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Series on Harmonisation of Regulatory Oversight in Biotechnology
No. 33

CONSENSUS DOCUMENT ON THE BIOLOGY OF PAPAYA (Carica papaya)

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No. 33

CONSENSUS DOCUMENT ON THE BIOLOGY OF PAPAYA (*Carica Papaya*)

Environment Directorate

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FOREWORD

The OECD's Working[1] Group on Harmonization of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on the development of ***consensus documents*** which are mutually acceptable among Member countries. These consensus documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, consensus documents are being published on the biology of certain plant species, on selected traits that may be introduced into plant species, and on biosafety issues arising from certain general types of modifications made to plants.

This consensus document addresses the biology of *Carica papaya* L. *(*Papaya*).* Included are descriptions of the taxonomy of the genus *Carica*; the natural habitat and the origins of the cultivated papaya; the botanical, physiological and agronomical characteristics of the cultivated papaya; the possibilities for intraspecific crosses; and the potential interactions with other organisms (insect pests, pathogens, and animals).

The United States served as the lead country in the preparation of this document. The document has been revised on a number of occasions based on the input from other member countries. It is intended for use by regulatory authorities and others who have responsibility for assessments of transgenic plants proposed for commercialisation, and by those who are actively involved with genetic improvement and intensive management of the genus.

At the 16th meeting of the Working Group (held 23-25 February 2005) it was agreed that the document be forwarded to the Joint Meeting of OECD's Chemicals Committee and Working Party on Chemicals, Pesticides and Biotechnology, which agreed that this document be declassified.

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[1] In August 1998, following a decision by OECD Council to rationalise the names of Committees and Working Groups across the OECD, the name of the "Expert Group on Harmonization of Regulatory Oversight in Biotechnology" became the "Working Group on Harmonization of Regulatory Oversight in Biotechnology."

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SECTION I. TAXONOMY AND GENERAL DESCRIPTION

A. Taxonomy

1.   Papaya, *Carica papaya* L., is an almost herbaceous (succulently soft-wooded), typically unbranched small tree in the family Caricaceae. Europeans first encountered papaya in the Western Hemisphere tropics by at least the early 1500s (Sauer, 1966), and various interests were soon disseminating it widely (Ferrão, 1992). Papaya is now cultivated worldwide in tropical and subtropical climates mainly for its melon-like fruit.

2.   The Caricaceae is classified in the order Brassicales (sometimes called Capparales), which characteristically express mustard-oil glucosides (glucosinolates) (Jørgensen, 1995; Rodman *et al.*, 1998; Olson, 2002). Recently, consensus has been developing that the genus *Carica* L. has only the one species *C. papaya*, and that the Caricaceae may comprise six genera (Aradhya *et al.*, 1999; Badillo, 2000; Van Droogenbroeck *et al.*, 2002, 2004; Kubitzki, 2003; Manshardt, 2002, Havaii University, pers. com.). Most of the genera are neotropical forest plants, occurring in South America and Mesoamerica or only in Mesoamerica. *Vasconcellea*, the largest genus with 21 species, had usually been considered as a section within *Carica*. The other neotropical genera are *Jacaratia* (7 spp.), *Jarilla* (3 spp.) and *Horovitzia* (1 sp.) (Badillo, 1993). The sixth genus, *Cylicomorpha* (2 spp.), occurs in montane forests in equatorial Africa (Badillo, 1971).

3.   The highland papayas, *Vasconcellea* (not "*Vasconcella*" – see Badillo, 2001; Kubitzki, 2003), are considered the closest relatives to *Carica papaya* (Badillo, 1993; Aradhya *et al.*, 1999; Van Droogenbroeck *et al., 20*02, 2004). *Vasconcellea* has many species with edible fruits (and a few cultivated varieties) (Badillo, 2000; Scheldeman and Van Damme, 2001); commercial cultivation of Caricaceae may be limited to the papaya and chamburo (ababai), babaco, and toronche or higacho (the names vary and sometimes are used locally for more than one species). The chamburo or mountain papaya, *V. cundinamarcensis* (often referred to as *V. pubescens*) is grown in the Americas; the fruits are usually cooked and eaten with sugar. There is commercial-scale cultivation in Chile, where the fruit is known as ababai (Scheldeman and Van Damme 2001). In western South America (particularly Ecuador) local consumers value babaco (often referred to as *V. pentagona*), which is also cultivated somewhat elsewhere, including New Zealand, South Africa, Spain and Italy (Scheldeman and Van Damme, 2001; Villarreal *et al.*, 2003). Babaco is generally considered to be an F$_1$ hybrid (known as *V. ×heilbornii* but sometimes still as its var. *pentagona*) (Jiménez *et al.*, 1999; Wiersema and León, 1999; Scheldeman and Van Damme, 2001; Morales Astudillo *et al.*, 2004). Higacho (or broadly toronche)*,* considered the hybrid *V. ×heilbornii* var. *chrysopetala* (sometimes referred to as *V. chrysopetala*) is also found in Ecuador, with a commercial variety also grown in New Zealand (NRC, 1989; Scheldeman and Van Damme, 2001).

4.   The International Plant Genetic Resources Institute (IPGRI) recognises eight different edible fruits from this family. Users from Mexico to South America collect fruits from wild plants or semi-wild plants, or may grow a few (thus incipient domestication). Siglalón silvestre, *V. stipulata*, is a local food in southern Ecuador. Col de monte (*V. monoica*) of Ecuador, Peru and Bolivia has small fruits eaten raw or cooked. Chungay or mito (*V. candicans*) is a familiar food in Peru (De Feo *et al.*, 1999). Papayuelo (*V. goudotiana*) of Colombia is small and apple-like. Other edible *Vasconcellea* include tapaculo (bonete,

papayito) or mountain pawpaw, *V. cauliflora*, whose fruit pulp is processed in various ways before consumption (Coppens d'Eeckenbrugge and Libreros Ferla, 2000), and higuera (calasacha), the collected nut *V. quercifolia*. Additionally, Scheldeman and Van Damme (2001) note for their edible fruits *V. crassipetala*, *V. microcarpa* (lechocillo), *V. palandensis* (papaillo), *V. parviflora* (coral) and *V. sphaerocarpa* (higuillo negro). The fruits of *Jacaratia digitata*, *J. mexicana*, *J. spinosa*, and *Jarilla heterophylla* also are eaten locally (Whitmore, 1978; Scheldeman and Van Damme, 2001).

B. Morphology

5.   *Carica papaya* is a usually unbranched, giant-herb-like tufted tree 2-10 m in height; commercial producers often remove plants if they are reaching a height from which fruits would not be harvested easily. Large, palmately lobed leaves with long stout leaf-stalks (to 125 cm) are attached densely (alternating more or less spirally) near the terminus of the straight trunk, and spreading to form a loose open crown. The leaf-stalks (petioles) end in a leaf blade 20-60 cm (to 75-100 cm) across (Campostrini and Yamanishi, 2001a), with each blade usually 5- or 7-lobed, and each lobe cut pinnately. The trunk tapers from a 10-30 cm wide base to 5-7.5 cm at the crown, and is patterned conspicuously with large leaf-scars; it is thin-barked and often hollow (between nodes) with aging (Elias, 1980). The soft pulpy wood is formed predominantly by phloem, with little secondary xylem (Whitmore, 1978; Carlquist, 1998). This fast-growing plant has *c*. 15-30 mature leaves, with a leaf persisting 2.5-8 months and new leaves arising at the rate of 1.5 to nearly 4 per week (Sippel *et al*., 1989; Allan *et al*., 1997; Mabberley, 1998; Nakasone and Paull, 1998; Fournier *et al*., 2003). Leaf senescence seems to be a function of the leaf's position within the plant's canopy (*i.e.* self-shading) rather than simply increasing age (Ackerly, 1999). All parts of the plant contain a thin, acrid latex, including the unripe fruits. The lifespan of feral trees is some 15-20 years (Anon, 2003). Plants infrequently may develop a forked trunk or a few branches when older or injured; in some places (*e.g.* Kenya) growers may encourage multiple trunks by pinching seedlings or cutting back established plants (Dodson and Gentry, 1978; Rao, 1993; Malo and Campbell, 1994).

6.   The flower-bearing stalks arise in leaf axils. There are three basic flower types in domesticated plants, but with a range of possible variation, resulting overall in about six distinctive kinds (Storey, 1941; 1967; Hsu, 1958a, 1958b; Mosqueda Vázquez and Molina Galán, 1973; Fisher, 1980; Nakasone and Lamoureux, 1982):

- Female flowers (globose-ellipsoid ovary) (sometimes agronomically termed as "type 1").

- Male flowers (of two kinds): morphologically typical (10 stamens, tiny rudimentary pistil) ("type 5"), or functionally male but a somewhat bisexual appearance ("type 4+").

- Bisexual flowers (of three kinds): decandrous (10 stamens, elongate ovary) ("type 4"), pentandrous (5 stamens, deep-furrowed ± ovoid ovary) ("type 2"), or irregular ("type 3") with stamens variably becoming carpel-like (*i.e.* carpellody).

7.   The morphology of inflorescences and flowers varies with the sex of the tree. Varieties typically are either dioecious (with unisexual flowers and exclusively male and female plants), or they are polygamous (with bisexual and unisexual flowers and hermaphrodite and single-sex plants). On female plants, the stalk (peduncle) is just 2.5-6 cm long and has one or a few large bell-shaped flowers with curvy separate petals. On male plants, hanging branching stalks (panicles) 60-100 cm (to over 150 cm) long have many much smaller trumpet-shaped flowers, with the petals (and stamens' filaments) joined in a long narrow tube which has flared lobes (Fisher, 1980; Calif. Rare Fruit Growers, 1997; Nakasone and Paull, 1998; Ronse Decraene and Smets, 1999). On hermaphrodite plants, these structures are intermediate to the unisexual types, with stalks less than 25 cm long having bisexual flowers that are shortly tubular with a

midpoint or lower constriction and the petal lobes larger. Hermaphrodite plants sometimes also bear male flowers (Crop Knowl. Master, 1993). Some plants produce male flowers on short stalks.

8.   The species thus has a richly complex capability in sexual expression and flowering. Some agricultural varieties (*e.g.* Solo and Eksotika) are gynodioecious — their trees are either hermaphrodite or female. Moreover, papaya sexuality can be labile. Bisexual flowers can be influenced by environmental conditions to change to male flowers through reductions in ovary size and function. Male (staminate) plants and andromonoecious plants (with male and hermaphrodite flowers) are phenotypically stable, or mutable. These types may exhibit seasonal sex reversal, developing staminate, bisexual, and pistillate flowers (Storey, 1958, 1976). Young hermaphrodite plants may have male flowers when first flowering, but bisexual flowers with maturity (Stambaugh, 1939). Female (pistillate) plants have stable sex expression; they are not known to develop flowers with masculine structures (Hofmeyr, 1939b; Nakasone and Paull, 1998). For details on conditions that may alter sexual expression and morphology, see Section V.D. Induced alterations to sexual development.

9.   Fruits hang from the stalks attached to the upper trunk, below the old leaves, with the younger fruits above those more mature. Fruit shape is a consequence of selection for the preferences of various local users and markets, but also reflects the flower type; the generally large fruits vary from spherical or ovoid to pear-shaped or elongate, and 10-50 cm in length (Storey, 1969, 1987). Fruit weight can vary substantially (*c.* 0.35-10 kg or even 12 kg) (Font Quer, 1958; Linnell and Arnoult, n.d.), again chiefly dependent on selection by local users and for specific markets. Storey (1969, 1987) reported preference for 2.5-6.0 kg fruits in South America and the South Pacific, 1.25-2.5 kg lobular fruits in South Africa, and just 400-500 g for Solo-type fruits (which were developed in Hawaii). For additional information on varieties and cultivars, see Table 1, and Section V.A. Reproductive types and locus of cultivation.

SECTION II. DISTRIBUTION AND CENTRE OF ORIGIN

10.   *Carica papaya* is native in the north-tropical Western Hemisphere. Some have suggested a centre of origin in Central America or the south of Mexico (de Candolle, 1883, 1884, from Singh, 1990; Storey, 1976). Manshardt and Zee (1994) found wild papayas (exclusively dioecious) in the Caribbean coastal lowlands of southern Mexico and northern Honduras. The wild female plants produced golf ball-sized fruits of less than 100 g, which usually were inedible (Manshardt, 1999). The musty bitter fruits (berries) have an extensive investment in seeds, which are about 25% smaller than domesticated papaya seeds and have stronger requirements for breaking dormancy. In experimental testing, wild seeds needed strong light to germinate, but 75% of domesticated seeds germinated in darkness. Also, fluctuating temperatures partially inhibited wild seeds from germinating whereas variable temperature did not affect the domesticated seeds' germination (Paz and Vázquez-Yanes, 1998). On the Caribbean coast of Central America, feral papaya have traits apparently indicating greater introgression from wild papaya compared to the feral papaya on the Pacific coast, which appear to have fewer wild traits (Manshardt and Zee, 1994). Successively greater introgression of domestication traits in the wild plants along with increasing presence of feral domesticated-type plants has been found westward and southward from the known wild papaya region.

