Applications of Biotechnology to Tropical Fruit Crops in Australia and Worldwide

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Abstract

Tropical fruits play an important role in the world economy. They make a substantial contribution to human nutrition and are used for medicine, timber, fuel and livestock feed. The major tropical fruit crops are banana, mango, pineapple, papaya and citrus; however, it is estimated that more than 400 species are harvested in the Asia, Pacific and Oceania region. Other regions such as Central and South America are rich in tropical fruit biodiversity. During the last 20 years, biotechnology has been applied to many tropical fruit species. In Australia, micropropagation systems have been developed for banana, pineapple, papaya, ginger, passionfruit and coffee; and good embryogenic protocols have been employed in banana, mango and papaya. Cryopreservation protocols are being developed for many of the major tropical fruit species. Transformation systems have been used to produce disease resistant cultivars of banana and papaya; and, to prevent blackheart, to control flowering and delay ripening of pineapple. The single significant commercial application of transformation has been the Papaya Ringspot resistant papaya in Hawaii. Molecular marker technology has been used to identify genotypes and to confirm intergeneric hybrids between papaya and related Vasconcellea species. Molecular maps have been developed for some species. Genetic diversity within populations and between related wild species has been determined for some fruits. Specific DAF markers have been identified for sex determination in papaya; a SCAR marker has been developed to identify dwarfism in bananas; and, a CAPS marker to identify a PRSV-P resistant gene in highland papaya. The major application in genomics has been the rapid progress in sequencing the papaya genome in Hawaii.

INTRODUCTION

Prior to 1990, biotechnology and its application to tropical fruit species were in their infancy and a review of literature reveals that only limited information was available on a narrow range of species (citrus, banana, papaya and pineapple). Despite the recalcitrant nature of many tropical fruit species in vitro, successful research in the area has since escalated. With consistent research and innovative approaches many of these hurdles have been overcome. Two species in particular, *Carica papaya* and *Citrus* spp., have been the focus of such extensive in vitro research that they have become the models for application of biotechnology to other tropical fruit species. Although much of the Citrus research has been conducted on subtropical Citrus species, there are many commercially important tropical citrus species to which this work is acutely relevant.

This paper documents biotechnology techniques in their application to an expanding range of tropical fruit species. Notable successes worldwide and in Australia are presented in plant tissue and cell culture, cryopreservation, genetic transformation, molecular markers and genomics.

MICROPROPAGATION

More information is available on micropropagation than on any other biotechnology applied to tropical fruits. Micropropagation from apical or axillary bud

explants (Tables 1 and 2) have been separated in this review from regeneration systems based on organogenesis or embryogenesis (Tables 3 and 4). Regeneration via callus is prone to somaclonal variation, whereas the meristematic tissue in buds is inherently the most genetically stable tissue in plants. Genetic stability in a micropropagation system is vital if it is to be applied to elite genotypes, particularly if the aim is germplasm conservation. A system that is genetically stable but has lower multiplication rates is based on production of micro-cuttings from axillary buds of nodal cuttings dissected from apically dominant shoots (Drew, 1992, 1996a). This protocol has been applied successfully in Australia to papaya (Drew, 1992), passionfruit (Drew, 1991a), coffee (Drew, 1991b) and neem (Drew, 1993), and to other tropical species worldwide. Micrografting, an innovative technique that is being applied to tropical and subtropical species (Raharjo and Litz, 2005), was developed in 1972 for Citrus. Micrografting of Citrus results in virus-free plants that are not juvenile (Murashige et al., 1972).

A summary of micropropagation protocols is presented for fruits of major importance (Table 1) and other tropical fruits (Table 2). With some exceptions (citrus, banana, papaya, pineapple), success has been achieved using juvenile bud explants, and in many cases, seedling tissue. Approximately half of the reports document acclimatisation of plantlets in soil. While the increase since 1990 in research effort on a wide range of tropical fruit species is encouraging, continued research is required. To be of practical value, it is important that micropropagation is achieved using adult material from elite genotypes.

