Australian Government
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The Biology of *Carica papaya* L. (papaya, papaw, paw paw)

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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 *Carica papaya* L. with particular reference to the Australian environment, cultivation and use. Information included relates to the taxonomy and origins of cultivated *C. papaya*, general descriptions of its 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 in risk assessments of genetically modified *C. papaya* that may be released into the Australian environment.

The plant is a short-lived, fast-growing, woody, herb-like tufted tree that can grow up to 10 m in height (Morton 1987; Du Puy & Telford 1993; OECD 2005). It generally branches only when injured. It is now grown as a fruit crop in all tropical countries and many sub-tropical regions of the world. It was deliberately introduced to Australia more than a century ago (Garrett 1995).

In Australia, red and pink-fleshed cultivars of *C. papaya* are often known as 'papaya' to distinguish them from the yellow-fleshed fruits, known as 'paw paw' or 'papaw' (Papaya Australia 2007), but both of these common names refer to the same plant species. Irrespective of its flesh colour, *C. papaya* is generally known as 'papaya' in other countries and this term will be used throughout this document to refer to plants/fruits of both flesh colours. In some areas, an unrelated plant, *Asimina triloba* (Annonaceae), native to north America, is also called pawpaw (Morton 1987).

SECTION 1 TAXONOMY

Carica papaya L. belongs to the small family Caricaceae and is a dicotyledonous, polygamous (having male, female or hermaphrodite flowers on the same plant)[1], diploid species with a small genome[2] of 372 Mbp/1C (Arumuganathan & Earle 1991) and nine pairs of chromosomes (Bennett & Leitch 2005). The genus name *Carica* is derived from the Latin name for a kind of fig which the leaves and fruits of *Carica papaya* resemble; the specific epithet *papaya* probably comes from the common name for the fruit (Du Puy & Telford 1993).

Until recently, the Caricaceae was thought to comprise 31 species in three genera (namely *Carica*, *Jacaratia* and *Jarilla*) from tropical America and one genus, *Cylicomorpha*, from equatorial Africa (Nakasone & Paull 1998). However, a recent taxonomic revision proposed that some species formerly assigned to *Carica* were more appropriately classified in the genus *Vasconcellea* (Badillo 2002). Accordingly, the family's classification has been revised to comprise *Cylicomorpha* and five South and Central American genera (*Carica*, *Jacaratia*, *Jarilla*, *Horovitzia* and

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[1] In nature, papaya plants are dioecious: male and female flowers are found on separate plants (De La Cruz Medina et al. 2002). Commercial papaya cultivars tend to be inbred gynodioecious (having bisexual/hermaphrodite flowers on some plants and only female flowers on other plants of the same species), or out-crossing dioecious (Kim et al., 2002) but there are also monoecious plants (having both male and female flowers). See Section 3.2 for further discussion.

[2] 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.

Vasconcellea) (Badillo 1971), with *Carica papaya* the only species within the genus *Carica* (Badillo 2002). The highland papayas, *Vasconcellea,* are considered the nearest relatives to *Carica papaya* although the relationship is not close (Aradhya et al. 1999; Van Droogenbroeck et al. 2002). A more recent study (Van Droogenbroeck et al. 2004) actually suggested that there are two lineages within the Caricaceae family and that some members of *Vasconcellea* are more closely allied to *Carica papaya* than others; this has implications for the successful use of *Vasconcellea* species in hybrid breeding programmes (see Section 2.4.1).

While there is considerable phenotypic variation within the genus *Carica papaya*, DNA fingerprinting of 63 accessions from different countries has indicated that there is limited genetic variation and that the level of genetic variation among dioecious cultivars is similar to that of the hermaphrodite cultivars (Kim et al. 2002).

SECTION 2 ORIGIN AND CULTIVATION

2.1 Centre of diversity and domestication

Although opinions differ on the origin of *C. papaya* in tropical America (Garrett 1995; Aradhya et al. 1999; OECD 2005) it is likely that *C. papaya* originated from the lowlands of eastern Central America, from Mexico to Panama (Nakasone & Paull 1998). Its seeds, which remain viable for several years if dried, were distributed to the Caribbean and south-east Asia (Philippines) during Spanish exploration in the 16th Century, from where it was further distributed to India, the Pacific and Africa (Villegas 1997). Papaya was introduced into Hawaii in the early 1800s by the Spanish explorer Don Francisco Marin and became an export crop of Hawaii in 1948 (Fitch 2005). Today, papaya is widely distributed throughout the tropical and warmer subtropical areas of the world (Villegas 1997) and has become naturalized in many areas (Morton 1987).

Undomesticated papaya was a spindly plant with nearly inedible fruits. During domestication the species has undergone considerable changes in fruit size, fruit flesh colour, mating system and growth habit (Manshardt & Moore 2003).

2.2 Commercial uses

Economically, *Carica papaya* is the most important species within the Caricaceae, being cultivated widely for consumption as a fresh fruit and for use in drinks, jams, jellies, ice-cream, pies and as dried and crystallised fruit (Morton 1987; Facciola 1990; Villegas 1997). Nutritionally, the ripe papaya fruit is a good source of calcium and an excellent source of vitamins A and C (Nakasone & Paull 1998) – see Table 9 in Section 5.3. Data from the 1995 Australian National Nutrition Survey showed that the average consumption of raw papaya fruit in Australia was around 135 g/person/day (FSANZ 2002).

Worldwide, the 2005 figures for papaya fruit show that some 6,634,580 tonnes were produced in 54 countries (FAO 2007a). The top 10 producers are given in Table 1.

Table 1. Top 10 papaya producing countries in 2005 (FAO 2007a)

Country	2005 Production (kilo tonnes)
Brazil	1,573.82
Nigeria	834.04
India	783.38
Mexico	709.48
Indonesia	646.65
Ethiopia	259.17
Congo	215.98
Peru	171.06
Colombia	137.66
Philippines	132.00

The major exporters of papaya are Mexico, Malaysia and Brazil – see Table 2. Much of the harvest in some countries is not exported, particularly in Southeast Asian countries, and the fruits are consumed or traded locally; the value of papaya to small farmers can be more significant than income derived from rice and in terms of daily consumption papaya ranks second only to banana in Southeast Asia (OECD 2005). The *Papaya Biotechnology Network of SE Asia* was formally launched in March 1998 with the primary objective of enhancing income generation, food production, nutrition, and productivity for resource-poor farmers by integrating proven biotechnology applications into their agricultural practices (ISAAA 1999). The network is composed of experts from Indonesia, Malaysia, Philippines, Thailand and Vietnam.

Table 2. Top 5 papaya exporting countries in 2005 (FAO 2007b)

Country	2004 Exports (kilo tonnes)
Mexico	81.88
Malaysia	46.74
Brazil	40.12
Belize	28.71
Netherlands	9.23

The unripe papaya fruit has a high latex content that may make it unsuitable for raw consumption although raw shredded green papaya is often used in Asian salads. Green fruit, if peeled, seeded and cooked is used in a variety of savoury Asian dishes including pickles and chutneys and for canning in sugar syrup (Morton 1987). Leaves and flowers may also be used as a cooked vegetable (Facciola 1990; Watson 1997); young leaves are cooked and eaten like spinach in the East Indies and sprays of male flowers are sold in Asian and Indonesian markets and in New Guinea to be boiled and eaten as a vegetable (Morton 1987). Papaya seeds have a peppery taste and can be dried in a dehydrator then ground in a mortar and pestle and used like pepper (Papaya Australia 2007).

Papaya also has several industrial uses. Biochemically, its leaves and fruit are complex, producing several proteins and alkaloids with important pharmaceutical and industrial applications (El Moussaoui et al. 2001). Of these, however, papain, is a particularly important proteolytic enzyme that is produced in the milky latex of all plant parts but especially in the green, unripe papaya fruits (see also Section 5). The latex is harvested by scarifying the green skin of the fruit to induce latex flow, which is allowed to dry before collection for processing (Nakasone & Paull 1998). The principal producers of crude papain are Zaire, Tanzania, Uganda and Sri Lanka and the principal importing countries are the United States, Japan, United Kingdom, Belgium and France (Practical Action 2006). In 2001, global world production of papain was in the order of 900 metric tonnes/year (AfricaBiz Online 2001).

Evolutionarily, papain may be associated with protection from frugivorous (fruit-eating) predators and herbivores (El Moussaoui et al. 2001). Commercially, however, papain has diverse uses. In food biotechnology, papain is used in the production of chewing gums, for chill-proofing beer, in tenderising meat, in the preparation of fish protein concentrates for animal feed, in the development of roast beef-like flavors by partial hydrolysis of proteins, for production of dehydrated pulses and beans, and in the improvement of the protein dispersibility index of soya flour (Morton 1987; Practical Action 2006; Papaya Genome Project 2007). In the pharmaceutical/cosmetic industries it is a component of soap, shampoo, lotions, skin care products and toothpaste (Morton 1987; Practical Action 2006). Papain has also been used in the textiles industry, for degumming silk and for softening wool (Villegas 1997) and for tanning leather. It also has a wide variety of medical and veterinary applications such as in drug preparations for various digestive ailments, in the preparation of vaccines, for deworming cattle, in the treatment of gangrenous wounds and hard skin, for reducing swelling, fever and adhesions after surgery, and dissolving membranes in diphtheria (Morton 1987; Cornell University 2001; Mezhlumyan et al. 2003; Practical Action 2006).

2.3 Cultivation in Australia

2.3.1 Commercial propagation

Australian papaya plantations are established mainly from seedlings, usually purchased from specialist papaya nurseries (O'Hare 1993). Growers can also obtain seeds directly from a professional seed supplier; as at April 2007 in Australia there was only one such commercial supplier (Max Bell[3] pers. com). Such suppliers need to take account of the sexual reproductive type and the genetic variability of the variety and need to adopt rigorous controlled crossing procedures (Watson 1997). Australia does not have a papaya seed certification scheme; most commercial seed is produced via hand-pollination of mature but unopened flowers to ensure purity of seed production (Max Bell pers. com). Both bisexual and dioecious seed is offered in Australia. Bisexual seed produces both bisexual (67%) and female (33%) trees; dioecious seed produces female (50%) and male (50%) trees (see Section 4.1). Hybrid seed is recommended as hybrids tend to be more vigorous than their parents, produce more fruit and are less susceptible to disease (Papaya Seed Australia 2007). All papaya fruits are affected by climatic changes but when grown under stable conditions hybrids are very consistent in fruit shape and size.

In Australia the seed is planted in December and January for seedlings to be ready for field planting in February and March; this allows young plants to reach a height of about 1 m before winter retards growth (O'Hare 1993).

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[3] As at April 2007, Max Bell was the Papaya Australia Industry Development Officer, based at Cardwell in Queensland

The practice of growing plants from seed gives rise to variation, and vegetative propagation is seen as a means of maximising profitability and uniformity. Plants can be grown from stem cuttings which should be hardened off for a few days and then propped up with the tip touching moist, fertile soil until roots form (California Rare Fruit Growers Inc. 1997; OECD 2005). Semihardwood cuttings planted during the summer root rapidly and should fruit the following year. Commercial papaya growers in South Africa use papaya cuttings (Hansen 2005). A variety of grafting techniques have been used with varying success (Sookmark & Tai 1975; OECD 2005). Micropropagation has also been attempted for a number of cultivars (George 1996; Chan & Teo 2002; Fitch 2005) and Hansen (2005) listed a number of commercial advantages that micropropagation has over seed propagation including reduced time to produce new varieties, ease of maintaining genetic uniformity, and production of plants that are all the same sex. Agronomically, there is evidence that micropropagated trees have a shorter juvenile phase than seedlings and thus produce fruits lower on the stem with the associated benefit of earlier and greater yields (Drew 1988; Chan & Teo 2002; Hansen 2005). One cost benefit analysis of using micropropagation has also shown that a micropropagated crop of a dioecious variety has a much higher return per hectare than a conventional crop grown from seedlings (Hansen 2005). Currently in Australia, a project is underway to micropropagate 16 elite lines produced in a breeding programme so that field trials of the lines can be planted in north Queensland by early 2008 (HAL 2006).