11.   The centre of diversity for the relatively large genus *Vasconcellea* (formerly in *Carica*) is South America along the Andes, especially in Ecuador (Badillo, 1993; Morales Astudillo, *et al., 20*04), with outlying species reaching as far as Mexico, Chile, Argentina and Uruguay (Aradhya *et al*., 1999; Van Droogenbroeck *et al*., 2004). This led some to propose South America for the origin for *C. papaya* (Prance, 1984). However, evidence to the contrary is provided by finding only domesticated-type feral *C. papaya* there (Manshardt and Zee, 1994; Morshidi, 1996), but finding unambiguously wild plants in Mexico and Honduras (Moreno, 1980; Manshardt and Zee, 1994; Paz and Vázquez-Yanes, 1998; Manshardt, 1999). Furthermore, both isozyme and RAPD (random amplified polymorphic DNA) analyses, and RFLP (restriction fragment length polymorphism) analysis of chloroplast and mitochondrial intergenic sequences, show appreciable divergence of *C. papaya* from what is now recognised as the genus *Vasconcellea* (Jobin-Decor *et al*., 1997; Aradhya *et al*., 1999; Kim *et al*., 2002; Van Droogenbroeck *et al*., 2004). This correlates well with the experimental difficulty in forming hybrids of *C. papaya* with other species in Caricaceae (see Section VI.A. Interspecific crosses with *Carica papaya*). Because *C. papaya* is genetically so distinct, and only feral papaya are known in South America, nowadays a South American origin of wild papaya appears hardly tenable.

12.   Papaya was probably domesticated in northern tropical America but a precise region has not been determined (Schroeder, 1958). Feral papayas occur in many tropical habitats of North America, Central America, the Caribbean and South America. In North America, subtropical areas of Mexico and Florida (USA) are the northernmost part of the species' current range; the southern range extends from Colombia and Venezuela to French Guiana, Brazil, Peru, Bolivia and Paraguay. In southern Florida there is evidence indicating pre-Columbian use of papaya by native people (Allen *et al*., 2002). The Spanish and Portuguese encountered cultivated papaya on the Caribbean coasts of Mexico (being used by the Maya) and Panama and Colombia reportedly by at least 1519 and 1526, respectively; cultivated papaya was reported in Jamaica by at least 1756 (Sauer, 1966; Singh, 1990). In the 1500s papaya was transported to the Philippines and India, and it was readily disseminated into tropical Asia, Africa, and Pacific islands (Singh,

1990; Ferrão, 1992). Less widely used names for the fruit, the tree, or both include papaw, paw paw (paw-paw, pawpaw) (but *Asimina* of the Annonaceae is known as pawpaw), papaye, papayer, papayo, lechosa, fruta bomba, melón zapote, mamón, mamonero, mamão and mamoeiro. *Carica papaya* is now well integrated into indigenous culture, agriculture and cuisine in numerous countries, and occurs beyond the cultivated areas as a feral or adventive plant, naturalised to various degrees in the tropics of the New and Old Worlds including Oceania.

SECTION III. USE AS A CROP, AND AGRONOMIC PRACTICES

13.   Extensive non-commercial production of papaya is common, and much of the harvest in some countries is not exported. Instead, growers consume the fruits or trade them locally. For example, Indonesia estimated that it produced 744,000 tons, of which less than 4 tons were exported (Setyobudi and Purnomo, 1999). In Vietnam, 50% of farm households cultivate papaya in home gardens, with 5 to 10 million or more growing 1-10 trees, whereas only 5,000-10,000 farmers produce papaya in monoculture gardens or large fields (Le Tran and Tran, 1999). In the Philippines, as many as 1.5 million farmers derive cash income from the sale of papaya from home garden, monoculture, or multiple-cropping system agriculture (Kositratana *et al*., 1999). Income from a unit of land in papaya cultivation may be two to four times more than the income from rice; papaya's entire value to the small farmer should not be underestimated (The Papaya Biotechnology Network of Southeast Asia-Workshop participants, 1999; ISAAA; *cf.* Cook, 2004).

14.   The commercially reported production of papaya in 52 countries in 2004 reached 6.5 million metric tons (FAO, 2005). The total area harvested was 365, 846 ha. By region, 7 of the production areas are in Middle America (Central America plus North America), 5 in the Caribbean, 10 in South America, 11 in Africa, 4 in the Near East, 10 in Asia plus Australia, and 5 in Oceania. The major producers were especially Brazil (24.6%), Mexico, Nigeria, India and Indonesia, as well as Ethiopia, the Democratic Republic of the Congo, Peru, Venezuela and China.

A. Uses, and adverse effects

A.1. Industrial uses

15.   Papaya is primarily a fresh-market fruit, and is used in drinks, jams, pectin, candies and as crystallised fruit. Green fruit may be cooked as a vegetable, as may the leaves, flowers and roots (Duke, 1967; Watson, 1997). Papaya has several well-known industrial uses, notably for the enzyme papain (one of its four major constituent cysteine proteinases) (El Moussaoui *et al*., 2001), which has properties similar to gastric pepsin. Producers induce latex to exude from longitudinal incisions made into unripe fruit; the papain purified from the extract is used in foods, beverages, pharmaceuticals, and other manufacturing (Mabberley, 1998; Wiersema and León, 1999). For example, the food industry uses papain in brewing, manufacturing baby food, and producing proteins for human and animal consumption. Papain is also used to shrinkproof wool and silk, and in the bating process to make leathers more pliable. For some applications however, synthetic enzymes and enzymes from other sources are displacing the use of the natural papain (Watson, 1997; ETA, 2001). The latex from papaya has been used in manufacture of chewing gum (de Wit, 1966). Oil from the fruit's many (200-1000) more or less spheroidal seeds (*c.* 2-5 mm × 3.5-6 mm) (Sharma and Singh, 1975), and other components of fruit and leaves have been used in cosmetics and soap (Quenum, 2001).

A.2. Nutritional and medical uses

16.   Papaya constituents contribute to human nutrition and health. Vitamins A and C from one medium papaya (edible portion 350 g) exceed the Dietary Reference Intakes established by the U.S. Food

and Nutrition Board (Inst. Medicine, Natl. Acad. Sci.) for adult minimum daily requirements (CRN, 2001; USDA, 2001), and papaya is a good source of the minerals K, Mg and B (Hardisson *et al*., 2001). Papaya has traditional and modern medical and dental uses; fruits, seeds, latex, and extracts have been used for treating at least forty human conditions, and are being investigated for others (*e.g.* Lewis and Elvin-Lewis, 1977; Mezhlumyan *et al*., 2003; Petitto, 2004). The efficacy of some of the uses is well documented (Animal Sci. Dept. Cornell Univ., 2001), including those as an antihelminthic (Satrija *et al*., 1995); an antiamoebic (To and Kyu, 1934), possibly mediated by the alkaloid carpaine (Burdick, 1971); and an enterobacteria antimicrobial (Osato *et al*., 1993). Papain is used in preparation or manufacturing of adjuvants and reagents for antibiotics or vaccines; chymopapain is a biologic used for treatment of herniated disks in the spine (Quenum, 2001; Mezhlumyan *et al*., 2003).

A.3. Adverse and other consequences

17.   Hypersensitive or allergic human responses to papaya have been described, including respiratory responses to the pollen (Blanco *et al*., 1998). Consumption of ripe fruit only infrequently produces such adverse consequences (Castillo *et al*., 1996; Iliev and Elsner, 1997). Skin may have such responses to fruit contact (Ezeoke, 1985) or extracts (Banik *et al*., 1992). Contact with latex derived from abraded green fruits and plant parts or extracts that contain papain or other proteinases may harm unprotected skin, but can also be used in healing wounds (Mezhlumyan *et al*., 2003). Tissues of papaya (including leaves and roots) which contain cyanogenic glycosides (Olafsdottir *et al*., 2002; Seigler *et al*., 2002) and tannins may provoke adverse reactions if consumed in quantity.

18.   Papaya enzymes may be injected for medical purposes. However, Moneret-Vautrain *et al*. (1985) have described the allergenic potential of injected chymopapain extracts — up to 1% of the population may have an adverse reaction. Injection may also evoke immune responses to papaya's other known cysteine proteinases, *i.e.* papain, caricain, and glycyl endopeptidase (Dando *et al*., 1995). The reactions to the fruit, pollen, and papain are mediated by an IgE mechanism (Blanco *et al*., 1998; Soto-Mera *et al*., 2000).

19.   Papaya has been investigated for possible effects on pregnancy, since some consider consumption a risk to fetal development, or to cause or alternatively to prevent miscarriage (Eno *et al*., 2000; Adebiyi *et al*., 2002a). In a controlled study of pregnant rats, juice from ripe fruits was considered safe (Adebiyi *et al*., 2002a). No effect of papaya juice was observed on isolated uterine muscle *in vitro*, but crude latex preparations caused spasm (Adebiyi *et al*., 2002a, 2002b). Additional physiological effects have been described from papaya parts not usually consumed, as for example on reproduction in male rodents and monkeys. Mice, rats and Hanuman langur monkeys (*Semnopithecus entellus*) given extracts of papaya seed appear to become infertile reversibly without indication of toxicity (Chinoy *et al*., 1994; Pathak *et al*., 2000; Lohiya *et al*., 2002). A papaya seed extract may offer control of a protozoan parasite that causes a major disease of fish in aquaculture (Ekanem *et al*., 2004).

B. Propagation

B.1. Seed

20.   Papaya producers usually grow the crop from seed; agronomic advisers encourage purchasing commercial seed for propagation (Muthukrishnan and Irulappan, 1985). Most commercial seed producers offer inbred selections, but some hybrid lines such as Rainbow and Eksotika II are available. Further discussion on the place of hybrid seed is found below in this section's subsection B.3. Varietal selection, and in Section VII.B.2. Cultivated varieties as sources of genetic variability. A list of frequently encountered varieties in commercial and breeding use is in Table 1.

21.   To assure seed quality, growers must take into account the sexual reproductive type and the genetic variability of the variety. Lines heterogeneous for many traits will produce considerable trait diversity in the progeny. Dioecious varieties are open-pollinated and much phenotypic variability can arise in the seeds of on-site fruit-bearing trees. Dioecious lines (described in Section V.A. Reproductive types and locus of cultivation) are more likely to be heterozygous for quality traits; the characteristics of tree and fruit are only maintained exceptionally. To maintain traits for generations, producers strictly control pollination using standard breeding techniques, and careful isolation of multiple lines. Rigorous crossing procedures are preferable (Watson, 1997). A strategy available for maintaining the consistency of some varieties is to obtain seed only from selfed male trees ("ambivalent males"), which produce fruit under limited (such as seasonal) circumstances (Aquilizan, 1987). Traits of superior plants can also be exploited by selection, especially when growers bag and hand-pollinate flowers to produce the seed.

22.   In the hermaphrodite lines self-pollination predominates, but outcrossing is not excluded (see also Section V.C. Pollination). Selection of seeds from only-selfed hermaphrodite plants will provide better trait uniformity (Singh, 1990). Carefully controlled production of hybrid seed is an alternative that may be increasing in importance. Seed producers pollinate selected female trees using pollen from selected hermaphrodite trees.

23.   Seeds, including the outermost layer — a gelatinous sarcotesta (Fisher, 1980), have inhibitors that prevent germination while contained in the fruit or prematurely after release (Yahiro and Hayashi, 1982; Ellis *et al*., 1985; Arumugum and Shanmugavelu, 1975; Tseng, 1992). Seeds freshly harvested from the fruits have very low and variable germination. Removal of the sarcotesta considerably increases germination in the fresh undried seeds. Seed treatment by drying and cool storage and soaking prior to planting can promote viability and the rate and uniformity of germination. Storage below 15ºC for 30-50 days greatly reduces the activity of growth inhibitors and enhances germination (Yahiro 1979; Yahiro and Hayashi, 1982). Soaking (with changes of water) also greatly increases germination (Paz and Vázquez-Yanes, 1998). For improved long-term storage, seed can be dried to moisture levels of 9-12% (Teng and Hor, 1976; Ellis *et al*., 1991); if dry and cool, papaya seeds may retain viability for 3 years (Malo and Campbell, 1994). After desiccation, heat shock can break the dormancy (Wood *et al*., 2000).