ORGANOGENESIS, EMBRYOGENESIS AND IN VITRO SELECTION

Regeneration of plantlets from callus can follow two distinct pathways. Organogenesis involves the development of meristematic tissue, which produces either shoots or roots, with vascular connections to the parental callus. Embryogenesis results in embryos that progress through characteristic developmental stages (globular, heart, torpedo and mature), have both a shoot and root meristem (bipolar) and become independent from the parental callus. Tropical and subtropical fruit species tend to regenerate by either organogenesis or embryogenesis (Tables 3 and 4), although occasionally there are reports of regeneration via both pathways (e.g. *Carica papaya*). As with micropropagation, most published successes via regeneration from callus have been achieved using juvenile tissue explants.

Many tropical fruit species are woody perennial dicots, which are in general a difficult group to culture in vitro. Most published successes of regeneration from callus have been achieved using immature embryos or very juvenile seedling explants, as these are often the most regenerative tissue in a plant. Much of the documented research on recalcitrant species has focussed on a detailed evaluation of a range of media components and concentrations. However, recent innovative protocols for embryogenesis and regeneration of *Musa* spp. from male flower explants (Teisson and Cote, 1997), and litchi and longan from leaf explants of leaf flushes (Litz and Raharjo, 2005) demonstrate the importance of testing a range of explants, as well as media, when working with tropical fruit species.

Results show that few species remain truly recalcitrant. With a combination of concentrated research effort and innovative approaches, regeneration is usually achieved. In vitro culture of papaya has been researched extensively worldwide and highly refined protocols have been developed. Efficient methods for embryogenesis from immature zygotic embryos have been used to develop both transgenic plants (Fitch et al., 1990) and encapsulated artificial seeds (Ye et al., 1993). Reports of culture of integuments of immature seeds and the development of embryos of maternal origin (Monmarson et al., 1995), and regeneration of plants via embryogenesis from root explants in Taiwan (S.D. Yeh, pers. commun.) should have important implications for rapid propagation and production of transformed ‘elite’ papaya genotypes. Regeneration of plantlets via embryogenesis following culture of nucellar tissue of mango, another recalcitrant species, (de Wald et al., 1989 a and b) demonstrates what can be achieved by innovative research.

Similarly, Zeng et al. (2000) transformed longan plantlets after infecting longan somatic embryos with *Agrobacterium rhizogenes.* This led to good production of secondary embryos from which transgenic plants were regenerated. Plantlets have been produced after embryogenesis from mature leaf tissue of mangosteen (Goh et al., 1990), and seedless triploid pummelo plants were produced following culture of endosperm (Wang and Chang, 1978; Yang et al., 2000).

Regeneration via organogenesis or embryogenesis is seen as having three major applications: micropropagation, cryopreservation and gene transfer. However, regeneration from callus can be prone to production of genetic off-types, thus any micropropagation technique should not be assumed to be clonal until large scale field testing has been undertaken to evaluate the protocol for genetic stability. Similarly, embryogenic cultures are well suited to cryopreservation studies; however, an assessment of genetic stability after large scale field evaluation is also necessary for each species and protocol, before it can be endorsed as a method of germplasm conservation. Regeneration protocols are basic to the development of plant transformation systems, as transformed plantlets have to be grown from transformed cells.

HAPLOIDY

Regeneration of haploid plants following anther or ovule culture has application to plant breeding and gene transfer programmes. However, there are limited applications to woody perennial species. There are several published reports of success with tropical fruit species. Plantlets have been regenerated following androgenesis with five species: *Annona squamosa* (Nair et al., 1983) *Carica papaya* (Tsay and Su, 1985), *Euphoria longan* (Yang and Wei, 1984), *Litchi chinensis* (Fu and Tang, 1983) and *Musa balbisiana* (Assani et al., 2003). Embryogenic callus has been produced from anthers of *Feijoa sellowiana* (Canhoto and Cruz, 1994), *Pouteria lucama* (Jordan et al., 1994) and *Psidium guajava* (Babbar and Gupta, 1986).

Although haploid plantlets have been regenerated from anthers of *Carica papaya* (Litz and Conover, 1978; Tsay and Su, 1985) work in the authors' laboratory has resulted in a very low success rate with many papaya genotypes, with only 1:1000 anthers producing embryogenic callus. Anther culture can be labour intensive, requiring plating of large numbers of explants, and a thorough investigation of factors that affect androgenesis. The stage of development of the microspore (usually best at the uninucleate stage), pretreatment of buds or anthers (e.g. cold treatment) as well as media factors and incubation conditions (light/dark treatment, daylength, temperature) should be considered when developing protocols for anther culture.

