Chapter 7
Passiflora

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7.1 Introduction

The species of the genus *Passiflora* L., commonly known as passionflowers, are recognized for their tasty fruits, pharmaceutical properties and ornamental flowers. Although *Passiflora* species are numerous, few have significant commercial value. The vast majority are wild and poorly known. However, they constitute an important source of unexploited genetic diversity for the improvement of cultivated *Passiflora* species and the introduction of new crops. In addition, wild *Passiflora* species have potential useful characters, such as the resistance to particular pathogens, which can be incorporated by traditional breeding or molecular methods in crop species. The knowledge of the relatedness among *Passiflora* species is essential for the identification of wild crop relatives for future breeding programs. In this chapter, we review the advances in genetics, breeding and conservation of *Passiflora* species.

7.2 Botany

The pantropical family Passifloraceae comprises more than 600 species (Vanderplanck 2000) accommodated in 18 genera. Of this, *Passiflora* is the largest with ca. 520 species (MacDougal and Feuillet 2004). The first report of a *Passiflora* species was made in 1553 by Pedro Cieza de León during the Spanish colonial period in South America (Linnaeus 1753). In 1574, the Spanish botanist Nicolás Monardes suggested that flowers of *Passiflora* symbolized the Passion of the Christ. Linnaeus (1753) named the genus *Passiflora*, from the latin *flos passionis* that means "suffering flower". Since Linnaeus' publications, in which he described 22 and 24 *Passiflora* species (Linnaeus 1745, 1753), more than 500 new species have been described (MacDougal and Feuillet 2004) and their number continues to increase (Coppens d'Eeckenbrugge et al. 2001a; MacDougal 2001, 2003; Cervi 2002, 2006; Feuillet 2002, 2004; MacDougal and Hansen 2003; Jørgensen 2004; Jørgensen and Weigend 2004; MacDougal 2004, 2006; Vitta and Bernacci 2004; Krosnick 2005; Porter-Utley 2007; Vásquez et al. 2007; Azevedo 2008).

The center of diversity of *Passiflora* is located in the neotropics, with South America accounting for 95% of all the species (Fig. 7.1). A few species are also found in subtropical, and even temperate, regions of North and South America and 24 species are native from Southeast Asia, Australia and the Pacific Islands (Krosnick and Freudenstein 2005). Overall, passionflowers are adapted to a wide range of climates (0–40° latitude), altitudes (0–4,500 m) and ecosystems (from tropical humid forest to arid regions).

Passiflora flowers are mostly pollinated by bees, hummingbirds and bats (MacDougal 1983, 1994; Endress 1994; Büchert 1998; Kay 2001), but other types of pollinators such as wasps, butterflies and moths have also been recorded (MacDougal 1983). Many species, such as *P. edulis* f. *flavicarpa* O. Deg. and *P. incarnata* L., are self-incompatible and their fertilization is done through cross-pollination. The coevolution between plants of *Passiflora* and larvae of butterflies of tribe Heliconiini has been the subject

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C. Kole (ed.), *Wild Crop Relatives: Genomic and Breeding Resources, Tropical and Subtropical Fruits*,
DOI 10.1007/978-3-642-20447-0_7, © Springer-Verlag Berlin Heidelberg 2011

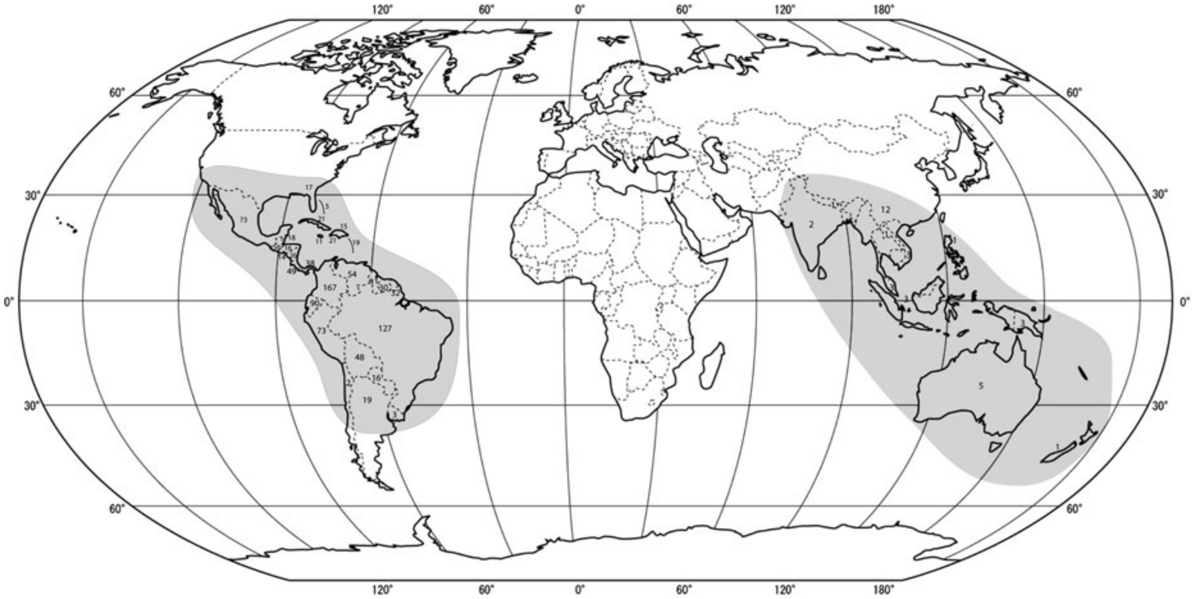

Fig. 7.1 Distribution of *Passiflora* richness according to Ocampo et al. (2007) and Shawn Krosnick (personal communication)

of several evolutionary studies (Gilbert 1971; Benson et al. 1975; Benson 1978; Gilbert 1980, 1982, 1983; Mitter and Brooks 1983; Spencer 1988). The caterpillars of these butterflies feed exclusively on *Passiflora* leaves.

7.2.1 Systematics

Based on previous classifications (Linnaeus 1753; Jussieu 1805a, b; De Candolle 1822; Roemer 1846; Harms 1923, 1925), Killip (1938) wrote the largest monograph on the genus including descriptions for 335 American species. His classification was based on floral characters and subdivided the genus into 22 subgenera. The Old World species were accommodated in the section *Disemma* of the subgenus *Decaloba* (Harms 1925). Escobar (1989) added the subgenus *Porphyropathantus*. The subgeneric classification of the genus has been recently challenged on morphological grounds by Feuillet and MacDougal (2003), who recognize only four subgenera which are subdivided into supersections, sections and series.

Cultivated species are essentially regrouped into four supersections of the largest subgenus *Passiflora* (see Sect. 7.4). At the subgenus level, the Feuillet and MacDougal classification is partly supported by recent molecular phylogenetic studies, as they clearly distinguish three major clades within *Passiflora*, corresponding to the three major subgenera (Muschner et al. 2003; Yockteng and Nadot 2004a; Hansen et al. 2006). The first problem is that this classification does not consider hundreds of species, such as the Old World species *Passiflora tetrandra* Banks ex DC. The second problem in the classification is the small subgenus *Deidamioides*, which regroups 13 species with dissimilar morphology. In fact, these species appear to be dispersed in phylogenetic reconstructions (Yockteng and Nadot 2004a; Krosnick and Freudenstein 2005). At lower levels, some supersections are supported by phylogenetic studies. For instance, the phylogeny based on nuclear sequences of glutamine synthase (ncpGS) supports mainly all supersections of subgenus *Decaloba* and the supersections *Coccinea, Passiflora* and *Tacsonia* of subgenus *Passiflora* (Yockteng and Nadot 2004a). However, the supersections *Stipulata* and *Laurifolia* of subgenus *Passiflora* do not form a clade in phylogenies. Members of the supersection *Stipulata* are dispersed in two non-related groups, in which section *Dysosmia* appears at the base of subgenus *Passiflora* and sections *Tacsonioides* and *Granadillastrum* are regrouped in one clade. Supersection *Laurifolia* is also divided into two well-supported but non-related clades. On one hand, the species of series *Tiliifolia* form a well supported clade closely related to species of supersection *Stipulata* except for the species in section *Dysosmia*. On the other hand, the species of series *Laurifoliae* and *Quadrangulares* form a clade closely related to supersection *Passiflora*. The results of this phylogenetic study point out the necessary revision of the classification by MacDougal and Feuillet. Molecular reconstructions are essential in this task; however, their robustness and resolution have not been sufficient for appropriate inferences on the divisions under the supersection level. Moreover, the interpretation of molecular data is highly complicated by the level of reticulation and the complexity of genome transmission in Passifloraceae. Interspecific hybridizations seem common in the genus, and chloroplast inheritance is often paternal or even biparental (see Sect. 7.5.3). Thus, phylogenetic inferences based on cpDNA sequences face the most severe problems anticipated by Harris and Ingram (1991) for classical phylogenetic methods, i.e., high intraspecific and even intraindividual variation and consequently lineage sorting, and also reticulate evolution of the chloroplast genome through hybridization and introgression. Studies based on nuclear ribosomal genes may suffer similar limitations. Many *Passiflora* species have originated from recent radiation, involving recent isolation and hybridization events, giving an incomplete concerted evolution of ribosomal gene copies in the genome (Lorenz-Lemke et al. 2005). Understanding the evolution of *Passiflora* is likely to be a long task that will impose many different molecular and morphological approaches as well as original methods for the interpretation of their data.

Although the classification of MacDougal and Feuillet (2004) needs to be revised and completed with the inclusion of many species, we have used it in the present text because it is the most recent to date.

1. Subgenus *Astrophea* (DC.) Mast. – 57 species
1.1. Supersection *Astrophea* Feuillet & MacDougal
1.1.1. Section *Astrophea* Feuillet & MacDougal
1.1.2. Section *Capreolata* MacDougal & Feuillet
1.1.3. Section *Leptopoda* Killip ex Feuillet & Cremers
1.2. Supersection *Pseudoastrophea* (Harms) Feuillet & MacDougal
1.2.1. Section *Pseudoastrophea* (Harms) Feuillet & MacDougal
1.2.2. Section *Botryastrophea* (Harms) Killip
1.2.2.1. Series *Botryastrophea* (Harms) MacDougal & Feuillet
1.2.2.2. Series *Carneae* Feuillet

2. Subgenus *Deidamioides* (Harms) Killip – 13 species
2.1. Section *Deidamioides* (Harms) Feuillet & MacDougal
2.2. Section *Polyanthea* DC
2.3. Section *Tetrastylis* (Bard. Rodr.) Harms
2.4. Section *Mayapanthathus* MacDougal & Feuillet
2.5. Section *Tryphostemmatoides* Harms

3. Subgenus Decaloba (DC.) Rchb. – 214 species
3.1. Supersection *Pterosperma* Gilbert & MacDougal
3.2. Supersection *Hahniopathanthus* (Harms) MacDougal & Feuillet
3.3. Supersection *Disemma* (Labill.) MacDougal & Feuillet
3.3.1. Section *Octandranthus* Harms
3.3.2. Section *Disemma* (Labill.) MacDougal & Feuillet
3.3.3. Section *Hollrungiella* Harms
3.4. Supersection *Multiflora* (Small) MacDougal & Feuillet
3.5. Supersection *Auriculata* MacDougal & Feuillet
3.6. Supersection *Cieca* (Medic.) MacDougal & Feuillet
3.7. Supersection *Bryonioides* (Harms) MacDougal & Feuillet
3.8. Supersection *Decaloba* (DC.) MacDougal & Feuillet
3.8.1. Section *Decaloba* DC.
3.8.2. Section *Xerogona* (Raf) Killip

4. Subgenus *Passiflora* Feuillet & MacDougal – 236 species
4.1. Supersection *Passiflora* Feuillet & MacDougal
4.1.2. Series *Passiflora* Feuillet & MacDougal
4.1.3. Series *Palmatisectae* Feuillet & MacDougal
4.1.4. Series *Pedatae* Killip ex Cervi
4.1.5. Series *Setaceae* Killip ex Cervi
4.2. Supersection *Stipulata* Feuillet & MacDougal
4.2.1. Section *Granadillastrum* Tr. & Planch
4.2.2. Section *Calopathanthus* Harms
4.2.3. Section *Tacsonioides* DC.
4.2.4. Section *Kermesinae* (Cervi) Feuillet & MacDougal
4.2.5. Section *Dysosmia* DC.
4.3. Supersection *Laurifolia* (Cervi) Feuillet & MacDougal
4.3.1. Series *Laurifoliae* Killip ex Cervi
4.3.2. Series *Quadrangulares* Feuillet & MacDougal
4.3.3. Series *Tiliafolia* Feuillet & MacDougal
4.3.4. Series *Marginatae* Killip ex Cervi