24.   Papaya producers either sow seed in the field, or start by germinating seed in a nursery. Germination may occur in 10-21 days after sowing, or in 4-10 days after pretreatment, and may continue intermittently for up to 35-40 days (Chen and Tseng, 1996; Bhattacharya and Khuspe, 2001). Nursery-grown seedlings may be transplanted to the field at about 60 days (Muthukrishnan and Irulappan, 1985). Because the sex of a plant is not known until flowering, growers often plant additional papaya in each mound, and later thin plants of the undesired sex. If growing hermaphrodite plants is intended, two to four (gynodioecious-type) plants may be transplanted per mound. Growers then remove the female saplings when the sex can be determined — in *c*. 4-8 months from sowing. If dioecious plants are grown, then surplus males will be discarded, leaving one male tree to pollinate 10-15 (sometimes more) female trees.

25.   However, several assays have recently been developed that will likely lead to routine molecular tests for determining the sex of seedlings. They include an assay for males and hermaphrodites using a sequence characterised amplified region (SCAR) marker developed from an RAPD marker (Urasaki *et al*., 2002a, 2002b); a pair of SCAR markers whose products are not produced in females (Deputy *et al*., 2002); a male-specific simple sequence repeat (SSR) (or microsatellite) and a SCAR marker (Parasnis *et al*., 1999, 2000); and a hermaphrodite-specific RAPD probe (Lemos *et al*., 2002). Moreover, Chan-Tai *et al*. (2003) are evaluating an exclusively hermaphrodite Sunrise Solo mutant that when selfed appears to be stable in its sexual phenotype, producing only hermaphrodites.

B.2. Vegetative propagation

26.   The cultivar Hortus Gold of South Africa is propagated vegetatively using leafy stem cuttings (Allan, 1974). Experimental success in propagating papaya by cuttings was reported by Allan (1964). Large leafy lateral shoots that developed after a winter season, were initially used for the cuttings, and rooted under intermittent mist. Induction and proliferation of suitable-sized lateral shoots (breaking apical dominance) is improved with application of cytokinin and gibberellic acid mixtures to developed plants (Allan, 1995; Ono *et al*., 2004). The cuttings root in about 3 weeks. Exceptionally, some varieties of papaya are seedless (Wettstein *et al*., 1944; de Wit, 1966).

27.   Clonally propagated plants may show greater uniformity, earlier fruiting, lower fruit-bearing height, and improved yield over plants from seed (Drew, 1988; Chan and Teo, 2002). Hawaiian Rainbow transgenic papaya propagated from cuttings flowered 1-3 months earlier and bore fruit 30 cm lower than progeny from seed (Fitch *et al*., 2002). Cloned plants also yielded significantly greater fruit weight, a difference more marked under less favourable environments. The technology for small-scale commercial and experimental micropropagation is well developed (Litz and Conover, 1978; Drew, 1992; Magdalita *et al*., 1997a). Field trials of *in vitro* plantlets have found that they propagate true to sex, without somaclonal reversion.

28.   Papaya can also be propagated by grafting. Airi *et al*. (1986) cleft-grafted scion shoots from cultivars Co-1 and Honey Dew onto uniformly established seedlings. Patch and T budding also can be used, but the success rate is poorer than with cleft grafting. In Malaysia, some growers use grafting in the orchard to supersede female-fruiting trees of the cultivar Eksotika (Cheah *et al*., 1993). As soon as a plant's sex is determined, propagators will side-cleft graft the female trees with scion shoots (basal diameter 2-3 cm) taken from hermaphrodite Eksotika trees; the scions fruit 6 months after the field grafting.

B.3. Varietal selection: Inbred lines and hybrid cultivars

29.   Although local papaya varieties are most common in some markets, producers frequently grow other varieties that originated elsewhere. Singh (1990) noted that in terms of phenotypic uniformity and stability, few varieties qualified strictly as cultivars, although Solo came closest. As described in Section VII.B.2. Cultivated varieties as sources of genetic variability, the Solo group of varieties developed in Hawaii has limited but inherent genetic variability. Other such uniform lines are Eksotika and Eksotika II from Malaysia, and the Tainung series (Formosa group) of hybrids and inbreds distributed by the Known You seed company of Taiwan (Manshardt, 2002, pers. com.). Commercial producers often grow Solo varieties, Khaek Dam from Thailand, and Tainung (Subhadrabandhu and Nontaswatsri 1997; Le Tran and Tran, 1999; Story, 2001); other Solo cultivars include Kapoho and Waimanalo (Watson, 1997; Beltraide, 2000). Larger-type fruits such as Maradol are also planted extensively. Table 1 lists some common varieties used in commerce and breeding.

Table 1. Common papaya varieties in commerce and breeding.

Variety	Origin	Average fruit size, Notable traits	Fruit characteristics (*e.g.* shape, color)
Bettina	Australia (Florida Betty × Queensland var.)	1.36-2.27 kg	Round-ovoid. Well-colored.
Cariflora	Florida, USA	0.8 kg Tolerant to PRSV.	Round. Dark yellow to light orange flesh.
Coorg Honey Dew [H]	India	2-3.5 kg	Long to ovoid. Yellow.
Eksotika [H]	Malaysia (Sunrise Solo × Subang 6)	0.6-0.9 kg	Elongate (from hermaphrodite). Orange-red flesh.
Eksotika II [H]	Malaysia (Eksotika lines 19 × 20)	0.6-1.0 kg Higher yield than Eksotika.	Fewer freckles on skin, and sweeter than Eksotika.
Sekaki [H]	Malaysia	1.0-2.5 kg	Long, cylindrical, with smooth skin. Red, firm flesh.
Hortus Gold (selection: Honey Gold)	South Africa	1 kg Propagated by cuttings.	Round-ovoid. Golden yellow.
Known You 1 [H]	Taiwan	1.6-3 kg Tolerant to PRSV.	Very long and slender. Yellow flesh.
Maradol	Cuba	2.6 kg	Elongate. Green or yellow skin.
Rainbow [H]	Hawaii, USA (SunUp × Kapoho Solo)	0.65 kg Transgenic resistance to PRSV.	Pear-shaped to ellipsoid. Yellow-orange flesh.
Red Lady 786	Taiwan	1.5-2 kg Tolerant to PRSV.	Elongate. Red flesh.
Red Maradol	Mexico	2.5-2.6 kg	Red flesh; yellow-orange skin.
Solo [H]	Developed in Hawaii, USA; from Barbados originally.	0.5-1 kg Bisexual flowers highly selfing.	Pear-shaped (from hermaphrodites). Orange-yellow skin; golden orange flesh.
Kapoho Solo [H]	Hawaii, USA	0.45 kg	Pear-shaped, but shorter neck than Sunrise Solo. Orange-yellow flesh.
Sunrise Solo [H]	Hawaii, USA	0.57 kg	Pear-shaped. Reddish pink flesh.
Tainung 1 [H]	Taiwan	1.1 kg	Pointed blossom-end (from hermaphrodite). Red flesh.

[H] Hermaphrodite variety (*i.e.*, gynodioecious)

30.   Historically, papaya researchers have not found hybrid production necessary for improvement of the crop. More recently, however, hybridisation has demonstrably improved crop potential. The heterosis in F_1 hybrids in some cases has increased plant vigor and yield in agronomic assessments (Subramanyam and Iyer, 1984; Dinesh *et al*., 1992; Chan, 2001) and seed producer trials (Grant, G., 2004, Papaya Seed Australia, pers. com.). In Malaysia, hybridisation of Eksotika Line 20 with its sib-line produced the F_1

hybrid Eksotika II, which has heterosis in vigor and yield (Chan, 1992). In Hawaii, the transgenic cultivar Rainbow was derived as the F_1 progeny of gynodioecious parental lines SunUp (transgenic) and Kapoho (a popular nontransgenic). In Australia, about 65% of commercial plantings over 10 ha are the dioecious Hybrid 1B (Grant, G., 2004, Papaya Seed Australia, pers. com.) and other hybrids are readily available from commercial sources and commonly planted. The Queensland government maintains parental varieties used for hybrid production and initially had a voluntary seed production scheme with a program for training hybrid seed producers (Dunn, J., 2004, Queensland Dept. Primary Indust. & Fisheries, pers. com.). In diallel crosses, desirable agronomic characters have shown good combining ability (Dinesh *et al*., 1992; Subhadrabandhu and Nontaswatsri, 1997).

C. Cropping practices

31.   Trees begin bearing within the 1st year of planting (some varieties within 7-9 months). Commercial life of the plant in the large-scale commercial production cycle is usually 3 years, but may be less or more in some areas (Singh, 1990; Watson, 1997). In the U.S. Virgin Islands, early, low-bearing plants have been developed for an annual crop to minimise damage from papaya ringspot virus and seasonal hurricanes (Zimmerman and Kowalski, 2004). In Hawaii production in the 4th year drops off precipitously, thus encouraging replanting after the 3rd year (Younge and Plucknett, 1981). Continuous production is possible even in subtropical regions if winter temperatures may be moderated such as by ocean buffering, but flowering during cooler months in some locations may result in reduced summer harvests (Watson, 1997). Even though fruit production may occur throughout the year in many regions, the month of planting can have an impact on the plant's development, the timing of harvest, and the total yield (Singh and Singh, 1998). Fruit may begin to ripen within 7-9 months, and full-production harvesting may be possible within another 2 months. Depending upon variety, the fruits may need to be thinned. For example, Sunrise Solo may bear up to 5 fruits per node, but is reduced by hand to 2 fruits (Watson, 1997).

32.   Density of planting depends upon the papaya variety and the region where cultivated; typical practice establishes 1160 to 1930 plants per ha (Watson, 1997), with trees spaced from 1.8 to 2.7 m apart in the row and a distance between rows of 2.7 to 3 m. Sometimes double rows are planted, *e.g.* $3.25 \times 1.75 \times 2.4$ m (PROSEA, 1991). Successful practices include provision of optimal soil cover for the orchard space between trees. Younge and Plucknett (1981) showed that clover (*e.g. Trifolium*) or grass reduces return compared to clean cultivation; weedy coverage of the space is similarly disadvantageous. Trash mulching may improve yields, as may a year of rotation with clover between several continuous years of papaya production. Mulching with coarse grass hay may substantially increase yields (Elder *et al*., 2002a).

33.   Papaya can be intercropped if timed appropriately. Before the papaya trees reach bearing age in India, short-term vegetable cropping may be accomplished with tomatoes (*Lycopersicon*), onions (*Allium*), or cabbage or cauliflower (*Brassica*) (Muthukrishnan and Irulappan, 1985), but it was recommended that any competition to the papayas be eliminated during papaya's many months of fruiting to avoid reducing yield. In Nigeria intercropping has been tested with jute (*Corchorus*), sweet potato (*Ipomoea batatas*), okra (*Abelmoschus esculentus*), and watermelon (*Citrullus lanatus*) (Aiyelaagbe and Jolaoso, 1992). However, the cotton or melon aphid (*Aphis gossypii*) can transmit papaya ringspot virus from cucurbits (Cucurbitaceae) (Ali *et al*., 2004). Some growers apparently use papaya itself as a short-term intercrop between rows of mangos (*Mangifera indica*) or litchis (*Litchi chinensis*) (Muthukrishnan and Irulappan, 1985). In Malaysia, sometimes papaya is the intercrop with oil palm (*Elaeis guineensis*) or rubber (*Hevea brasiliensis*) on developing plantations (Chan *et al*., 1999). As papaya is often a 2- or 3-year crop, such interplantings have little impact on the longer lived trees before they reach production age.

D. Cultivation requirements

34. Adequate irrigation is essential for plant growth and fruit quality. Rainfall in the 1000 to 2500 mm range may be optimal (Watson, 1997), and seasonal variability needs to be taken into account. The pattern of rainfall may lead to soil water deficits, so that supplemental water must be provided for fruit production (Terra de Almeida *et al.*, 2003b). Practices include overhead or modified drip or undertree irrigation. Overhead irrigation may be least suitable, since leaf diseases may increase (Watson, 1997). For Australia, Watson (1997) recommended recharging the root zone twice a week to attain soil water capacity. A pH of 5.0-7.0 is favorable for papaya cultivation (Nakasone and Paull, 1998); lime is commonly used to increase alkalinity.