Despite the limited number of reports of successful application of this technology to tropical and subtropical fruit species, the successes reported above are sufficient to suggest that this could be both a novel and rewarding field of research for further studies. The potential to detect and exploit recessive character traits in one generation via production of doubled haploids, has enormous potential for species such as woody perennial fruit species with long juvenile periods. This potential also applies to gene transfer projects where transformed homozygous diploids could be produced in one generation, or flowers could be fertilised with transformed pollen.

Embryo Culture

Production of plants from mature embryos is one of the most straightforward in vitro techniques. Furthermore, because immature embryos contain the most regenerable tissue in most species, its culture has facilitated both in vitro regeneration of recalcitrant species and rescue of interspecific and intergeneric hybrids.

Kantharajah et al. (1992a) demonstrated the effectiveness of embryo culture when working with a recalcitrant species, *Litchi chinensis*. Litchi had previously proven to be one of the most difficult tropical fruit species to establish and grow in vitro. However, immature embryos of litchi as small as 3mm in length were cultured. Ability to produce adventitious buds varied with genotype; however, cultivar 'Bengal' produced 15 shoots

after pretreatment of immature embryos with BAP. Root formation was achieved with 65% of adventitious shoots, and resulting plantlets acclimatised. Other reports of regeneration via embryogenesis of immature zygotic embryo explants have been reported (Tables 3 and 4), and include avocado, custard apple and papaya. The potential for further research with embryo culture is obvious, given the success already achieved with recalcitrant tropical fruit species.

Embryo rescue has facilitated the production of intergeneric hybrids between *Carica papaya* and related *Vasconcellea* species and the successful backcrossing from these F_1 hybrids to *papaya* (Drew et al., 2006 a,b). This has allowed the transfer of PRSV-P resistance from *V. quercifolia* to *C. papaya* and offers an alternative to gene transfer.

Protoplast Culture and Somatic Hybridisation

Although protoplasts can be isolated from a range of tissues of almost any plant species, regeneration of plants from protoplasts is one of the most difficult in vitro techniques. Reports of success with recalcitrant woody species are limited, and applications to tropical and subtropical fruit species are rare. Recently however, there have been reports of plantlet regeneration from mango protoplasts (Ara et al., 2000), litchi protoplasts (Yu et al., 2000; Huang and Lai, 2006) and avocado protoplasts (Witjaksono et al., 1998). In contrast to other fruit species, there are many reports of protoplast culture of *Citrus* species and these have been reviewed by Ochatt et al. (1992). There have been reports of protoplast isolation of non-woody tropical fruit species: papaw (Litz, 1986) and banana (Krikorian et al., 1988), although sustained cell division was not achieved by these early workers. More recently there have been reports of plant regeneration from protoplasts of banana (Assani et al., 2001, 2006).

The principal uses of protoplasts are as targets for direct methods of gene transfer and to facilitate interspecific hybridisation. Direct methods of gene transfer requiring protoplasts are obsolete. Although protoplast fusion may provide a method of interspecific and intergeneric hybridisation, the difficulties in achieving sustained cell division and plantlet regeneration in many species generally outweigh the advantages. In reality, protoplast fusion is an advantage only when prezygotic barriers prevent interspecific hybridisation. If zygotic embryos are produced, embryo rescue and culture is a superior technique. A comparison of these techniques has been demonstrated with intergeneric hybridisation of *Carica papaya* and related *Vasconcellea* species. An efficient method has been developed for embryo rescue, embryogenesis and plantlet production for hybridisation between *C. papaya* and *V. cauliflora* (Magdalita et al., 1996) and between *C. papaya* and *V. pubescens, V. quercifolia, V. parviflora* and *V. goudotiana* (Drew et al., 1998). By contrast, attempts to hybridise *C. papaya* and *V. pubescens* via protoplast fusion have resulted in callus growth but no plants (Jordan, 1992). Similar difficulties have been experienced in the authors' laboratory when protoplasts of *C. papaya* were fused with those of *V. pubescens, V. quercifolia* and *V. stipulata*.