4.4. Supersection *Coccinea* Feuillet & MacDougal
4.5. Supersection *Distephana* (DC.) Feuillet & MacDougal
4.6. Supersection *Tacsonia* (Juss.) Feuillet & MacDougal
4.6.1. Section *Rathea* (Karst.) Harms
4.6.2. Section *Insignes* Feuillet & MacDougal
4.6.3. Section *Colombiana* Esc.
4.6.3.1 Series *Leptomischae* Esc.
4.6.3.2. Series *Colombianae* Esc.
4.6.3.3. Series *Quindiensae* Esc.
4.6.4. Section *Parritana* Esc.
4.6.5. Section *Fimbriatistipula* Esc.
4.6.6. Section *Tacsoniopsis* Tr. & Planch
4.6.7. Section *Elkea* Feuillet & MacDougal
4.6.8. Section *Tacsonia* (Juss.) Feuillet & MacDougal
4.6.9. Section *Boliviana* (Harms) Feuillet & MacDougal
4.6.10. Section *Trifoliata* Feuillet & MacDougal
4.6.11. Section *Manicata* (Harms) Feuillet & MacDougal

7.2.2 Morphology

Passiflora species exhibit a highly diversified morphology. Passionflowers are in general lianas, vines or herbs, mostly climbing with woody or herbaceous stems and axillary tendrils. Some species are arborescent and are regrouped in subgenus *Astrophea*. The stem can be cylindrical, angular or even winged. All species present stipules, sometimes deciduous, differing widely in size and shape. Leaves are alternate, simple, entire, lobed or palmate; rarely compound, such as in *P. cirrhiflora* Juss., *P. deidamioides* Harms, *P. pedata* L. and *P. trifoliata* Cav. The margins of the leaves range from serrate to entire. The extreme diversity of leaf morphology in *Passiflora* has been attributed to the pressure exerted in their coevolution with their main herbivores, the larvae of the Heliconiine butterflies (Gilbert 1982). The genus is also characterized by the presence of extrafloral nectaries that vary in form, position and number. They are common on the leaf petiole and along leaf margins, and can be also found on sepals or bract margins. In subgenus *Decaloba*, they are most often found in the lamina. These extrafloral nectaries (EFN) attract and reward ants that often have a protective role against herbivores, especially butterfly caterpillars, and nectar robbers (Smiley 1986; Apple and Feener 2001; Leal et al. 2006). Most passionflowers have three bracts, rarely less. Bracts can be foliar, elliptic, oblong or oval, persistent or deciduous with entire or dentate margin. The flowers are axillary, regular and hermaphroditic. Only *P. tetrandra* Banks ex DC. is dioecious. The calyx can be patelliform, campanulate or tubular. The perianth is composed of five sepals and five petals often similar in color and shape, and its color varies from flat green to showy violet or red. The most striking floral feature is the corona that is constituted of filaments in one or several series. These can be long, short or fused into a tube, such as in *P. murucuja* L. This character plays an essential role in the attraction and selection of pollinators (Endress 1994; Kay 2003; Yockteng 2003). A circular flower nectary is at the base of the corona. The reproductive organs are borne by an androgynophore holding the five stamens and three carpels, except in some Asiatic species (Krosnick et al. 2006). The ovary has one locule with multiple ovules disposed in three parietal placentas. The fruits are small, purple or blackish indehiscent berries with one or few seeds, commonly in subgenus *Decaloba,* or yellow or orange to red capsules with many seeds, mostly edible and measuring up to 30 cm long, commonly in subgenus *Passiflora*.

7.2.3 Cytology

Cytological data are essential to study the relationship between wild and cultivated species and to plan out interspecific hybridizations for future breeding programs.

Until now, chromosome counts have been reported for 94 *Passiflora* species (Table 7.1). The most common chromosome numbers are $2n = 12$, $2n = 18$ and $2n = 24$, which correspond roughly to the three main subgenera. The most common chromosome numbers of subgenera *Passiflora* and *Decaloba* are $2n = 18$ and $2n = 12$, respectively. Few species of subgenus *Astrophea* have been examined but the results indicate that the predominant number in the group is $2n = 24$. Divergent hypotheses about the base chromosome number of the genus have been proposed. A recent study based on a phylogenetic analysis proposed $x = 12$ as the base number (Hansen et al. 2006). Karyotype analyses have shown that several characters (number and position of satellites, number and length of chromosomes and the position of the

Table 7.1 Chromosome numbers of *Passiflora* species[a]

Taxa	Number of chromosomes
Supersection *Astrophea*	
P. lindeniana Triana & Planchón; *P. pentagona* (Cervi) Killip, 5S = 2 45S = 4	$n = 12$
P. pittieri Mast.; *P. haematostigma* Mart. Ex Mast.- *P. pentagona* (Harms) Killip	$2n = 24$
Supersection *Decaloba*	
P. adenopoda DC.; *P. biflora* Lam.; *P. aurantia* var. *aurantia* G. Forst.; *P. bryonioides* Kunth ex Spreng.; *P. candollei* Triana & Planch.; *P. capsularis* L. 5S = 2; 45S = 2; *P. capsularis* var. *acutiflora* Mast.; *P. cinnabarina* Lindley; *P. citrina* MacDougal; *P. cobanensis* Killip; *P. conzattiana* Killip; *P. coriacea* Juss.; *P. costaricensis* Killip; *P. cubensis* Urban; *P. dioscoreaefolia* Killip; *P. escobariana* MacDougal; *P. gilbertiana* MacDougal; *P. gracilis* J. Jacq. Ex Link.; *P. herbertiana* Lindley; *P. juliana* MacDougal; *P. karwinskii* Mast.; P. misera Kunth, 5S = 2. 45S = 4; *P. morifolia* Mast., 5S = 2 45S = 2; *P. nubicola* MacDougal; *P. oaxacensis* MacDougal; *P. obtusifolia* Sessé & Mociño; *P. penduliflora* Bertero; *P. perfoliata* L.; *P. porphyretica* Mast. var. *porphyretica*; *P. pterocarpa* MacDougal; *P. pulchella* Kunth; *P. quinquangularis* Calderón; *P. rovirosae* Killip; *P. rubra* L., 5S = 2 45S = 2; *P. sanguinolenta* Mast. & Linden; P. sexflora Jusssubsp. *itzensis* MacDougal ; *P. standleyi* Killip; *P. suberosa* L.; *P. tricuspis* Mast., 5S = 2 45S = 4; *P. warmingii* Mast.; *P. xiikzodz; P. xiikzodz* subsp. *xiikzodz* MacDougal	$n = 6$; $2n = 12$
P. holosericea L.; P. lobata (Killip) Hutch. Ex. MacDougal	$2n = 14$
P. gracilis J. Jacq. Ex Link.; *P. microstipula* Gilbert & MacDougal	$2n = 18$
P. gracilis J. Jacq. Ex Link	$2n = 20$
P. exsudans Zucc.; *P. lutea* L.; *P. punctata* L.; *P. suberosa* L., 5S = 4, 45S = 10, 1C = 1.85; *P. tenuiloba* Engelm.	$n = 12$; $2n = 24$
P. misera Kunth, 5S = 6, 45S = 12; *P. suberosa* L.	$n = 18$; $2n = 36$
P. lutea L.	$2n = 84$
Supersection *Passiflora*	
P. actinia Hook, 5S = 2 45S = 6; *P. alata* Curtis, 5S = 2 45S = 4; *P. amethystina* Mikan, 5S = 2 45S = 6; *P. antioquiensis* Karst.1C = 1.5 4, 2C = 3.0 4; *P. caerulea* L., 1C = 1.45 2C = 2.9; *P. cincinnata* Mast., 5S = 2 45S = 4; *P. coccinea* Aubl.; *P. edmundoi* Sacco, 2C = 3.43, 5S = 2 45S = 6; *P. edulis* Sims; *P. edulis* fo. *flavicarpa* Sims. Deg., 2C = 3.19, 2C = 3.2, 5S = 2 45S = 4; *P. edulis* Sims; *P. edulis* Sims fo. *edulis*, 2C = 3.16; *P. elegans* Mast.; *P. foetida* L.; *P. galbana* Mast.2C = 3.52 6, 5S = 2 45S = 6; *P. gibertii* Brown, 2C = 3.92; *P. glandulosa* Cav., 5S = 2 45S = 6; *P. incarnata* L.; *P. jilekii* Wawra; *P. kermesina* Link & Otto; *P. laurifolia* L., 2C = 3.88, 5S = 2 45S = 4; *P. ligularis* Juss.; *P. magnifica* L. K. Escobar; *P. malacophylla* Mast.; *P. maliformis* L., 2C = 3.78; *P. manicata* (Juss.) Pers.; *P. mixta* L. f.; *P. mucronata* Lam. 2C = 3.4, 5S = 2 45S = 6; *P. nitida* Kunth 2C = 4.82; *P. quadrangularis* L., 2C = 5.36; *P. racemosa* Brot.; *P. riparia* Mart. ex Mast.; *P. seemanii* Griseb.; *P. serratodigitata* L.; *P. serrulata* Jacq.; *P. setacea* DC.; *P. subpeltata* Ortega; *P. tarminiana* Coppens & Barney; *P. tripartita* (Juss.) Poir.; *P. tripartita* var. *mollissima* (Kunth) Holm-Niels. & Jørg.; *P. trisulca* Mast.; *P. umbilicata* (Griseb.) Harms; *P. vitifolia* Kunth	$n = 9$; $2n = 18$
P. incarnata L.	$n = 18$; $2n = 36$
P. foetida L. 5S = 4 45S = 6; *P. foetida* var. *gossypifolia* (Desv.) Mast.	$n = 10$; $2n = 20$
P. foetida L.	$2n = 22$
P. subpeltata	$2n = 72$

[a] Chromosome numbers (Heitz 1926; Nakajima 1931; Simonet and Miedzyrzecki 1932; Nishiyama and Kondo 1942; Baldwin 1949; Bowden 1940; 1945; Darlington and Janaki Ammal 1945; Storey 1950; La Cour 1951; Simmonds 1954; Beckett 1960; Heiser 1963; Lloyd 1963; Harvey 1966; Beal 1969a, 1969b, 1971, 1973; Diers 1961; MacDougal 1983, 1994; Gill et al. 1984; Guerra 1986; Berry 1987; Lepper and Duharte Gongora 1988; Turner and Zhao 1992; Snow and Macdougal 1993; Oliveira and Coleman 1996; Barbosa and Vieira 1997; Soares-Scott 1998; Gilbert and MacDougal 2000; Melo et al. 2001; Olaya Arias et al. 2002; Melo and Guerra 2003; Souza et al. 2003a, 2003b; Yockteng 2003). Nuclear content (2C or 1C) (Souza et al. 2004; Zonneveld et al. 2005; Souza et al. 2008) and number of sites 45S and 5S of rDNA (Melo and Guerra 2003) are also indicated

centromere) are specific to each subgenus (Snow and Macdougal 1993). The majority of species studied so far are diploid, but some species display various ploidy levels such as *P. misera* Kunth. with $2n = 12$, 36, *P suberosa* L. with $2n = 12$, 24 and 36, *P. subpeltata* Ortega with $2n = 18$, 72 and *P. incarnata* with

$2n = 18, 36$. Tetraploid hybrids ($2n = 36$) have also been obtained from somatic hybridization of diploid species ($2n = 18$) (Soares-Scott et al. 2005). However, the main commercial species and horticultural hybrids, obtained through sexual hybridization, are in general diploids (Vieira and Carneiro 2004).

Genome size values (2C) obtained for 10 diploid species of subgenus *Passiflora* range from 3.16 to 5.36 pg while the genome size of a tetraploid species of subgenus *Decaloba* is 1.83. Data of genome size can be useful in the assessment of somatic and sexual compatibility in *Passiflora* species. Further studies are, therefore, needed to increase data of genome size in *Passiflora*.

Examining the sites of 5S and 45S of rDNA, Melo and Guerra (2003) observed that species with $x = 6$ present only two 5S sites and two or four 45S sites whereas other species with $x = 9$ or 10 display more than two sites for both 45S and 5S (Table 7.1). These data suggest a diploid origin for the species with $x = 6$ and a polyploid origin for genomes with $x = 9$ or 10. In addition, the numbers of 45S and 5S sites should correspond to the ploidy level of the individual analyzed. In fact, they allow differentiating the two cytotypes of *P. misera* in which the number of 5S and 45S is three times larger in the hexaploid cytotype than in the diploid cytotype. In addition, interspecific hybrids derived from species of supersection *Passiflora* can be differentiated by their number of 45S rDNA sites (Melo and Guerra 2003).

Wild and cultivated *Passiflora* species generally present meiotic stability (Barbosa and Vieira 1997; Melo et al. 2001; Souza et al. 2003b). In contrast, hybrids exhibit meiotic instability, but sexual hybrids seem more stable than somatic ones (obtained by protoplast fusion) (Soares-Scott et al. 2003). Pollen viability in cultivated species is 80%, whilst in wild species it varies from 78.2% to 99.5% (Barbosa and Vieira 1997; Souza 2002).