35. Balanced nutrition should be provided from the date of planting through harvesting for this fast-growing, heavy-bearing crop (Cunha and Haag, 1980; Watson, 1997). Nitrogen, phosphorus and potassium are important for good growth (Shoji *et al.*, 1958; Awada *et al.*, 1986; Nakasone and Paull, 1998). Nitrogen deficiency coupled with declining air temperatures can produce carpellodic flowers in some varieties and unmarketable fruits (Awada and Ikeda, 1957). Boron deficiency causes "bumpy" fruit and latex exudation (Chan and Raveendranathan, 1984), which can be remedied by foliar spray of boric acid or ground application of borax.

E. Yield parameters

36. The yield of papaya fruit varies widely in different countries, and is dependent on soil characteristics, varieties grown, pest and pathogen incidence, and local good management practices (Singh, 1990). Productivity of an orchard is also a function of the number of bearing trees; hermaphrodite and female plant types; average number of fruits per tree, which may be 25-100; and average weight of fruit, which commonly ranges between 350 g and 3000 g. The average yield worldwide in weight of fruit for the 10 years of 1991-2000 was 15,000 kg per ha (FAO, 2001). Optimal production is between 27,000 to 35,000 kg per ha in India (Singh, 1990); 12,500 to 62,500 kg per ha in Trinidad; and experimentally up to 100,000 kg per ha in Hawaii, although the typical Hawaiian yields are 20,000 to 30,000 kg per ha (excluding culled fruit) (Manshardt, 2002, pers. com.). Yield over the lifetime of the tree varies; with intensive cultivation, the highest yield is in the 1st year following planting.

37. Several thousand metric tons of papaya latex are obtained each year from the unripe fruits. An orchard of not less than 10 ha is usually required to produce one metric ton of dry latex annually (El Moussaoui *et al.*, 2001).

38. Papaya seed production for agriculture varies greatly with variety, growing conditions, cultivation practices (*e.g.* open-pollination in isolated fields, or controlled hand-pollination), and purpose (*e.g.* production of foundation seed for the market, or breeding seed). In India (Bihar) for example, the dioecious Pusa Dwarf and Pusa Giant produced more seeds at lower cost under hand-pollination than the gynodioecious Pusa Delicious and Pusa Majesty. The seed yield of Pusa Dwarf in isolation plots at one site was 579 kg/ha, whereas under controlled pollination at another site the yield was 362 kg/ha. The yield of hand-pollinated Pusa Majesty was just 52 kg/ha (Ram and Majumdar, 1990; Ram, 1996).

SECTION IV. PESTS AND PATHOGENS

39.   *Carica papaya*'s milky latex is stored in a dense network of anastomosing articulated laticifers (joined cells) throughout the plant, but not within the fruit when ripe (Roth and Clausnitzer, 1972; Fisher, 1980; Zeng *et al*., 1994). The latex may provide defense mechanisms by sanitising and healing wounds. The soluble fraction of the latex (which is *c.* 85% water) contains a rich diversity of biomolecules, including some possibly involved or recognised to be directly involved in deterring insects or pathogens — such as glycosyl hydrolases (*e.g.* a class II papaya chitinase), proteinase inhibitors (papaya cystatins), and nine proteinases (El Moussaoui *et al*., 2001; Azarkan *et al*., 2004). Papain (which is not papaya's major cysteine proteinase) is a crucial factor in defense against some lepidopteran larvae (*Samia*, Saturniidae; and *Mamestra* and *Spodoptera*, Noctuidae) (Konno *et al*., 2004). Nonetheless, papaya seedlings experimentally exposed to key damaging mite species (*Tetranychus* and *Calacarus*) and the powdery mildew fungus *Oidium caricae* did not show induced resistance, but instead weak induced susceptibility after being sanitised and transplanted to the field in Hawaii (Fournier *et al*., 2004). Major pests and pathogens evade defenses, which can also enhance infestation by other such species.

A. Pest species: Mites, insects and nematodes

40.   A small number of mite and insect species are major pests of papaya, though many such species infest the plants (Singh, 1990; Pantoja *et al*., 2002). Aphids often increase in number on weeds surrounding or within the orchards and when the weeds have dried up, attack papaya (Singh, 1990). Green peach aphid (*Myzus persicae*), cotton or melon aphid (*Aphis gossypii*) and cowpea aphid (*A. craccivora*) may transmit papaya ringspot virus. Other insect pests include onion thrips (*Thrips tabaci*) in Hawaii; various scale insects, such as *Aonidiella orientalis* in Queensland; and mealybugs (Pseudococcidae). Fruit flies, such as oriental fruit fly (*Bactrocera dorsalis*) and Mediterranean fruit fly (*Ceratitis capitata*), are principal infesting species in Hawaii (Manshardt, 2002, pers. com.), as are papaya fruit fly (*Toxotrypana curvicauda*) in the Caribbean region (Malo and Campbell, 1994); fruit flies are of most importance in the export market (Nakasone and Paull, 1998). Leafhoppers can be significant pests, including *Empoasca papayae* in Brazil (Firko and Podleckis, 1996) and *E. stevensii* in Hawaii (Manshardt, 2002, pers. com.). Most insect infestations can be treated with appropriate pesticides; aphids may be controlled best by prophylactic removal of host weeds in the vicinity of the orchards (Singh, 1990).

41.   Mite species are likely to be more important pests than insects, with false spider mites (*e.g. Brevipalpus phoenicis*) and spider mites (*e.g.* carmine mite, *Tetranychus cinnabarinus*) occurring in most growing areas (Singh, 1990). Tarsonemid mites (*e.g. Polyphagotarsonemus latus*) are pests in Brazil (Firko and Podleckis, 1996). Suitable acaracides may be employed to control mite damage (Singh, 1990). Root knot nematodes (*Meloidogyne* spp.) and reniform nematode (*Rotylenchulus reniformis*) may limit production in some countries (Singh, 1990). Producers use various halogenated soil fumigants to control nematodes, along with cultural strategies such as removing papaya debris and rotating papaya with other crops.

B. Pathogens: Fungi, viruses and bacteria

42.   More important than mite and insect pests are the pathogens that infect various developmental stages and parts of the plant. The severity of infection depends upon cultural practices and environmental conditions. Singh (1990) reported up to seventeen papaya diseases, of which about six are principal diseases found in many growing areas. Many of the areas are affected by collar rots, damping off, anthracnose, mosaic, and leaf curl diseases. Nishijima (1999) lists a larger number of papaya disease organisms and the associated disease conditions; a recent description of the principal diseases is provided by Persley and Ploetz (2003).

43.   Several fungi produce damping off diseases in nursery plants (younger than 60 days following seeding); the causal agents are *Phytophthora*, *Pythium* and *Rhizoctonia* species. Collar rots are important diseases, affecting seedlings and older plants (stems rot and crack, leading to death); *Pythium* and *Phytophthora* along with *Calonectria* are the causal agents. An anthracnose is in most areas, infesting leaf petioles and fruits; *Colletotrichum gloeosporioides* causes this major disease. Fungal infections of leaf blades and petioles include Corynespora leaf spot, which may be caused by *Corynespora cassiicola* (Carribean region). Powdery mildews affecting the fruit or other parts include *Oidium caricae* (Hawaii), *Sphaerotheca* spp. and *Leveillula taurica* (*Oidiopsis taurica*) (Queensland), and *Ovulariopsis papayae* (East Africa) (Morton, 1987).

44.   Postharvest fungal diseases also cause losses. Phytophthora stem-end rot (*Phytophthora nicotianae* var. *parasitica*), Phomopsis rot (*Phomopsis caricae-papayae*), anthracnose (*C. gloeosporioides*), black stem-end rot (*Phoma caricae-papayae* and *Lasiodiplodia theobromae*) and Alternaria rot (*Alternaria alternata*) may follow inadequate temperature maintenance or mechanical injury (Kader, 2000). Anthracnoses and Phytophthora blights may be controlled by various fungicides (Pernezny and Litz, 1999). Unspecified replant or yield decline problems (which are probably caused by fungal pathogens) have been treated by replacement of infected soil with virgin soil, or by fumigation (CTAHR, 1985).

45.   Viruses usually impose the most significant limits to papaya cultivation; the importance of some viruses seems to be increasing in many growing areas. Papaya ringspot virus (PRSV), a potyvirus, has produced major crop loss, for example in Hawaii, Mexico, the Caribbean, South America, Africa and Southeast Asia (Persley and Ploetz, 2003). Diagnostic are dark green rings on fruit, and yellow mosaic on leaf lamina accompanied by stunting and shoestring-like leaves (Gonsalves, 1993). PRSV is spread by mechanical means, and also green peach aphid and cotton or melon aphid (Bhargava and Khurana, 1970). Declines in production may occur despite vigorous efforts using cultural strategies to limit spread. Control strategies have included roguing infected plants, but this cannot stem the disease once established (Queensland Dept. Primary Indust. & Fisheries 2003). Treatment with aphicides has been ineffective, because transmission by insertion into the plant occurs before the aphids are killed (Pernezny and Litz, 1999). If non-host crops are interplanted between papaya rows, vectors feed on the non-hosts before feeding on papayas, which can reduce disease transmission and incidence (Gonsalves, 1998). Researchers in Taiwan have developed some tolerant varieties. Seedlings were inoculated with a mild strain of PRSV or a mutated virus to produce cross protection from the more devastating form (Yeh, 1990). However, because of the apparent mutability of the virus, this protection is not completely effective and may not be permanent (Lin *et al*., 1989). Also, the present tolerant varieties (*e.g.* Tainung No. 5) have had poor acceptance because of inferior consumer qualities (Japan Intl. Res. Centre Agric. Sci., 2003).

46.   Collaborators in Cornell University and Hawaii developed transgenic plants to provide resistance to PRSV by expression of viral coat proteins. The newly introduced cultivars brought about a rapid reversal of decline in the papaya industry in Hawaii (Lius *et al*., 1997; Manshardt, 1999; Gonsalves, 2000). Small field trials were conducted in 1992; a scale-up and the release of seeds commercially were

completed in 1998. In 2003, nearly half the commercial crop in Hawaii consisted of the PRSV-resistant Rainbow transgenic papaya (Pacific Bus. News 2003). For details about the coat protein-based resistance, see Section VII.B.4. Molecular approaches for agronomic improvement.

47.   Other viruses include papaya mosaic virus (PapMV), a potexvirus identified in parts of South America and Florida (USA) (Malo and Campbell, 1994). PapMV appears to be mechanically transmitted, without a biological vector (Buchen-Osmond and Hiebert, 1988). The incompletely characterised papaya leaf-distortion mosaic virus (PLDMV), a potyvirus, has been analysed experimentally (Maoka *et al*., 1996); it has no more than 59% amino acid sequence homology to PRSV. Chen *et al*. (2001) have shown that the Taiwan isolate DL-1 is antigenically different from PRSV; this virus is also known in Japan (Maoka, 2002). Papaya droopy necrosis virus (PDNV), a rhabdovirus, is found in Florida (Zettler and Wan, 1993). A similar rhabdovirus called papaya apical necrosis virus ("PANV") (but not recognised by the International Committee on the Taxonomy of Viruses) is often a severe pathogen in Venezuela (Zettler and Wan, 1993); it is vectored by a leafhopper (Lastra and Quintero, 1981). Croton yellow vein mosaic virus (CYVMV), a bigeminivirus, causes severe leaf curling and twisting of petioles, leading to death before flowering or fruiting (Singh, 1990; Brunt *et al*., 1996). This can be a devastating pathogen in some areas, such as India; it appears to be transmitted by the whitefly *Bemisia tabaci* even though papaya is not a preferred host. Papaya leaf curl virus (PLCV), a whitefly-transmitted geminivirus, is found in India and Taiwan (Chang *et al*., 2003); it has been analysed for molecular similarity to other viruses (Saxena *et al*., 1998). Papaya lethal yellowing virus (PLYV), with substantial sequence similarity to *Tombusvirus* (Silva *et al*., 1997), can be economically important in Brazil. Tomato spotted wilt virus (TSWV), a tospovirus, has caused sporadic outbreaks in Hawaii; it is hosted by common weed species and vectored by thrips (Gonsalves and Trujillo, 1986; Bautista *et al*., 1995). PRSV type P (papaya) infects papaya and cucurbits; PRSV type W (watermelon) naturally only infects cucurbits, but experimentally it has infected papaya (Purcifull *et al*., 1986). Also detected have been diseases attributed to distortion ringspot virus, which may actually be a synonym for PRSV (Brunt *et al*., 1996). A regionally important virus in Brazil called papaya meleira virus ("PMeV") (which is currently not ICTV-sanctioned) is a double-stranded DNA virus with no similarities to other viruses (Maciel-Zambolim *et al*., 2003). Control strategies for the other virus diseases of papaya are similar to those for PRSV, but resistance strategies have not yet been developed.