However, a major success in this field has been the production of somatic hybrids between *Citrus* species. Somatic hybridisation between pumello and mandarin (Grosser et al., 2004), pumello and orange (Calixto et al., 2004), and mandarin and orange (Ananthakrishnan et al., 2006) has produced potential new rootstocks to replace sour orange which has been devastated by citrus tristeza virus. Citrus cybrids have been produced by somatic hybridisation using a cytoplasmic male sterile cultivar, Satsuma mandarin, in an attempt to produce seedless cultivars (Guo et al., 2004). There has been a report of somatic hybrids between *Passiflora* species (Cuco et al., 2005).

As with most difficult aspects of in vitro culture, intensive research efforts, which require sustained funding, usually result in success. Protoplast culture of tropical and subtropical fruit species is no exception and, given sufficient attention, new and improved protocols would undoubtedly be developed. However, because protoplast culture is a very difficult technique and many tropical fruit species are recalcitrant woody dicot species, reports of successes are limited.

Transformation

In the last decade there have been reports of gene transfer to ten tropical and subtropical fruit species (Table 5). The first successful transformation of a tropical fruit species was papaya (Fitch et al., 1992) and this has lead to the only commercial application of this technology to tropical fruit crops, i.e. production of Papaya Ringspot (PRSV-P) resistant papayas in Hawaii. Transgenic papayas resistant to PRSV-P have now been developed for 10 countries in addition to Hawaii (Gonsalves et al., 2006).

Further commercial application of transgenics has been limited by two factors. Firstly, the majority of tropical fruit species are woody perennial dicots, for which protocols for regeneration of plantlets via embryogenesis or organogenesis (which is essential for gene transfer) have been developed only recently. Some species, e.g. rambutan, remain recalcitrant in vitro. Secondly, many governments are still reluctant to accept genetically modified crops as food plants. This is despite the fact that more than a billion acres of transgenic crops have been produced worldwide and no adverse effects on human health have been reported due to genetically modified plants in the past 25 years.

However, good progress is being made in the application of this technology to tropical fruit species (Table 5). Delay in fruit ripening (Mason and Botella, 1997) and control of *Phytophthoza* (Zhu et al., 2004) have been reported for papaya. In Australia, transgenic work in pineapples has resulted in control of ethylene production which influences flowering and fruiting (Trusov and Botella, 2006) and development of pineapples not susceptible to the postharvest disorder, blackheart (Graham et al., 2000). In Brazil, transgenic passionfruit are being developed with an antisense construct to the ACC oxidase gene (Quoirin et al., 2004) and that are resistant to passionfruit woodiness virus.

Genomics and Molecular Makers

The most significant contribution to genomics of tropical fruit species is the sequencing of the papaya genome at the University of Hawaii (http://asgpb.mhpcc.hawaii.edu**)**. Not only will this make a major contribution in the identification and use of genes in papaya and related species, but major benefits will also flow to other tropical fruit species in the identification and control of genes with homologous sequences that control a wide range of character traits. This will be particularly useful in species with long juvenile phases and thus long breeding cycles. Other contributions in this field include the construction of a bacterial artificial chromosome library of banana (Vilarinhos et al., 2003) and an online pineapple bioinformatics resource (Moyle et al., 2005).

Good progress has been made with molecular markers in the last 5 years. Genetic linkage maps have been produced for pineapple (Carlier et al., 2004), litchi (Liu and Mei, 2003), passionfruit (Carneiro et al., 2002) and two *Vasconcellea* species (Dillon et al., 2005). Microsatellite markers have been developed for six species (Table 6). A CAPS marker to identify a PRSV-P resistant gene in highland papaya (Dillon et al., 2006) should facilitate intergeneric hybridisation between *Carica papaya* and wild *Vasconcellea* species and backcrossing to introgress PRSV-P resistance into papaya. Markers have been identified for sex determination in papaya; both male (Somsri et al., 1998) and hermaphrodite (Lemos et al., 2002). A SCAR marker has been developed to identify dwarfism in bananas (Ramage et al., 2004a) and will facilitate the early detection of dwarf off-types after micropropagation. Markers have been developed to identify genes for resistance to major diseases: *Fusarium* (Javed et al., 2004) and *Mycosphaerella* (Zapater et al., 2004) in banana; and, *Xanthomonas* in passionfruit (Lopes et al., 2006). The mode of inheritance of chloroplast (cp) and mitochondrial (mt) DNA has been studied in papaya and some passionfruit species. Intergeneric hybrids between papaya as the female parent and *Vasconcellea* species demonstrated maternal inheritance of cpDNA and mtDNA (Van Droogenbroeck et al., 2005). Four hybrids between species of the subgenus *Passiflora* showed paternal inheritance of cpDNA while one hybrid of species of the subgenus *Decaloba* showed maternal inheritance of cpDNA; however, all mtDNAs of the 5 hybrids were maternally inherited (Muschner et al., 2006).