Despite the stated advantages of vegetative propagation, commercial propagation of papaya continues to be done largely via seed and probably reflects the ease of processing and lower start-up costs associated with seed propagation.

2.3.2 Scale of cultivation

In 2006, prior to cyclone Larry, Australia was producing around 12.4 kilo tonnes of papaya fruit (Max Bell, pers com). Most of this was for local consumption (see Table 3 for export trends).

As it grows best in warmer climates (see Section 6.2), papaya is predominately grown commercially in Northern Queensland areas including Innisfail, Mareeba, Proserpine, Yarwun, Yeppoon, Gympie and the Sunshine Coast districts; it is also grown in northern NSW, Western Australia (Kununurra and Carnarvon) and the Northern Territory (Humpty Doo) but Northern Queensland accounts for > 95% of Australia’s production (Garrett 1995). In home gardens where fruit does not need to meet flavour criteria, papaya can be grown as far south as the south coast of New South Wales in warm, sheltered spots (Baxter 1997). A climate statistics comparison of the range of locations in which papaya can be grown in Australia is given in Appendix 1.

The papaya industry in Australia is relatively small and there are a few major growers with plantations of approximately 50 ha and around 200 smaller producers with plantations in the 5 – 10 ha range (Max Bell pers. com). Adverse weather conditions in the early 2000’s caused problems to the industry. Continuing drought in central Queensland saw most growers there cease papaya production (HAL 2006). The occurrence of cyclone Larry in March 2006 resulted in 95% loss of fruit bearing trees in Australia’s two main growing areas of Innisfail and Mareeba. It was estimated that it would take 9 to 18 months for production to return to pre-cyclone levels (Papaya Australia 2007).

Table 3 gives the recent history of papaya production and value in Australia prior to cyclone Larry. Most of Australia's papaya production is consumed within the country.

Table 3. Papaya supply, disposal and value in Australia*

	Unit	2001	2002	2003	2004
Production					
Volume	tonnes	9,622	11,314	8,976	9,952
Area	ha	537	457	623	650
Yield	t/ha	17.9	24.7	14.4	15.3
Gross value	$'000	7,300	12,500	9,900	15,233
Exports, fresh					
Volume	tonnes	8.4	0.7	0.0	1.4
Value	$'000	15	1	0	5
Unit value	$/kg	1.79	2.02	0.00	3.50
Imports, fresh and dried					
Volume	tonnes	22.4	6.9	5.5	18.6
Value	$'000	26	7	5	37
Unit value	$/kg	1.18	1.05	0.91	1.97

* table taken from Foster et al. (2005)

Both dioecious and gynodioecious (bisexual) varieties of papaya are grown commercially in Australia, but the Queensland industry has been based on dioecious outcrossed varieties (see Table 4) that are generally recommended because they have high fruit yields (Drew et al. 1998; Chay-Prove et al. 2000). In bisexual varieties, fruit production on hermaphrodite trees may be affected by air temperatures leading to decreased yields and/or poorly shaped fruit (Organisation for Economic Co-operation and Development (OECD) 2003). These bisexual papaya are affected by a condition known as carpellody or "cat-facing" (Papaya Seed Australia 2007) which is caused by the fusing of the ovary and stamens during adverse weather conditions (see Section 4.1.1). The resulting fruit is deformed and unmarketable and these lines are only recommended for coastal north Queensland and the Atherton Tableland, where the relatively predictable tropical climate does not affect fruit shape unduly. The fruits from hermaphrodite trees are pyriform in shape whereas fruits from female plants are spherical (Urasaki et al. 2002a; Crane 2005) – see also Table 6.

Table 4 lists the varieties that are grown in Queensland. Varieties that are grown in north Queensland include the established yellow hybrid varieties, Hybrid 1B and Hybrid 11B, the red-fleshed Hawaiian 'Sunrise Solo' varieties and Hybrid 29 grown in the lower rainfall areas. In central Queensland the yellow-fleshed hybrid varieties Hybrid 29 and Hybrid 14 are popular and in south-east Queensland the inbred yellow-fleshed PG lines and 'Richter Gold' lines are recommended (O'Hare 1993; Ross et al. 2000). Numerous other varieties and lines are suited to, or have been developed for, Australian conditions (eg 'Petersen', 'Improved Petersen', 'Sunnybank', Arline/57', 'Bettina', 'OE', 'Yarwun Yellow', 'Guinea Gold', 'NT Red').

Table 4. Papaya varieties most commonly grown in various areas in Queensland*

Area	Variety	Papaya Type
Atherton Tableland	Hybrid 1B	Yellow dioecious
	Hybrid 11B	Yellow dioecious
	Hybrid 14	Yellow dioecious
	Sunrise Solo	Red gynodioecious
Coastal North Queensland	Hybrid 1B	Yellow dioecious
	Hybrid 11B	Yellow dioecious
	Hybrid 13	Yellow dioecious
	Hybrid 14	Yellow dioecious
	Sunrise Solo	Red gynodioecious
Central Queensland	Hybrid 1B	Yellow dioecious
	Hybrid 11B	Yellow dioecious
	Hybrid 13	Yellow dioecious
	Hybrid 29	Yellow dioecious
South-east Queensland	PG	Yellow dioecious
	Richter Gold	Yellow dioecious

* Data taken from Ross et al. (2000)

Despite the wide range of varieties available, approximately 60% of commercial production in Australia is accounted for by Hybrid 1B and approximately 30% by 'Sunrise Solo' (Hansen 2005). Although Hybrid 1B fruit has good appearance, it does not have good flavour whereas 'Sunrise Solo', while having excellent flavour, has poor fruit shape, is thin fleshed and is susceptible to winter spot that causes blemishing of the fruit skin (Drew 2005). Hansen (2005) noted that there appears to be a genetic linkage between the desirable character of 'musk' flavoured fruit and the deleterious character of susceptibility to winter spot. Considerable effort has been invested in breeding programmes to develop commercial lines of both yellow and red fleshed varieties that have fruits with both good flavour and appearance (Drew 2005; Hansen 2005; HAL 2006).

Ross et al. (2000) listed the fruit types preferred by the Australian market as follows:

- Yellow-fleshed (1-2 kg): eg Hybrids 1B, 11B, 13, 14, 29, Richter Gold.
- Red, pink or orange-fleshed (1-2 kg): eg New Guinea Red types
- Pink, red or scarlet-fleshed (500 g – 1kg): eg Sunrise Solo, Eksotika
- Pink or red-fleshed (1-3 kg): eg New Guinea Red and Paris-Sunrise Solo crosses
- Pink or red-fleshed varieties sold in hard green condition: used in traditional Asian cuisine as a vegetable or salad ingredient.

2.3.3 Cultivation practices

Conditions for commercial planting of papaya (eg plantation layout, planting spacings, drainage, irrigation, fertilising, cropping cycles) are given by O'Hare (1993) and Benson & Poffley (1998). The more important points are considered below.

Commercially planted papaya performs best on well-drained soils with a minimum topsoil depth of 0.5 m, a pH of 5.5 – 6.5 and shelter from strong winds (O'Hare 1993; Elder et al. 2000a). Plants grow best on the high organic content soils of the tropics but are adaptable to a range of soil types (Benson & Poffley 1998) except heavy clay soils (O'Hare 1993). It is recommended that soil should be analysed for nutrients at least 3 months prior to planting and appropriate fertiliser applications made at least 2 months prior to planting (O'Hare 1993). The recommended soil nutrient levels for south Queensland are given in Table 5.

Table 5. Recommended soil nutrient levels for commercial growing of papaya in South Queensland*

Nutrient	Optimum range
pH	5.5 – 6.5
Organic carbon	> 2%
Nitrate nitrogen	> 40 mg/kg
Sulphate sulphur	> 20 mg/kg
Phosphorus	> 30 mg/kg
Potassium	> 0.6 meq/100 g
Calcium	> 3.0 meq/100 g
Magnesium	> 1.0 meq/100 g
Sodium	< 10% exchangeable cations
Chloride	< 250 mg/kg
Conductivity	< 0.2 mS/cm
Copper	0.3 – 10 mg/kg
Zinc	2 – 10 mg/kg
Manganese	4 – 45 mg/kg
Iron	> 2.0 mg/kg
Boron	1.0 – 2.0 mg/kg

* data taken from O'Hare (1993)

Under reasonable conditions, trees yield well for two years, after which production declines. It is therefore advisable to make fresh plantings each year to ensure continuity of supply (O'Hare 1993). While planting may be done at any time of year, it is recommended that in Queensland 8 – 10 week old, hardened-off seedlings are planted out in February and March (or, in very hot areas, delayed until April) so that they are well established by winter (O'Hare 1993).

As the sex of plants can be difficult to determine before they start flowering (but see Section 4.1), several plants are established in each planting site within the plantation to ensure that the optimum ratio of sex types is achieved. Seedlings will be supplied at least 3/pot and the contents of each pot are planted in a single hole/site (O'Hare 1993). When the sex can be determined, plants are thinned to achieve the desired sex ratio and to reduce the competition that may affect fruit production. Seedlings planted in February and March will usually begin flowering from October to December, with the male flowers forming first (O'Hare 1993). Thinning involves cutting off unwanted plants at ground level although some growers cut females at a single site at 300 mm above ground level so that they can re-shoot and become available as replacements should the first female die. For dioecious varieties, a ratio of one male to 8-10 female plants is recommended to maximise yield whereas for bisexual varieties, the aim of thinning is to have one bisexual plant in each planting position (Nakasone & Paull 1998; Chay-Prove et al. 2000). Male pollinators should be in such a position that the pollen will drift through cropping trees on the wind at the time of flowering (Benson & Poffley 1998).

The spacing of plants in a plantation depends on the slope and management system and, in Australia, there are basically two practices (O'Hare 1993; Benson & Poffley 1998). Single rows are recommended on locations where the slope is greater than 8% and therefore where the slope is too great to allow machine access. The rows are 3 m - 3.5 m apart with planting sites being 1.5 m apart in the rows. This gives a plant population of 1,900 plants per hectare. On land where the slope is less than 8% and therefore where machinery needs access, double rows are used. In this conformation, which gives a higher planting density than single rows, two rows are planted 1 m – 2 m apart and then there is a space of 3.5 m - 4 m to the next double row; planting sites are 1.5 m apart in the rows.

Ideal plants start fruit set at as low a height as possible; this is achieved by maximising leaf growth in young trees by irrigating and fertilising (O'Hare 1993). Yield and fruit quality vary with location, variety and season as well as agronomic practices such as irrigation (Elder et al. 2000a).

Under commercial conditions, irrigation is essential during periods where the minimum monthly rainfall drops below about 100 mm (Nakasone & Paull 1998) – see Section 6.1.3 for a discussion of the effect of water stress. Irrigation can take the form of undertree sprinkling, trickle or overhead depending on water availability (O'Hare 1993). In many instances fertigation (irrigation of plants with water containing fertilizer) may be an efficient way of applying nutrients to the crop. Runoff and drainage in a plantation needs to be controlled and, again, the type of measure taken depends on the slope of the land (O'Hare 1993). Contour drains are used in land with a slope of less than 8%. and are constructed so as to divert runoff into a grassed waterway. Mounds, where the soil is built up to 30 – 40 cm high along the rows, are recommended for land with a slope of greater than 8%. In addition highly sloped land should also utilise infall roads. These roads are usually spaced six rows apart up the slope and facilitate both plantation management and erosion control as well as interception of runoff.

Providing that adequate fertiliser has been applied at planting, no further applications are necessary until flowering unless the plantation is in a high rainfall area where nutrients are leached from the soil (O'Hare 1993). Potassium is particularly important for the production of high quality fruit. Boron deficiency is common and is manifested by the occurrence of ‘bumpy fruit’ and poor fruit flavour. Addition of borax or a foliar spray such as Solubor® at six-monthly intervals is sufficient to overcome the problem (Benson & Poffley 1998). Once optimum soil levels of nutrients have been achieved, annual applications of a complete NPK fertiliser will maintain the levels (O'Hare 1993).