48.   Multiple viruses or other pathogens may occur as coextensive diseases in papaya-growing regions, as do PLYV and PRSV in Venezuela (Marys *et al*., 2000). Evidence for coinfection by PapMV and PRSV has been found in one of ten Mexican states that were assessed (Noa-Carrazana *et al*., 2000). Simultaneous occurrences of zucchini yellow mosaic virus (ZYMV), PRSV, and papaya bunchy top disease have also been detected (Fewerda-Licha, 2002).

49.   Bacterial diseases of papaya are more or less common depending upon the growing region. Species of *Erwinia* initially induce lesions on the lower surface of leaves; yellowing, wilting and death of foliage occur and rotting of the plant follows (Seaver, 2000). This disease is more economically significant in the Caribbean and Venezuela than PRSV (Coppens d'Eeckenbrugge, G, IPGRI Cali, Colombia, pers. com.). To control *Erwinia* in the Virgin Islands, Webb (1985) recommended resistant cultivars and barrier crops that did not support the pathogen, as bactericides and antibiotics were not effective. In the Northern Mariana Islands, disease caused by *Erwinia* is spread by the giant African snail *Achatina fulica* and disease incidence is reduced by snail control.

50.   A severe dieback of papaya in Australia had been attributed to *Phytoplasma australiense* (Liefting *et al*., 1998). Two diseases were indentified, papaya yellow crinkle disease and papaya dieback disease, caused by two different phytoplasma groups (Padovan and Gibb, 2001). A small incidence of a third phytoplasma disease in Australia, a papaya mosaic disease, has been reported (Elder *et al*., 2002b). Leafhoppers (*e.g. Orosius*) infrequently harbored the phytoplasmas, suggesting transmittal but the attribution for causation of the disease is qualified because papaya is not a preferred host. Papaya bunchy

top disease appears to be produced by rickettsial bacteria in the laticifers, which are transmitted by the leafhopper *Empoasca papayae* (Davis *et al*., 1998, 1999). Control strategies for bunchy top have included roguing infected plants, topping to allow production of uninfected axillary shoots, and control of vectoring aphids (Davis, 1993).

SECTION V. REPRODUCTIVE BIOLOGY

A. Reproductive types and locus of cultivation

51.   Papayas may be cultivated as dioecious varieties (with separate male and female plants), or gynodioecious varieties (having both hermaphrodite and female plants). In subtropical areas dioecious lines are usually planted because the phenotype of gynodioecious plants is unstable under variable and extreme seasonality (Manshardt, 1999). Gynoecious and androecious plants are mixed in the orchard with a ratio of 10 to 25 female plants to 1 male.

52.   Gynodioecious lines are usually confined to tropical areas because flower development in hermaphrodite plants is highly sensitive to climatic stresses and the tropical climate can be more stable and benign for this tropical species. The hermaphrodite plants are susceptible to carpel abortion, or to transformation of stamens into carpel-like fleshy structures (carpellody) so ovarian development is variably expressed. Either female-type or deformed fruits are produced; both are unmarketable. In gynodioecious lines, all plants may be fully productive, as fruit is borne on both the hermaphrodite and the female (gynoecious) plants. In some gynodioecious lines, the hermaphrodite plants frequently produce irregular fruits and their crop also is not as heavy as from the female plants (Shetty, 1953; Persley and Ploetz, 2003). However, in some gynodioecious lines the hermaphrodite fruits are preferred in some areas, and the female plants are removed. For example, the hermaphrodite plants of the variety Solo produce pear-shaped fruits with more flesh and a smaller seed cavity, which are favored in Hawaii over the spherical fruits on female plants (Arkle and Nakasone, 1984).

B. Sexual reproduction

53.   The categories of unisexual and bisexual flower types occurring variously on plants have been described by many investigators, and have resulted in conflicting descriptions of plant sexual types (Sakai and Weller, 1999). The categories of the papaya sexual types from crosses are complex, but can be summarised simply; Table 2 shows the results of such crosses.

Table 2. Formation of individual plant sexual types following papaya crosses (adapted from Storey, 1976).

Flowers and plant: S = staminate (male); P = pistillate (female); H = hermaphrodite (male & female)

Mating	S				P	H	(Non-viable zygote)
S × P	1				1	0	0
H × P	0				1	1	0
S × H	1				1	1	1
H × H	0				1	2	1
S × S*	2	1	0	1			

*Cross accomplished when sex reversal occurs on staminate (*e.g.* ambivalent male) plants.

54.   The genetic or chromosomal mechanism for this complicated pattern of reproduction is not understood fully; a simple explanation has been used to represent the underlying condition. M is designated as a gene's dominant allele for maleness, M_H the dominant allele for hermaphroditism, and m the recessive allele for femaleness. Zygotes with homozygous dominant alleles (MM, MM_H, M_HM_H) are considered lethal; thus only Mm (male plants), M_Hm (hermaphrodite plants), and mm (female plants) are viable phenotypes (Hofmeyr, 1938a, 1938b, 1939a, Storey, 1938; Muthukrishnan and Irulappan 1985; Ma *et al*., 2004). Storey (1953) furthermore proposed that tightly linked genes on a chromosome, determining sex, lethality, and additionally other sexual characteristics (*e.g.* inflorescence branching and number of flowers, petal fusion, stamen number, ovary shape), would be consistent with the crossing results. Hofmeyr (1967) hypothesised that M (M1) and M_H (M2) represent regions of slightly different length from which vital genes are missing. Sondur *et al*. (1996) accounted for the observations using recent knowledge about development of floral organs in other plants. They proposed that *trans*-acting regulatory proteins induce the sexual forms: an M allele of the sex locus (*Sex1*) induces male floral parts while inhibiting carpel development, an M_H allele induces male parts while only reducing carpel size, whereas the m allele has no ability to induce male parts. Lethality in the dominant homozygotes could result from loss of an essential function when the m allele is lacking. Sex reversal is rare in males, but its occurrence occasionally in hermaphrodites might result from the interaction between M_H and the gene's target (a promoter sequence or another protein factor) being less stable than the interaction between M and the target. Embryos from anther culture have produced only female plantlets (perhaps haploids or polyploids, *e.g.* dihaploids), which presumably originated from microspores, with only the m genotype involved because of the lethality related to the dominant alleles (Rimberia *et al*., 2005).

55.   A mutation recently discovered in a hermaphrodite Sunrise Solo cultivar produces exclusively hermaphrodite plants following self-pollination (*i.e.* no females in the expected 2:1 H:P ratio) (Chan-Tai *et al*., 2003). Pollen of the mutant fertilising typical hermaphrodite plants produced a 3:1 ratio of hermaphrodites to females, indicating that all genotypes survived. Randomly self-pollinating these F_1s produced segregating F_2s that confirmed there were surviving homozygous dominant plants ($M_HM_@$) apparently with a new hermaphrodite allele (a variant of M_H designated as $M_@$). Furthermore, a new recessive lethality gene (l) was inferred that is linked to m, and lethal in female (mm) genotypes when homozygous recessive (mlml).

56.   Based on interspecific hybridisation research in Caricaceae, Horovitz and Jiménez (1967) proposed an XX-XY system of sex determination. Micheletti de Zerpa (1980) studied the meiosis of their BC_2 of *Vasconellea cundinamarcensis* into *V. stipulata*, finding that 2 (only) of the 18 chromosomes had limited pairing and they sometimes behaved as univalents. This was taken as evidence that the Y chromosome of a *V. cundinamarcensis* with a bisexual phenotype had been transferred with its bisexuality genotype to produce the bisexual BC_2, as *V. stipulata* is dioecious. (Both parental species showed no heteromorphic chromosomes.) Liu *et al*. (2004) found that the sex-determining genes in *Carica papaya* are located in a 4.4 Mb region of chromosome LG1 (linkage group 1), *c.* 10% of the chromosome, which shows suppressed recombination (Ma *et al*., 2004). Thus LG1 acts like an incipient Y chromosome, in which a part is Y-like but the rest is autosome-like. This male-specific Y region (equating to *c.* 100-200 genes in average parts of the papaya genome) contains the non-female DNA coding, *i.e.* for male or hermaphrodite characteristics (Viskot and Hobza, 2004). The X-Y sequence divergence may be 10-20% (Charlesworth, 2004).

C. Pollination

57.   Cross-pollination may be common or infrequent, depending upon the papaya variety, flowering behavior (including flower type), and the environment. In some instances, male plants may more effectively pollinate hermaphrodites in adjacent orchards than the hermaphrodites can self pollinate. There

may be genotype differences in variety lines, and seasonal changes in flower receptivity affecting pollination (Louw, 2000; A. Louw, 2003, Inst. Trop. & Subtrop. Crops, South Africa, pers. com.; Parés *et al., 20*02; Parés-Martínez *et al*., 2004). In gynodioecious plants, seed set was ten times greater when Coorg Honey Dew plants in India were hand-pollinated after being open-pollinated (Purohit, 1980), but hand-pollination did not increase papaya fruit set in Jamaica (Free, 1975). These results depend upon the pollinators available as well as the papaya variety; for example, bagging of hermaphrodite flowers of the variety Sunrise resulted in 90% fruit set, whereas for the variety Higgins it was only 33% (Rodríguez-Pastor *et al*., 1990). In the dioecious condition the male and female plants are separate, so outcrossing is requisite to fertilisation.

58.   In male flowers, stalked anthers (in an upper whorl) are exserted well beyond the floral tube's opening, whereas nearly sessile anthers (in a lower whorl) are inside the tube and dehisce (open) into it (Wiggins and Porter, 1971). In a dioecious variety (Washington), anther dehiscence was completed 36 to 18 hrs before flower opening (anthesis), and stigmas became receptive a day before anthesis (Khuspe and Ugale, 1977). In gynodioecious varieties, self-fertilisation is possible in hermaphrodite flowers. Anthers dehisce before anthesis, facilitating cleistogamy (Rodríguez Pastor *et al*., 1990; Chan *et al*., 1999; Ronse Decraene and Smets, 1999). The anthers of male, and functionally male (type 4+) flowers have been found to dehisce 2 days before anthesis, whereas the anthers of hermaphrodite flowers dehisce 1 day before anthesis (Parés *et al*., 2002; Parés-Martínez *et al*., 2004). Maximum stigma receptivity has been found to occur on the day of anthesis, although stigmas may become receptive 3 days earlier, and remain so for up to 5 days after anthesis (Subramanyam and Iyer, 1986; Dhaliwal and Gill, 1991). A hermaphrodite flower's pollen may be released before its stigmas' are receptive (protandrous dichogamy), with the stigmas becoming receptive only at anthesis (*e.g.* in the variety Cartagena Amarilla) (Parés *et al*., 2002).

59.   Pollen can be produced year-round. The grains are relative large (32-39 μm diam), and in the subtropics can be larger in local warmer areas (Sippel and Holtzhausen, 1992); the surface is finely reticulate (Allan, 1963a; Fisher, 1980). Viability of pollen (measured by stainability and germination) may vary seasonally, being highest in the rainy season and spring (Singh and Sharma, 1997), and much reduced in winter in subtropical locales such as Australia (Garrett, 1995, in OGTR, 2003a; Allan, 2002). Pollen may be relatively long-lived; in a Petri dish at room temperature, 16% of pollen grains remained viable for 16 days (Sharma and Bajpai, 1969; *cf.* Vahidy and Nafees, 1973).

60.   Some pollen transport may occur by wind transfer, but the detection of pollen near plants seems to be meager (Allan, 1963c). Nontransgenic plants were grown *c.* 396 m (1300 ft) downwind of 0.4 ha of GUS-marked transgenic Rainbow papaya in Kapoho, Hawaii; no GUS expression was detected in the progeny of the nontransgenics (Manshardt, 2002, pers. com.). Purseglove (1968) noted that isolated female trees were pollinated as far as 244 m away from male trees, but Baker (1976) speculated that the observations might be explained by parthenocarpy, which is known to occur in some varieties (*e.g.* Wettstein *et al*., 1944; Free, 1975; Rodríguez Pastor *et al*., 1990; Garrett,1995, in OGTR 2003a). In a study designed to differentiate wind and insect importance, pollination was 38% in open-pollinated plants (Cera-type) but only 26% in controls that were muslin-bagged at the point of anthesis, thus suggesting a substantial contribution by insect pollinators at the suboptimum test site in Veracruz, Mexico (Mateos Sánchez *et al*., 1995). After excluding medium and larger sized insects with wire gauze in South African papaya, no normal fruit set was observed (Allan, 1963c). In some areas, hand-pollination is infrequently undertaken to assist fruit set (Calif. Rare Fruit Growers, 1997).