Cryopreservation

For a number of reasons, seed storage of tropical fruit species is often not successful. Many have recalcitrant seeds that are high in moisture content and lose viability when desiccated. Others are cold sensitive and will not tolerate being chilled for storage purposes (Chin and Krishnapillay, 1989). Seed of some fruit species have either no natural dormancy mechanism (mango and rambutan), or have a short life of only a few days (mangosteen). Some tropical fruit species have no seeds (banana and breadfruit), while others are highly heterozygous (papaya) and elite genotypes cannot be conserved by storing seed. Given the rapid loss of forests and germplasm in tropical regions, cryopreservation is of vital importance for conservation of valuable plant genetic resources. Cryopreservation research is well advanced for only a few tropical fruit species, with the bulk of species still requiring much work.

Cryopreservation of banana is more advanced than any other tropical fruit species. Embryogenic cell suspensions have been frozen using a classical protocol (Panis et al., 1990). Cryopreservation of proliferating meristems has been applied to 36 banana accessions belonging to 8 different genomic groups (Panis et al., 2002). This protocol is being implemented for cryopreserving the whole in vitro Musa collection maintained by the International Network for the Improvement of Banana and Plantain (INIBAP). Similarly, protocols for cryopreservation of *Citrus* species have been well defined. Whole seeds can be cryopreserved for species which display a sufficient level of desiccation tolerance (Normah and Serimala, 1997). Embryogenic calluses and cell suspensions (Engelmann et al., 1994), somatic embryos (Marin and Duran-Vila, 1988; Gonzalez-Arnao et al., 2003), ovules (Gonzalez-Arnao et al., 2003) and shoot tips (Wang et al., 2002) have been successfully cryopreserved. Of the *Citrus* species that are important to Thailand, protocols for micropropagation, embryogenesis and cryopreservation have been developed for *C. reticulate* and *C. grandis* (S. Somsri, pers. comm.).

In the author's laboratory, we demonstrated that *Carica papaya* seeds are sufficiently desiccation tolerant to withstand freezing with high survival percentages after partial desiccation. Apical and axillary shoot tips sampled from in vitro plantlets have been cryopreserved using the vitrification technique with recovery rates of 70% for some genotypes (Ashmore et al., 2001; Drew et al., 2005). Shoot tips of in vitro plantlets of 8 commercial pineapple varieties were successfully frozen using a vitrification protocol, with survival ranging between 10 and 65% (Gonzalez-Arnao et al., 1998). High survival (average of 89% for the 16 cultivars tested) was achieved with shoot tips of persimmon from dormant axillary buds after freezing using a vitrification protocol (Matsumoto et al., 2001).

CONCLUSIONS

The increase in reports of successes in biotechnology of tropical fruit crops in the past fifteen years is encouraging, however, relative to other major horticultural crops, research on tropical fruit species still lags behind. Many of the reports are at an early research stage or have been applied to juvenile tissue and must yet be extended to mature tissue. The outstanding exception is the progress on biotechnology of papaya. In vitro culture protocols have been refined over the past 25 years so that we now have excellent control of in vitro development (Manshardt and Drew, 1998). Micropropagation and embryo culture protocols underpin research on breeding and conservation strategies. The accumulated experience in papaya cell and tissue culture has facilitated development of cryopreservation protocols. Gene transfer in papaya is now routine and molecular markers have been developed for important genetic traits. Sequencing of the papaya genome is almost complete and should result in rapid advances in the understanding and control of papaya genes. Our comprehensive understanding of the crop has opened the door to so many more possibilities. The future of papaya research is exciting, and we look forward to a time when biotechnology of all topical fruit species reaches a similar stage.

