 150ppm Deficiency 60ppm or below	▪Reduces plant growth and fruit mass ▪Affects slip production ▪Fruits with reduced fruit acidity and aroma and are prone to sunburn. ▪Short leaves, leaf tip death and necrosis
P	Low requirement Optimal soil levels 20ppm Deficiency at 5ppm or below	▪All plant parts depressed in growth ▪Erect, long narrow leaves, older leaf tips show die back and chlorosis.
Ca	High requirement Optimal soil levels 100ppm Deficiency at 25ppm or below	▪Abnormal leaves (short) with grey-green colour. ▪Severe deficiency affects growth ▪Fruit aroma and translucence reduced ▪Death of growth tips
Mg	Low requirement Optimal soil levels of 50ppm Deficiency at 10 ppm or below.	▪Reduces chlorophyll concentration, photosynthesis and growth. ▪Leaves turn bright yellow ▪Short stems ▪Weak root system ▪Fruits low in acid and sugar content and lack aroma
S	Low requirement Rare deficiency in pineapple plants	▪Leaf yellowing and narrowing ▪Plants stunted ▪Fruits reduced in size
Fe	Low requirement Optimal soil levels 27-78ppm Deficiency at 3.0ppm or below.	▪Interveinal chlorosis, yellowing and mottling of leaves ▪Small, hard and red coloured fruits ▪Crown light creamy or white in colour
Zn	Low requirement Optimal soil levels 4ppm Deficiency at 3ppm or below.	▪Centre cluster of leaves curved in young plants ▪Yellow-brown blister like spots on leaves of old plants

Data compiled from (Py et al. 1987) and (Swete Kelly 1993) (Py et al. 1987; Swete Kelly 1993).

6.1.2 Temperature stress

Temperature is an important factor in pineapple plant growth, flowering and yield. Pineapple can survive in hot, dry tropical environments as well as in cool sub tropics where freezing temperatures may occasionally occur (Bartholomew et al. 2003). For information on optimal temperature range for pineapple cultivation and the effects of high and low temperatures on plant development refer to Section 2.3.

6.1.3 Water stress

Pineapple leaves are arranged in a dense rosette which channels light rains and dew to the base of the plant resulting in water economy of the plant. In addition large trichomes cover the upper and lower surfaces that assist in reducing water loss. Morphological features of the leaf that include thick cutinized epidermis and multicelled hypodermis, small number of stomata and stomatal pores and presence of other features permit the pineapple to cope with reduced water. Half the volume of the leaf contains water storage parenchymatic cells. The leaf and canopy transpiration rates of pineapple are lower than most cultivated crops. These morphological and anatomical features are an adaptation to low evapotranspiration (Krauss 1959;

Sanford 1962). The pineapple plant can withstand drought to a certain extent; however prolonged extreme droughts can adversely affect growth and yield significantly (Rohrbach & Apt 1986; Bartholomew et al. 2003).

In regions of heavy or high rainfall, growth of the plant can be affected and results in susceptibility to disease. Waterlogging can lead to death of plants within 15 days as seen in the Mekon delta (Le Van Thuong 1991). Good drainage is essential and ridging practices have been adopted in Australia, West and South Africa to prevent the risk of water logging during the rainy season. In flooded situations apart from plant growth, fruit weight is also affected. During water logging root and plant rot pathogens are of great concern and could lead to loss of plants (Bartholomew et al. 2003).

6.1.4 Other stresses

Irradiance is also an important abiotic factor. A 10 to 20% decrease in solar radiation resulted in reduced growth and yield (Sanford 1962). Although wind is a minor factor, prolonged winds decrease plant size by 25% (Nightingale 1942b).

6.2 Abiotic tolerances

Pineapples can normally grow in acid soils and have the capacity to tolerate high levels of soluble aluminium, calcium and manganese. In soils that contain these elements, plants can absorb large amounts of soluble manganese and aluminium; however they cannot utilise the absorbed iron, which often leads to severe iron deficiency (Bartholomew et al. 2003). Manganese induced iron deficiency is managed by regular iron sprays in the form of iron sulphate. Pineapple plants can tolerate high concentrations of potassium (Purseglove 1972; Bartholomew et al. 2003).