7.2.4 Agricultural Status

Since prehistoric times, people have consumed fruits of *Passiflora* species. Passionfruits are rich in minerals, alkaloids, flavonoids, caretonoids and vitamins A and C, indicating their nutritional quality. More than 80 *Passiflora* species produce edible fruits (Coppens d'Eeckenbrugge 2003). About half of these species belong to subgenus *Decaloba* and their fruits are generally small, rarely more than 1.5 cm in diameter, so they are only collected on wild plants in rural areas. Although fruits produced by subgenus *Decaloba* are rich in qualitative terms, their potential for the development of economic fruit crops is very limited. Species with larger fruits belong to subgenus *Passiflora*. More precisely, species of economic potential for fruit production belong to supersections *Passiflora*, *Laurifolia* and *Tacsonia* (Fig. 7.2). Table 7.2 provides a list of 48 species of which more than 20 have been cultivated as fruit crops at very different scales.

Although passionfruits were widely known and grown by Native Americans (Patiño 1963), their development into commercial crops is fairly recent. *Passiflora edulis* f. *flavicarpa* (Fig. 7.3) was long overshadowed by the purple maracuja, published as a distinct taxon only in 1932 in the Flora of Hawaii, as an introduction from Australia (Degener 1932). For this country, Winks et al. (1988) mention that *P. edulis* was introduced in 1861; however, commercial development started only 60–70 years later, the yellow form and its hybrids becoming important only in the late 1950s. In 1951, Hawaiian plantings of this form amounted to less than five acres, from which a few vines were selected. By 1958, 1,200 acres were devoted to this crop as a basis of a well-established Hawaiian passionfruit juice industry. It was introduced in Venezuela in 1954, and trials took place in the Cauca Valley (Colombia) in 1963 with materials from Hawaii, Brazil and Venezuela (Torres and Giacometti 1963; Morton 1967). Among Andean passionfruits, Castañeda (1956) only mentions sweet granadilla (*P. ligularis* Juss.) as a highly demanded

Fig. 7.2 Diversity of edible fruits of subgenus *Passiflora*. Photo from Geo Coppens d'Eeckenbrugge

Table 7.2 Cultivated species of *Passiflora*[a]

Species	Cultivation	Uses	Origin	Common vernacular names	Close relatives with potential
Supersection *Passiflora*					
Series *Passiflora*					
P. bahiensis	Possibly tolerated	Fresh fruits, drinks	NE Brazil		
P. cincinnata	Garden ornamental with edible fruit	Fresh fruit, drinks	Bolivia, S Brazil, Paraguay	Pachio del monte	
P. edulis f. flavicarpa	Pantropical fruit crop	Fruit juice, drinks, medicinal	Brazil, Paraguay, N Argentina	Yellow passionfruit, maracuja	
P. edulis f. edulis	Tropical highland fruit crop	Fresh fruit, drinks	S Brazil, Paraguay, N Argentina	Purple passionfruit, purple maracuja	
P. incarnata	Ancient native crop of N America; ornamental	Desserts, drinks, vegetable, garden ornamental	E North America (USA and N Mexico)	Maypop, may-apple	
Supersection *Laurifolia*					
Series *Laurifoliae*					*P. acuminata*, *P. odontophylla*, *P. capparidifolia*, *P. crenata*, *P. cerasina*, *P. rufostipulata*, *P. pergrandis*, *P. tolimana*, *P. chaparensis*
P. ambigua	Sporadically in native countries	Fresh fruit	From S Mexico to Ecuador and Brazil	Granadilla de monte	
P. laurifolia	Home gardens – West Indies	Fresh fruit, drinks	Tropical South America	Golden apple, water lemon	
P. nigradenia	Occasionally in native countries	Fresh fruit	Bolivia, Peru	Pachio amarillo	
P. nitida	Small commercial plots dispersed in Panama and South America	Fresh fruit	Panama, Colombia, Venezuela, French Guiana, Brazil and E Peru	Bell apple, maracujá de cheiro	
P. popenovii	Small commercial plots in S Ecuador and S Colombia	Fresh fruit	Ecuador	Curubejo, granadilla de Quijos	
P. riparia	Occasionally in native countries	Mature fruits eaten raw	Amazon	Chinchorcon	
Series *Quadrangulares*					*P. trialata*
P. alata	Cultivated commercially in southern Brazil, sporadically in other South American countries	Fresh fruit, desserts, drinks	Amazon and riverine forests of Central Brazil	Winged-stem passionflower, sweet maracuja	
P. quadrangularis	Minor commercial crop in South and Central America; tropical home gardens	Fresh fruit, desserts, drinks, candied mesocarp	Uncertain, probably N South America	Barbadine, giant granadilla	

(*continued*)

Table 7.2 (continued)

Species	Cultivation	Uses	Origin	Common vernacular names	Close relatives with potential
Series *Tillifoliae*					*P. danielli, P. fieldiana,* *P. magnifica,* *P. seemannii ,* *P. palenquensis,* *P. triloba, P. serrulata,* *P. multiformis,* *P. platyloba*
P. ligularis	Tropical highlands of Central and South America	Fresh fruit	Mexico to Bolivia	Sweet granadilla	
P. maliformis	Small commercial cultivation in Colombia, home gardens in other countries	Fruit drinks	N Andes	Stone granadilla, couch apple, sweet calabash, water lemon	
P. tiliifolia	Rarely cultivated, in home gardens	Fruits eaten raw, drinks	Colombia, Ecuador, Peru	Machimbi, granadilla tripona	
Supersection *Stipulata*					
P. caerulea	Ornamental, under subtropical and Mediterranean climates	Bright red edible pulp, scarce and insipid	S Brazil, Argentina, Paraguay	Blue passionflower	
Supersection *Coccinea*					
P. coccinea	Rarely cultivated, in Guyana and Guadeloupe, as ornamental plant	Edible fruit	Amazonia	Scarlet passionflower	*P. quadriglandulosa,* *P. speciosa*
P. glandulosa	Rarely cultivated, in Guyana and Guadeloupe, as ornamental plant	Edible fruit	Amazonia	Maracuja cabeza de gado, markoesa	
P. vitifolia	Rarely cultivated, in Guyana and Guadeloupe, as ornamental plant	Edible fruit	From Honduras to NW South America	Cuchubao, curuvito	
Supersection *Tacsonia*					*P. ampullacea, P. mandonii*
P. antioquiensis	Becoming rare in home gardens in Colombia	Fresh fruit, medicinal	Colombia	Red banana passion-flower, curuba antioqueña	
P. cumbalensis	Cultivated around Bogotá, Colombia	Juice, drinks, sherbets	Andes (2,000–3,000 m) from N Colombia to C Peru	Rosy passionfruit, tacso, curuba roja	
P. mixta	Rarely cultivated, in home gardens	Juice, drinks, sherbets	Andes (2,500–3,600 m)	Curuba de indio	

P. pinnatistipula	Home gardens in the Andes	Fresh fruit	Andes (2,500–3,800 m) from Colombia to N Chile	Mountain granadilla, coldland granadilla, gulupa
P. tarminiana	Commercial and home gardens in native countries	Juice, drinks, sherbets	In high altitude in NW South America	Banana passionfruit, banana poka
P. tripartita var. azuayensis	Rarely, in home gardens of Ecuador	Juice, drinks, sherbets	Andes of Ecuador (2,600–3,300 m)	Tacso
P. tripartita var. mollissima	Commercial and home gardens in native countries	Juice, drinks, sherbets	Andes (2,000–3,200 m) from Venezuela to Bolivia	Yellow banana passionfruit, yellow curuba
P. tripartita var. tripartita	Rarely, in home gardens of Ecuador	Juice, drinks, sherbets	Andes of Ecuador (2,600–3,300 m)	Tacso

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[a] This list was produced following the classification of Feuillet and MacDougal (2003). Species presenting the same potential are also listed in relation to the affinity to cultivated species

Fig. 7.3 *Passiflora edulis* Sims. f. *flavicarpa* Deg. Photo from Geo Coppens d'Eeckenbrugge

Fig. 7.4 *Passiflora edulis* f. *edulis* Sims. Photo from Geo Coppens d'Eeckenbrugge

Fig. 7.5 *Passiflora ligularis* Juss. Photo from Geo Coppens d'Eeckenbrugge

fruit while the banana passionfruit (*P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen and Jørgensen) is only mentioned for its organoleptic qualities and its absence from two of the three Colombian cordilleras. The first experiment for the commercial cultivation of this species was reported by Jaramillo (1957).

Nowadays, 15 species are cultivated and a dozen are commercialized. The maracuja, *P. edulis* Sims, is the most important one. Its yellow form is cultivated in most tropical lowlands, particularly in tropical South America. Brazil is by far the main producer and consumer, with about 70% (half a million tons) of the world production. Ecuador is the main provider for the international market of passionfruit concentrate (Linden 2007). Colombia, the third main producer, has an appreciable home market and its contribution to international trade is variable. The purple form of *P. edulis*, *P. edulis* f. *edulis* (Fig. 7.4), originating from higher latitudes in southern South America, is confined to cooler climates. It has shown adaptation to tropical highlands, particularly in the Andes and in eastern Africa, as well as to subtropical climates, in Australia. The purple maracuja is present in small quantities on the international market, mostly provided by East African countries. While the yellow maracuja appears to be a cultigen, the purple form still exists in the wild in its birth place. Interestingly, the closest relative of *P. edulis* is *P. incarnata*, which was a common fruit crop of North America in Pre-Columbian times. The sweet granadilla, *P. ligularis* (Fig. 7.5), is cultivated for the fresh fruit market in the northeastern Andes, at moderate altitudes, and in Central America. Colombia is the main producer and consumer, and regularly provides small quantities at high price for the international market. The banana passionfruits, or curubas, are also widely cultivated in the Andes, above 2,000 m, and consumed in juices, sherbets and pastries. They mostly correspond to two cultigens, *P. tripartita* var. *mollisssima* (Fig. 7.6) and *P. tarminiana* Coppens and Barney. *Passiflora cumbalensis* (H. Karst.) Harms is commercialized at a very small scale around the city of Bogota in Colombia (Fig. 7.7). The ancient cultivation in home gardens of *P. antioquiensis* Karst. has been abandoned. Similarly, *P. pinnatistipula* (Harms) Killip is losing ground in High-Andean home gardens. The giant granadilla, *P. quadrangularis* L. (Fig. 7.8), is a cultigen present on the national markets in all tropical America. A close

Fig. 7.6 *Passiflora tripartita var. mollissima* (Kunth) Holm-Niels. & Jørg. Photo from Geo Coppens d'Eeckenbrugge

Fig. 7.7 *Passiflora cumbalensis* (H. Karst.) Harms. Photo from Geo Coppens d'Eeckenbrugge

relative, *P. alata* Curtis, has been recently selected and developed in Brazil, for the fresh fruit market (Kavati et al. 1998). Among the section *Laurifoliae* of subgenus *Passiflora*, *P. popenovii* Killip (Colombia, Ecuador) (Fig. 7.9), *P. nitida* Kunth (northern South America) and *P. riparia* Mart. ex Mast. (Amazon) are sold in local markets. *Passiflora nitida* is often confused with *P. laurifolia* L., which occurs wild in northeastern South America, and is still, albeit rarely, cultivated in the Antilles.

Fig. 7.8 *Passiflora quadrangularis* L. Photo from Geo Coppens d'Eeckenbrugge

Fig. 7.9 *Passiflora popenovii* Killip. Photo from Geo Coppens d'Eeckenbrugge

The peculiar beauty of their flowers has made passionflowers particularly interesting for the industry of ornamental plants. The development of the ornamental potential of passionflowers is still confined to circles of amateurs, who have developed a number of interspecific hybrids. The earliest was obtained by Thomas Milne in 1819. Since then, more than 400 hybrids have been generated to obtain more showy flowers (Peixoto 2005). Breeders have also used tetraploidization to obtain larger flowers (Fischer 2004). This spectacular diversity of shapes and colors has not been translated into commercial success, mostly because potential market is essentially concentrated at high latitudes. Indeed, as a garden ornamental, the most successful species is *P. caerulea* L. Its winter hardiness has allowed it to take a relative importance under mild temperate climates. Thus, much remains to be done to develop passionflowers for the tropical garden (Abreu et al. 2009).