Weeds compete with papaya plants for water light and nutrients – see Section 7.1 for a discussion of weeds and their chemical control. In double row plantations, the main interrow is usually grassed and kept mown (O'Hare 1993). Ground covers such as Pinto peanut (*Arachis pintoi*) and Maku lotus (*Lotus pedunculatus*) may also assist in weed control but compete with the papaya plants for moisture (O'Hare 1993). Mulching is a common weed control practice. Mulching seedlings with coarse grass hay has also been shown to produce plants with thicker stems and to promote earlier flowering and increasing fruit set, yield and average fruit weight The response to mulching was probably due to a number of factors including better use of the total soil volume, lower soil temperatures in the first few centimetres, reduced soil and water loss, improved conditions for soil mycorrhiza and decreased nematode populations (Elder et al. 2000b; Elder et al. 2002). Walsh & Ragupathy (Walsh & Ragupathy 2007) confirmed improved arbuscular fungal colonisation of papaya roots in mulched plants.

The major pests and diseases of papaya in Australia, together with their control are discussed in Section 7.2. Monitoring for pests and diseases at two-weekly intervals is advised (O'Hare 1993).

Seedlings usually begin flowering 9 - 12 months after they germinate (California Rare Fruit Growers Inc. 1997) and it then takes from 5 – 9 months for fruit maturation (O'Hare 1993). In the annual cropping cycle of an Australian plantation, the bulk of the crop flowers between November and March and is harvested between September and December (O'Hare 1993). In a tropical plantation, each plant ripens 2 – 4 fruits per week (Morton 1987) and the crop may require harvesting and packing at least once a week all year round (Papaya Australia 2007). In subtropical climates fruit set declines, or may even cease, during the colder winter months (Allan 2002).

Commercial harvesting and packing is done by hand and fruits must be handled carefully so as to avoid blemishes and bruising that will make the fruit unmarketable. The fruit must have started to colour before it is picked (O'Hare 1993). In cooler months, fruits are ethylene ripened under controlled conditions which provide a temperature of 29 – 32^{o} C, good air circulation, humidity of 85 – 90% and an ethylene atmosphere supplied either continuously or as single shots every 12 hours (O'Hare 1993). In warmer months, fruit is allowed to ripen naturally. Ideally, fruit should reach the market with between half and three-quarters colour in summer and between three-quarters to full colour in the winter months. Storage and transport of fruit should be done at a temperature of 13^{o} C and 90% humidity (O'Hare 1993).

2.4 Crop Improvement

2.4.1 Breeding

Papaya is generally regarded as a cross-pollinated species but self-fertilization does not result in inbreeding depression and inbred lines have been used to advantage to help fix useful genetic characteristics in both gynodioecious and dioecious lines (Aquilizan 1987).

The open-pollinated dioecious varieties of papaya that formed the basis of the Queensland industry tend to be highly variable in characteristics such as fruit shape, taste, size, flesh-colour, firmness and yield (Elder et al. 2000a). In particular, fruit shape is an important component in the production of uniform fruit packs for which the market will pay premium prices. The development of inbred dioecious lines by self-fertilising male plants (ambivalent males – see Section 4.1.1) has led to the availability of these lines for the production of hybrids with more uniform characteristics; the system is called the *Yarwun (Queensland) System* for fixing dioecious type inbred lines (Aquilizan 1987).

Disease resistance, increased yields and improved quality and storage traits are the most important breeding objectives (Nakasone & Paull 1998). Worldwide, papaya ringspot virus (PRSV - see Section 7.2.3) presents the most significant problem to production. Genetic resistance to PRSV does not exist in *Carica papaya*; PRSV-tolerance is found in some lines which have been used to introgress tolerance into cultivars such as 'Cariflora' (Conover et al. 1986). The genus *Vasconcellea* contains a number of species with resistance to PRSV and some of these have been crossed with papaya to obtain resistant interspecific hybrids (*Papaya* x *cauliflora*, *Papaya* x *quercifolia* and *Papaya* x *pubescens [cundinamarcensis]*) (Drew et al. 2005b). However, such crosses are problematic due to genome incompatibility (Magdalita et al. 1997) - see also Sections 9.2 and 9.3 - and only *Papaya* x *quercifolia* hybrids have shown some levels of fertility and hence may prove of use in back-crossing programmes. Sajise et al. (2004) showed that a *Papaya* x *quercifolia* hybrid had cross compatibility with two Philippine local inbred selections but not with inbreds from other countries; this highlights the importance of the genotype of the *Carica papaya* parent in such crosses. Studies have also been done to characterize molecular markers for PRSV resistance in *Vasconcellea* species (Dillon et al. 2005a; Dillon et al. 2005b) and should assist attempts to transfer this trait into papaya.

Some species of *Vasconcellea* are considered to possess other traits (eg high quality fruits, high level of proteolytic enzymes, cold tolerance) that could be useful in breeding programmes for papaya improvement (National Research Council 1989; Scheldeman & Van Damme 2002). In particular, the babaco (a natural sterile hybrid derived from crosses between *V. cundinamarcensis* and *V. stipulata*) has high yields and is the only *Vasconcellea* species cultivated intensively (although on a small scale) in Ecuador, Australia and New Zealand (Morton 1987). The plant is slender and no more than 3 m high, but the 5-angled fruits reach 30 cm in length and are usually seedless. The plant is not known in the wild and is propagated by cuttings.

Fitch (2005) discussed a number of papaya varieties that have been developed to meet a range of breeding objectives including tolerance to *Phytophthora* and improved fruit quality and yield. Some varieties are grown worldwide particularly the 'Solo' group (developed in Hawaii), 'Tainung' (developed in Taiwan), 'Eksotika' and 'Eksotika II' (developed at the Malaysian Agricultural Research and Development Institute), 'Maradol' (developed in Cuba) and 'Hortus Gold' (developed in South Africa) (OECD 2005).

In Australia, two recent breeding projects have been funded by Horticulture Australia Limited (Drew 2005; Hansen 2005). Cycles of random mating (to break the linkages between traits like high sugar level and susceptibility to winter spot), coupled with micropropagation of promising individuals has resulted in saving time and money in not having to genetically fix good individuals through the production of inbred lines (Hansen 2005). These projects have resulted in the production of a number of promising lines with good yields of high quality, good tasting fruit that can be maintained in tissue culture storage until required for further breeding programmes or for direct commercialisation. Transcript and carotenoid profiling, and identification of genes expressed during papaya fruit development is also being undertaken in Australia and provides an alternative way of approaching molecular breeding or genetic modification strategies for altering fruit quality traits (Devitt. et al. 2006a; Devitt. et al. 2006b).

Linkage maps have been developed to assist breeding through mapping candidate genes, searching for quantitative trait loci of agronomic traits (Sondur et al. 1995) and developing marker assisted selection. Most linkage maps have been concerned with markers for traits such as sex determination and fruit flesh colour (Fitch 2005). Sex determination has been particularly studied because of its close link to efficient commercial fruit production. Liu et al. (2004) used chromosome walking and fine mapping to locate the sex determination locus in papaya and also found that there was suppression of recombination around the locus indicative of degeneration of the Y chromosome. Molecular markers and DNA diversity have been used to study the relationships among papaya and other members of the Caricaceae (Van Droogenbroeck et al. 2002; Van Droogenbroeck et al. 2004) and such studies are considered important for being able to exploit genetic potential in breeding programmes for improvement of papaya.

In 2004, an integrative multi-institutional consortium, based at the University of Hawaii, was formed to sequence the papaya genome (Papaya Genome Project 2007). The project was 88% completed in April 2007 and had an estimated genome completion date of December 2007. The project aim is to map and clone papaya genes related to improvement of economic value and efficiency of cultivation.

2.4.2 Genetic modification

Early experiments with papaya established plant tissue culture regeneration systems – a necessary precursor to successful transformation. The main pathway of regeneration is via somatic embryogenesis and although embryogenic cultures have been induced from various explant types, the most successful explants are immature zygotic embryos (Fitch & Manshardt 1990) and young seedling tissues (Fitch 2005). Transformation protocols involving both *Agrobacterium tumefaciens* and microprojectile bombardment were developed in the early 1990s (Fitch et al. 1990; Fitch et al. 1993) and both procedures have been improved over time to give good results (Fitch 2005). In Australia, Mahon et al. (1996) found that a biolistic system using somatic embryos, derived from immature zygotioc embryos (Drew et al. 1994), of an Australian dioecious cultivar (OE) as target tissue resulted in efficient transformation that yielded 41% successful transformants (kanamycin resistance) and transformed plantlets within 6 months of bombardment. Drew et al. (2005b) pointed out, however, that a drawback of using zygotic embryos as target tissue is that it is not possible to apply the technology directly to an elite female or hermaphrodite cultivar, only to progeny.

The first commercial trait used in genetic modification experiments was resistance to PRSV and fruits from commercial lines have been available since around 1998; papaya was thus the first genetically modified (GM) fruit crop used for human consumption. GM PRSV-resistant papaya was developed in Hawaii in response to the devastating impacts of the disease in Hawaii and south-east Asia; for a historical account of the research see Gonsalves (1998). Two cultivars ‘SunUp’ (red-fleshed) and ‘Rainbow’ (yellow-fleshed) that resist the virus by expressing PRSV coat protein (a concept known as parasite-derived resistance) were successfully developed in Hawaii (Gonsalves & Manshardt 1996) and their commercial production rapidly reversed the declining Hawaiian papaya industry (Manshardt 1999; Ferreira et al. 2002; Gonsalves et al. 2004). The mechanism of the resistance is thought to be via post transcriptional gene silencing and there is a suggestion that a threshold level of expression must be attained before silencing is effective (Gaskill et al. 2002). ‘Rainbow’ seedlings take much longer to develop resistance to PRSV than ‘SunUp’ and this is thought to be due to the fact that ‘SunUp’ seedlings reach the threshold level more quickly because they are homozygous for the transgene (Gaskill et al. 2002). ‘SunUp’ shows no resistance to PRSV strains from Thailand and Taiwan. The two lines were approved as food in the USA in 1997 (FDA 1997) and in Canada in 2003 (Health Canada 2003) and were approved for commercial growing in the USA in 1996 (USDA/APHIS 1996).

A number of other countries are also attempting to develop commercial lines of GM PRSV-resistant papaya lines (Fitch 2005). *The Papaya Biotechnology Network of Southeast Asi*a was launched in March 1998 and seeks to expand the biotech capacity of its members through information exchange and transfer of proprietary technology from the private-sector of developed countries to national institutes in Southeast Asia (ISAAA 1999). In the region encompassing Australia, Southeast Asia and China:

- Stable PRSV resistance was obtained in GM plants derived from two Australian cultivars (OGTR 1998; Lines et al. 2002). The technique involved using a transformation and regeneration protocol based on the microprojectile bombardment of secondary somatic embryos mentioned above (Mahon et al. 1996) and plants did not show infection after 18 months of field exposure to the virus. These field trials have now ceased and no further trials are currently underway in Australia.

- Small field trials of PRSV-resistant papaya are underway in the Philippines (ABSP II 2004; Magdalita et al. 2004)

- The Department of Agriculture in Thailand started field trials of GM PRSV-resistant papaya in 1999 at the Khon Kaen Horticulture Experiment Station in Tha Pra. In mid-2004 unapproved GM plants were found in a large number of plantations; this led to the destruction of the field trials and a government ban on any further trials.

- China has been undertaking field trials and is likely to approve the commercial release of PRSV-resistant lines in the near future (ABSP II 2006).

Fitch (2005) listed other priorities for papaya transformation. Of these, the following genetic modifications have reached field trial stage: resistance to fungi, resistance to arthropods, and delayed ripening. In Australia there has been a field trial testing GM papaya plants modified for delayed fruit ripening (OGTR 2000). Currently there is a field trial growing six different types of GM papayas that have been genetically modified to delay fruit ripening by downregulating ACC (1-amino-cyclopropane-1-carboxylic acid) synthase, an intermediate enzyme in the biosynthesis of the plant hormone, ethylene; there is also one type that has been modified to delay fruit ripening by a change in the perception of ethylene (OGTR 2003).