SECTION 7 BIOTIC INTERACTIONS

7.1 Weeds

Weeds are a major problem in pineapple plantations, the management of which is important during the early stages of growth because weeds compete for water, nutrients and light. Severe weed problems can reduce plant yield by up to 80%. In addition weeds are potential hosts for pests and viruses (Bartholomew et al. 2003; Torres & Garcia 2005).

Approximately 20 species of weeds belonging to 10 families have been identified that can affect pineapple plantations. In Australia Smooth Cayenne plantations are affected by both broad leaf and narrow leaf weeds; 12 species of broad leaved and 8 species of narrow leaved weeds have been identified (Bartholomew et al. 2003). The most important narrow leaf weeds of the grass species include *Panicum maximum* var. *maximum*, *Sorghum halepense*, *Cyanodon dactylon* L., the *paspalums* (*Paspalum dilatatum* and *urvillei*) and nut grass (*Cyperus rotundus*). Significant broad leaved weeds include morning glories and perennial weeds such as *Saccharum spontaneum* and *S. halepense*, *Imperata cylindrica*, which are generally eradicated in Queensland by deep ploughing (Bartholomew et al. 2003; Torres & Garcia 2005).
Pineapple plants in general are relatively slow in establishing a complete ground cover. Therefore eliminating weed cover could result in high levels of soil erosion. Manual, mechanical and chemical means of weed control are employed to eradicate

weeds in Smooth Cayenne plantations. Before the 1950's and prior to introduction of pre-emergence herbicides, weeds were managed primarily by physical removal or tillage (Bartholomew et al. 2003). In Australia, pre emergence herbicides like diuron and bromacil (Reid 1990; Glennie 1991) are used to control grasses and broad leaf weeds; spraying is usually done on moist soils after cultivation or just on emergence of weeds. However it is difficult to control all weeds by the use of one herbicide (Reid 1990; Bartholomew et al. 2003; Torres & Garcia 2005).

Herbicide alternatives include hand weeding or tillage, which is adopted after the canopy has closed. Use of plastic mulch laid during field preparation helps in water management, soil temperature control and weed control but at the same time prevents tillage (Torres & Garcia 2005). Post emergence herbicides usually sprayed when plants are young and actively growing include ametryn, bromacil, diuron and glyphosate (Reid 1990; Bartholomew et al. 2003; NSF for Integrated Pest Management 2007).

7.2 Pests and pathogens

Many characteristics of the pineapple plant and commercial pineapple production systems have contributed to the severity of several pest and disease problems (Rohrbach et al. 2003). Pineapple plants are subject to a minimum of pests and diseases if proper care and pest management practices are employed. Apart from diseases caused by bacteria, fungus and virus there are a number of insect pests of pineapple. Diseases also occur due to mineral deficiency. In addition to these pests, diseases like heart rot, root rot, fruit rot and butt rot pose major problems during handling, storage or planting of fresh materials.

Cultivar Smooth Cayenne is sensitive to pests like fruit borers, mites, symphillids, nematodes and diseases like mealybug wilt, fusariosis, fruitlet core rot, butt rot and internal browning (Rohrbach & Schmitt 1994). However it is resistant to fruit collapse caused by *Erwinia Chrysanthemi* Burkbolder (Lim 1985) and *Phytophthora spp.* (Py et al. 1987).

Characteristics of pests and pathogens affecting pineapple plants and their occurrence in cultivated areas of Australia are summarised in Table 6

Table 6. Pest and pathogens in pineapple plantations of Australia

Types of pests and pathogens	Sub class with Biological names	Occurrence in Australia	Characteristics
Major Insects and Invertebrate pests	Mealy bugs (*Dysmicoccus brevipes*)	All pineapple growing regions of Queensland	▪Infect roots, stem, leaves, butt, flower and fruit (Waite 1993). ▪Feed on plant sap and produce honey dew, which accumulates, encouraging growth of sooty mould. ▪Can potentially transmit closterovirus that causes mealybug wilt (Rohrbach et al. 2003).
	Ants (Argentine, fire and big-headed)	Queensland during the fallow period	(Bartholomew et al. 2003)
	Mites (*Dolichotetranychus floridanus*)	Yeppoon district of Queensland (during dry climatic conditions)	▪Feed on base of leaves causing lesions and allow rot organisms to invade the tissues