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Tables

Table 1. Micropropagation of tropical fruit species that are of major importance.

Genera/Species	Common name	Explant	Results	Reference
Ananas comosus	pineapple	axillary buds	rapid multiplication	Drew 1980
		lateral buds	high multiplication rates, mature plants*	Rangan 1984**
		in vitro shoots / TIS	rapid multiplication	Escalona et al. 1999
		axillary buds/ bioreactor	rapid multiplication	Escalona et al. 2003
Artocarpus heterophyllus	jack fruit	shoot apices	rooted plantlets	Rajmohan et al. 1988
		shoot buds	rooted plantlets *	Roy et al. 1993
		adult axillary buds	rooted plantlets *	Rajendra et al. 1998
Carica papaya	papaya papaw	apical and lateral shoots	mature plants *	Drew 1992 Drew 2003**
Citrus grandis	pummelo	juvenile shoot tips	rooted shoots	Paudyal et al. 2000
		nodal segments	rooted plants*	Begum et al. 2004
Dimocarpus longan	longan	shoot tips	rooted shoots	Chen et al. 1999
		mature shoot tips	plantlets*	Wang et al. 2000
Litchi chinensis	litchi	shoot segments	shoots grafted to seedlings	Yu 1991
		seeds	multiple shoots, roots	Das et al. 1999
Mangifera indica	mango	shoot tips	explant survival	Thomas et al. 1997
		apical buds / adult	explant survival	Chavan et al. 2001
		stem nodes	rooted shoots	Shahin et al. 2003
Musa spp.	banana	shoot tips	mature plants*	Teisson et al. 1997**

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Table 2. Micropropagation of other tropical fruit species.

Genera/Species	Common name	Explant	Results	Reference
Annona atemoya	atemoya custard apple	nodal cuttings	rooted plantlets*	Rasai et al. 1994
Annona cherimola	cherimoya	nodal sections	multiple shoots	Jordan et al. 1991
	custard apple	nodal sections	rooted plantlets *	Encina et al. 1994
Annona muricata	soursop	internodal sections	adventitious shoots	Lemos et al. 1998
		nodal sections	plantlets	Zobayed et al. 2002
Annona squamosa	sugar apple	nodal sections	rooted plantlets*	Lemos et al. 1996b
	custard apple	nodal sections	plantlets	Zobayed et al. 2002
Arerrhoa carambola	carambola five corner fruit	nodal sections	rooted plantlets *	Khalekuzzaman et al. 1995
		shoot tips	rooted plantlets *	Li et al. 1999
Eugenia javanica	java apple	shoot tips	rooted plantlets	Kataoka et al. 1993
Feijoa sellowiana	pineapple	seedlings	shoots	Bhojwani et al. 1987
	guava	explants	shoots	Bertoni et al. 1996
Passiflora spp.	passionfruit	apical or lateral buds	rooted plants*	Drew 1996b**
Persea americana	avocado	nodal segments	rooted shoots	Biasi et al. 1994
		adult shoots	plantlets*	Barcelo-Munoz et al. 1999
		juvenile shoots	rooted plants*	Premkumar et al. 2003
Psidium guajava	guava	nodal segments	leaf development	Broodrijk 1989
		shoot tips	shoots, roots	Fitchet-Purnell 1990
		shoot tips	rooted shoots*	Papadatou et al. 1990
		shoot tips	shoot growth	Khattak 1990
		stem nodes	rooted plantlets*	Mohamed-Yasseen et al. 1995
Syzygium cumini	jambu java plum	nodal and shoot tips	rooted plantlets*	Yadav et al. 1990
Tamarindus indica	tamarind	nodal segments	rooted plantlets	Kopp et al. 1992
		mature embryos	rooted shoots	Mehta et al. 2000
Vasconcella pubesans	mountain papaya	shoot tips	rooted plants	Jordan 1992
Ziziphus sativa	jujube	microcuttings	shoots, roots	Vashakidze et al. 1988
Ziziphus mauritana	Indian jujube	nodal explants	rooted plantlets	Rathore et al. 1992

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Table 3. Caulogenesis, rhizogenesis and embryogenesis following callus induction from various tissue explants of tropical fruit species that are of major importance.