61.   The flowers open in the early night-time (Mekako and Nakasone, 1975a; Sippel *et al*., 1989; Parés *et al*., 2002), or the morning (Khuspe and Ugale, 1977; Azad and Rabbani, 2004), and since they are strongly dimorphic or polymorphic, provide different cues to potential insect pollinators. Staminate flowers may be more fragrant and open for 24 hrs, and they produce calcium oxalate crystals in the anthers and nectar basally (from the rudimental pistil), thus being an attractant for insects. The pistillate flower has no

nectar, but a sweet non-sugar exudate seems available on its flared large antler-like stigmas (or stigmatic lobes) (Ronse Decraene and Smets, 1999; Parés *et al*., 2002), and in these ways it may mimic the male flower (Baker, 1976). The female flowers may remain open for 7 days (Mabberley, 1998).

62.   The main pollinators are somewhat unclear. Details of pollination especially by hawkmoths (Sphingidae), and apparently also mosquitoes, midges and thrips have been described (Heide, 1923; Free, 1975; Baker, 1976; Knudsen and Tollsten, 1993; Garrett, 1995, in OGTR 2003a; Morrisen *et al*., 2003). In the Galápagos Islands, hawkmoths often visit the flowers after dark (McMullen, 1999); in mainland Ecuador, visitors to the male and female flowers include beetles, flies and mosquitoes (Nielsen, 1998, in Ronse Decraene and Smets, 1999). In Venezuela, 17 species were identified as pollinators (or visitors), including *Trigona* and *Xylocopa* bees (Marín Acosta, 1969). In Mexico (Veracruz), 712 insects in 68 families and 12 orders were recovered from 100 flowers, but only 38% pollination was attained (Mateos Sánchez *et al*., 1995). In Central Amazonia (Brazil), papaya pollen is among the preferred foods of the bee *Trigona williana* almost year-round (Marques-Souza *et al*., 1996). Similarly, honeybees were found transporting papaya pollen in South Africa (Allan, 1963c).

63.   In some countries the role of insects in papaya pollination is factored as prominent, whereas in others wind-borne pollen appears to be more the concern. Accordingly, different recommendations for appropriate isolation distances from other papaya may reflect the specific conditions at different locations of production. Recognising both insects and wind as agents for pollen movement, Singh (1990) recommended 2-3 km isolation for production of foundation seed, but cited no experimental observations supporting this distance. The Hawaiian Identity Preservation Protocol for non-GMO papaya seed production specifies at least 1320 ft (400 m) isolation from other varieties (Hawaii Dept. Agric., 2003), based on the transgenic field test reported earlier in this subsection. The Papaya Biotechnology Network of Southeast Asia proposed that nontransgenic papaya should be separated by 400 m from any transgenic papaya plants that could bear anthers in field tests (Anon, 1999). USDA-APHIS approves an isolation distance of 500 m for papaya field tests in Florida. The Gene Technology Regulator (Australia) allows field testing only under conditions of complete insect exclusion by netting and removal of all male inflorescences (OGTR, 2003b).

D. Induced alterations to sexual development

64.   Changes in environmental conditions (temperature, humidity, soil water, nitrogen) can induce various alterations in flowering and reproduction of papaya (Lange, 1961; Singh *et al*., 1963; Rojas *et al*., 1985; Terra de Almeida *et al*., 2003a). When gynodioecious trees develop in hot and dry conditions, the inflorescence at each node may form a terminal bisexual flower but become subtended by male (staminate) axillary flowers (Manshardt, 2002, pers. com.). The male flowers can attain to 80% of all inflorescences on Solo cultivars during such conditions (Nakasone and Paull, 1998). When cooler conditions predominate, the axillary flowers may revert towards a preponderant bisexual morphology.

65.   Sex reversals are also observed in the opposite direction, toward female structures. In both dioecious and gynodioecious lines, high temperatures and increased humidity can cause a shift towards female flowers (Singh, 1990). Lower night-time temperatures in the winter months in Hawaii may occasionally induce carpellody, in which stamens develop to resemble carpels, but associated with a developing fruit (Awada, 1958; Hsu, 1958a). The result is fruits of irregular shape, which are unmarketable (Chandrasekaran *et al*., 1950; Watson, 1997). Carpellody may routinely reach 10-15% in hybrid and inbred lines in subtropical Australia (Grant,2004).

66.   In dioecious cultivars, where trees bear either male or female flowers, night-time temperatures below 12ºC may induce the formation of bisexual flowers on male plants (Allan *et al*., 1987), and short-day warm conditions may support this change (Aquilizan, 1987). Resistance to sex reversal of male trees is

greater in spring compared to the cooler seasons (Allan *et al*., 1987). In subtropical climates, fruit set on male trees (ambivalent males) may occur predictably (Watson, 1997). This conditional reversal is used to insure inbreeding of basically dioecious lines in Queensland (Aquilizan, 1987). In the tropics, the trauma of a few machete slashes to the trunk may stimulate male trees to produce bisexual flowers (Duke, 1967).

67.   The female reproductive structures are stable, in contrast to the bisexual and male structures. Nonetheless, the fertility of female plants can be altered by environmental conditions. Low moisture levels or low nitrogen can induce female sterility (Awada and Ikeda, 1957).

SECTION VI. HYBRIDISATION

A. Interspecific crosses with *Carica papaya*

68.   By the traditional methods of hybridisation, most attempts to transfer traits from *Vasconcellea* species into *C. papaya* have resulted in endosperm failure (Horovitz and Jiménez, 1958, 1967; Mekako and Nakasone, 1975b; Manshardt and Wenslaff, 1989a). Using embryo rescue and micropropagation techniques, some intergeneric hybrids have been generated (Manshardt and Wenslaff, 1989a, 1989b). Although F_1 plants from crosses with *C. papaya* were produced, they generally were sterile, and produced no F_2s (Manshardt and Drew, 1998). Failure of meiosis resulted in formation of unreduced gametes, which in backcross to *C. papaya* have produced sterile sesquidiploid plants (Manshardt and Drew, 1998). In the Philippines, sterile F_1 hybrids of *C. papaya* with *V. cundinamarcensis* (synonym *V. pubescens*) and as well with *V. quercifolia*, *V. stipulata*, and *V. cauliflora* have been reported (Magdalita *et al., 19*97b, 1998; Siar *et al., 19*98; Villegas, 1999). Crossing various *C. papaya* with *V. cauliflora* in Venezuela achieved 0-76% fructification (Vegas *et al*., 2003). All crosses using *V. cundinamarcensis* with *C. papaya* have produced infertile female hybrids (Drew *et al*., 1998; R. Drew, 2001, Griffith, Univ., Australia, pers. com.).

69.   Drew *et al*. (1998) achieved a limited fertile crossability of *C. papaya* with *V. quercifolia*. Large numbers of F_1s were formed following embryo rescue, and backcrossed to *C. papaya*, which produced one male (BC_1) that was fertile and tolerant to papaya ringspot virus; further development by backcrossing it was planned (Drew 2004, pers. com.). Sajise *et al*. (2004) have backcrossed an F_1 (from Drew) with elite papaya lines in the Philippines and obtained 24 BC_1 plantlets. Also, some *C. papaya* crosses with *V. parviflora* have produced F_1 plants with viable pollen (Drew *et al*., 1998).

70.   Using RAPD techniques (with 14 primers), Jobin-Decor *et al*. (1997) estimated relatedness of some species of Caricaceae. *Carica papaya* had a mean dissimilarity of 69% with six *Vasconcellea* species; it had a dissimilarity of 84% with *Jacaratia spinosa* (and no isozymes in common). There were similar results for *C. papaya* with these *Vasconcellea* species using isozyme analysis — 70% dissimilarity. Using the amplified fragment length polymorphism (AFLP) technique (with 5 primer combinations to generate nearly 500 polymorphic bands), Van Droogenbroeck *et al*. (2002) grouped taxonomic accessions; cluster analysis revealed evidence for strong genetic divergence of *C. papaya* from all eight (plus unidentified) *Vasconcellea* species. In another AFLP study, Kim *et al*., (2002) found that six *Vasconcellea* species were only 43% similar to *C. papaya*, but were 73% similar to one another. Using RFLP analysis of chloroplast and mitochondrial non-coding DNA, Van Droogenbroeck *et al*. (2004) found six *Vasconcellea* species to be more similar to *C. papaya* than to eleven other *Vasconcellea* species, which suggests further possibilities for interspecific crossing with papaya. These more closely related taxa include *V. quercifolia*, *V. weberbaueri* and *V. ×heilbornii*, and less closely also *V. parviflora* and *V. stipulata*, but do not include *V. cundinamarcensis* or *V. cauliflora*.

B. Interspecific crosses within *Vasconcellea*

71.   Workers hope to find a *Vasconcellea* bridge species for crossing with other *Vasconcellea* species, and so interbreeding with *Vasconcellea* known to cross with *C. papaya*. Natural hybrids between some species of *Vasconcellea* occur in the Andes (Badillo, 1971, 1993; Van Droogenbroeck *et al*., 2004). The

parentage of the sterile *V. ×heilbornii* is uncertain, as molecular data (Jobin-Decor *et al*., 1997; Aradhya *et al., 19*99; Van Droogenbroeck *et al*., 2002, 2004) do not clearly support the usual interpretation that these wild and semi-domesticated plants (babaco, higacho) came from *V. cundinamarcensis* × *V. stipulata* (Badillo, 1967; NRC, 1989; Jiménez *et al*., 1999). Organellar genome patterns identical with *V. weberbaueri* were found (Van Droogenbroeck *et al*., 2004). *Vasconcellea stipulata* nevertheless has been well documented experimentally to produce fertile hybrids with *V. cundinamarcensis*. Similarly, when *V. stipulata* is the pollen parent in crossing with *V. ×heilbornii*, progeny with 10-20 full seeds are produced (Horovitz and Jiménez, 1967; Micheletti de Zerpa, 1980). Sterile F$_1$ crosses have been made between *Carica papaya* and *V. ×heilbornii* (as well as *C. papaya* and *V. stipulata*).

SECTION VII. GENETIC VARIABILITY

A. Cytology and genome

72.   The diploid (2*n*) number of chromosomes of *C. papaya* is 18 (Meurman, 1925; Asana and Sutaria, 1929; Chen, 1993). No heteromorphic chromosomes have been detected (Datta, 1971; see Section V.B. Sexual reproduction), although differing chromosomal length and constriction morphologies have been found in various varieties. Tetraploids have been induced experimentally (Hofmeyr, 1945).

73.   An analysis of the papaya nuclear genome has been undertaken by constructing a genetic linkage map (Sondur *et al.*, 1996). Using RAPD techniques for the analysis of a breeding line and a commercial line, evidence for 11 linkage groups was presented, and a total map distance of *c.* 1000 cM, compared to an expected genome size of *c.* 1350 cM. There was an overall low frequency of polymorphisms per primer (0.16) in comparison to other agronomic plants, suggesting either a relatively low genome size (including polymorphic repetitive DNA) in papaya, or low genetic diversity in the lines. The genome is small, with a 2C of 0.77 picograms and haploid DNA content of 372 Mbp (Arumuganathan and Earle, 1991). Making a map of the entire papaya genome is underway, with a constructed bacterial artificial chromosome (BAC) library of papaya that has nearly 40,000 clones (Ming *et al.*, 2001).

B. Genetic variation within *Carica papaya*

74.   The breadth of genetic variation readily available for papaya breeding and improvement is difficult to estimate. Papaya germplasm banks often hold a number of accessions, but the genetic resources in these repositories typically are modestly characterised. A typical collection contains a diverse assortment of *Carica* breeding material, cultivated types and cultivars, and often accessions of some *Vasconcellea* species as well. Surveys or analyses have been carried out to assess agronomic characteristics classically, and increasingly by molecular techniques (*e.g.* Santos *et al.*, 2003). Many agronomic descriptors for habit, flower, fruit, seed, etc., have been standardised by IBPGR (1988), including a range of alternative categories for the character. In a conventional analysis of a total of 125 accessions of the Solo group and the Formosa group (Tainung series) and a few intercrosses (holdings in one Brazilian repository), promising variability was found mainly in fruit size and tolerance to *Phytophthora* spp. (Dantas and Firmino de Lima, 2001). An AFLP analysis of 63 accessions from most growing areas (*c.* 17 countries) found an average similarity of 0.880 among them (Kim *et al.*, 2002).