Types of pests and pathogens	Sub class with Biological names	Occurrence in Australia	Characteristics
			(Waite 1993). ▪Problem on stored vegetative propagales (Waite 1993).
	Scale (*Diaspis bromeliae*)	All pineapple growing regions of Australia	▪Fruits and suckers damaged if ratoon planting shaded. ▪Affects fruit appearance decreasing fruit value (Waite 1993). ▪When fruits highly infested, cracks may develop in fruitlets (Py et al. 1987).
	Thrips and symphlids (*Hanseniella spp.*)	All pineapple growing regions of Queensland	▪Feed on meristematic regions of young roots, root hairs and root tips resulting in short, branching roots leading to reduced yields during dry climatic conditions ▪Damage to root permits wound pathogens to enter (Sakimura 1966; Py et al. 1987; Waite 1993; Bartholomew et al. 2003)
	Beetles African black beetles (*Heteronychus arator*) Native black beetle (*Metanastes vulgagus*)	Queensland	▪Feed on leaf and stem bases and cause sever damage to young plants (Christensen 2004).
	Grubs [White grub (of the family *Scarabaeidae*)]	Yeppoon, Hervey Bay and Woombye of Queensland	▪Affect uptake and transport of nutrients and water by the roots. (Carter 1967; Petty 1978; Waite 1993). ▪Feeding leads to damage to roots and infection by secondary plant pathogens (Carter 1967; Waite 1993)
	Cane grubs (19 species),	Queensland	Total ratoon failure in Woombye in 2002 (Bartholomew et al. 2003)
Minor Insect and invertebrate pests	grasshoppers, cane weevil borer, pineapple mites, common armyworm, Rutherglen bug, grey cluster bug, moth larva, bud moths, wireworms and termites	Most occur in Queensland.	In Wamuran on summer tops in January 2003 Termites have been reported active in pineapple soils and colonise old woody plant butts (Waite 1993)
Fungal pathogens	*Phytophthora cinnamomi,* *P. Parasitica and Pythium spp.*	Queensland (Mary Valley and Mackay)	▪Heart rot and root rot disease (Carter 1967; Pegg 1969; Bartholomew et al. 2003).
	Ceratocystis paradoxa	All pineapple growing regions of Australia	▪Causes black rot (Bartholomew et al. 2003)
	Thielaviopsis paradoxa	All pineapple growing regions of Australia	▪Causes butt rot (Carter 1967)
	Penicillium funicolosum & Fusarium moniliforme Saccharomyces spp.	All pineapples growing regions of Australia	▪Causes white fruitlet core rot (Bartholomew et al. 2003; Petty & Tustin 2006).

Types of pests and pathogens	Sub class with Biological names	Occurrence in Australia	Characteristics
Bacterial and Viral diseases	*Erwinia chrysanthemi*	All pineapples growing regions of Australia	▪Causes heart rot and fruit collapse (Lim 1985)
	Erwinia carotovora, E. ananas, Gluconobacter oxydans and *Acetobacter aceti*	All pineapples growing regions of Australia	▪Causes pink disease (Bartholomew et al. 2003)
	Closterovirus *Tomato spotted wilt virus*	All pineapple growing regions of Australia	(Carter 1967)
Nematodes	Root knot *(Meloidogyne javanica & M. incognita)*	All pineapple growing regions of Queensland	▪Terminal shaped galls resulting from infection of root tips (Bartholomew et al. 2003).
	Reniform (*Rotylenchulus reniformis)*	Northern pineapple plantations of Queensland	▪Stunting of plants (Bartholomew et al. 2003).
	Root lesion (*Pratylenchus brachyurus*)	All pineapple growing regions of Queensland	▪Roots and root hair destroyed (Bartholomew et al. 2003).

7.3 Other biotic interactions

Other animal pests include the Australian crow (*Corvus orru*), Eastern swamphen (*Porphyrio porphyrio*), Native rodents (*Rattus sordisus*, *Melomys cernivipes, M. burtoni*), Feral pigs (*Sus scrofa*), which occur in all the pineapple growing regions of Australia (Broadley et al. 1993).