SECTION 3 MORPHOLOGY

3.1 Plant morphology

Morphological description of papaya can be found in a number of sources (Morton 1987; Du Puy & Telford 1993; OECD 2005). The hollow green or deep purple trunk can grow to 10 m, is straight and cylindrical with prominent leaf scars, and can become 30-40 cm thick at the base, thinning to 5 – 7.5 cm at the crown. The leaves emerge directly from the upper part of the stem in a spiral on nearly horizontal petioles 25 – 100 cm long and form a loose open crown. The leaf blade, deeply divided into 5 to 9 main lobes, varies from 25 – 75 cm in width, and has prominent yellowish ribs and veins. Colleters (short-lived multicellular stalked globules) are present at leaf bases and along vein margins and their secretions may aid in protection against desiccation and/or protection against insect predators (Ronse Decraene & Smets 1999). The life of a leaf is 2.5 to 8 months and new leaves arise at the rate of 1.5 – 4 per week. All parts of the plant contain white latex.

3.2 Reproductive morphology

The flowers (see references at the bottom of Table 6) are born on inflorescences which appear in the axils of the leaves. Papaya has a highly complex capability in sexual expression (see also Section 4). Some plants bear only short-stalked pistillate (female) flowers, or hermaprodite (perfect) flowers (having female and male organs), borne on short stalks, while others may bear only staminate (male) flowers, clustered on long panicles. There are also monoecious plants having both male and female flowers. Pistillate trees tend to be stable while staminate and hermaphrodite trees may be ‘ambivalent’, going through seasonal sex reversals (Storey 1976). Table 6 gives details of the various characteristics associated with the main flower types. There is a range of possible variation and the proportion and type of flowers produced may vary even on the same tree (Villegas 1997). Hermaphrodite flowers are of two main types – elongata and pentandria - with an intermediate type between these two.

Table 6. Characteristics of the major flower types in papaya*

Character	Male (staminate)	Female (pistillate)	Hermaphrodite: elongata	Hermaphrodite: intermedia	Hermaphrodite: pentandria
inflorescence	Pedunculate pendulous panicle 25 – 100 cm long	solitary or few flowered cyme, stalk 3.5 – 5 cm long	short peduncled cluster, stalks less than 25 cm	short peduncled cluster, stalks less than 25 cm	short peduncled cluster, stalks less than 25 cm
corolla	trumpet-shaped, 2.5 cm long, 5 lobes, light yellow/cream	5 almost free petals (fused at base); petals fleshy, yellow/cream	5 partially united petals, fused from ¼ - ¾ of their total length	Undefined: petals may be fused up to 2/3 of their length or free	5 almost free petals; petals fleshy, yellow/cream
stigmas	NONE	5, fan-shaped on a short style	5, fan-shaped	5, fan-shaped	5, fan-shaped
ovary	rudimentary non-functional ovary (or pistillode)	ovoid oblong, 2-3 cm long, central cavity, numerous ovules	elongate	distorted, irregular shape	ovoid oblong, 2-3 cm long, 5-furrowed
stamens	10 in 2 whorls alternating with petal lobes	NONE	10 borne at the throat of the corolla in 2 clusters (5 long, 5 short)	2-10, some or all of which are distorted	5 attached by long filaments near base of ovary
Shape of resulting fruit	n/a	Spherical/ovoid	cylindrical to pear-shaped	carpelodic (cat face)	ovoid and lobed

* data compiled from McGregor (1976); Villegas (1997); Du Puy & Telford (1993); De La Cruz Medina et al. (2002); Ronse Decraene & Smets (1999)

The fruits are technically classified as fleshy berries (Villegas 1997) sometimes called pepo-like berries since they resemble melons by having a central seed cavity. They are borne axillary on the main stem, usually singly but sometimes in small clusters. The fruit has a smooth exocarp (peel) and thick, fleshy mesocarp and in shape may be globose, ovoid, obovoid, or pyriform, 7-35 cm long, and 0.250-10 kg in weight. Female plants produce medium to large round-shaped fruit of good quality with a large seed cavity; hermaphrodite plants produce small to medium elongated fruit of good quality but with a smaller seed cavity; male plants with bisexual flowers may produce a few, elongated, poor quality fruit (Crane 2005).

SECTION 4 DEVELOPMENT

4.1 Reproduction

Fruit production in papaya plants may occur following either cross-pollination (out-crossing), self-pollination or parthenocarpy (a form of asexual reproduction in which fruits may be produced without fertilisation), depending on whether dioecious or gynodioecious lines are planted and the particular cultivar that is grown (Rodriguez-Pastor et al. 1990; Nakasone & Paull 1998; Louw 2000; Organisation for Economic Co-operation and Development (OECD) 2003). Rodriguez-Pastor et al. (1990) demonstrated that when out-crossing is limited experimentally by bagging flowers to prevent pollen flow, 90% and 94.7% of fruit from hermaphrodite flowers of ‘Sunrise Solo’ and ‘Kapoho Solo’, respectively, may be produced following either self-pollination or parthenocarpy. Of these, potentially 35% of the Sunrise Solo fruit were produced parthenocarpically and *ca* 65% were produced following self-pollination. Kapoho Solo produced no parthenocarpic fruit (Rodriguez-Pastor et al. 1990). Parthenocarpic fruit were reported to be of adequate commercial size and quality.

Garrett (1995) also investigated the potential for alternative papaya lines to produce fruit parthenocarpically. She demonstrated that such fruit may be produced at much lower frequencies and are of poor size and quality, compared to sexually derived fruit. Garrett (1995) also indicated that low numbers of seeds are produced by parthenocarpic fruit and that approximately 4% of such seeds may be viable, depending on the variety of papaya. It is not clear whether these seeds were produced sexually (perhaps by inadvertent contamination with pollen) or asexually. Nevertheless, many researchers (Gillaspy et al. 1993; Vivian-Smith et al. 2001) contend that, by definition, parthenocarpic fruit contain no viable seeds.

4.1.1 Sexual reproduction

Papaya flowers can be grouped into three basic forms that reflect whole plant gender: female, male or bisexual (hermaphrodite). With controlled cross-pollinations between flowers of each gender, the ratio of female, hermaphrodite and male offspring are predictable, as summarised in Table 7 and as follows:

i. pistillate flowers pollinated by staminate flowers give equal numbers of male and female progeny
ii. pistillate flowers pollinated by pollen from bisexual flowers give an equal number of female and bisexual progeny
iii. bisexual flowers either self or crossed-pollinated with other bisexuals give a ratio of one female to 2 bisexual

iv. bisexual flowers pollinated by staminate ones produce equal numbers of female, male and bisexual progeny.

The second and third combinations thus produce the maximum number of fruit-bearing plants.

Table 7. Summary of gender ratios following pollinations between male (M), female (F) and bisexual (B) *C. papaya* gender forms*

Pollination	No. of resulting Females	No. of resulting Males	No. of resulting Bisexuals
F x M	1	1	-
F x B	1	-	1
M x M†	1	2	-
B x B	1	-	2
B x M	1	1	1
M x B	1	1	1

* summarised from Storey (1976)

† note that because of gender reversals or alterations, 'males' may bare functional carpels and set fruit.

The genetic or chromosomal basis for this complicated reproductive pattern is poorly understood (Villegas 1997; Organisation for Economic Co-operation and Development (OECD) 2003). However, as summarised by Somsri et al. (1998), a common hypothesis is that sex is controlled by a single locus with three alleles — M_1 (male), M_2 (hermaphrodite) and m (female). Male/staminate (M_1m) and hermaphrodite plants (M_2m) are heterozygous whereas female/pistillate plants (mm) are homozygous recessive. Combinations of dominants, namely M_1M_1, M_1M_2, or M_2M_2 are lethal, leading to post-zygotic abortion of such ovules; the lethal effect of these homozygous dominant sex-determining alleles is further evidence of the degeneration of the Y chromosome (see also discussion in Section 2.4.1). Accordingly, this hypothesis predicts that viable males can only be M_1m (dioecious) and viable hermaphrodites can only be M_2m (gynodioecious). A cross of two hermaphrodites normally yields a 2: 1 (hermaphrodite:female) ratio.

Recently, Chan-Tai et al. (2003) obtained a hermaphroditic papaya mutant from 'Sunrise' that has a genotype designated $M_{@}ml$. Selfing of this mutant resulted in all progeny being hermaphrodite as the female genotype is lethal because of a lethal gene (l) being linked to the homozygous recessive genotype (ie mlml) in this particular mutant, and the dominant $M_{@}M_{@}$ genotype is not lethal. Crossing of the mutant with another hermaphrodite (M_2m) resulted in a 3:1 (hermaphrodite:female) ratio because neither the $M_{@}M_2$ genotype nor the mlm genotypes were lethal.

Crosses within, among and between the normal dioecious and gynodioecious papayas result in a complex array of sex-type ratios with a further layer of complexity being added by environmental influences such as temperature that can lead to the production of a range of functional male and female flower types (Fitch 2005; OECD 2005) and can even cause sex reversals. Of particular importance in the Australian breeding system is the occurrence of sexually ambivalent (fruit-bearing) male trees; these have been used to fix dioecious inbred lines (Aquilizan 1987) – see also Section 2.4.1. A high proportion of dioecious cultivars in Queensland produce sexually ambivalent male plants which, under short warm days and low night temperatures, form hermaphrodite flowers at the tip of the inflorescence (Aquilizan 1987).

Considerable effort has been invested recently in developing molecular tests to determine the sex of papaya seedlings (Somsri et al. 1998). These would be advantageous commercially, as plant sex could be determined before reproductive maturity. Male-specific (Parasnis et al. 2000) and hermaphrodite-specific (Lemos et al. 2002; Deputy et al. 2002) tests have been developed using a variety of molecular techniques. Urasaki et al. (2002b)} also developed a molecular test to distinguish male and hermaphrodite plants from females and further refined the procedure (Urasaki et al. 2002a) to minimize the risk of false negatives and provide a single-step DNA extraction method for routine sex testing. Chaves-Bedoya & Nuñez (2007) developed a SCAR (sequence characterized amplified region) marker to determine the sex type of papaya plants.

Efforts to identify molecular markers for sex are complicated by environmental variables including temperature, humidity, soil nutrients that may modify the functional gender of plants (Organisation for Economic Co-operation and Development (OECD) 2003). In hot (>35 ºC) and dry conditions, for example, bisexual flowers may become functionally male, with poorly developed and non-functional female parts (Watson 1997; Nakasone & Paull 1998). At low (<20º C) temperatures, by contrast, bisexual flowers may become functionally female because of carpelloidy, a condition in which the stamens resemble carpels but remain associated with the developed fruit, leading to distorted fruit shape (Organisation for Economic Co-operation and Development (OECD) 2003). Bisexual flowers of variety 'Solo' may produce 100% carpellodic flowers when minimum temperatures are less than 17º C (Nakasone & Paull 1998). Such changes in functional gender can be either temporary or permanent.

Changes in functional gender in response to environmental variables have been used advantageously in papaya breeding programs and to help select the most appropriate varieties for commercial cultivation in particular regions (Chay-Prove et al. 2000; Organisation for Economic Co-operation and Development (OECD) 2003).

4.2 Pollination and pollen dispersal

As might be expected from the variety in flower types (see Section 3.2) the occurrence of cross-pollination can vary considerable eg hermaphrodites can self-pollinate or they can be pollinated from adjacent male plants, while in dioecious plants where males and females are separate, cross-pollination is essential. In addition, factors such as environmental conditions, floral characteristics associated with the various flower types and flower receptivity may affect the level of cross-pollination (OECD 2005). Commercial fruits are best obtained following the transfer of pollen from staminate flowers to pistillate flowers.

In Australia, seasonally variable papaya fruit production (in terms of both quantity and quality) has been attributed to several factors including low pollen viability and an absence of suitable pollinators.