Table 7.3 Theraupetic properties of *Passiflora* species[a]

Species	Theraupetic properties
P. alata	Analgesic (M), anthelmintic, antiashmatic, antibacterial, anticancer, antidiarrheal, antifungal, antioxidant , antiviral, anxiety (R), burn, cough, diabetes, diuretic, emetic, emmenagogues, fever, hemorrhoids, hypertension, hysteria, insomnia, internal inflammation (M), maintenance of natural killer (NK) cell activity, morphine deaddiction, sedative (M), seizure, skin inflammation (Iv), venom antidote
P. actinia	Anxiety (R), sedative (M)
P. caerulea	Anthelmintic, antibacterial, diuretic, sedative, seizure
P. clathrata Mast.	Sedative
P. capsularis	Emmenagogues
P. contrayerva Sm.	Venom antidote
P. coriacea	Antioxidant (Iv)
P. edulis	Analgesic, anthelmintics, antibacterial (Iv), anticancer (Iv), antidiarrheal, antifungal (Iv), antiviral (Iv), anxiety (R), diuretic, hypertension, internal inflammation (M), sedative, skin inflammation (M)
P. edulis var. flavicarpa	Anticancer (Iv), internal inflammation (M)
P. foetida	Analgesic, anthelmintics, antibacterial (Iv), anticancer (Iv), anxiety (H), cough, emetic, emmenagogues, fever, hysteria, insomnia, skin inflammation
P. incarnata	Anthelmintics, antiashmatic, anxiety, burn, diarrhea, dysmenorrheal, hemorrhoids, hysteria, insomnia, maintenance of natural killer cell activity (R), morphine deaddiction, neuralgia, sedative, seizure (M)
P. laurifolia	Venom antidote (Iv)
P. maliformis	Analgesic, fever, hypertension
P. mexicana Juss.	Sedative
P. mixta (and *P. tripartita*)	Antiseptic for ulcers, diuretic, febrifuge, hepatic and bilious affections, "intestinal fevers"
P. mucronata	Anthelmintic
P. nitida	Antibacterial (Iv), antioxidant (Iv)
P. palmeri Rose	Antibacterial (Iv), antioxidant (Iv)
P. pedunculata Hort. ex Mast.	Venom antidote
P. pentagona	Anthelmintic
P. quadrangularis	Anxiety (R), diabetes, hypertension
P. salvadorensis (Donn. Sm.) MacDougal	Diuretic
P. sexflora	Venom antidote
P. suberosa	Skin inflammation
P. tenuifila	Antioxidant (Iv)
P. trifoliata	Antiseptic, sedative
P. vitifolia	Venom antidote

[a] Properties according to Uphof (1968), Girault (1984), Braga and Junqueira (2000), Dhawan et al. (2004), and others cited in Sect. 7.7.3. Some properties have been tested in mice (M), in rats (R), in humans (H) or In vitro (Iv).

Passionflowers are also known for their medicinal properties (Table 7.3). In particular, *P. incarnata* is exploited in the pharmaceutical industry for its sedative, antispasmodic and analgesic properties (McGuire 1999; Dhawan et al. 2004).

Several common species of *Passiflora* have become weeds, as is the case of *P. capsularis* L., in the coffee growing zone of Colombia. Some have extended their range to other continents early after the great voyages of the XVI and XVII centuries, and some are even considered invasive. *Passiflora foetida* L. and *P. suberosa* have become pantropical weeds, for upland rice and other field crops. Nevertheless, the competitive ability of *P. foetida* has been used to control erosion and the grass *Imperata cylindrica* in coconut fields in Philippines and in sweet potato fields in Papua New

Guinea, while their young leaves are used in Surinam and Java as a vegetable (Waterhouse 1994). Several species of supersection *Tacsonia* have naturalized in New Zealand (Heenan and Sykes 2003). The most surprising case is that of *P. tarminiana,* a cultigen showing limited potential of escaping cultivation in the northern Andes, but invading protected areas in Hawaii, New Zealand and Australia. The considerable impact of *P. tarminiana* on native floras generated prevention against the introduction of passionflowers in many tropical countries. The problem of invasive passionflowers is treated more thoroughly in Sect. 7.9.

7.3 Conservation Initiatives

7.3.1 Evaluation of Genetic Erosion

Passiflora species are essential components of natural and semi-natural habitats and are critical to maintain ecosystem health. Their conservation and sustainable use are vital for improving their agricultural production and preserving the environment. Furthermore, the disappearance of *Passiflora* species from the ecosystem would entail the loss of other organisms depending on them, such as the butterflies *Heliconius* and many nectar feeding insects and birds.

Characterization and evaluation of the genetic diversity of wild and cultivated *Passiflora* species are necessary to identify and prevent genetic erosion. The genetic diversity of different *Passiflora* species has been studied using various molecular tools as isoenzymes (Segura et al. 1998, 2003b, 2005; Fore and Spira 2002; Tague and Fore 2005), random amplified polymorphic DNA (RAPD; Fajardo et al. 1998, Aukar et al. 2002; Crochemore et al. 2003; Viana et al. 2003; Bellon et al. 2007; Junqueira et al. 2007), cpDNA (Sanchez et al. 1999), amplified fragment length polymorphisms (AFLPs; Segura et al. 2002; Ocampo et al. 2007) and sequences of chloroplast and nuclear regions (Lorenz-Lemke et al. 2005; Koehler-Santos et al. 2006a, b).

These genetic studies show that wild and cultivated *Passiflora* species have, in general, high intraspecific and interspecific genetic variability. Only one species, *P. elegans* Mast., has been reported to have low genetic variability (Lorenz-Lemke et al. 2005). The genetic diversity of some cultivated and wild species has been compared (Segura et al. 1998, 2002, 2003b, 2005; Bellon et al. 2007). In the group of banana passionfruits, cultigens (*P. tripartita* var. *mollissima* and *P. tarminiana*) show very limited variation, contrasting with the high diversity of wild species (*P. mixta* L. f.) (Segura et al. 1998, 2002, 2003b, 2005). In contrast, Bellon et al. (2007) report no differences in genetic diversity among wild and commercial accessions of *P. edulis*. Ocampo et al. (2007) emphasize a surprisingly high diversity in the same species. However, the susceptibility of cultivated species to many pathogens is a probable indication of genetic erosion (Vieira and Carneiro 2004). Furthermore, human activities can facilitate new encounters between plants and pathogens, causing damage in wild populations (Webster et al. 2007).

There are in situ and ex situ approaches to conserve biodiversity and different ways of using genetic resources. We review the different attempts to conserve germplasm of *Passiflora*.

7.3.2 In Situ Conservation

In situ approaches for the conservation of *Passiflora* species have been mainly limited to protected areas. These measures may be appropriate for particular species, such as those located in sparsely populated rain forests, but they may be insufficient when human pressure is high. In Colombia, Ocampo et al. (2007) showed that most of the genus diversity was particularly concentrated on the hillsides of the coffee growing zone (81% of the total 167 species), i.e., in a highly populated and perturbated region, out of protected areas. Several common species thrive in disturbed habitats, so their distribution even benefits from the human pressure. However, most of the 58 Colombian endemic species are found in these increasingly deforested hillside areas, which puts them at a high risk. Furthermore, the *Passiflora* diversity hotspots correspond strikingly well to particular ecotopes, hence the necessity of integrating biodiversity conservation measures in the general management of agricultural activities, recreational areas and water resources (Ocampo et al. 2007). Applying IUCN criteria, Ocampo et al. (2007) consider that 71% of the Colombian Passifloraceae are under some degree of threat, 10% being critically endangered, 6.1% vulnerable and only 16% of the species are placed in the two “least concern” and “near threatened” categories, indicating the necessity of establishing conservation measures, at least in this country.

A proper documentation of *Passiflora* genetic diversity in relation with the geographic distribution of species is essential. Jørgensen et al. (2009), from the Missouri Botanical Garden (USA), have conducted a study to establish the geographical distribution of *Passiflora* species based on herbarium data and subsequently estimated their threat status. Preliminary results focused on subgenus *Decaloba*, Jørgensen (2009) found that 40% of these species are vulnerable or endangered, while another 40% are not currently threatened.

For a same level of habitat fragmentation or perturbation, the erosion risk varies according to several factors, such as the situation of the species in the ecological succession, its reproductive biology and its dependence on particular pollinators and dispersors. For instance, high genetic diversity at the local level with little differentiation among regions in *P. incarnata*, an early successional species, suggests that this genetic structure is related to founder effects and long-distance pollen-mediated gene flow (Fore and Spira 2002; Tague and Fore 2005). This situation contrasts with that of *P. mixta*, a similar weed that is affected by the fragmentation of the habitat of its pollinator, the hummingbird *Ensifera ensifera* (Lindberg and Olesen 2001).

7.3.3 Ex Situ Conservation

Conservation of *Passiflora* genetic resources out of their natural habitat is mainly done in botanical gardens and germplasm collections, maintained by national institutes. More than 50 *Passiflora* germplasm collections are maintained around the world (Ferreira 2005) and the *Passiflora* accessions in collections have increased in recent years, from 524 accessions in 1994 to 1,235 in 2004 (Ferreira 2005).

Figure 7.10 illustrates the information available of *Passiflora* germplasm obtained from several databases. A total of 2,203 *Passiflora* accessions are currently reported for a total of 159 species; 19% of these accessions correspond to the widely cultivated *P. edulis* and 24.7% are unclassified. When compared to other collections of crop genetic resources, the proportion of wild species is much more important (28.3%). The global effort may appear important; however, it must be related to the number of species, and also to their potential usefulness for breeding. Thus, Fig. 7.10 should be taken with caution. Many accessions are usually exchanged among collections, so duplication may be relatively important. While this is positive in terms of safety, the genetic diversity may be less important than suggested by the numbers.

The living plant collections of botanical gardens represent a significant source of conserved genetic resources. For instance, the Royal Botanic Gardens of Kew (UK) holds in their greenhouses 113 living passionflowers representing 72 different species and 21 hybrids or ornamental varieties. The Missouri Botanical Garden conserves 24 individuals of 15 species and 2 hybrids. In vivo plant collections with a scientific research purpose are also maintained by academic institutions, such as the Lawrence Gilbert’s laboratory at University of Texas in Austin (USA), which maintains 101 species and 30 hybrids (Gilbert 1998). Unexpected sources of ex situ genetic resources of *Passiflora* are the living collections maintained in greenhouses by plant societies and amateurs (Passiflora Society International 2008). Private societies regrouping amateurs are created for the sole purpose of studying, collecting and preserving *Passiflora* seeds and plants. Many members of these societies have large in vivo collections with more than a hundred species collected around the world. These societies have also seed banks available for their members. In France, the collection maintained by C. Houel, including 359 accessions from 241 species, has received the status of national collection (Houel 2009).

An appropriate documentation of germplasm is indispensable to make this stored diversity useful to everyone. The germplasm collection should be systematically classified and evaluated. For instance, Crochemore et al. (2003) used molecular markers to evaluate the samples of *P. edulis* obtained from the germplasm collection of the Instituto Agronômico do Paraná (IAPAR) in Brazil, facilitating by this way the identification of misclassified samples and the classification of unidentified ones. In addition, it is necessary to continuously increase the genetic variability of germplasm collection. This initiative requires identification of the most suitable populations. For instance, genetic studies in banana passionfruits showed that it would be preferable to collect samples of *P. tripartita*

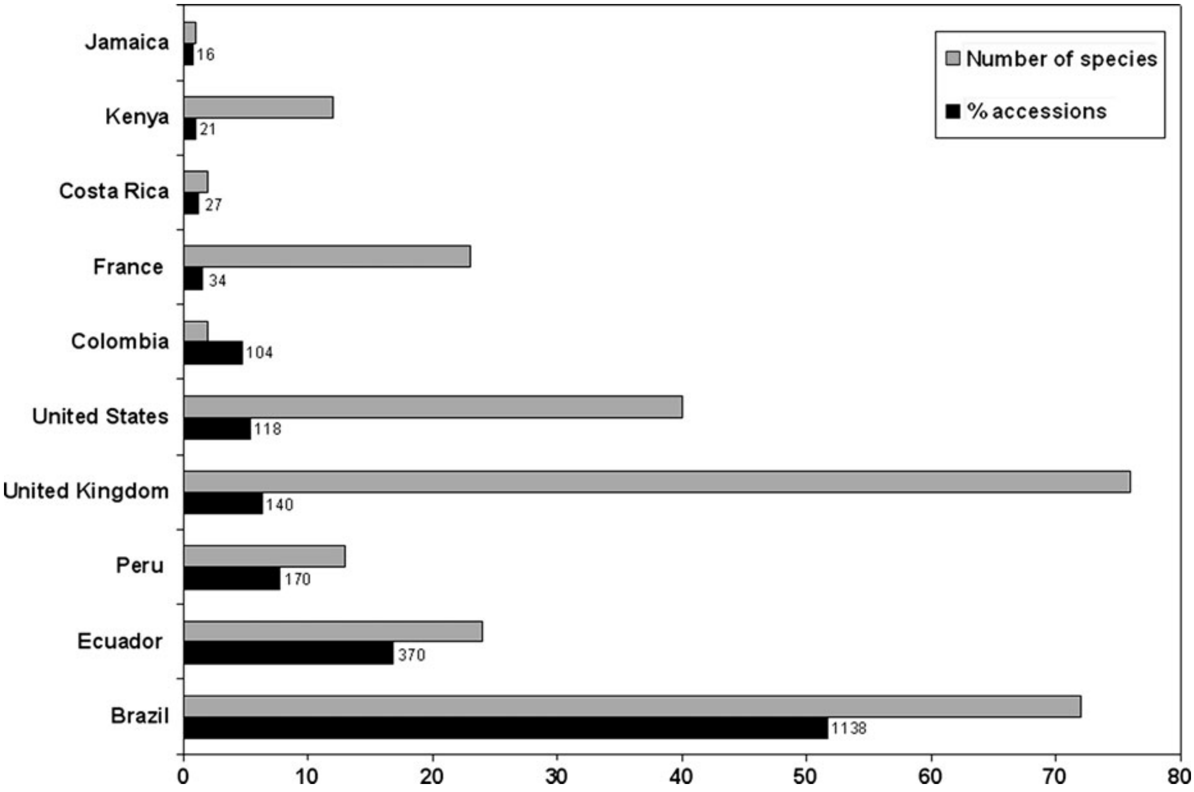

Fig. 7.10 Percentage of accessions and number of species represented in germplasm collections in each country. The number of accessions per country is also indicated. The information was obtained from the Germplasm Resources Information Network of the USDA-ARS (GRIN) (USDA 2010), the New World Fruit Database of the Biodiversity International that save information of many ex situ germplasm collections worldwide (Biodiversity International 2009), the Kew Botanical Garden and the Missouri Botanical Garden. The information about Brazil collections have been obtained from Ferreira (2005). Only data from the first ten countries with more abundant collections are illustrated in this chart

var. mollissima in southern populations (Ecuador and Peru) with high genetic variability, rather than in northern populations (Colombia and Venezuela), in order to enlarge the genetic diversity of these species in germplasm banks (Segura et al. 1998, 2002, 2003b, 2005).