SECTION 8 WEEDINESS

Typical characteristics of problematic weeds include prolonged seed dormancy, persistence in soil as seed banks, germination under adverse environmental conditions, rapid vegetative growth, a short life cycle, very high seed output, high seed dispersal and long-distance dispersal of seeds (Pheloung et al. 1999). An important indicator of potential weediness of a particular plant is its history of weediness in any part of the world and its taxonomic relationship to declared weeds (Panetta 1993; Pheloung et al. 1999).

A. comosus and its relatives do not possess any of the above mentioned weedy characteristics. Pineapple plants are slow growing and have a long life cycle. Cultivated pineapple plants are self incompatible and self sterile and do not produce seeds even if pollinated, and fruit development is parthenocarpic (Purseglove 1972; Bartholomew et al. 2003). It is desirable to have fruits without seeds in commercial cultivations and therefore in Queensland and other parts of the world pineapples are mostly cultivated as a monoculture. Cross pollination due to vectors does not occur because major pollinators like hummingbirds are not present in Australia. In general, only minor pollinators like honeybees, ants and native bees are present in Australia and do not contribute significantly to cross pollination in pineapple plantations (Coppens d'Eeckenbrugge et al. 1997; Bartholomew et al. 2003). In the unlikely event of successful pollination, the seeds, if produced remain contained in the fruit as pineapples have no seed releasing mechanisms. For information on seed dormancy and germination refer Section 4.4 (Purseglove 1972).

Under breeding and experimental conditions pineapple hybridises with other subspecies of *A. comosus* to produce fertile offsprings (refer Section1 for more details). Hand-pollinated crosses between *A. comosus* var. *comosus* (diploid, 2n=50) and *A. macrodontes* (tetraploid, 4n=100) produced 5-10% fertile seeds, most of which were tetraploid and grew to be fully fertile (Collins 1960). Although pineapple plants can be grown from seeds, fertility in commercially grown cultivars of pineapple is very low and consequently seed production is rare (Coppens d'Eeckenbrugge et al. 1993).

Commercial propagation of pineapple is not through seeds but by the use of vegetative plant parts. Vegetative propagules can only be distributed by natural disasters like flooding or human/animal intervention. These propagules cannot establish easily in the natural environment as they require cultivated conditions. The viability of seeds and vegetative propagules in the field is substantially reduced after six months (Holm et al. 1997a; Parsons & Cuthbertson 2001; Weeds Australia 2007; USDA 2007a; USDA 2007b). Pineapple plants can occasionally re-shoot from large pieces of stem that are left intact and buried within commercially cultivated areas if the plants from the previous crop are not completely destroyed. Although stem pieces could theoretically survive outside the cultivated environment they are unlikely to become weeds as they are slow growing and sensitive to common herbicides; in addition some cultivars like Queen (not Smooth Cayenne) are susceptible to common fungi like *Phytophthora cinnamomi* (Py et al. 1987).

Abiotic factors like major and minor nutrients discussed in Table 5 of Section 6.1, temperature, water and solar radiation are also important considerations that determine the success in growth and fruit production of pineapple plants. Therefore the spread and persistence of pineapple plants outside the cultivated environment is unlikely to lead to its successful establishment due largely to its dependence on optimal abiotic factors. Conventional breeding has not succeeded in producing herbicide tolerant cultivars. All the attributes mentioned above do not qualify pineapple plant as a potential weed (Stanley & Ross 1989).

8.1 Weediness status on a global scale

Pineapple plants are not considered a weed in natural or agricultural ecosystems in pineapple growing countries (Holm et al. 1997a; Parsons & Cuthbertson 2001; CRC Australia 2005; Weeds Australia 2007). None of the members of the family *Bromeliaceae* including *Ananas* spp. have been reported as weeds in any country (Holm et al. 1997b).

8.2 Weediness status in Australia

Pineapple is an introduced crop in Australia and to date has not been classified as a ‘naturalised’ or ‘agricultural’ weed. It is grown exclusively as a managed commercial crop in Queensland and in very small areas of the Northern Territory, northern New South Wales and central Western Australia (Reid 1990). Only one variety, *A. comosus* var. *comosus*, is grown exclusively in the cultivated environment in Australia. None of the pineapple cultivars have become naturalised in south-east Queensland or in any other part of Australia (Sanewski & Scott 2000).