Pollen can be produced all year around. However, Garrett (1995) observed that pollen production by papaya trees varies seasonally and according to the variety of plant that is cultivated, but a general trend is for decreased quantities of pollen during winter/early spring. The viability of pollen that is produced also varies seasonally and according to variety (Magdalita et al. 1998) with viability being low in winter.

Garrett (1995) determined that, on average, 90% of freshly dispersed pollen grains were viable but that in winter, viability dropped to about 45% in some lines and as low as 4.5% in others. No information was provided on the duration of pollen viability, but Allan (1963) indicates that extremes of humidity reduce the storage life of papaya pollen which, under ideal (artificial) storage conditions, potentially remains viable for about 5-6 years.

Garrett's (1995) observations of seasonal variation in pollen viability are broadly consistent with similar studies conducted in South Africa (Allan 1963) and Israel (Cohen et al. 1989), where it was concluded that minimum temperatures below 10º C significantly affect pollen viability, possibly as a consequence of degenerated pollen mother cells (Allan 1963).

In contrast to pollen production and viability, the receptivity of papaya stigmas remains high throughout the year. If pollinated with viable pollen, both female and hermaphrodite flowers can successfully produce fruit, even in winter (Garrett 1995).

Garrett (1995) provided no data regarding the numbers of flowers (female, male or hermaphrodite) that are produced in each season. It is difficult, therefore, to determine the relative importance of variable pollen viability and likely seasonal variations in the number of actual flowers, particularly female flowers, in affecting total fruit production.

Pollinator efficiency or abundance may also affect fruit production. There may be 1,000 seeds in a single fruit, indicating that 1,000 viable pollen grains would have been deposited on a receptive stigma (McGregor 1976). The more seeds in a fruit, the larger the fruit grows; fruits with less than 300 seeds are not generally marketable (McGregor 1976).

In a detailed series of experiments done in Central Queensland, Garrett (1995) demonstrated that pollination by native and European honeybees, or by wind, is rare. Rather, Garrett (1995) determined that hawkmoths (Lepidoptera: Sphingidae: Macroglossinae), many in the genus *Hyles*, are the primary pollinators of papaya in central Queensland. Hawkmoths are also primary pollinators of papaya in Kenya (Martins 2004). In Queensland it was observed that seven hawkmoth species pollinate papaya flowers and that four additional species are likely to be pollinators (Garrett 1995). Of these eleven species, eight were active at dusk (18:00 – 19:00); the remaining three were active during the day. Usually, moths spent about three seconds at each flower before moving to another. Foraging focussed on groups of up to three trees, with each tree in the group being visited in turn, before flying to another part of the orchard. This behaviour did not appear to be affected by wind direction (Garrett 1995). Total foraging time and the distance between groups of trees visited by pollinating moths were not recorded.

Plants that are pollinated by hawkmoths are described as being 'sphingophilous'. The flowers of such plants are typically white to cream in colour, have long tubes, produce copious nectar and open at sunset or during the night emitting a characteristic odour (Gibson 2001). Nectaries of staminate papaya flowers are located on the central rudimentary pistil. Pistillate flowers actually do not produce nectar but have a fragrant stigmatic exudate (Ronse Decraene & Smets 1999). Irrespective of nectar production, both flower types have nectar guides that provide hawkmoths with tactile and contact chemosensory stimuli (Astridge & Hansen 2005). Hawkmoths are regarded as long distance and fast flyers (Ronse Decraene & Smets 1999; Gibson 2001) but there are no data on likely gene flow distances in papaya as a result of hawkmoth pollination. However, there have been studies in other genera pollinated by hawkmoths and, for example, pollen dispersal of up to 65 m has been reported in the African orchid *Disa cooperi* (Johnson et al. 2005) and up to 350 m in the central American rainforest tree *Pithecellobium elegans* (Chase et al. 1996).

If a papaya plant is inadequately pollinated, it will bear a light crop of fruits lacking uniformity in size and shape. In particular, fruit weight and yield of trees in central Queensland may drop in January following the reduced pollination in the previous winter months of July and August by hawkmoths (Garrett 1995). Hand-pollination in July and August in commercial plantations that are not entirely bisexual (and, hence self-pollinating) has the potential to increase yields (Garrett 1995) but is labour intensive and unlikely to be justified on economic grounds.

Despite floral morphology suggesting insect pollination, several authors have indicated that wind pollination may also be important (Nakasone & Paull 1998; OECD 2005) especially in some countries. For example, very high papaya pollen counts (10 – 18% of total aeropollen) have been recorded in the outskirts of Calcutta (Chakraborty et al. 2007). Species in which both wind and insect pollination occur are described as having an amphiphilous pollination mechanism.

4.3 Fruit/seed development and seed dispersal

The first crop of fruit is low on the stem. The fruits range in size from 10-50 cm long and vary in mass from about 350 g to as much as 12 kg (OECD 2005). Fruits from female trees are spherical whereas the shape of fruit from bisexual trees is affected by environmental factors, particularly temperature, that modify floral morphology during early development of the inflorescence (Nakasone & Paull 1998).

Unripe fruits are green and hard and rich in latex. Ripe papaya fruits have smooth, thin yellow-orange coloured skin and contain no latex. Depending on the cultivar, flesh thickness varies from 1.5 to 4 cm (Nakasone & Paull 1998) and flesh colour may be pale yellowish to red (Villegas 1997; Nakasone & Paull 1998). In immature fruits, the developing seeds have white seed coats (Lange 1961). Mature fruits contain numerous grey-black spherical seeds 5 mm in diameter and coated with a transparent, gelatinous aril/sarcotesta (Villegas 1997). There are usually 60 – 65 dried seeds per gram (10288). The cold temperatures experienced over winter months in subtropical climates may affect seed development; under-developed seeds may be found in fruits that set in autumn and seed abortions occur in the coldest months (Allan 2002). Trees yield well for two years, after which production declines (Benson & Poffley 1998).

The ripe fruit is indehiscent and therefore seeds are not dispersed without assistance. Worldwide, many birds and animals eat the fruit and disperse the seeds (OECD 2005). 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 papaya (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*) occur along coastal eastern Australia and have been observed in NSW, feeding on papaya fruits (ABS 2001).

Other species that also occur in papaya growing areas include the Black Flying-fox (*Pteropus alecto*), Little Red Flying-fox (*Pteropus scapulatus*), Spectacled Flying-fox (*Pteropus conspicillatus*), Tube-nosed flying fox *(Nyctimene robinsoni*), and Common blossom bat (*Syconycteris australis*). There appears to be no scientific literature specifically detailing papaya seed dispersal by these species but it could be assumed that at least some of these species feed on papaya fruit and could disperse seeds. 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 means that seeds are not digested and can germinate after being passed in the faeces. The observation of volunteer papaya plants in old campsites and house sites (Max Bell pers. com) indicates that humans also play a role in seed dispersal.

4.4 Seed dormancy and germination

Seed of papaya is photoblastic (has an absolute requirement for light in order to germinate) (Vasquez-Yanes & Orozco-Segovia 1996). Seed should be mature to maximise viability (Lange 1961). Nonetheless germination of seeds of papaya has been reported to be slow, erratic and incomplete (Ellis et al. 1985). The seeds have inhibitors that prevent germination while they are still inside the fruit or if they are released prematurely. Significant early germination of seeds that fall onto the soil would be hampered by the presence of the sarcotesta which would first have to decompose (Lange 1961). In commercial nurseries, the sarcotesta should be removed at harvest to reduce the time taken to germinate (Lange 1961).

Queensland growers have reported inconsistencies in germination rates and loss of viability during drying and storage of seeds (Ashmore & Drew 2006). Freshly harvested seeds that are not dried have very low and variable germination (OECD 2005). Air-dried papaya seeds stored in the dark at room temperature and room atmosphere lose viability after 3 years (Vasquez-Yanes & Orozco-Segovia 1996) but Bass (1975) noted only small viability losses in papaya seed stored for 6 years at 10^{o} C and moisture content in equilibrium with 50% Relative Humidity (9-10% moisture content). Thus, desiccated storage at low temperature would seem to be advantageous and, for example, Ellis et al. (1985) recommended that freshly extracted papaya seeds are rubbed to remove the sarcotesta then thoroughly washed in running water before being dried for storage under desiccation and below 15^{o} C. However, desiccation to too great a level can present problems. Three categories of *ex situ* seed storage of mature seeds have been defined (Roberts 1973; Hong & Ellis 1996):

- ‘Orthodox’ seeds are those that are able to be dried, without damage, to low levels of moisture content [2-6%], and the period of viability is extended by lowering their temperature and moisture content during storage;
- ‘Recalcitrant’ seeds are those that cannot be dried without loss of viability and there is no satisfactory method for maintaining the viability of intact seeds over the long term;
- ‘Intermediate’ seeds are those that cannot be dried to below about 10% moisture content without showing stress and have medium-term storage under optimal conditions.

Papaya seeds have been classed as being ‘intermediate’ with regard to desiccation tolerance and show stress at moisture contents of less than 8% - 10% (Ellis et al. 1991). However, Wood et al (2000) concluded that desiccation resulted in dormancy being induced rather than reducing seed viability and showed that heat shock (4 h at 36^o C) followed by a return to a lower temperature (26^o C) could be used to break dormancy following storage under desiccation. Clement et al. (2004) suggested the presence of papaya seeds in the seed bank and the heat rise that accompanies clearing and burning as explanation for the spontaneous appearance of papaya plants in Amazonian Dark Earths where papaya is not currently cultivated or where volunteers are destroyed as weeds.

Photoblastic seeds can also survive storage under moist conditions if kept in the dark and around 38% of papaya seeds stored artificially for 5 years under such conditions still germinated (Vasquez-Yanes & Orozco-Segovia 1996). Some 55% of papaya seed remained viable for 2 years after burial 5 cm below the surface in the wet soil of a tropical rainforest (Vasquez-Yanes & Orozco-Segovia 1996).

Even under non-ideal conditions, papaya seeds can persist and remain viable in the soil. For example, in the subtropical Mt Kuwanoki Forest Reserve on Hahajima Island, viable papaya seeds (papaya is an introduced species) were found in samples taken from the soil profile to a depth of 20 cm (Naoko et al. 2003) – the length of time the seeds had spent in the seed bank was not determined.

Treatment with gibberellins may promote germination of papaya seeds and reduce the time taken to germinate and a preapplication for 24 hours with giberrellic acid (GA_3) has been suggested (Ellis et al. 1985; Bhattacharya & Khuspe 2001). Germination can occur in 16 - 20 days continuing up to 40 days; much faster germination (5 – 9 days) has been obtained with *in vitro* germination (Bhattacharya & Khuspe 2001). Percentage germination may vary from 3 – 71% depending on the cultivar and temperature, with 30^o C being optimal (Bhattacharya & Khuspe 2001).

Cryopreservation of shoot tips and seeds of papaya has been successful (Azimi et al. 2005; Drew et al. 2005a) as a method of providing long-term conservation of the species. Ashmore & Drew (2006) reported that North Queensland seed that was desiccated and cryostored for 6 months had better germination than desiccated seed stored at temperatures ranging from – 20^o C to 15^o C.

4.5 Vegetative growth

Developing papaya trees can produce a new node every 3 -4 days (Sondur et al. 1995). Under unmanaged conditions, trees can live for 15 -20 years (OECD 2005) and reach 8-10 metres in height but in cultivation, they are usually destroyed when they reach heights that make harvesting of fruit difficult (Villegas 1997).

Varieties such as Hybrid 29, a semi-dwarfed hybrid, that set fruit at a comparatively low height can be advantageous as they can remain in production for longer because of ease of harvesting. On the other hand, the short internodes of a dwarf tree can lead to undesirable compaction of the fruits as they develop (Sondur et al. 1995). Cultivated trees in Australia are usually replaced after approximately 4 years when they exceed 4 m in height (O'Hare 1993).