7.4 Role in Elucidation of Origin and Evolution of Allied Crop Plants

The evolution of cultivated passionflowers has not been extensively investigated. However, despite the difficulties and inconsistencies in the taxonomic treatment of *Passiflora*, most of them show a close morphological relationship with several wild species, suggesting strong evolutionary affinities. The best approach is to identify the likely crop gene pools around these cultivated species. The closest relatives would be the taxa in the primary gene pool; slightly more distant relatives would constitute the secondary gene pool and so on.

The situation is different for ornamental plants, where vegetative propagation is the normal rule. Many crosses have been attempted according to the amateur creativity and potential genitors in the collection, with some surprising successes between what seem distantly related species. However, most of these hybrids set no fruits or empty fruits.

The present section is essentially devoted to the relatives of established fruit crops, all from subgenus *Passiflora* (Table 7.2). In each case, species exhibiting strong morphological affinities are considered. Elements from molecular studies are added at the end of each section, when available.

7.4.1 *Series* Passiflora *(Supersection* Passiflora*)*

P. edulis f. *flavicarpa* (yellow maracuja), *P. edulis* f. *edulis* (purple maracuja) and *P. incarnata* (maypop) can only be distinguished by a very limited number of morphological traits. They are much more clearly differentiated in their ecology. The first one is a vigorous tropical cultigen producing large yellow fruits. Although its origin is most probably Amazonian or periamazonian, the precise origin of yellow maracuja remains mysterious since it was developed out of South America. According to Vanderplanck (1991), the first documented cultivation was based on the seeds of a few fruits bought in a London market and sent to Argentina. Their descent would have been sent to the United States Department of Agriculture, and redistributed to Australia, New Zealand and later to Hawaii. This very narrow genetic base was somewhat widened through crosses with *P. edulis* f. *edulis*. The yellow maracuja shows strong self-incompatibility, even if a few pseudo-self-compatible clonal cultivars were selected in the 1950s. When reintroduced into South America, these selections were newly in contact with their natural pollinators and propagated again through seeds; so this trait was lost. Many cultivated populations still show the segregation for fruit color testifying that the yellow form was once crossed with the purple form. In contrast with our ignorance for the yellow maracuja, the origin of *P. edulis* f. *edulis* is clearly in southern South America, where it is still commonly found growing spontaneously, under subtropical conditions. Its adaptation to cool conditions allowed it to naturalize in other subtropical areas as well as in tropical highlands. The purple maracuja produces a fruit smaller than the yellow one, and appears at least partially self-fertile. The cross between the two forms of *P. edulis* is only fertile when the yellow form is used as the male genitor. Hybrids are intermediate and vigorous (Nakasone et al. 1967) with a regular meiosis, but have a lower chiasma frequency (Beal 1975).

The maypop was a common North American fruit crop in Pre-Columbian times. However, it is no more cultivated commercially, except for ornamental or pharmaceutical purposes. Crosses with *P. edulis* have shown limited success. Several authors report the obtention of fertile hybrids (Beal 1972; Anderson 1976; Winks et al. 1988), with more fertile F_2 and backcross progenies (Kajewski 1941) while others had to double their hybrid genome to restore fertility (Knight 1991). Thus, independent of the strong affinity between the two species, *P. incarnata* must be considered to be part of the secondary or tertiary gene pool of *P. edulis*. Similarly, *P. edulis* has been crossed with *P. cincinnata* Mast., with variable success (Howell 1989). The hybrid of Howell did not flower, while those obtained by Ruberté-Torres and Martin (1974) were intermediate and produced an edible fruit. Afterwards, species of different supersections, such as *P. caerulea* and *P. manicata* (Juss.) Pers., have also been crossed successfully with *P. incarnata* or *P. edulis* (Escobar 1985; Vanderplanck 1991) showing that morphological and genetic affinity are poor predictors of crossability in *Passiflora*.

7.4.2 *Series* Tiliifolia *(Supersection* Laurifolia*)*

This series includes two groups of species showing particularly large morphological and genetic similarity. The first one involves the cultivated *P. ligularis*, as well as the wild *P. tiliifolia* L. (Fig. 7.11) that can be often observed in close vicinity, in the same highland conditions. Despite its striking resemblance with *P. ligularis*, *P. tiliifolia* is rarely cultivated. Other very similar species are *P. palenquensis* Holm-Niels. & Lawesson, and *P. fieldiana*, which grow under very different ecological conditions (low to mid elevations). A close relative (*P.* af. *palenquensis*) has been observed under cultivation in the Pacific lowlands of

Fig. 7.11 *Passiflora tiliifolia* L. Photo from John Ocampo

Fig. 7.12 *Passiflora maliformis* L. Photo from John Ocampo

western Colombia. All these species produce fruits that are round to ovoid, tapering at apex, with a thin, smooth and brittle epicarp and sweet grayish arils, easy to consume in hand. Hybrids have not been reported between these species.

The second group involves the stone granadilla, *P. maliformis* (Fig. 7.12), and its close relatives, *P. platyloba*, *P. serrulata* Jacq. and *P. multiformis* Jacq. All of them exhibit yellow stipules, a same fruit shape and similar habit and habitat. In fact, intraspecific variation in these four species is so wide, as compared to presumed interspecific variation, that species delimitation should be re-examined objectively, on both morphological and genetic grounds. The only morphological trait that discriminates them is leaf lobation, but it may be highly variable within many species. The two groups are slightly differentiated in the molecular study of Yockteng and Nadot (2004a). Amplified fragment length polymorphism (AFLP) markers show a close affinity between *P. ligularis* and *P. tiliifolia*, but no particular affinity with *P. maliformis* (Segura et al. 2002; Ocampo et al. 2007).

7.4.3 *Series* Laurifoliae *(Supersection* Laurifolia*)*

The morphological similarity prevailing within this series made the identification and classification of species particularly difficult (Killip 1938). Several species may coexist in the same region such as *P. nitida*, *P. laurifolia*, *P. crenata* Feuillet & Cremers and *P. cerasina* Annonay & Feuillet in the lowland forests of French Guiana or *P. nitida*, *P. nigradenia* Rusby, *P. riparia*, *P. fernandezii* Escobar, *P. chaparensis* Vásquez and *P. venusta* Vásquez & Delanoy in Bolivia (Vásquez et al. 2007). The origin of *P. laurifolia* populations cultivated in the Antilles has to be clarified, and their relationship to wild conspecific materials from South America. In the northern South America, the most commonly cultivated *Laurifoliae* species is *P. nitida*, while *P. laurifolia* seems to occur only in the wild in the Guianas. No wild representative of *P. popenovii* has been reported, and the species is so difficult to propagate through seeds that vegetative propagation is often preferred. Its vernacular name "granadilla de Quijos" refers to an ancient Native American culture, and also a province of Ecuador, where it may have its origin (Patiño 1963). The situation is different for *P. nigradenia*, which is still found in both wild and cultivated conditions in Bolivia (Vásquez 1998).

The species of series *Laurifoliae* present a particular high potential. Indeed, they not only produce a highly aromatic fruit pulp, but also they exhibit at the same time a high genetic diversity and a high uniformity in most essential traits, so they could allow the breeder to create original and adapted cultivars without facing the problems of an excessive genetic segregation. However, their taxonomy should be first clarified, delineating species on an objective basis and establishing their affinities. The exceptional capacity to grow on flooded soils and their resistance to soil parasites is of outmost interest for developing rootstocks or transferring the corresponding genes to other passionfruit species. However, these species have several traits reflecting their lack of domestication. Their seeds tend to germinate very irregularly, often with marked latency, and they often allocate too many resources to vegetative growth. Thus, they cannot be accommodated on artificial supports, because they could invade other fruits trees in the orchard. In addition, their harvest season is short and impredictable. These problems should be addressed in order to fully develop their economic potential.

7.4.4 *Series* Quadrangulares *(Supersection* Laurifolia*)*

In contrast with the situation prevailing in other series of supersection *Laurifolia*, the high morphological similarity of *P. alata* and *P. quadrangularis* reflects their close genetic affinity and fertile hybrids are easily obtained (JC de Oliveira personal communication). Their progeny segregates for resistance traits (Oliveira et al. 1996). Both species have been used successfully in crosses with *P. caerulea* (Vanderplanck 1991).

7.4.5 *Supersection* Tacsonia

The supersection *Tacsonia* comprises 61 species, 11 of which are cultivated and known with the name of banana passionfruits. The fruits of *P. tripartita* var. *mollissima* and *P. tarminiana* are present all the year on the Andean markets and a small quantity is even exported to Europe. Their thin leathery pericarp and generous orange, succulent arils ensure the highest pulp yields among passionfruits (around 60% for the two cultigens). *Tacsonia* species are differentiated by their large flowers presenting a long floral tube mostly pollinated by hummingbirds. In most of them, the hypanthium length varies between 7 and 13 cm, restricting the normal access to nectar to only one species, the sword-billed hummingbird, *Ensifera ensifera* (Snow and Snow 1980; Lindberg and Olesen 2001). As for this bird, their native distribution is limited to the Andean mountains between 1,400 and 4,000 m, from Venezuela to Chile.

Although this has not been established systematically, interspecific barriers are much more labile in this supersection as compared to supersection *Passiflora*. Spontaneous hybrids have been relatively frequently reported, involving the cultivated *P. arminiana*, *P. tripartita* var. *mollissima*, *P. pinnatistipula* as well as the wild *P. tripartita*, *P. mixta*, *P. cumbalensis* and *P. antioquiensis* (Killip 1938; Escobar 1981; Geo Coppens d'Eeckenbrugge personal observations). The most distinct species, *P. manicata*, has also been involved in artificial crosses, giving fertile hybrids (Escobar 1985). However, Schoeniger (1986) in an attempt to exploit the intercompatibility of *P. tripartita* var. *mollissima* with *P. mixta* and *P. cumbalensis* for the genetic improvement of the former, observed phenomena of unilateral incompatibility, loss of fertility, seed germination and general viability in advanced hybrid and backcross generations.

Segura et al. (2002, 2003a) have studied the relationships between cultivated species and some of their wild relatives with isozyme and AFLP markers. The four most common species, *P. tarminiana*, *P. cumbalensis*, *P. tripartita* and *P. mixta* were differentiated from the others. In the isozyme study, the accessions of the two latter species showed particular affinity, as they clustered together, following a more geographic than taxonomic pattern. A wider study (Segura et al. 2005) confirmed the existence of a gene flow between *P. mixta* and *P. tripartita*, as well as a higher genetic diversity in Ecuador, as compared to Colombia and Venezuela, two countries where the genetic diversity of the two cultigens appeared very low. The closer genetic affinity between *P. tripartita* and *P. mixta* seems consistent with their closer morphological affinity (Villacis et al. 1998); however, *P. tripartita* var. *mollissima* hybridizes easily with both *P. mixta* and *P. tarminiana*. The observation of meiosis in a few hybrids indicates a better chromosome pairing between the two cultigens than with the wild *P. mixta* (Olaya 2002). However, the two parental phenotypes of the cultigens are recovered in less than four generations in the progenies of their hybrids, suggesting very limited exchanges at the genome level. The nature of interspecific barriers among species of supersection *Tacsonia* is not clear yet.

7.5 Role in Classical and Molecular Genetic Studies

The genetics of species *Passiflora* is mainly known from cultivated species. Therefore, the genetics of wild species is not known except for a few population genetic studies. Data from gene actions, physiological pathways and genetic mapping are only available for the cultivated species *P. edulis*. However, the studies based on crop species constitute a reference for future research in wild species. They can even provide new tools, as could be the case of transferable microsatellite markers.