Genera/ Species	Common name	Explant	Organs/embryos produced in vitro	References
Ananas comosus	pineapple	axillary buds	somatic embryos	Daquinta et al. 1997
		axillary buds	synthetic seeds*	Soneji et al. 2002
Carica papaya	papaya papaw	seedling stem and cotyledon	caulogenesis embryogenesis, plantlets	Litz 1986** Fitch et al. 1990
		immature zygotic embryos	encapsulated artificial seeds	Ye et al. 1993
		embryogenic suspension culture	embryos of maternal origin	Monmarson et al. 1995
		integuments of immature seeds		
Citrus grandis	pummelo	endosperm	triploid plantlets	Wang et al. 1978
		endosperm	triploid plantlets	Yang et al. 2000
		epicotyl and root	rooted shoots	Goh et al. 1995
		juvenile leaf explants	rooted shoots	Huang et al. 2002
Dimocar-pus longan	longan	leaf	embryogenesis, plantlets	Litz 1988
		nodes	embryogenesis, plantlets	Celo et al. 1997
Garcinia mango-stana	Mango-steen	leaf	rooted shoots*	Goh et al. 1990, 1994
		seed segments	rooted shoots*	Normah et al. 1992, 1995
		leaf explants	plantlets	Te-chato et al. 1999, 2000
Litchi chinensis	Litchi, lychee	immature embryos	embryogenesis, plantlets	Zhou et al. 1993
		somatic embryos	plantlets*	Liao et al. 1998
		protoplasts	somatic embryos,	Yu et al. 2000
		young leaves	plantlets	Litz et al. 2005
			embryogenesis, plantlets	
Mangifera indica	mango	nucelli from immature seed	embryogenesis,	Mathews et al. 1992**
		nucellus	plantlets*	Litz et al. 1998
		protoplasts	embryogenic cultures	Ara et al. 2000
		nucellus	plantlets	Patena et al. 2002
			plantlets	
Musa spp.	banana	young male flowers	embryogenesis, plantlets	Teisson et al. 1997**
		protoplasts	plantlets	Assani et al. 2001
		somatic embryos	bioreacter	Kosky et al. 2002

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Table 4. Caulogenesis, rhizogenesis and embryogenesis following callus induction from various tissue explants of other tropical fruit species.

Genera/Species	Common name	Explant	Organs/embryos produced in vitro	References
Annona atemoya	atemoya, custard apple	leaf	shoots	Nair et al. 1984
		hypocotyls	rooted shoots*	Rasai et al. 1994
Annona cherimola	cherimoya, custard apple	petioles	shoots, roots	Jordan 1988
		zygotic embryos	shoots	Jordan et al. 1991
Annona muricata	soursop	hypocotyls	rooted shoots*	Bejoy et al. 1992
Annona squamosa	sugar apple, custard apple	hypocotyls	rooted shoots *	Lemos et al. 1996a
Averrhoa carambola	carambola, five-corner fruit	leaf	shoots	Litz et al. 1989
		root	rooted shoots	Rashid et al. 1992
		root	rooted shoots*	Kantharajah et al. 1992b
		hypocotyl and cotyledon	rooted shoots	Amin et al. 1993
		cotyledons	rooted shoots*	Khalekuzzaman et al.1995b
Carica pubescens	mountain papaya	axillary buds	embryogenesis	Jordan et al. 1996
Feijoa sellowiana	Feijoa pine-apple, guava	cotyledons	embryogenesis	Cruz et al. 1990
		cotyledons	embryogenesis	Canhoto et al. 1996
		zygotic embryos	embryogenesis	Vesco et al. 2001
		floral tissues	embryogenesis	Stefanello et al. 2005
Feronia limonia	elephant apple	cotyledon	rooted shoots*	Hossain et al. 1994
Passiflora spp.	passionfruit	stem and leaf sections	rooted shoots	Drew 1996b**
Persea americana	avocado	immature zygotic	embryogenesis	Pliego-Alfaro et al. 1988
		embryos	plantlets	Witjaksono et al. 1998
		protoplasts	micrografted plants	Raharjo et al. 2005
		embryos / shoots		
Psidium guajava	guava	fruit	callus	Madhavi et al. 1992
		hypocotyl explants	organogenesis	Singh et al. 2002
		mesocarp tissue	embryos / plantlets	Chandra et al. 2004
Tamarindus indica	tamarind	cotyledons	shoots, roots	Jaiwal et al. 1991
		hypocotyl segments	organogenesis plantlets*	Sonia et al. 1998
Zizyphus spinosus	sour jujube	leaves	shoots	Sun et al. 2002
Zizyphus jujuba	Chinese jujube	leaves	rooted plantlets	Du et al. 2005

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Table 5. Genetic transformation of tropical fruit species.