Papaya trees normally grow as single-stemmed trees with a crown of large palmate leaves emerging from the apex of the trunk, but trees may become multi-stemmed when damaged (Villegas 1997). Under cultivation, a process known as ratooning is sometimes employed to allow fruits to develop closer to the ground and also to help overcome dieback (which is localized in the apex); the stem of a tall tree is cut back to approximately 1 m above ground and three strong shoots equidistant around the stem are allowed to grow back (O'Hare 1993). Growers believe that ratooning is more economical than replanting because land preparation and irrigation lines are already in place. Also, production is re-established two (or more) months sooner than if replanting was undertaken (Elder et al. 2002). However, the advantages need to be balanced against the possible decrease in average fruit weight of the ratoon crop compared with a newly planted crop (Elder et al. 2002).

SECTION 5 BIOCHEMISTRY

Papaya plant parts contain many biologically active compounds, a selection of which are listed in Table 8.

Table 8. Some chemical compounds occurring in *Carica papaya**

Chemical	Main plant part in which chemical occurs	Recorded level/concentration
alkaloids	leaves	1,300 – 1,500 ppm
carpaine	leaves	150 – 4,000 ppm
dehydrocarpaines	leaves	1,000 ppm
flavonols	leaves	0 - 2,000 ppm
tannins	leaves	5,000 – 6,000 ppm
nicotine	leaves	102.8 ppm
prunasin (cyanogenic glycoside)	leaves	No data
benzylglucosinolate	latex	116,000 ppm
caoutchouc	latex	45,000 ppm
chymopapain a & b	latex	No data
lysozyme	latex	No data
Malic acid	latex	4,400 ppm
papain	latex	51,000 – 135,000 ppm
butanoic acid	fruit	1.2 ppm
carpaine	fruit	200 ppm
cis-and *trans*- linalool oxide	fruit	250 – 2,238 ppm
α-phellandrene	fruit	No data
α-terpinine	fruit	No data
methyl-thiocyanate	fruit	No data
caricin	seeds	No data
benzyl-isothiocyanate	seeds	2,000 – 5,000 ppm
carpasamine	seeds	3,500 ppm
linoleic acid	seeds	5,389 ppm
oleic acid	seeds	193,545 – 202,400 ppm
palmitic acid	seeds	28,791 – 30,107 ppm

* data compiled from Duke (2007)

Papaya belongs to a group of plant species known as laticiferous plants. These plants contain specialised cells (laticifers), dispersed throughout most plant tissues, that secrete a substance known as 'latex'. Latex is a complex mixture of chemical compounds with diverse chemical activities. Collectively, these compounds are thought to be involved in defence of the plant against a wide range of pests and herbivores (El Moussaoui et al. 2001).

The latex of papaya plants is rich in enzymes known cysteine proteinases, which are used widely for protein digestion functions in the food and pharmaceutical industries. Commercially, papaya latex is harvested from fully grown but unripe fruit, the skin of which contains numerous laticifers. Ripe papaya fruit contains no latex (Villegas 1997), possibly because the latex-producing cells cease functioning or breakdown with age.

Cysteine proteinases may constitute as much as 80% of the enzyme fraction in papaya latex (El Moussaoui et al. 2001). The most well studied proteinases from papaya are papain, chymopapain, caricain and glycyl endopeptidase. Other enzymes known from papaya latex include glycosyl hydrolases such as β-1,3-glucanases, chitinases and lysozymes, protease inhibitors such as cystatin and glutaminyl cyclotransferases and lipases (El Moussaoui et al. 2001).

Unripe papaya fruit, papaya seeds and latex extracts have been implicated in numerous toxic and allergenic responses in mammals, including humans, as discussed in Sections 5.1 and 5.2, below.

5.1 Toxins

The use of papaya leaf, fruit and root extracts as traditional medicines (Akah et al. 1997; Eno et al. 2000) and the complex, largely uncharacterised, chemical composition of papaya latex, suggests the potential for effects on the health of humans or other organisms. A compound present in crushed papaya seed that is believed to have activity against helminthic intestinal parasites, benzyl isothiocyanate (BITC – derived from benzylglucosinolate), has been shown to have an effect on vascular contraction using a canine carotid artery *in vitro* model (Wilson et al. 2002). Other studies have suggested possible purgative effects of root extracts (Akah et al. 1997) and antihypertensive activity of fruit extracts (Eno et al. 2000). The presence of cyanogenic compounds in papaya has also been reported (Seigler et al. 2002). *Carica papaya* is a rare example of a species in which a glucosinolate (benzylglucosinolate) and a cyanogenic glycoside (prunasin) co-occur (Olafsdottir et al. 2002); generally plants that produce glucosinolates do not produce a cyanogenic glycoside and *vice versa*. Excessive consumption of plant parts that contain cyanogenic glycosides (leaves and roots, in the case of papaya) may induce adverse reactions, due to the formation of cyanide in the digestive system of the consumer, although none have been recorded for papaya.

5.2 Allergens

Papain, a product of papaya latex, is widely used in both the food manufacturing and pharmaceutical industries. Sensitisation to papain among workers in these industries is well known (Baur et al. 1988; Iliev & Elsner 1997). Immunoglobin E (IgE) antibodies against all four of the major papaya cysteine proteinases in latex (papain, chymopapain, caricain and glycyl endopeptidase) have been identified in people who show an allergic response to a pharmaceutical product derived from papaya latex (Dando et al. 1995). The presence of these antibodies demonstrates that all four cysteine proteinases are allergenic.

Papaya may also have allergenic properties when ingested. For example, an allergic reaction, manifesting as a skin rash, has been reported following use of throat lozenges containing papaya, which appeared to be due to the papaya extract contained in the lozenges (Iliev & Elsner 1997). Around 50% of patients with latex allergy have hypersensitivity to certain plant foods, especially fruits; Diaz-Perales et al. (1999) noted that papaya fruits contain class I (allergenic) chitinases that correspond to proteins detected with a pool of sera from patients with latex-fruit allergy. Latex-allergic patients may develop oropharyngeal itching (the oropharynges is the part of the pharynx at the back of the mouth) and angioedema (rapid swelling of the skin, mucosa and submucosal tissues, particularly around the mouth/throat and hands; sometimes followed by itchiness) if they eat papaya (De Clerck. et al. 2007).

An extreme allergic reaction to skin contact with unprocessed papaya fruit has also been reported (Ezeoke 1985). Papaya fruit pickers manually harvesting fruit are advised to wear gloves and protective clothing, as latex oozing from the fruit stalk may cause skin irritation (Morton 1987).

Papaya pollen is able to induce respiratory IgE-mediated allergy (Blanco et al. 1998) and one IgE-reactive, 100k Da protein component with esterase activity has been identified (Chakraborty et al. 2007). The pollen can contribute significantly to the aeropollen and aeroallergen load in areas where papaya plants occur (Chakraborty et al. 2007).

5.3 Other undesirable effects of phytochemicals

The antifertility properties of papaya, particularly of the seeds, have been the subject of significant evaluation using animal models, especially in India where there is interest in the development of a safe and effective oral male contraceptive (Lohiya et al. 1999). A complete loss of fertility has been reported in male rabbits, rats and monkeys fed an extract of papaya seeds (Lohiya et al. 1999; Pathak et al. 2000; Lohiya et al. 2002), suggesting that ingestion of papaya seeds may adversely affect the fertility of human males or other male mammals.

In India and parts of south-east Asia and Indonesia, consumption of papaya fruit is widely believed to be harmful during pregnancy, since papaya is believed to have abortifacient properties (induces miscarriage during pregnancy) or teratogenic properties (causes malformations of the foetus) (Adebiyi et al. 2002). For example, Adebiyi et al. (2002) suggest that unripe papaya fruit may induce miscarriage in susceptible pregnant human females. Conversely, a papaya fruit extract is used for prevention of miscarriage by traditional African healers (Eno et al. 2000). A number of early studies, largely conducted in India, suggested that unripe papaya fruit, latex extracts or papaya seeds have deleterious effects on pregnancy in laboratory animals (Schmidt 1995). However, more recent analysis suggests that ripe papaya fruit or purified papain do not cause malformations of rat foetuses.

Ingestion of unprocessed ripe papaya fruit has no impact on the number of viable foetuses or foetal weight in rats (Adebiyi et al. 2002). Likewise, purified papain derived from latex of unripe papaya did not impact adversely on prenatal development when administered orally to pregnant rats (Schmidt 1995). However, *in vitro*, crude latex derived from unripe papaya fruit stimulates contractions in non-pregnant rat uterus (Adebiyi et al. 2002).

5.4 Beneficial phytochemicals

The vitamin A and C content of one medium papaya fruit (approx 350 g edible portion) exceeds the Dietary Reference Intakes established by the US Food and Nutrition Board for adult minimum daily requirements (OECD 2005). The vitamin C content is much higher than in either tomatoes or oranges (Benson & Poffley 1998).

Papaya fruit is marketed as a source of a wide variety of vitamins and minerals necessary for wellbeing (Papaya Australia 2007). Table 9 gives key nutritional elements of the fruit.

Table 9. Papaya Fruit Nutritional Values (Per 100g edible portion only)*

Nutrient	Value – Papaya Australia	Value – USDA Nutrient Database
Water	89.3g	88.83g
Energy	123kJ / 29kcal	163kJ/39kcal
Protein	0.4g	0.61g
Fat	0.1g	0.14g
Carbohydrate (total)	6.9g	9.81g
Carbohydrate (sugar)	6.9g	5.9g
Dietary fibre	2.3g	1.8g
Cholesterol	Nil	Nil
Sodium	7mg	3mg
Potassium	140mg	257mg
Calcium	28mg	24mg
Magnesium	14mg	10mg
Iron	0.5mg	0.1mg
Zinc	0.3mg	0.07mg
Beta-carotene	910ug	276ug
Thiamin	0.03mg	0.027mg
Riboflavin	0.03mg	0.032mg
Niacin	0.3mg	0.338mg
Vitamin C	60mg (171% of RDI)	61.8mg
Vitamin A Eq	150µg	N/A

[*] nutritional data taken from the Papaya Australia (2007) website and the USDA National Nutrient Database for Standard Reference (2006).

SECTION 6 ABIOTIC INTERACTIONS

6.1 Abiotic stresses

6.1.1 Nutrient stress

Papaya is a fast-growing, heavy-producing crop and, as such, commercial plantings generally require fertiliser applications, particularly nitrogen to maximise fruit quality and yield. The literature would suggest that nutrients are not limiting to growth in non-managed environments and that papaya is able to grow in a range of nutrient conditions albeit at the expense of general vigour and fruit quality as nutrition declines.

6.1.2 Temperature stress

Under commercial conditions, papaya has exacting climate requirements for vigorous growth and fruit production. It must have warmth throughout the year and will be damaged by light frosts (O'Hare 1993); even brief exposure to O° C is damaging and prolonged cold without overhead sprinkling will kill the plants (California Rare Fruit Growers Inc. 1997). Temperatures below 12-14º C strongly retard fruit maturation and adversely affect fruit production (Nakasone & Paull 1998) but hotter temperatures, if accompanied by dry conditions, can also adversely affect fruit set (Elder et al. 2000a). Similarly, soil temperatures below 15º C limit growth (O'Hare 1993). An ambient temperature range between 21 and 33º C is ideal (Villegas 1997; Nakasone & Paull 1998; OECD 2005).

6.1.3 Water stress

While drought reduces tree growth, fruit set, fruit size and quality, and canopy cover (O'Hare 1993; Crane 2005) papaya plants are considered to be relatively resistant to drought (Marler et al. 1994). During water deficit, plant growth is arrested, leaf abscission is induced and photosynthetic rate is greatly reduced but the plants are able to increase mineral solutes such as Na, K and Cl and this is thought to contribute to osmotic adjustment (Mahouachi et al. 2006), a factor that delays dehydration (Marler et al. 1994). Re-supply of water can bring about plant morphological and physiological recovery without irreversible effects of water stress.

Papaya plants are intolerant of waterlogging (Marler et al. 1994; California Rare Fruit Growers Inc. 1997; Benson & Poffley 1998) and well-drained soils are essential. Waterlogged plants die within a matter of days following stomatal closure and abscission of expanded leaves (Marler et al. 1994). Plants that are not killed do not recover well.