7.5.1 *Population Genetic Studies*

Genetics studies conducted in wild and crop *Passiflora* species reveal their genetic diversity, the geographic structure of populations and the relationship among species. Passionflowers generally present high interspecific and intraspecific genetic variability except for *P.* elegans (Fajardo et al. 1998; Segura et al. 1998, 2002, 2003b, 2005; Sanchez et al. 1999; Aukar et al. 2002; Fore and Spira 2002; Crochemore et al. 2003; Viana et al. 2003; Lorenz-Lemke et al. 2005; Tague and Fore 2005; Bellon et al. 2007; Junqueira et al. 2007).

Species belonging to the same supersections are in general closely related. For instance, *P. elegans* and *P. actinia* of supersection *Stipulata* are close relatives (Lorenz-Lemke et al. 2005), as well as *P. tarminiana*, *P. tripartita* var. *mollissima* and *P. mixta* of supersection *Tacsonia* (Segura et al. 1998, 2003b). The genetic proximity among species has facilitated interspecific hybridization events. Genetic studies also permit to know how historical geological, climatic and ecological conditions have affected the distribution of species. For example, the high intraspecific variability of *P. actinia* is structured along a north–south gradient in Brazil, where northern populations are more diversified than the southern. This study gives evidence of migration of northern populations of *P. actinia* to the south probably caused by a change in temperature and humidity in southern region at the beginning of the Holocene (11,000–10,000 years BP). Populations of *P. elegans* show a low genetic variability not structured geographically, probably as a consequence of severe bottleneck events during Pleistocene glacial stage (Lorenz-Lemke et al. 2005). The genetic variation of banana passionfruit species, *P. tarminiana*, *P. tripartita* var. *mollissima* and *P. mixta,* is structured along a south–north gradient giving evidence that their center of diversity is probably in the southern region of their range (Segura et al. 2005). *Passiflora nitida* also has a high genetic variability with a geographical structure and a higher variation among populations than within populations (Junqueira et al. 2007). The opposite is found in *P. alata* in which the greater variation is found within populations while a geographical structure is absent, possibly due to high levels of gene flow between populations (Koehler-Santos et al. 2006a). Genetic variability among populations of *P. incarnata* is lower than within populations. The strong gene flow between geographically distant populations, enhanced by the combined action of self-incompatibility and long distance pollen transfer by pollinators, explain the low differentiation among *P. incarnata* populations (Tague and Fore 2005).

The study of geographical structure of genetic diversity is essential to prioritize the conservation of genetically diversified areas.

7.5.2 Genetics of Self-Incompatibility

The genetic control of self-incompatibility in *Passiflora* has been studied since 1959 only in cultivated species (Bruckner et al. 2005). In the yellow passionfruit species (*P. edulis* f. *flavicarpa*), self-compatibility is controlled by the combination of a gametophytic and a sporophytic systems (Rego et al. 1999, 2000; Suassuna et al. 2003; Souza et al. 2006). The gametophytic system is regulated by the *S* gene that has multiple alleles. A single allele is expressed in the haploid pollen grain that germinates only in a diploid pistil, which does not express the same allele. The sporophytic system is regulated by a cluster of three genes encoding for proteins with a role in the reception and recognition of pollen (Hiscock and Tabah 2003). Pollen will not germinate on the diploid stigma of a flower that contains either of the two alleles of the sporophyte parent that produced the pollen.

Self-incompatibility of *Passiflora* species facilitates the outcrossing of individuals and promotes the creation of new genotypes. Therefore, it must be taken into account in breeding programs to improve crop species, ensuring sufficient diversity of *S* haplotypes to provide fertilization and good fruit production.

7.5.3 Organellar Inheritance

Besides, mitochondria and chloroplast in *Passiflora* are inherited by different mechanisms. Studies present evidence that mtDNA is maternally inherited in passionflowers, while the inheritance of cpDNA can be maternal, paternal or biparental (Muschner et al. 2006; Hansen et al. 2007). The biparental plastid transmission, suspected by Corriveau and Coleman (1988) on the basis of observations in epifluorescence microscopy, was confirmed by Do et al. (1992) in crosses involving the two forms of *P. edulis*. Only the chloroplasts of *P. edulis* f. *flavicarpa* were found in the reciprocal hybrids. In a cross with *P. coccinea* Aubl. as female parent, *P. edulis* f. *flavicarpa* also transmitted its chlorotype to the progeny. Mrácek (2005) observed that the plastids of *P. menispermifolia* Kunth. and *P. oerstedii* Mast. are biparentally transmitted. The heteroplasmy of hybrids also permitted to evidence that the progeny's plastome–genome was incompatible with the parental genome of *P. menispermifolia* (Mrácek 2005). The heteroplasmy could cause many problems in phylogenetic inferences based on chloroplast gene sequences. In species of subgenus *Passiflora*, the cpDNA is reported to be inherited paternally or biparentally whilst it appeared maternally inherited in two species of subgenus *Decaloba* studied so far (Muschner et al. 2006; Hansen et al. 2007). Although the differential inheritance of plastids could bring new evidence to support the subdivision of these two subgenera, it underlines that interpretation of phylogenies based on cpDNA sequences has to be very cautious. Moreover, the phenomenon of heteroplasmy could explain the incongruences between phylogenetic studies based on chloroplast sequences (Muschner et al. 2003; Hansen et al. 2006). In addition, it is not possible to infer the paternal origin of the pollen and seeds of hybrid individuals (Hansen et al. 2007).

7.5.4 Construction of Genetic Linkage Maps

Linkage maps are useful for identification of important plant genes controlling simply and quantitatively inherited traits. They could facilitate the identification of genomic regions that might affect the variation of important *Passiflora* traits involved in fruit production, fruit quality and disease resistance.

In self-incompatible species, like many *Passiflora* species, linkage maps are constructed using a strategy known as two-way pseudo-testcross, based on monoparental dominant markers that segregate in a 1:1 proportion (Grattapaglia and Sederoff 1994). The final result is the generation of two individual maps, one for each parental genotype. This method was used to generate genetic linkage maps of *P. edulis* f. *flavicarpa,* based on random amplified polymorphic DNA (RAPD) and AFLP markers in three different studies (Carneiro et al. 2002; Moraes 2005; Lopes et al. 2006). The linkage maps were obtained from the same F_1 population derived from a single cross between two clones of *P. edulis* f. *flavicarpa*, "IAPAR 123" (female parent) and "IAPAR 06" (male parent) (Carneiro et al. 2002; Moraes 2005; Moraes et al. 2005; Lopes et al. 2006).

Moreover, the development of specific microsatellites markers to yellow passionfruit (Oliveira et al. 2005) and the use of a maximum likelihood approach (Wu et al. 2002) permitted to generate a first integrative linkage genetic map using the same F_1 population. In this study, individual parental maps were integrated into one map based on the segregation of codominant markers (microsatellites) and dominant markers (AFLP) in one or both the parents (Oliveira et al. 2008). The integrated map is more saturated in markers and the linkage groups are longer than those in individual maps, which will probably facilitate the mapping of crucial traits for the crop species.

7.5.5 Mapping Genes and Polygenic Clusters

Once the genetic linkage map has been developed, the next step is to identify or map the genes controlling the traits of interest by quantitative trait loci (QTL) mapping.

Fruit phenotype is, in general, the result of the interaction of multiple genes as well as environmental factors. Therefore, QTL mapping is necessary to determine the genetic architecture underlying the fruit phenotype. Several fruit characters in yellow passionfruit (*P. edulis* f. *flavicarpa*) show a wide genetic variability and also a high coefficient of heritability (52.6–83%) (Moraes 2005; Moraes et al. 2005). Using an AFLP linkage map, Moraes (2005) mapped genomic regions associated with eight fruit-related traits (fruit yield, number of fruits, average fruit weight, average fruit length, average fruit width, percentage of pulp, soluble solids content and average of fruit size). A total of 41 QTLs were mapped with four to seven QTLs by trait (Moraes 2005). Most (90%) of the QTLs have small or medium effects on fruit traits explaining 15% of the trait's phenotypic variance. These values are higher than those found in some recent studies conducted in other plant species such as cucumber (Yuan et al. 2008) and melon (Obando et al. 2008). The expression of some traits such as fruit yield and the number of fruits are correlated and probably controlled by the same genes or proximal genes. QTLs for important fruit quality traits in passionfruit were, therefore, located on the linkage map (Moraes et al. 2005). The key markers most closely linked to these QTLs can be further developed to provide tools for breeding and selection in *Passiflora*. A future QTL analysis in wild species would permit to locate genes coding desirable fruit traits that can be incorporated into cultivated species.

QTL mapping in *Passiflora* has also been used to identify genomic regions related to the resistance to one of the common pathogen *Xanthomonas campestris* pv. *passiflorae* (Lopes et al. 2006). This bacterial pathogen causes a disease in *Passiflora* that leads to a premature death of the plant. A unique quantitative resistance loci (QRL) was found in genetic linkage map explaining only 15.8% of the total phenotypic variance in the segregating population (Lopes et al. 2006). The results in *Passiflora* are not sufficient (Lopes et al. 2006) compared to the studies in other plant species that detected several QRLs explaining a large percentage of phenotypic variance for resistance to *X. campestris* (Studer et al. 2006; Soengas et al. 2007). However, it is necessary to continue this first effort in order to progress in the detection of genes controlling the resistance against pathogens in particular in wild resistant species.

7.5.6 Assessment of Gene Actions and Physiological Pathways

Some of the pathways studied in *P. edulis* are the ethylene pathway and its role in growth and development of the plant (Arjona and Matta 1991; Shiomi et al. 1996) and the jasmonate pathway and its role in defense response (Siqueira et al. 2008). The inositol phosphate biosynthesis pathway has also been studied. This pathway produces signal molecules having vital roles encompassing regulation of many processes indispensable to organism homeostasis (Abreu and Aragao 2007). One enzyme implicated in this pathway has been detected not only in *P. edulis* but also in *P. eichleriana* Mast., *P. caerulea, P. nitida* and *P. coccinea* Aubl.

Pelegrini et al. (2006) also described a new defense peptide *Pe*-AFP1 (*Passiflora edulis* antifungal peptide-1) that is a pathogen inhibitor. In vitro, this defense peptide inhibits the development of the filamentous fungi *Trichoderma harzianum*, *Fusarium oxysporum* and *Aspergillus fumigatus* but not of *Rhyzoctonia solani*, *Paracoccidioides brasiliensis* and *Candida albicans* (Pelegrini et al. 2006). The discovery of *Pe*-AFP1 can lead to the development of antifungal drugs against human and plant diseases and of transgenic plants resistant to fungal pathogens. Besides, these results are promising to conduct studies in the detection of new plant defense peptides in other *Passiflora* species, particularly in species already described as resistant to pathogens.

7.5.7 Host–Parasite Interactions

Species of *Passiflora*, especially crop species, suffer different diseases caused by virus, bacteria and fungi. In Table 7.4, the most common pathogens are listed. New descriptions of pathogens affecting *Passiflora* species appear frequently (Parry et al. 2004; Baker and Jones 2007; Tang et al. 2008; Villalobos et al. 2009). Some of these diseases produce considerable losses in passionfruit production. The harmful diseases are the fruit woodiness caused by the virus *Passiflora* woodiness virus (PWV) and cowpea aphid-borne mosaic virus (CABMV), the anthracnose, scab and septoriose caused, respectively, by the three fungi, *Colletotrichum gloeosporioides*, *Cladosporium* spp. and *Septoria passiflorae* and bacteriosis caused by the bacteria *Xanthomonas axonopodis* pv. *passiflorae*.