Genera/Species	Common name	Tissue Explant / Gene Delivery	Gene (s) transferred	Reference
Ananas comosus	pineapple	embryogenic callus	Blackheart R*	Graham et al. 2000
		embryogenic callus *Agrobacterium*	Chlorsulfuron R	Firoozabady et al. 2006
		embryogenic callus *Agrobacterium*	Basta R	Sripaoraya et al. 2006
		embryogenic callus	Flowering control	Trusov et al. 2006
Carica papaya	papaya papaw	embryogenic callus particle bombardment	PRSV-P Resistance	Fitch et al. 1992
Citrus grandis	pummelo	cotyledons *A. rhizogenes*	marker	Yang et al. 2005
Diospyros kaki	persimmon	embryogenic callus *Agrobacterium*	Fungal resistance	Tamura et al. 2004
Dimocarpus longan	longan	somatic embryos *Agrobacterium*	marker	Zeng et al. 2000
Litchi chinensis	litchi	leaves *Agrobacterium*	Green-fluorescent protein	Puchooa 2004
Musa spp.	banana	embryogenic callus particle bombardment	marker	Sagi et al. 1995
Passiflora edulis f. *flavicarpa*	passionfruit	leaves *Agrobacterium*	antisense ACC oxidase	Quoirin et al. 2004
Persea americana	avocado	embryogenic callus	marker	Litz et al. 2005
Zizyphus jujuba	sour jujube	stem sections *Agrobacterium*	antisense ACC synthase	He et al. 2004

* Resistance

Table 6. Use of molecular markers in tropical fruit species.

Genera/Species	Common name	Marker	Application	Reference
Ananas comosus	pineapple	RAPD/SSR AFLP	genetic linkage mapping	Carlier et al. 2004
Annona cherimola	cherimoya custard apple	MicroS*	species identification	Escribano et al. 2004
Carica papaya	papaya	DAF	male marker	Somsri et al. 1998
	papaw	RAPD	hermaphrodite marker	Lemos et al. 2002
		MicroS*	identify microsatellite markers	Perez et al. 2006
Citrus grandis	pummelo	RAPD/SSR	assess genetic diversity	Corazza-Nunes et al. 2002
Dimocarpus longan	longan	AFLP	assess genetic diversity	Lin et al. 2005
Garcinia mangostana	mangosteen	RAF	assess genetic diversity	Ramage et al. 2004b
Litchi chinensis	litchi	RAPD	genetic linkage mapping	Liu et al. 2003
Mangifera indica	mango	RAPD	assess genetic diversity	Karihaloo et al. 2003
		MicroS*	identify microsatellite markers	Duval et al. 2005
		MicroS*	identify microsatellite markers	Honsho et al. 2005
		MicroS*	identify microsatellite markers	Schnell et al. 2005
Musa spp.	banana	SCAR	detection of dwarf off-types	Ramage et al. 2004a
		RAPD	*Fusarium oxysporum* resistance	Javed et al. 2004
		RFLP	*Mycosphaerella* resistance	Zapater et al. 2004
		MicroS*	identify microsatellite markers	Creste et al. 2006
Passiflora edulis f. *flavicarpa*	passionfruit	RAPD	genetic linkage mapping	Carneiro et al. 2002
		MicroS*	identify microsatellite markers	Oliveira et al. 2005
		AFLP	*Xanthomonas* resistance genes	Lopes et al. 2006
Persea americana	avocado	MicroS*	assess genetic diversity	Ashworth et al. 2003
Vasconcellea spp.	wild papaya relatives	RAF	genetic linkage mapping	Dillon et al. 2005
		CAPS	PRSV-P resistant gene marker	Dillon et al. 2006
Zizyphus spp.	jujube	AFLP	assess genetic diversity	Singh et al. 2006

* Microsatellite markers