8.3 Weediness in agricultural ecosystems

Pineapple is not a weed in agricultural ecosystems either because it was not considered a problem or because it was not known to occur in agricultural areas at present (Groves et al. 2003). None of the members of the family *Bromeliaceae* have been reported as a weed or as a noxious weed in any State or Territory of Australia. *Tillandsia usneoides* is the only member of subfamily *Tillandsioideae* of *Bromeliaceae,* that is reported to be present in agricultural ecosystems in the States of Queensland and NSW. Subfamilies *Bromelioideae* and *Tillandsioideae* in which *A. comosus* and *Tillandsia usneoides* are respectively placed, are monophyletic, share a common ancestor and are related at the species level (Parsons & Cuthbertson 2001; Groves et al. 2003). *Tillandsia usneoides* like *A. comosus* has the same status (Groves et al. 2003).

8.4 Weediness in natural ecosystems

Pineapple may be a minor problem but is not considered important enough to warrant control at any location; its seeds are not listed in the Queensland weed seeds category (Friend 1983; Groves et al. 2003).

8.5 Control measures

Destruction of plant residue from the preceding crop is a common practice before replanting. Complete decomposition is important not because they can potentially regenerate, but the remaining plant material can host parasites like mealy bugs or nematodes. In addition decomposed plant material can add to soil fertility and a proportion of the mineral elements will be available for the next crop. Common management practices include shredding (carried out using a rotary chopper), permitting cattle to feed (undesirable because soil compaction may occur) and using herbicides like paraquat dichloride to dry out the leaves before burning (Py et al. 1987; Bartholomew et al. 2003). Subsequently the following operations are carried out *viz* subsoiling, levelling, cross-ploughing to a depth of 45-50cm, finishing with disc harrow or rotary harrow (depending on the soil type), ridging and heating the soil in order to achieve complete decomposition (Py et al. 1987).

SECTION 9 POTENTIAL FOR VERTICAL GENE TRANSFER

Potentially, genes could be transferred to:

- naturalised, commercially and domestically grown pineapples, which includes *A. comosus* species, subspecies, varieties and cultivars (includes clones)
- wild pineapple
- other unrelated plant genera

For vertical gene transfer to occur, physical factors like geographic distance, differences in flowering and anthesis times, pollen vectors and mating systems should be overcome. Other important considerations include genetic incompatibility, selective abortion and hybrid fitness that play a crucial role in determining successfully gene transfer.

9.1 Intraspecific crossing

There are a number of factors that limit intraspecific crossing in pineapple including:

- pineapples are not naturalised in Australia
- the main pollinator of pineapple (hummingbirds) is absent in Australia

- pollen is short lived and not wind dispersed
- inbuilt self incompatibility mechanism
- only one variety of pineapple dominates in commercial cultivation in Australia

Given that pineapples are not naturalised in Australia and are an introduced crop, intraspecific gene transfer relates only to commercially and domestically grown pineapple varieties and cultivars/clones. In this context it is important to note that approximately 70% of commercial cultivation of pineapple in the world (Loeillet 1996) and approximately 94% in Australia comprises of the clones of the cultivar Smooth Cayenne (Sanewski & Scott 2000).

In the pineapple growing areas of Queensland occasional pollinators like honeybees (*Apis mellifera*), pineapple beetles, native bees (*Trigona* spp.) and ants play a minor role in pollination when compared to Hummingbirds in Hawaii and therefore do not pose a major problem (Bartholomew et al. 2003). Pollen grains are sticky, heavy, not wind dispersed and remains viable for very short periods of time. Therefore even if pollinators carried pollen, it would be transported only over short distances and would become non-viable quickly.

It is the practice in commercial cultivations to plant one cultivar (monoculture) to avoid cross pollination/gene transfer and the remote chance of seed production (Sanewski & Scott 2000; Bartholomew et al. 2003). In Australia only one cultivar of one variety is almost exclusively cultivated. The related varieties (refer Section 1 for details of varieties) of *Ananas* are not present in agricultural ecosystems. Therefore intraspecific gene transfer can potentially only occur within this variety/cultivar and its clones. However even within a single plantation the cultivars and clones of *A. comosus* are naturally self incompatible forming fruits parthenocarpically without seeds (Coppens d'Eeckenbrugge et al. 1993; Leal 1997).