Larger transportation linked to human activity allows pathogens to encounter potential new hosts and can thus promote the emergence of new epidemics when pathogens could adapt to these novel hosts. Rarely these pathogens are specific to one species and thus they have the capacity to shift from a primary host to a new host species. For example, in Australia the *Passiflora* woodiness virus (PWV) described firstly in the indigenous species *P. aurantia* G. Forst. is now also infecting introduced species such as *P. edulis, P. caerulea* and *P. foetida* (Webster et al. 2007). Other examples are the infection by the *Passiflora* latent virus of the non-native species *P. tarminiana* in New Zealand (Tang et al. 2008) and the infection by fungus *Phytoplasma* spp. of introduced species *P. edulis* in Costa Rica (Tang et al. 2008; Villalobos et al. 2009). Pathogen species described

Table 7.4 Diseases affecting *Passiflora* species[a]

Pathogen	Species susceptible	Known resistant species
Bacteria		
Xanthomonas axonopodis pv. passiflorae	*P. alata, P. amethystina, P. cincinnata, P. coccinea, P. edulis* f. *edulis, P. edulis* f. *flavicarpa, P. nitida, P. setacea*	*P. actinia, P. amethystina, P. caerulea, P. edulis* f. *edulis, P. edulis f. flavicarpa, P. foetida, P. gibertii, P. laurifolia, P. maliformis, P. morifolia, P. mucronata, P. nitida, P. odontophylla, P. serrato-digitata, P. setacea, P. Tenuifila*
Fungi		
Alternaria spp.	*P. edulis* f. *flavicarpa*	*P. manicata*
Cladosporium cladosporioides	*P. edulis* f. *flavicarpa*	
Cladosporium herbarum	*P. nitida, P. cincinnata*	
Colletotrichum gloeosporioides	*P. alata, P. caerulea, P. cincinnata, , P. cirrhiflora, P. coccinea, P. edulis f. flavicarpa, P. garckei, P. gibertii, P. serratodigitata, P. setacea, P. tenuifila, P. tripartita* var. *mollissima*	*P. amethystina, P. caerulea, P. candida, P. coccinea, P. fuchsiiflora, P. gibertii, P. mucronata, P. nitida, P. serrato-digitata, P. odontophylla, P. setacea, P. Tenuifila*
Fusarium oxysporum f. sp. passiflorae	*P. edulis* f. *edulis, P. edulis* f. *flavicarpa, P. capsularis, P. cincinnata, P. foetida, P. laurifolia, P. Ligularis, P. morifolia, P. tripartita* var. *mollissima*	*P. alata, P. caerulea, P. edulis* f. *edulis* (wild), *P. gibertii, P. ligularis, P. macrocarpa, P. nitida, P. quadrangularis, P. Setacea*
Fusarium solani (*Nectria haematococca*)	*P. edulis* f. *edulis, P. edulis f. flavicarpa, P. caerulea, P. cincinnata, P. maliformis, P. pohli, P. setacea, P. sidaefolia, P. suberosa*	*P. actinia, P. alata, P. amethystina, P. caerulea, P. coccinea, P. edulis* f. *edulis, P. gibertii, P. mucronata, P. nitida, P. odontophylla, P. serrato-digitata, P. setacea, P. Tenuifila*
Glomerella cingulata	*P. edulis*	
Oidium neolycopersici, Oidium passiflorae	*P. caerulea, P. edulis, P. foetida*	
Phytophthora nicotianae var. nicotianae.	*P. edulis* f. *edulis, P. setacea, P. sidaefolia*	*P. caerulea* (tolerant)
Phytophthora parasitica	*P. edulis*	
Phytoplasma spp.	*P. edulis*	
Pseudocercospora spp.	*P. foetida, P. setacea*	
Virus		
Bean yellow mosaic virus (BYMV)	*P. caerulea*	
Chrysanthemum B carlavirus (CVB)	*P. caerulea*	
Citrus tristeza closterovirus (CTV)	*P. gracilis*	
Cowpea aphid-borne mosaic virus (CABMV)	*P. edulis* f. *flavicarpa*	*P. coccinea, P. incarnata, P. macrocarpa, P. Suberosa*
Cucumber Mosaic virus, cucumovirus (CMV)	*P. edulis, P. caerulea*	
East Asian *Passiflora* virus (EAPV)	*P. edulis*	
Maracuja mosaic tobamovirus (MarMV)	*P. edulis*	
Okra mosaic tymovirus (OkMV)	*P. edulis*	
Passiflora chlorosis potyvirus	*P. incence*	
Passiflora latent carlavirus (PLV)	*P. edulis, P. caerulea, P. foetida , P. suberosa, P. subpeltata, P. tarminiana*	
Passiflora virus Y (PaVY)	*P. edulis, P foetida*	
Passionfruit crinkle virus (PCV)	*P. edulis* f. *edulis, P. edulis* f. *flavicarpa, P. suberosa*	
Passionfruit mottle virus (PFMoV)	*P. edulis*	
Passionfruit rhabdovirus (PRV).	*P. edulis*	

(*continued*)

Table 7.4 (continued)

Pathogen	Species susceptible	Known resistant species
Passionfruit ringspot virus (PFRSV)	*P. edulis, P. foetida, P. quadrangularis*	
Passionfruit Sri Lankan mottle potyvirus (SLPMV)	*P. edulis* f. *flavicarpa, P. foetida, P. tripartita var. mollissima*	*P. suberosa*
Passionfruit vein-clearing rhabdovirus	*P. edulis*	
Passionfruit woodiness potyvirus (PWV)	*P. alata, P. amethystina, P. aurantia, P. edulis* f. *edulis, P. edulis* f. *flavicarpa, P. foetida, P. gibertii, P. mucronata, P. nitida, P. odontophylla, P. serrato-digitata, P. suberosa, P; subpeltata, P. tenuifila*	*P. actinia, P. coccinea, P setacea*
Passionfruit yellow mosaic tymovirus [PFYMV (PaYMV)]	*P. edulis f. flavicarpa*	
Purple granadilla mosaic virus	*P. edulis, P. alata, P. serrato-digitata, P. caerulea, P. maliformis, P. gibertii, P. edulis* f. *flavicarpa.*	
Nematodes		
Meloidogyne incognita		*P. caerulea, P. edulis, P. cincinnata, P. Quadrangularis*

[a] The diseases are listed according the following references: Delanoë (1991), Ploetz (1991), Chang (1992), Cole et al. (1992), Chang et al. (1994), Brunt et al. (1996), Pares et al. (1997), Gonzalez et al. (2000), Wolcan and Larran (2000), Davis et al. (2002), Gioria et al. (2002), Morales et al. (2002), Parrella and Castellano (2002), Pegg et al. (2002), Parry et al. (2004), Fischer et al. (2005), Junqueira et al. (2005), Iwai et al. (2006b), Liberato (2006), Nascimento et al. (2006), Ploetz (2006), Baker and Jones (2007), Dianese et al. (2008), Jankovics et al. (2008), Santos et al. (2008), Tang et al. (2008), Villalobos et al. (2009). Resistant *Passiflora* species of a specific disease are also listed: Delanoë (1991, 1992), Junqueira et al. (2005), Meletti et al. (2005)

initially in a phylogenetically distant host plant can also be found in species of *Passiflora*. For instance, the bean yellow mosaic virus infects now plants of *P. caerulea* in Italy (Parrella and Castellano 2002) and the worldwide *Citrus tristeza* closterovirus (CTV) infects the wild species *P. gracilis* J. Jacq. ex Link (Brunt et al. 1996). Closely related virus can develop the same disease symptoms in *Passiflora* plants. The fruit woodiness has been described to be caused primarily by only the PWV virus. However, Nascimento et al. (2006) found that the disease is also caused by the related CABMV potyvirus. While Brazilian plants are primarely infected by the CABMV, the Australian and Asian plants are mostly infected by the PWV.

Strategies of selection could be performed to choose the more resistant genotypes of cultivated species in order to reduce the susceptibility to diseases. Among the yellow passionfruit, Martins et al. (2008) found some genotypes moderately resistant to *Colletotrichum gloeosporioides*. Moreover, the resistance to the scab caused by the fungus *Cladosporium cladosporioides* has been enhanced by the selection of more resistant individuals of yellow passionfruit (Santos et al. 2008). However, the variability of resistance to different diseases of cultivated species appears in general to be very low (Junqueira et al. 2003).

Therefore, the identification of resistant species is essential to increase the variability of resistance in susceptible cultivated species by breeding strategies. The numerous wild species of *Passiflora* are a potential source of genotypes resistant to particular pathogens. Several wild species are resistant to the most common pathogens such as *P. actinia* that is non-susceptible to the PWV, the CABMV and the fungus *Colletotrichum gloeosporioides* (Junqueira et al. 2005) (Table 7.4). The feasibility to produce hybrids from interspecific crosses enhances the probability of obtaining resistant varieties of crop species (see Sect. 7.6.4).

7.6 Crop Improvement Through Traditional and Advanced Tools

7.6.1 On-Farm Selection and Genetic Resource Management

Passionfruits' genetic improvement owes much to the efforts of the native growers in South America. For most species, even those of economic importance, many farmers still select a few good-looking fruits from higher yielding vines to establish the next orchard. In banana passionfruit, some growers select those seeds in the median part of the fruit. The intensity of selection is relatively weak particularly if the crop cycle is long (about 10-year-old banana passionfruit orchards). Growers may detect interspecific hybrids and favor them in their orchard. In Colombia, in a valley where *P. tripartita* var. *mollissima* cultivation has recently been established, the growers favor hybrids with *P. mixta* in an attempt to reduce the impact of anthracnose on fruit appearance. Other farmers bring spontaneous *P. mixta* × *P. tripartita* var. *mollissima* from the wild to grow them in their own home garden. Conversely, conservative farmers often discard those seedlings exhibiting particularly thin leaf lobes, indicative of hybridization with *P. mixta*, because hybrids tend to bear less fruits. Similar situations may exist in other cases where cultivated and wild species look very similar; some farmers tolerate wild vines of *P. tiliifolia* on the borders of their *P. ligularis* plots. Partial sympatry of similar cultivated and wild species also occurs in the series *Laurifoliae* in the lowlands.

As passionfruits have become more important commodities and even local markets have offered higher prices for more standardized products, plot size and planting densities have increased, favoring, unfortunately, the development of a wide cohort of pests and diseases. Although the shortening of crop cycles benefits the higher yield and better sanitary conditions of young vines, it increases both the costs of establishment of the crop and the need to get a higher and faster economic return. Such intensification has necessarily run parallel to the development of formal breeding in the passionfruit crops of wider importance. Local strains have been developed through mass selection for the sweet granadilla and banana passionfruit, while the development of yellow maracuja cultivars has been shared by the public and private sectors.

7.6.2 Development of Clonal Cultivars

Yellow maracuja breeding was initiated in Hawaii to improve yield and quality of the crop for the juice industry. Yields were multiplied fourfold, and juice yield improved from 25% to 35% (Morton 1967). To face the increasing phytopathological constraints of the crop, breeders attempted to widen its depleted genetic basis through hybridization with the purple form (Nakasone et al. 1967). Selection was most often carried out on an individual basis and the selected elite material was propagated clonally, which led to prefer pseudo-self-compatible genotypes (Fouque and Fouque 1980). When the elite material was strongly self-incompatible, cross-pollination had to be organized by interplanting distinct clones in the orchard (Knight 1972; Ito 1978).

In the context of clonal propagation of planting materials, another solution was attempted in Australia by grafting the plants on rootstock resistant or tolerant to the most severe soil pathogens. This practice imposed on the development of two parallel programs – a breeding program for scions and a rootstock program – without solving the problem of viral transmission via the planting materials (Coppens d'Eeckenbrugge et al. 2001b). Distinct species have been tested as rootstocks for *P. edulis*. *Passiflora incarnata* and *P. caerulea* were appreciated for their general resistance to soil pathogens as well as cool temperature at subtropical latitudes, but the latter was discarded because of its abundant suckering. Hybridization was attempted between both species and *P. edulis* f. *flavicarpa* for obtaining of better rootstock. Interspecific crosses involving *P. incarnata* were used as well for the scion, in order to improve the cold and virus resistance of commercial fruit types (Winks et al. 1988). However, their outcome is not clear, as the use of clones and pure *P. edulis* f. *flavicarpa* rootstock is still recommended in Australia (Department of Employment Economic Development & Innovation 2005).

7.6.3 Synthetic Population and Hybrid Breeding

When the Hawaiian selections of yellow maracuja came back to their home continent, they returned to sexual propagation, which had two major consequences. First, seed propagation reduced the impact of viral diseases as this planting material was not contaminated. Second, a higher level of agromorphological variation appeared in the crop, notably the segregation for fruit colors, still observed in many

South American populations, and also in all important agronomical traits. Considerable genetic gains for yield and fruit size and quality were made possible, first through mass selection, then through the development of synthetic varieties (see Meletti et al. 2005 for a review), initially composed by selected clones (Maluf et al. 1989) and then by half-sib or full-sib progenies (Meletti 1998). Early producing cultivars were developed for the fresh fruit market and for the juice industry, showing yields up to 50 tons/ha, pulp yields close to 50% and soluble solids around 15–16°Brix (Meletti et al. 2000). However, no similar success was obtained in terms of disease resistances (Vieira and Carneiro 2004), which have a considerable impact on production, mostly because no sources of appreciable resistance/tolerance had been identified within *P. edulis*. A similar partial success allowed the development of *P. alata* from a home garden or from the wild to a commercial crop for the fresh fruit market, through selection and standardization of fruit shape (Kavati et al. 1998). As limitations in yield and quality had been overcome, the focus of breeding efforts shifted towards genetic resistances, through the characterization of other species (see Sect. 7.5.7) and introgression programs (Sect. 7.6.4).

In Brazil also, the yellow and purple forms of *P. edulis* have been crossed to generate varieties with better fruit qualities. Although these varieties are, in general, highly susceptible to diseases (Vieira and Carneiro 2004), they permitted the selection of plants with good fruit yield and also some degree of resistance to bacteriose and anthracnose (Junqueira et al. 2005).

7.6.4 Introgression of Traits Through Interspecific Hybridization

The search of resistance traits is the most frequent reason for attempting many different crosses and the subsequent introgression at the interspecific level. A few projects have been justified on other grounds, such as adapting the crop to temperate latitudes and/or to smaller pollinators through a reduction in flower size, or introducing self-compatibility to improve pollination efficiency (Knight 1991).