B.1. Germplasm collections

75.   FAO's Seed and Plant Genetic Resources Service (AGPS) has a list of locations that cultivate papaya germplasm; these include nearly 90 research stations or seed production sites (FAO, 2001; *cf.* Bettencourt *et al.*, 1992). However, world germplasm resources for papaya are not organised in an accessible database. CIRAD-FLHOR (Centre de coopération internationale en recherche agronomique pour le développement) and IPGRI have a project for improvement of neotropical fruits which includes establishing a database with limited objectives. A regional effort for collecting and evaluating germplasm holdings of Caricaceae is being developed with a focus on resistance or tolerance traits, particularly for PRSV, bacterial decline, and anthracnoses — the regionally most important pathogens (Coppens, 2001,

pers. com.). Other goals for Caricaceae germplasm collections may include development of *Vasconcellea* with potential as commercial fruits, and for new sources of enzymes such as papain (*e.g.* Colombo *et al.*, 1989; Villarreal *et al.*, 2003).

76.   Breeding programs in various countries have established germplasm collections to co-ordinate with varietal improvement programs. The U.S. National Plant Germplasm System's USDA site in Hilo, Hawaii reports 153 accessions of *C. papaya* and several *Vasconcellea* spp. (GRIN, 2001); agronomic characters associated with specific accessions can be retrieved in a database *via* the Internet. Large holdings include those by Brazil (Coppens, 2001, pers. com.; Dantas and Firmino de Lima 2001) at EBDA-Bahia (82 accessions), EMBRAPA Mandioca e Fruticultura, Cruz das Almas, Bahia (141 accessions) and IAC-Campinas, São Paulo (169 accessions); Colombia at Univ. Nacional Medellín and CORPOICA (83 accessions) with additional accessions at other locations; India (90 *C. papaya* accessions) (Giacometti *et al.*, 1987); and Malaysia (72 accessions) (Chan *et al.*, 1999).

77.   Most of the germplasm collections consist of living plants, but some include seeds (Giacometti *et al.*, 1987). Seed may be stored for up to 12 months at 12 C if capped in a tightly fitting jar, and longer under conditions specified by IBPGR (Giacometti *et al.*, 1987). Pollen likewise can maintain viability if stored appropriately, such as for 6 months either at 10ºC and 10% relative humidity (Allan, 1963b) or at -18ºC (Cohen *et al.*, 1989), or for 10-16 months cryogenically — even with several thawings and refreezings (Ganeshan, 1986).

B.2. Cultivated varieties as sources of genetic variability

78.   Many varieties of papaya are typically cultivated within a country, and each is often quite localised. A catalogue made in one of the high production areas of East Java, Indonesia recorded at least 24 such varieties (Baswarsiati *et al.*, 1985, in Setyobudi and Purnomo, 1999). Some papaya varieties have found international acceptance and are grown extensively worldwide. One is Solo, from which other lines have been selected (such as Sunrise Solo). Eksotika, bred from backcrossing Subang 6 with recurrent parent Sunrise Solo, is the flagship variety in Malaysia for export (Chan *et al.*, 1999).

79.   To determine variability among papaya varieties and the degree of relatedness of some cultivars, Stiles *et al.* (1993) used RAPD molecular techniques (with 11 primers amplifying 102 distinct fragments). The comparison among 10 varieties from Malaysia, Mariana Islands, Hawaii and Florida showed their least relatedness was *c.* 70%, and the most closely related cultivars at *c.* 95%. The genetic similarities were generally those expected from knowing the region of origin and breeding history of the variety. Kim *et al.* (2002) analysed 186 AFLPs to estimate genetic diversity within 63 papaya accessions from many international sources; the genetic diversity was quite limited. The average similarity was 0.880, and in a single growing region, such as within Solo-type hermaphrodite cultivars in Hawaii, the average was 0.921. Analysis using isozymes is also possible — a total of 29 alleles have been found in 11 loci that segregate independently (Morshidi, 1998).

80.   Surprisingly, Kim *et al.* (2002) found that the dioecious cultivars (which are open-pollinated) did not have more genetic variability than the hermaphrodite cultivars, which are thought to be mainly self-pollinated and so presumed to be less genetically variable. The literature on papaya breeding includes a considerable number of reviews (Singh, 1990), and no inbreeding depression has been detected (Hamilton, 1954). Indeed, after the initial selection for new traits, inbreeding by sib-mating for about four generations is often the practice to establish new varieties. Hybridisation was typically not used in developing new varieties (Storey, 1953), reinforcing the belief that inbreeding depression is not an important issue in cultivating papaya. Not withstanding, in development hybridisation is increasing, as shown by Australian varieties and Malaysia's success with Eksotika II (see also Section III.B.1. Seed and B.3. Varietal selection).

B.3. Genetic variability in resistance to pathogens

81.   Several research programs have looked for plants with the ability to develop tolerance (*i.e.*, an ability to be infected but with limited effects) or resistance (lack of susceptibility to infection) to PRSV, one of the most devastating pathogens of papaya. Complete resistance is preferable, but tolerance is a useful option. The dioecious line Cariflora developed in Florida has shown a high level of tolerance (Conover *et al.*, 1986). Researchers in the Thailand Department of Agriculture have selected a PRSV-tolerant variety called Thapra 2; the plants may become infected, but have mild symptoms or remain symptom free. A second tolerant Thailand cultivar, Pakchong 1, was developed at Kasetsart University (Kositratana *et al.*, 1999). In the Philippines, the variety Sinta has exhibited high tolerance (Villegas *et al.*, 1996). In Malaysia, hybrids have been made of the popular variety Eksotika with Tainung No. 5, which has tolerance to PRSV, and the later generations have reasonable or high levels of field tolerance and are under continuing selection (Chan and Ong, 1996; Chan *et al.*, 1999; Chan, 2004; Chan, Y.K., pers. com.). See Section IV. Pests and pathogens for details about the results of these approaches. Since the development of transgenic varieties expressing a virus coat protein to confer resistance to PRSV, less effort has been expended to develop tolerant varieties; the genetically engineered resistance is providing more substantial benefits (Ferreira *et al.*, 2002).

B.4. Molecular approaches for agronomic improvement

82.   Mutagenesis has augmented common breeding practices for improvement, resulting for example in a dwarf papaya with higher fruit yield per unit area (Ram and Majumdar, 1981). An RAPD-based genetic linkage map (Sondur *et al., 19*96) has been used to locate and characterise genes affecting growth (height and stem diameter) and time of first flowering, by an analysis of quantitative trait loci (QTLs) in an F_2 papaya population derived from the cross of a gynodioecious, tall, late-flowering variety and a dioecious, semi-dwarf, early-flowering selection (Sondur *et al., 19*95). Three QTLs affecting rate of height increase and final height were detected, four QTLs affecting rate of stem diameter increase and final diameter, and two QTLs affecting node at first flowering. This is viewed as the lower limit of major QTLs for these traits. Five of the QTLs were on linkage group 1 (LG1) and one QTL each on LG3, LG4, LG5 and LG10, considered a non-random distribution. The height-influencing QTLs accounted for 64% of the phenotypic variance in height increase, the stem-influencing QTLs accounted for 52% of the variance in diameter increase, and the QTLs influencing node at first flowering accounted for *c.* 30% of the variance in node (in which the first flower-bearing node ranged from the 15th to the 36th). Variance due to environment was estimated to be 20% for height increase and 25% for increase in diameter.

83.   Because practical methods for transforming papaya have been developed and the biotechnology is becoming well refined (Fitch *et al.*, 1990; Pinto *et al.*, 2002; Zhu *et al.*, 2004; Wall *et al.*, 2004), and transgenic commercial lines have been approved and available since 1998 (Cai *et al.*, 1999; Ying *et al.*, 1999; Gonsalves, 2000), papaya is a focus for improvement using genetic engineering approaches. Programs are using such tools to transform various varieties, for example co-ordinated under the Papaya Biotechnology Network of Southeast Asia (ISAAA, 2001a), with a current focus on delayed ripening characteristics and resistance to PRSV. Commercial interests have developed papaya with altered fruit ripening to allow extended marketing. Field testing in Australia has been authorised for papaya transformed with genes (*capacs1* and *capacs2*) that alter expression of ACC synthase, and with an ethylene expression gene (*ETR1*) (OGTR, 2003b). To increase tolerance to aluminum (common in tropical acidic soils), a transgenic papaya has been made in Mexico that overexpresses a citrate synthase gene from *Pseudomonas aeruginosa* (de la Fuente *et al.*, 1997). Transgenic papaya also is being researched as a delivery vehicle for an edible vaccine against tuberculosis (Zhang *et al.*, 2003).

84.   Genes identified in papaya include some whose expression might be employed to modify various agronomic traits or enhance industrial production. Identified sequences (NCBI, 2001) include those affecting the following (Table 3):

Table 3. Selected Papaya Genes For Which Sequence Information Is Available

Industrial/Agronomic product	Carbohydrate metabolism	Others
a male-specific SCAR marker	sucrose synthase	arginine decarboxylase (ADC)
chymopapain	cell wall invertase	ATP synthase
papain	β-galactosidase	membrane channel proteins
metallothionein-like protein	α-galactosidase	glutamine cyclotransferase
1-aminocyclopropane-1-carboxylic acid (ACC) synthase	xyloglucan endo-transglycosylase	caricain (proteinase omega) cysteine protease cysteine protease inhibitor
ethylene receptor	pectinesterase	Cu/Zn superoxide dismutase maturase K

85.   Breeders and molecular biologists have a goal of developing resistance to various papaya diseases. Many pathogen-associated sequences have been cloned and identified (NCBI, 2001), which potentially could be employed in transformed papaya to provide endogenous resistance to pathogens that use papaya as host. Large numbers of viral genes have been sequenced, including coat proteins of numerous PRSV biotypes from different locations, a replicase, mRNA products of the virus, and an RNA polymerase gene (*NIb*). The whole PRSV and PapMV genomes have been sequenced. Other genes identified include two genes from PLDMV — an *NIb* gene and a coat protein (capsid protein) gene, a gene from the phytoplasma that causes papaya dieback (tuf) disease, the succinate dehydrogenase gene from the rickettsial bacteria that may cause papaya bunchy top disease; and an ileu tRNA.

86.   Engineered resistance to viral diseases of papaya may require expression of geographically specific viral proteins. Many strains of the widespread PRSV may be virulent to papaya varieties even after they have been transformed with viral capsid sequences. For example some Florida (USA) isolates were molecularly similar to Mexican and Australian isolates, but dissimilar to those from Asia (Davis and Ying, 1999). The genetically engineered resistance may be less or not effective if the origin of the capsid sequence is from a different region than the local viral strain (Tennant *et al., 19*94, 2001, 2002). Recombination involving as few as 5 nucleotides in a virus coat protein gene can cause a susceptible response when a resistant papaya variety expressing the non-mutant coat protein is inoculated with the altered virus (Chiang *et al*., 2000). However, not sequence similarity alone, but also gene dosage, plant stage, and other PRSV genes have important consequences for the expression of field resistance to PRSV (Tennant *et al*., 2001; Tripathi *et al*., 2004).

87.   A consortium of scientists from universities, business and the U.S. Department of Agriculture (USDA-ARS) developed the first resistant papaya, which expressed a Hawaii-specific PRSV coat protein (Fitch *et al*., 1992). Projects to deploy PRSV-resistant transgenic papayas are variously underway for example in Mexico, Guatemala, Jamaica, Venezuela, Brazil, Uganda, Tanzania, Bangladesh, Taiwan, Australia, and the countries that are members of the Papaya Biotechnology Network of Southeast Asia — Malaysia, Thailand, Vietnam, Philippines and Indonesia (Cai *et al*., 1999; Flasinski *et al., 20*02; Tennant *et al., 20*02). Brazilian researchers working at Cornell University (USA) have transformed five papaya varieties using Brazil-specific PRSV capsid sequences, and planned field tests (ISAAA 2001b; Lima *et al*., 2002). Thailand has developed a PRSV-resistant variety using a sequence from a PRSV strain specific to Southeast Asia; field tests were planned for 2002 (ISAAA, 2001c). Localised research efforts have succeeded in providing coat protein-based immunity in Australian and Venezuelan varieties (Lines *et al*., 2002; Fermin *et al*., 2004).