SECTION 7 BIOTIC INTERACTIONS

7.1 Weeds

In Australia, a large number of weed species (especially broadleaf and grass species) are known to be a problem in papaya plantations. An InfoPest search performed by GrowSearch Australia (Department of Primary Industries and Fisheries, Queensland) in September 2006 listed 143 genera from 43 families as being weeds of papaya. The main herbicide chemical recommended for use on these weeds is glyphosate with the other main chemicals being glufosinate-ammonium, oxyfluorfen, diuron, haloxyfop and fluazifop.

A study of the growth and yield response of the variety 'Sunrise Solo' to various weed management strategies (Akinyemi et al. 2004) showed that herbicide usage is the most sustainable practice and, when compared to other strategies such as hoe weeding and intercropping, had beneficial effects on commercially important parameters in terms of reduction in days to 50% flowering, and an increase in fruit yield.

7.2 Pests and diseases

7.2.1 Invertebrate pests

Singh (1990) reported that about four insect and mite species are major pests of papaya worldwide, although 35 other arthropods may infest the plants. In Australia, fruit-spotting bugs (*Amblypelta lutescens* and *A. nitida*), two-spotted mite (*Tetranychus urticae*) and broad mite (*Polyphagotarsonemus latus*) are the most serious pests (Chay-Prove et al. 2000). Oriental scale, once a significant problem, has become a minor and infrequent problem since release of a wasp (C*omperiella lemniscata*) for biological control (Astridge & Elder 2005).

Far north Queensland was the site of an outbreak of the Asian Papaya fruit fly (PFF), *(Bactrocera papayae*) in papayas near Cairns on October 17, 1995 (DPI & F 2007). Regarded as a serious threat to the horticultural industry, the outbreak was controlled by an eradication campaign that began within 10 days of detection. PFF populations were reduced by 99% in the first 12 months and the program was formally closed in mid-1999 following declaration of eradication of PFF from mainland Queensland on 30 April 1999.

Appendix 2a lists the major invertebrate pests of papaya and the chemicals used for their control. A number of these pests have native or exotic insect parasitoids and/or predators capable of reducing the size of pest populations (Appendix 2b). These can contribute to an Integrated Pest Management approach providing that the ecology of both the pest and the beneficial organism are understood (Blanche et al. 2002).

Konno et al. (2004) concluded that the papain produced in latex of papaya leaves is an important factor in protecting the plant from lepidopteran larvae. The protease activity of the papain in fresh latex exuded from leaves is extremely high (195.8 unit mg^{-1}) although activity in leaves as a whole is quite low (0.362 unit mg^{-1}); insects thus confront a highly condensed toxin immediately after eating the leaves.

7.2.2 Other pests

Flying foxes (*Pteropus* spp.) are the chief mammalian predator of papaya fruit in Australia (Tidemann et al. 1997). Birds (especially currawongs) and possums may attack the ripe fruit (Baxter 1997) and there has been an estimate of 20% crop loss due to the combined foraging of flying foxes, birds and possums (Walsh et al. 2006). Commercially, fruit may be picked when it is beginning to colour and then be ripened under ethylene to reduce losses from these pests (O'Hare 1993). Exclusion netting has been suggested as a means of protecting fruit but can be cost prohibitive (Tidemann et al. 1997).

Rats and wild pigs can cause severe damage to young plants (Max Bell pers. com.)

7.2.3 Diseases

Because of extensive monoculture and a narrow gene pool, papaya is susceptible to numerous diseases (see Appendix 3).

In Australia, the major fungal pathogens of papaya include phytophthora root and fruit rot (*Phytophthora palmivora*), black spot (*Asperisporium caricae*), brown spot (*Corynespora cassiicola*), anthracnose (*Colletotrichum* spp.) and powdery mildew (*Oideum caricae*.). Several fungal species (eg *Rhizopus* spp., *Stemnophyllum* spp., *Phomopsis* spp.) also cause postharvest fruit rots that are controlled by pre-harvest fungicide treatments or post-harvest dipping of fruit in a fungicide such as perchloraz.

Yellow crinkle, mosaic and dieback are phytoplasma-associated diseases of papaya (Guthrie et al. 1998; Fitch 2005); yellow crinkle and mosaic may be symptoms of the same disease complex (Fitch 2005) while dieback is caused by a different phytoplasma group (Padovan & Gibb 2001). Papaya dieback is the major limiting factor to the papaya industry in southeast and central Queensland (Drew et al. 2005b; Walsh et al. 2006). There is currently no commercial strategy for controlling these diseases.

Papaya ringspot virus (PRSV) (see also Section 2.4.1) has become the limiting factor for commercial papaya production in many areas of the world (Nakasone & Paull 1998). PRSV is a member of the potyvirus family of single-stranded RNA viruses and strains are found in nearly every papaya-growing region (Gonsalves 1998). There are two types of PRSV: Type P (PRSV-p) that infects cucurbits and papaya; and Type W (PRSV-w) that only infects cucurbits. Internationally, PRSV-p has significantly reduced crop productivity in Hawaii, the Carribean, Brazil, south-east Asia and other papaya growing areas. Control measures such as roguing and quarantine have had only limited success in most countries and considerable effort has been put into the development of genetic modification for resistance (see Section 2.4.2) and resistance through interspecific hybridisation (see Section 2.4.1).

PRSV-p was first identified in Australia in 1991 (Thomas & Dodman 1993) near Caboolture (Queensland Sunshine Coast) and suburban Brisbane and was subsequently recorded in Bundaberg and Beaudesert (Chay-Prove et al. 2000). PRSV-p is transmitted by aphids, mechanical transmission of sap and the movement of infected plants (Chay-Prove et al. 2000). Its spread in Australia is being managed by a quarantine zone, which limits movement of papaya and cucurbits (eg. cucumber, pumpkin and watermelon); the area south of latitude 24º30' S, and east of longitude 150º00' E (vicinity of Moura, arrowed on Fig. 1) is declared to be a pest quarantine area for papaya ringspot (Queensland Government 2002).

PRSV-p remains restricted in distribution in Queensland. Several outbreaks have occurred in south-east Queensland, but these were contained by removing and destroying infected plants. The virus is relatively common in backyards of some northern suburbs of Brisbane, but the rate of spread appears to be low (Persley 2003).

Figure 1. Map of Central and South-east Queensland showing location of pest quarantine area (enclosed in dotted line) for papaya ringspot (arrow shows the approximate location of latitude 24°30' S and longitude 150° E)

SECTION 8 WEEDINESS

There have been numerous attempts to characterise the 'typical' traits of weeds (Baker 1965; Bazzaz 1986; Noble 1989; Roy 1990; Williamson & Fitter 1996), but the most successful predictors of weediness remain taxonomic affinity to other weedy species and the history of a given species' weediness elsewhere in the world (Panetta 1993; Pheloung et al. 1999).

In managed agricultural systems, papaya is easily controlled by herbicide spraying (see Section 8.3) and volunteer plants are not regarded as a weed problem (OECD 2005). With regard to factors relevant to the potential weediness of papaya in unmanaged environments there are two types of considerations. Firstly, there are those attributes that might predispose papaya to weediness; these include:

- Papaya may persist after cultivation and spread along roadsides and disturbed habitats where other plants have not established (OECD 2005). Space et al. (2000) suggested that in Rota, of the Mariana Islands, papaya may be invasive in highly disturbed habitats. Similarly, Kwit et al. (2000) observed the establishment of exotic *C. papaya* seedlings following disturbance of forest canopies by a hurricane in Florida. Persistence and spread in the Australian ecosystem has not been observed apart from observations of volunteer plants in a few old campsites and housesites in Queensland (Max Bell, pers. com) and the occurrence of naturalised populations in two Australian territories (see Section 8.2)
- Worldwide, papaya fruit is consumed by a wide range of vertebrates that could potentially spread seeds into ecological habitats (OECD 2005).
- Papaya has a pioneer ecology due to a number of features that include fast growth, short life cycle, prolific seed production, seed dormancy, and capacity to establish significant seed banks (OECD 2005). Wood et al. (2000) concluded that papaya seeds would be able to form a semi-persistent seed bank in the soil and still retain the capacity to respond to heat shock (see Section 4.4).
- Plants can flower and bear fruit all year round under optimal conditions.
- Genetic diversity within commercial cultivars provides adaptability and allows cultivation of the plant under a relatively wide range of conditions (OECD 2005).

Secondly, there are those attributes that do not favour the establishment of the plant as a serious weed; these include:

- Optimal growth of the plant is restricted by requirements for warm temperature, adequate moisture and good nutrition (see Section 6).
- Trees yield well for two years, after which production declines (Benson & Poffley 1998).
- The plant does not have any significant asexual reproduction mechanism (see Section 4)
- Because of the highly complex capability in sexual expression (see Section 4) sex ratios for obtaining optimal fruit (and seed) set would be unlikely to occur without human intervention.
- *Carica papaya* has limited taxonomic affinity to other weedy species (see Section 8.1 below).

8.1 Weediness status on a global scale

Papaya has naturalised in many tropical and sub-tropical countries (Randall 2002) but, on balance, it is not considered to be a significant weed in any region of the world (OECD 2005).

Internationally, the small shrub, *Vasconcellea pubescens* (formerly *Carica pubescens*; ‘mountain papaya’), is the only relative of papaya that has been recorded as a weed (Randall 2002). Mountain papaya has naturalised in New Zealand where it occurs in scattered open and shrubland communities on the north island (Landcare Research 2007). It is considered to be 'moderately invasive' in some tropical areas (Bingelli et al. 1999; Randall 2002).

8.2 Weediness status in Australia

Groves et al. (2003) assigned a rating of '1'to *Carica papaya* in natural ecosystems indicating that it is "naturalised and may be a minor problem but not considered important enough to warrant control at any location". In agricultural ecosystems, papaya is also not considered a problem (Groves et al. 2003).

Herbarium records and associated specimen notes indicate that in Queensland, *C. papaya* may form small, low-density self-perpetuating populations (data provided by the Queensland Herbarium). However, seedlings are often out-competed by Guinea Grass (*Panicum maximum*) (Max Bell pers. com) which is a coloniser of disturbed sites, including roadsides, and particularly untended areas in many parts of Queensland. Seed spread by pests such as flying foxes would appear not to be a significant problem (see Section 4.3).

Papaya is established along roadsides and bush tracks throughout Christmas Island (an Australian Territory in the Indian Ocean) and is naturalised on North Keeling Island (also an Australian Territory in the Indian Ocean) in disturbed *Pisonia grandis* forest (Du Puy & Telford 1993).

Vasconcellea pubescens does not occur in Australia (Groves et al. 2003; Australian Plant Name Index 2005; Australia's Virtual Herbarium 2007) and no other Caricaceae species have naturalised in Australia (Groves et al. 2003).

8.3 Control measures

In agricultural habitats volunteer plants can be killed by spraying with a herbicide such as paraquat, glyphosate or triclopyr (OECD 2005). An InfoPest search performed by GrowSearch Australia (Department of Primary Industries and Fisheries, Queensland) in September 2006 listed oryzalin as a spray for use on non-bearing trees.

During the tree thinning process that is practiced when the sex of trees becomes evident (Section 2.3.1), plants cut off at ground level will not reshoot whereas those cut about 300 mm above ground can reshoot (O'Hare 1993).

SECTION 9 POTENTIAL FOR VERTICAL GENE TRANSFER

The possibility of genes transferring from *C. papaya* to other organisms is addressed below. *Potentially*, genes could be transferred to: (1) commercially and domestically cultivated papaya and naturalised papaya populations, (2) wild papaya (*Vasconcellea*) species, (3) other plant genera, and (4) other organisms. With particular regard to the possibility of gene transfer to other plants (including other papaya plants), each of two potential barriers must be overcome before gene flow can occur successfully. *Pre-zygotic* barriers include geographic separation, differences in floral phenology, different pollen vectors and different mating systems such as stigmatic or stylar incompatibility systems. *Post-zygotic* barriers include genetic incompatibility at meiosis, selective abortion, lack of hybrid fitness and sterile or unfit backcross progeny.