The cultivars and varieties of *A. comosus* are sexually compatible and can potentially outcross to produce seeds artificially under breeding conditions. Therefore hybridization between other *Ananas* spp. including varieties, cultivars and clones can be achieved artificially. Although *A. comosus* var. *comosus* exhibits low levels of fertility the crosses exhibit high fertility due to crosses with other varieties. Hand-pollinated crosses between *A. comosus* var. *comosus* (diploid, 2n=50) and *A. macrodontes* (tetraploid, 4n=100) produced 5-10% fertile seeds (the remainder having mostly flat empty seed coats), most of which were tetraploids that grew vigorously to be fully fertile, while the triploids were sometimes self sterile (Collins 1960). Sanewski (2000) hybridised *A. macrodontes* with *A. comosus* var. *erectifolius* and *A. comosus* var. *bracteatus* and reported low levels of fertility.
Sanewski (2000) reported no seed production in a pineapple farm that cultivated 4-5 different cultivars on small areas (Sanewski & Scott 2000). A similar study in Hawaii reported that no cross pollination occurred even when different compatible pineapple cultivars were planted in adjacent rows (Collins 1960; Westerkamp & Gottsberger 2000). Pseudo self incompatibility is exhibited very frequently by wild pineapples (*A. comosus* var. *ananassoides*, var. *parguazensis*, and var. *bracteatus*) (Sanewski & Scott 2000).

9.2 Natural interspecific and intergeneric crossing

9.2.1 Gene transfer to naturalised pineapple species

Neither *A. comosus* var. *comosus* nor any variety of *A. comosus* nor any species of *Ananas* are naturalised in Australia (Sanewski & Scott 2000). In addition wild varieties of pineapple are not present in Australia. It is mostly a cultivated species with one variety (var. *comosus*) and cultivar (Smooth Cayenne) dominating the Australian commercial plantations. Therefore there is no chance of gene transfer from cultivated pineapple to naturalised pineapple species (Bartholomew et al. 2003).

9.2.2 Gene transfer to other Ananas spp.

Under experimental and breeding conditions, *A. comosus* and its varieties are compatible and can cross fertilise to produce hybrids. *A. comosus* var. *comosus* can hybridise with other subspecies of *A. comosus*. Hand-pollinated hybrids have been obtained from crosses between *A. comosus* var. *comosus* and *A. comosus* var. *ananassoides*, *A. comosus* var. *bracteatus*, and *A. comosus* var. *erectifolius* to produce viable seeds and fertile off springs (Sanewski 1998; Sanewski & Scott 2000). For more details refer Sections 9.1.

9.2.3 Experimental gene transfer to unrelated plants

In Australia gene transfer and successful production of seeds or progeny from pineapple to unrelated plants has not been reported. However there are a few reports on intergeneric hand-pollinated crosses between *Ananas* and some members of the family *Bromeliaceae*. Hand-pollinated crosses were carried out between *A. comosus* and *Neoreglia*, *Aechmea serrata* and *A. comosus*, *Cryptanthus* and *Ananas* (species not given), *A. bracteatus* and *Aechmea* sp and *Tillandsia fasciculata* and *A. comosus* var. *comosus*, but failed to produce any hybrids (Lawn 2007; Geoff 2007). Sanewski and co workers (2000) were unsuccessful in obtaining intergeneric hybrids from *Aechmea* sp x *A. comosus* and *Aechmea* sp x *A. macrodontes,* even with controlled hand pollination (Sanewski & Scott 2000).

In the wild, *Bromeliad* bigenerics (crosses between plants from two different genera, i.e. genus x genus) do not occur, which may be due to fertility barriers, different flowering times, need for specialised pollinators and geographical range that prevents most species in different genera from producing hybrids. The biggest obstacle appears to be genetic incompatibility between potential parents present in the same family (Lawn 2007). There are no other reports of hybridisation between *Ananas* and other unrelated plants.

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