88.   Several biotechnological solutions have been explored to supply the resistance needed to protect the crop from the prevalent PRSV of various regions. Chiang *et al.* (2001) suggested transforming papaya to express chimeric PRSV coat proteins, which possibly can be protective against these variable viral challenges. Bau *et al.* (2003) showed that a single coat protein sequence from a local Taiwan strain was adequate to provide complete immunity from heterologous strains arising in Mexico, Hawaii and Thailand, and this line did not produce any coat protein. Another approach may be to use the PRSV replicase gene to provide resistance (Chen *et al.*, 2001). An approach that produces an untranslatable product, which may result in an RNA-meditated immunity to PRSV, has been successful in protecting Australia cultivars (Lines *et al.*, 2002) and Florida cultivars (Davis and Ying, 2002). Also, programs for multiple protections against pathogens are attempting to combine coat proteins from PRSV with coat proteins from PLDMV (Maoka, 2002).

SECTION VIII. ECOLOGY

A. Dispersal

89.   In Cameroon, forest elephants (*Loxodonta cyclotis*) seek papaya fruits beyond their protected reserve and disperse the seeds (Tchamba and Seme, 1993; Barlow, 2000). Wild *Carica papaya* seems to have many characteristics that fit the hypothesised megafaunal dispersal syndrome (Janzen and Martin, 1982; Barlow, 2000). The non-domesticated fruits are fairly large (5-8 cm in diameter) and visually nondescript (greenish unless fully ripened) but with a penetrating aroma, and are held high up on a trunk with suppressed branching. The fruits are indehiscent (without structural opening), and pulpy within but have peppery mustard-tasting seeds (Sharma and Singh, 1975; Passera and Spettoli, 1981) that are grouped centrally. Non-domesticated *Vasconcellea* fruits can be larger. Such unusual species may have evolved in response to consumption of fruits whole and seed dispersal by large (now extinct) mammals such as ground sloths (*Eremotherium*) and mastodon-like gomphotheres (*Cuvieronius*) (Simpson, 1969, 1980; Barlow, 2000).

90.   A great many vertebrates with a wide variety of ecological roles eat papaya fruits and may disperse viable seeds. Coyotes (*Canis latrans*) in coastal western Mexico (Jalisco) habitually seek out papaya as food, sometimes taking fruits directly from the trees and causing important economic loss (Hidalgo-Mihart *et al*., 2001). Pacas (*Agouti paca*), large forest rodents which range from Mexico to Paraguay, when in captivity selectively prefer papaya fruits because of their relatively high energy content (Laska *et al*., 2003). Brow-ridged langur monkeys (*Trachypithecus* spp.) in eastern India (Tripura) raid the crop, and can cause tree mortality (Das, 1998). Arboreal neotropical monkeys consume papayas, such as wild cotton-top tamarins (*Saguinus oedipus*) and captive capuchins (*Cebus*) — which pass the seeds in less than 2 hrs (Wehncke *et al*., 2003). Great fruit-eating bats (*Artibeus lituratus*), which are common from Mesoamerica and the Lesser Antilles to northern Argentina, disperse seeds found viable when tested (Garcia *et al*., 2000). In Papua New Guinea (Madang), papaya was found in fecal samples of lesser bare-backed fruit bats (*Dobsonia minor*) netted in the Kau Wildlife Area (Bonaccorso *et al*., 2002).

91.   In the Yucatán (southern Mexico), the plant is appropriately called papaya de pájaro (bird papaya). Many birds eat the fruits and may disperse seeds, such as Montezuma oropendolas (*Psarocolius montezuma*), a blackbird ranging from southern Mexico to central Panama (Webster, 1997), and Guianan cocks-of-the-rock (*Rupicola rupicola*) (Gilliard, 1962). Papaya was 29% of the diet of West Indian red-bellied woodpeckers (*Melanerpes superciliaris*) studied on Grand Cayman Island (Cruz and Johnston, 1984). Endangered Ouvéa parakeets (*Eunymphicus cornutus uvaeensis*) of New Caledonia preferentially consume papaya which are available throughout the year in Melanesian gardens (Robinet *et al*., 2003). Various bird species in India (Punjab) seek out the fruit (in rind-forming through ripening stages), and can result in crop damage of at least 3.4% (Mahli, 2001).

B. Weediness

92.   Papaya in different regions is variously described as an incidental escapee from cultivated sites, an opportunist, a pioneer species, or sometimes as an invasive or potentially invasive species. Papaya may persist beyond cultivation for indefinite periods. Little and Wadsworth (1964) state that "Through the

tropics they grow almost as weeds, bearing fruit the first year from seed and spreading along roadsides and in waste places"; they report that in Puerto Rico papaya is widely cultivated, escaping, and naturalised. In the Galápagos Islands (Santa Cruz), papaya was found along a new road from the coast inland in the arid, transition, and humid zones, but did not persist along the old road (Haro Martínez, 1975). Papaya is usually not characterised as an invasive species (USDA-APHIS, 1997).

93.   *Carica papaya* is regarded as a pioneer species in fairly natural habitats. Papaya can occur in forest gaps and within the early succession, since it has such characteristics as rapid growth in response to disturbance and high light intensity, and prolific production of seeds and an attractive fruit. Its pioneering ecological strategy includes a short life cycle with seed dormancy and a seed bank.

94.   As an opportunist, papaya has the capacity to establish significant seed banks. In Central Amazonia, Brazil (Santarém region) at some old Dark Earth locations (aboriginally cultivated soils), papaya comes up after the long-standing tropical rain forest has been cleared and burned (Clement *et al*., 2004). In a post-hurricane study of regeneration that compared feral *C. papaya* with a similar-sized native pioneer tree species (*Trema micrantha*) in Florida hammock habitats, papaya had a broader niche for regeneration (Kwit *et al*., 2000). They averred that dormant seed supply seed for population return following natural disturbance. Moist wild papaya seeds kept in total darkness in Petri dishes at room temperature remain viable and dormant (Vázquez-Yanes and Orozco-Segovia, 1996; *cf.* Pérez-Nasser and Vázquez-Yanes, 1989). In Japan's Bonin Islands (Hahajima) in mesic subtropical forest, the seed bank at 16 sites was sampled (0-20 cm) in three layers. Viable papaya seeds occurred in all three, with the most seeds at a depth of 4-10 cm, where their density was *c.* 18 per m^2 (Yamashita *et al*., 2003).

95.   Nakasone and Paull (1998) characterise papaya as "a rapid volunteer in areas where the tree vegetation has been disturbed". Subsequent to major hurricane damage (1992) in southern Florida (USA), papaya recruited abundantly and rapidly in unmanaged and managed areas. In the 1st and 2nd years, it comprised 76% and 40% of all stems respectively in the unmanaged areas (Horvitz and Koop, 2001). In an inventoried natural semi-evergreen forest of southeastern Mexico on the Yucatán Peninsula (Quintana Roo) where no papaya had been recorded, papayas were infrequently present just 5 months after an extreme hurricane had altered the region (Sánchez-Sánchez and Islebe, 1999).

96.   Randall (2002) reported weedy papaya infestations on some tropical islands and in localised areas of New Zealand. On Christmas Island (Indian Ocean) and in the Mariana Islands (Rota) and Samoa (Savaií), papaya is a colonising invader of disturbed or burned habitats (Craig, 1993; Space *et al*., 2000; Elmqvist *et al*,. 2001; Green *et al*., 2004). On Tongatapu, papaya was found in 44% of 52 sample plots in a range of land-cover types (especially fragmented interior forest). Following from these observations, Wiser *et al*. (2002) stated that it should be considered a potentially serious invader. In coastal Queensland (Australia), "small, low-density self-perpetuating populations" may be found (OGTR, 2003a). In the Hawaiian Islands, papaya is sparingly naturalised on four main islands, with some plants even occurring on nearly vertical rock faces (Wagner *et al*., 1999; Oppenheimer and Bartlett, 2000). In a wet-forest region of coastal Ecuador near the Andean foothills, Dodson and Gentry (1978) found papaya to be common in second-growth areas, including a forest regenerating from an agricultural clearing about 18 years previously.

97.   Papayas are sensitive to most herbicides and volunteer plants in agricultural habitats can be eliminated using paraquat, glyphosate, or triclopyr (Lee, 1989; Kline and Duquesnel, 1996). Reports are scarce on efforts to reduce feral *C. papaya* in relatively natural habitats (*e.g.* Horvitz and Koop 2001), which may be important for ecological restoration or to reduce genetic contamination in orchards from feral off-types.

C. Optimal habitats

98.   *Carica papaya* requires a tropical or semitropical habitat that is always rather warm and provides high illumination. Depending on latitude, cultivated varieties may thrive at elevations from sea level to 600 m and may range up to about 1200 m, being limited by the occurrence of killing frost (Arntzen and Ritter 1994; Bhattarai *et al., 20*04). Temperatures below 11ºC negatively affect growth and fruit set, and strongly retard fruit maturing and ripening (Shetty, 1953; Allan 2002). At higher elevations fruit tends to be insipid.

99.   Rainfall must attain to at least 350 mm and should not exceed about 2500 mm, as excessive moisture is detrimental to the plant or fruit (Singh 1990). Within its probable native range in Veracruz (central-eastern Mexico) (Moreno, 1980), a study correlated regional parameters with 62 botanical collections (including 25% from scarcely or slightly modified habitats; *cf.* Del Angel-Pérez and Mendoza-Briseno 2004). Most plants were in Köppen's Am(f) subclimate type; the annual estimated total precipitation was 1200-1400 mm, with 100-150 days having considerable rain (an average 30-40 mm possible in 24 hrs), and with 20-40 days per year having essentially no rain (Gómez-C. 2000). Relative humidity of more than 60% may be optimal for papaya (FAO 1986); nevertheless, in South Africa the best-quality fruits are grown in low humidity regions (Malan 1953).

100.   Acceptable growth of papaya can occur in a variety of soils. An optimal soil that promotes growth is well drained, and flooding is not tolerated (Malaysia Dept. Agric. 2001). A pH of 5.0-7.0 is favorable for its cultivation (Nakasone and Paull, 1998); uniform, rich loams of pH 6.5-7.0 are considered optimal (Singh, 1990). For Hawaiian soils, Younge and Plucknett (1981) recommended an optimum pH of 5.8-6.2; if the pH reaches 6.2-6.5, increased damage by *Phytophthora* may occur (Adlan, 1969). Arbuscular mycorrhizal fungi are strongly beneficial in cultivation (Jaizme-Vega and Azcón 1995; Vierheilig *et al., 20*00; Trindade *et al., 20*01). Compacted soils that impede root penetration (Yamanishi *et al., 19*98) will also limit net CO_2 assimilation (Campostrini and Yamanishi 2001b).

101.   Optimal growth is in sheltered locations; strong winds in combination with rain or low temperatures can cause fruit loss as a consequence of lodging that can easily occur in these fairly shallow-rooted plants. Most roots occur in the soil's upper 20 cm and they may extend radially to 80 cm (Fisher and Mueller 1983; Masri 1993; Malaysia Dept. Agric. 2001). Under optimal conditions taproots may reach a depth of about 1 m, and papaya rooting can adapt to slopes (Marler and Discekici 1997). With minimal pre-plant preparation or an absence of fertiliser applications, only a fibrous root system may develop (Younge and Plucknett 1981).

D. Optimal geographic location

102.   The genetic diversity within the present commercial cultivars provides relatively wide adaptability for papaya and permits cultivation in many locations. Production of this world crop is generally found between 30ºN and 40ºS, but commercial production is compressed to a circumferential region around the equator from 25ºN to 25ºS (Singh 1990). When grown outside these tropical latitudes, optimal growth is in well-protected areas near sea level (Nakasone and Paull 1998). Photosynthetic saturation occurs at rather high irradiance, and shade induces major morphological and cellular changes (Imai *et al., 19*82; Buisson and Lee 1993; Marler 1994); papaya has been described as a shade-avoiding species (Grime 1981). Papaya is cold-sensitive, wind-sensitive, flooding-intolerant, and moderately salt-sensitive (Marler 1994; Clemente and Marler 2001). Nevertheless, it has been successfully adapted as a dooryard treelet, and has naturalised in many locations. On most continents and on many islands, the usefulness of papaya's products and its wide range of traits have allowed the papaya a place in many gardens, local markets and commercial enterprises.

SECTION IX. REFERENCES

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