9.1 Intraspecific crossing

Cross-pollination of one *C. papaya* plant to another mediated via an insect pollen vector is the most likely means by which papaya genes could be transferred from papaya to other organisms, including cultivated and naturalised *C. papaya*. In Australia, hawkmoths (Lepidoptera: Sphingidae) are the most likely pollen vectors (see Section 4.2).

Viable seeds and potentially fertile progeny would be produced when pollen is transferred between papaya plants, irrespective of whether the transfer occurred to cultivated or naturalised papayas. As naturalised papayas occur throughout the range of papaya cultivation (Australia's Virtual Herbarium 2007), gene transfer between naturalised and cultivated papayas is likely.

Various organisations and agencies have specified isolation distances for growing papaya; these are cited in OECD (2005). The Hawaiian Identity Preservation Protocol for non-GM papaya seed production specifies a minimum of 400 m isolation from other varieties; the Papaya Biotechnology Network of Southeast Asia proposed that non-GM papaya should be separated by 400 m from GM papaya; USDA-APHIS approved an isolation distance of 500 m for GM papaya field trials. Manshardt (2002) reported that A series of experiments conducted in Puna, Hawaii in 1997 indicated that when commercial fields of hermaphrodite plants are separated by more than 400 m, cross-pollination will be a rare event (Manshardt 2002; Manshardt et al. 2007). Note however, that the type of flowers that are present on a papaya plant will influence the level of cross-pollination that will occur with female plants showing a higher frequency than hermaphrodite plants. Further experiments conducted in Oahu, Hawaii in 2003 confirmed that transgene dispersal through pollen drift between hermaphrodite papayas is an inefficient process (Manshardt et al. 2007).

9.2 Natural interspecific and intergeneric crossing

The closest relatives of *C. papaya* and, therefore, the species with which *C. papaya* is most likely to hybridise and exchange genes are species of *Vasconcellea* (formerly, *Carica*)(Badillo 2002). None of these species occurs in Australia, eliminating the likelihood of genes transferring naturally to wild papaya species.

Nevertheless, wild papayas (*Vasconcellea* spp.) naturally posses a number of desirable traits including resistance to pathogens, cold tolerance and higher sugar content of fruit (Drew et al. 1998), that breeders have sought to introduce into *C. papaya* using traditional plant breeding techniques. Difficulties in producing hybrids between *C. papaya* and *Vasconcellea* spp. underscore the negligible risk of gene transfer from *C. papaya* to wild papayas in Australia. For instance, several investigations (Manshardt & Wenslaff 1989a; Manshardt & Wenslaff 1989b; Drew et al. 1998) have indicated that following pollination of *C. papaya* with pollen from wild papayas (and vice versa), pollen grains germinate on the stigma successfully and pollen tubes grow through the style and penetrate the ovules, thereby facilitating fertilisation. Subsequently, however, abortion of these ovules, or endosperm failure, prevents further development of hybrid embryos or production of viable mature seed.

The inability of papaya to hybridise naturally with its closest relatives and the infertility of such hybrids when they are formed artificially (see below), illustrates the reproductive isolation of *C. papaya* from other plant groups (Manshardt & Wenslaff 1989a) and indicates that the likelihood of gene transfer between *C. papaya* and other plant species in the wild is negligible.

9.3 Crossing under experimental conditions

The post-zygotic barriers to successful hybrid formation have limited the success of traditional breeding programs (Manshardt & Drew 1998) and indicate that the generation of inter-specific hybrids is only possible with significant human intervention, including techniques such as embryo rescue (Manshardt & Drew 1998). When hybrids are generated using these techniques, they appear as morphological intermediates between the two parental species (Magdalita et al. 1997).

In Australia, an embryo rescue protocol developed for 90 day old *Carica papaya* embryos (Magdalita et al. 1996) was used successfully to produce hybrids between *C. papaya* and wild papaya (*Vasconcellea*) species including *V. quercifolia*, *V. pubescens*, *V. goudotiana* and *V. parviflora* (Drew et al. 1998). However, many hybrids were of low vigour and did not survive when transplanted to the field. Although other hybrids survived to reproductive maturity and a few produced viable pollen (Drew et al. 1998), the backcross progeny (derived from re-crossing to the original *C. papaya* parent) were infertile, probably because of large changes to the chromosomes (OECD 2005). The success of intergeneric crosses may, to some extent, depend on the genotype of the *Carica papaya* parent used as well as the time of year at which pollen is collected and the post-pollination time at which hybrid embryos are rescued (Magdalita et al. 1998).

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APPENDICES

Appendix 1. Comparison of monthly temperature and rainfall statistics in areas where papaya is grown in Australia*

Kununurra, Humpty Doo, Mareeba, Gympie and Alstonville represent areas where commercial production occurs. Narooma, on the south coast of NSW is unsuitable for commercial growing of papaya but represents climatic conditions under which growth is possible but far from optimal.

1. Kununurra – Western Australia

	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

2. Darwin (Humpty Doo) – Northern Territory

	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

3. Mareeba – Northern Queensland

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	31.2	30.8	29.9	28.6	27.1	25.5	25.2	26.5	28.2	30.4	32.1	31.9	29.0
Mean min temp (°C)	20.9	21.2	20.0	17.7	15.3	12.3	11.2	11.7	13.5	16.0	18.7	20.3	16.6
Mean rainfall (mm)	201.9	238.5	191.1	47.4	22.6	14.2	7.1	6.9	5.1	14.5	53.8	103.0	844.5

4. Gympie – Southern Queensland

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (°C)	31.3	30.4	29.4	27.3	24.5	22.1	21.9	23.3	26.0	28.3	30.2	31.3	27.2
Mean min temp (°C)	19.6	19.6	18.1	14.6	10.8	7.9	6.2	7.1	10.1	13.8	16.4	18.5	13.6
Mean rainfall (mm)	165.1	169.2	146.2	84.9	73.4	61.1	54.9	39.6	47.2	72.1	89.1	135.3	1133.2

5. Alstonville – Northern New South Wales

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (oC)	27.2	26.7	25.9	24.0	21.2	18.9	18.6	19.9	22.3	24.1	25.4	26.9	23.4
Mean min temp (oC)	19.5	19.4	18.3	15.9	13.3	10.9	9.9	10.6	12.7	14.8	16.6	18.5	15.0
Mean rainfall (mm)	177.6	234.3	283.7	196.8	198.6	151.5	91.9	73.0	52.4	108.3	132.2	160.6	1743.7

6. Narooma – South Coast of New South Wales

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean max temp (oC)	23.4	23.7	22.8	21.0	18.6	16.6	16.0	16.7	18.2	19.4	20.5	22.0	19.9
Mean min temp (oC)	16.3	16.6	15.3	12.7	10.1	7.7	6.6	7.2	9.0	11.1	12.9	15.0	11.7
Mean rainfall (mm)	92.7	85.6	105.6	80.4	80.5	86.4	50.6	49.7	62.1	71.9	71.8	73.1	868.5

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

Appendix 2a Major invertebrate pests of papaya in Australia*

Common Name	Species	Family	Chemical control
Banana-spotting bug	*Amblypelta lutescens* ssp. *lutescens*	Coreidae	endosulfan; trichlorfon
Fruitspotting bugs	*Dasynus fuscescens; Amblypelta nitida*	Coreidae	endosulfan; trichlorfon
Oriental scale	*Aonidiella orientalis*	Diaspididae	Petroleum oil
Loopers	various species	Geometridae	spinosad
Sorghum head caterpillar	*Cryptoblabes adoceta*	Pyralidae	spinosad
Yellow peach moth	*Conogethes punctiferalis*	Pyralidae	endosulan; spinosad; fenthion
Broad mite	*Polyphagotarsonemus latus*	Tarsonemidae	dicofol
Cucumber fly	*Bactrocera cucumis*	Tephritidae	dimethoate
Mediterranean fruit fly	*Ceratitis capitata*	Tephritidae	dimethoate
Queensland fruit fly	*Bactrocera tryoni*	Tephritidae	dimethoate
Two-spotted (Red spider) mite	*Tetranychus urticae*	Tetranychidae	dicofol
Redbanded thrips	*Selenothrips rubrocinctus*	Thripidae	spinosad
Leafroller moths	various species	Tortricidae	spinosad

* information taken from an InfoPest search, performed by GrowSearch Australia (Department of Primary Industries and Fisheries, Queensland) in September 2006; O'Hare (1993); Chay-Prove et al. (2000)

Appendix 2b Parasitoids and predatory insects attacking papaya insect pests*

Insect Pest	Australian native parasitoids	Australian native predatory insects	Exotic parasitoids	Exotic predatory insects
Banana-spotting bug	*Pentatomophaga bicincta* (tachinid fly) + unidentified wasp	*Pristhesancus papuensis* (assassin bug)		*Pheidole megacephala* (ant)
Oriental scale		*Chilocorus baileyi* (coccinellid)	*Encarsia citrina* + *Aphytis* spp. (wasps) + *Comperiella* spp. (wasps)	*Chilocorus circumdatus*
Yellow peach moth	*Argyrophylax proclinata* (tachinid fly)	*Pristhesancus plagipennis* (assassin bug)		
Queensland fruit fly		*Pristhesancus plagipennis* (assassin bug) + praying mantises	*Diachasmimorpha longicaudata* (wasp) + *Fopius arisanus* (wasp)	
Two-spotted (Red spider) mite		*Stethorus histrio* (coccinellid) + lacewing larvae		
Redbanded thrips		Lacewings, predatory thrips, predatory bugs		

* information taken from Blanche et al. (2002).

Appendix 3. Major diseases of papaya in Australia*

Category	Disease name	Causal agent	Symptoms	Chemical control
Fungal	anthracnose	*Colletotrichum gloeosporioides*	first symptoms are small well defined dried pink spots on the surface of ripening fruit; lesions grow to 5 cm diameter, become rounded, sunken and brown to black in colour; lesions also occur on petioles; post-harvest infection usually produces stem-end rot.	prochloraz
	black spot	*Asperisporium caricae*	Black pustules on the abaxial surface of the leaf; pustules also occur on fruit but are superficial.	chlorothalonil; tebuconazole; mancozeb
	brown spot	*Corynespora cassicola*	lesions in which spores are produced occur on the stem, fruits, petioles and leaves	chlorothalonil
	Phytophthora fruit rot and root rot	*Phytophthora palmivora*	fruit surface is covered by a whitish mycelium and numerous sporangiophores; the fruits become brown-blackish and drop; firm dark brown lesions appear on the roots and stem base; leaves wilt; roots develop a soft, wet rot.	metalaxyl-M
	powdery mildew	*Oidium caricae; Oidiopsis taurica*	crown leaves develop yellow patches and white fungal growth; fruit shows circular white patches	triadimenol; sulphur
	Pythium root rot	*Pythium* spp.	Yellowing and wilting of leaves; soft rot in the roots that may extend into the trunk	metalaxyl-M
Viral/ Phytoplasma	yellow crinkle	unknown phytoplasma	old leaves turn yellow and then dry and fall; juvenile leaves develop a clawed appearance	
	dieback	*Candidatus* Phytoplasma australiense	inner crown leaves become bunched and yellow then die; stem begins to die back from the top; fruit shrivels	
	mosaic	unknown phytoplasma	crown leaves turn yellow and have shrivelled edges	
	papaya ringspot virus (PRSV)		early symptoms include yellowing and vein clearing in young leaves and sometimes severe blistering and leaf distortion. Dark concentric rings and spots or "C"-shaped markings develop on the fruit which may turn tan-brown as the fruit ripens.	
	papaya meleira virus		necrosis of the tip and borders of young leaves; on green fruits, there is exudation of watery latex on the surface, which later becomes stained and darkened due to the oxidation of the latex	

* information taken from an InfoPest search, performed by GrowSearch Australia (Department of Primary Industries and Fisheries, Queensland) in September 2006; PaDIL (2005); OECD (2005); Walsh et al. (2006).