Some species seem to be amenable to hybridization more easily than others, as in the case for *P. caerulea*. Self-incompatibility of many cultivated species, such as *P. edulis* and *P. incarnata,* could be a functional component of interspecific incompatibility, explaining cases of unilateral incompatibility as in the cross between the two forms of *P. edulis* (Coppens d'Eeckenbrugge et al. 2001b). According to the difficulty of particular crosses, the production of interspecific seeds has involved controlled crosses or more sophisticated techniques, such as hormones, to retard floral abscission or/and intra- and interspecific double pollination (Payan and Martin 1975). The frequent sterility of the resulting F_1 hybrids poses a further problem. Knight (1991) doubled the chromosome number of hybrids between *P. incarnata* and the two forms of *P. edulis* to restore their fertility. The subsequent tetraploid progenies were self-incompatible, which is consistent with the sporophytic system, remaining functional in polyploids. Their fruits gave a pleasant juice, despite a relatively clear color, with characteristics closer to maracujas than to maypops (Senter et al. 1993). Knight concluded that they had promise as a new fruit crop for warm–temperate zones. However, the only documented outcome today is the ornamental cultivar "Byron Beauty" derived from this hybrid (Knight et al. 1995).

Junqueira et al. (2005) attempted to transfer the resistance of *P. setacea* DC. against the anthracnose and PWV to *P. edulis* f. *flavicarpa* by introgression. The initial cross is fertile in both directions. The F_1 hybrids appear vigorous, closer to the *P. setacea* parent in many respects, and resistant. However, they face pollination problems related to abnormal floral morphology. Four backcross generations were obtained using the recurrent genitor as pollen-donor, allowing the recovery of a *P. edulis* phenotype. However, genetic resistance to the PWV seems to be inherited in a quantitative manner, diminishing with successive generations. The BC_3 still showed resistance to anthracnose; however, fruit yield was very low in comparison to susceptible cultivars, probably in relation to their very long androgynophore. The same authors report very similar results using *P. coccinea* instead of *P. setacea*, with hybrid vigor, general resistance transfer, abnormal floral proportions and very low fruit set in the F_1 and BC_1 generations. When exploring the potential of the cross with *P. caerulea*, they obtained sterile hybrids with good resistance to bacteriosis and anthracnose, but susceptible to the PWV and attractive to caterpillars of *Dione* butterflies. Fertility was partly restored in the BC_2 generation. Many more such crosses within subgenus *Passiflora* have been attempted by the same group, including triple hybridizations. The compatibility of species has also been evaluated and some appear totally compatible, producing fertile seeds (Junqueira et al. 2005). For instance, the widely cultivated *P. edulis* f. *flavicarpa* seems totally compatible with *P. glandulosa* and very compatible with *P. coccinea* (79.2%) and *P. setacea* (85.7%) but it is totally incompatible to *P. actinia* and very incompatible with *P. caerulea* (8.6%) (Junqueira et al. 2005). Recently, 17 interspecific F_1 hybrids were generated from the crosses *P. laurifolia* × *P. nitida, P. edulis* f. *flavicarpa* × *P. coccinea*, *P. caerulea* × *P. amethystina* J.C. Mikan, *P. glandulosa* Cav. × *P. galbana* Mast., *P. coccinea* × *P. actinia, P. glandulosa* × *P. edulis* f. *flavicarpa, P. sidaefolia* M. Roemer × *P. actinia, P. galbana* × *P. actinia,* F_1 (*P. coccinea* × *P. setaceax P. coccinea*), F_1 (*P. coccinea* × *P. setacea*) × *P. mucronata* Lam., *P. eichleriana* × *P. gibertii* N.E. Br., *P. galbana* × *P. edulis* f. *flavicarpa, P. glandulosa* × *P. edulis edulis, P. glandulosa* × *P. sidaefolia, P. coccinea* × *P. setacea*. Their success was confirmed using RAPD markers (Junqueira et al. 2008).

Schoeniger (1986) conducted a long series of experiments of interspecific crosses in the supersection *Tacsonia*, with the aim of introgressing genetic resistance to oidium and anthracnose from wild *P. mixta* and *P. cumbalensis* into *P. tripartita* var. *mollissima*. In this case, F_1 hybrids also showed remarkable vigor, with larger leaves, stipules, bracts and flowers. According to Escobar (1981), pollen viability is equal to or higher in the hybrids, as compared to parental species. However, fertility strongly decreases in F_2 and BC_1 generations, following a lack of flowering and low fruit set, aggravated by poor seed germination and high mortality. Considerable variation appeared for all organs, including fruits (production, size, shape, succulence and flavor of arils), with cases of transgressions in the segregation and abnormal leaf and flower shapes. Selfing F_2 and BC_1 plants produced similar results, and some plants exhibited traits that were unknown in the parent species (Schoeniger 1986). Later, Coppens d'Eeckenbrugge crossed *P. tripartita* var. *mollissima* with *P. tarminiana* and *P. mixta* and characterized the resulting F_1 hybrids; crosses were fully fertile. The hybrids were morphologically intermediate, with a tendency to be more similar to their maternal parent. They showed high vegetative vigor, with large leaves and larger, but somewhat rarer, fruits, of intermediate characteristics. Concerning resistance to anthracnose, which produces black dots depreciating the fruits, the hybrids between the susceptible *P. tripartita* var. *mollissima* and the resistant *P. tarminiana* expressed the symptoms at an intermediate level, suggesting a quantitative inheritance of the resistance and presaging difficulties for its effective introgression (Primot et al. 2005). These examples show that the introgression of resistance traits into cultivated passionfruits through interspecific crosses will be a long process. Sexual compatibility is not a synonym to genome compatibility and disease resistances are complex traits whose inheritance often seems to depend on a dosage effect. Lack of resistant germplasm in *P. edulis* f. *flavicarpa* leaves few other solutions than pursuing the effort. The situation may be different in species, such as *P. tripartita*, for which resistant conspecific materials may be explored, particularly in wild botanical varieties. *P. mixta*, a wild species, which shows spontaneous genetic exchanges with the cultigen, is also worth exploring.

The success of introgression at the interspecific level will depend not only on the number of crosses and generations obtained, but also probably more on the development of specific tools to understand and follow the transfer of targeted traits. A particular investment is necessary in cytogenetics, studying the chromosomal structure of the parents and recombination in the hybrids, as well as molecular tools, such as genetic maps and trait markers. Furthermore, cytogenetics could provide some keys for a better understanding of interspecific incompatibility in *Passiflora*.

7.6.5 Somatic Hybridization

Somatic hybrids of *Passiflora* species have been generated from protoplasts isolated from leaf tissues or callus derived from suspension cultures. These somatic hybrids are artificial polyploids and present, in general, chromosomal instability. For example, despite their high pollen viability, meiotic irregularities have been found in somatic allotetraploid hybrids ($4n = 36$) obtained from the cross between the diploid parents *P. edulis* f. *flavicarpa* ($2n = 18$) and *P. amethystina* ($2n = 18$) (Vieira and Carneiro 2004). In contrast, the somatic allotetraploid hybrids generated from protoplasts of *P. edulis* f. *flavicarpa* and *P. cincinnata* do not present aneuploidy. They have stable meiotic behavior and normal pollen viability suitable for the introgression of genes such as the resistance against *Xanthomonas campestris* pv. *passiflorae* present in *P. cincinnata* (Vieira and Carneiro 2004). Other desirable traits such as cold tolerance have been transmitted via somatic hybridization from *P. incarnata* to *P. edulis* f. *flavicarpa* (Otoni et al. 1995).

7.6.6 Genetic Transformation

To counteract the negative effects of pathogens, resistant transgenic plants of yellow passionfruit (*P. edulis* f. *flavicarpa*) have been generated. For instance, transgenic plants have become resistant to the virus passionfruit woodiness virus (PWV), introducing the gene codifying for the virus coat protein (CP) (Trevisan et al. 2007).

In another study, an antiapoptotic gene (*p35*) from a baculovirus, which is supposed to lead resistance to environmental stress and to a broad spectrum of diseases, was introduced to the genome of *P. edulis* f. *flavicarpa* by biobalistics (Freitas et al. 2007). Although it failed to confer resistance against the cowpea aphid-borne mosaic virus (CABMV) to transgenic passionfruit plants, it was able to increase their resistance against the bacterium *Xanthomonas axonopodis* pv. *passiflorae*, and their tolerance against the herbicide, glufosinate (Syngenta) (Freitas et al. 2007).

7.7 Genomics Resources Developed

7.7.1 Gene Sequences

In the NCBI genebank database (NCBI 2009), there are 1,648 *Passiflora* entries corresponding to 1,196 nucleotide sequences and 452 translated protein sequences. Approximately 95% of these entries were produced in phylogenetic studies and correspond to the sequences of plastid fragments, such as *rcb*L, the spacer *trn*H–*psb*A, the spacer *trn*L-F, and nuclear sequences, such as Internal Transcribed Spacer (ITS) and glutamine synthetase (GS2) (Muschner et al. 2003; Yockteng and Nadot 2004a, b; Krosnick and Freudenstein 2005; Hansen et al. 2006).

Population genetic studies have also generated molecular sequences. In a phylogeographical study, internal transcribed spacers (ITS) sequences of 32 individuals of *P. actinia* and 20 individuals of *P. elegans* from 41 different localities were obtained (Lorenz-Lemke et al. 2005). Besides, the study of genetic variation of populations of *P. alata* has provided new nuclear and chloroplast sequences (Koehler-Santos et al. 2006a). ITS of a fragment of glyceraldehyde 3-phosphate dehydrogenase (G3pdh) gene, the chloroplast intergenic spacers *trn*L–*trn*F and *psb*A–*trnL* and the intron *trn*L were sequenced to study 88 individuals of *P. alata* from 52 different localities of Brazil. For the first time, the second intron of gene *LEAFY*, which regulates the establishment of the floral meristem and flowering time in *Arabidopsis,* was sequenced in a *Passiflora* species. One novelty of this study was also the use of the first set of 12 microsatellite markers in a *Passiflora* species (Padua et al. 2005; Koehler-Santos et al. 2006a). A set of ten microsatellites specific *to P. edulis* f. *flavicarpa*, the yellow passionfruit, is also available (Oliveira et al. 2005) and was already used to construct a genetic linkage map (Oliveira et al. 2008) (see details in Sect. 7.5). Twenty-eight unpublished microsatellites specific to *P. alata* are also accessible in the NCBI database.

Several chloroplast and mitochondrial sequences of hybrids, product of interspecific crosses of *Passiflora* species, have been deposited in the database and used to determine the process of organellar inheritance in *Passiflora* (Muschner et al. 2006).

Besides, eight sequences of homolog isoforms of the allergenic compound of the pollen of Betulaceae (Bet v1) from *Passiflora morifolia* Mast., *Passiflora* sp., *P. suberosa*, *P. misera* and *P. organensis* Gardner are accessible in NCBI (Finkler et al. 2005). The aim of the study of Finkler and co-workers was to make a first characterization of Bet v1 homologs in *Passiflora* species and to identify the utility of this gene for future evolutionary and applied researches.

7.7.2 Expressed Sequence Tags

A few expressed sequence tag (EST) sequences of *Passiflora* are available in the NCBI database and all are obtained from the cultivated species *P. edulis*. Mita et al. (1998) were first to deposit five cDNA sequences of molecules playing an important role in the ethylene pathway. Their study generated two cDNA sequences of the ethylene receptor of *P. edulis*, called *PE*-ERS1 and *PE*-ETR1, which have a length of 2,297 bp with an open reading frame (ORF) encoding 637 residues of amino acids and 2,715 bp with an ORF encoding 738 amino acids. They also obtained cDNA sequences from two copies of the ACC synthase (*PE*-ACS1 and *PE*-ACS2) and one copy of the ACC oxidase (*PE*-ACO1), each having a sequence length of 1,054 bp with an ORF encoding for 351 amino acids, 1,063 bp with an ORF encoding for 354 amino acids, and 785 bp with an ORF of 261 amino acids. A subsequent study of ethylene pathway identified a third cDNA sequence of an independent copy of an ethylene receptor (*PE*-ERS2) measuring 2,357 bp that include an ORF codifying for 634 amino acids (Mita et al. 2002). The cDNA sequence of an antifungal protein (*PE*-AFP1) with a length of 25 amino acids residues was purified from seeds of *P. edulis* and constitutes the first defense peptide with antifungal properties identified in *Passiflora* (Pelegrini et al. 2006). Besides, the Myo-inositol-1L-phosphate synthase (MIPS) cDNA, component of Inositol phosphate biosynthesis pathway, as well as two cDNAs of translation elongation factor 1a-1 of *P. edulis* was sequenced (Abreu and Aragao 2007). MIPS cDNA isolated from developing passionfruit seeds measures 1,951 bp in length contains one open reading frame of 1,533 bp encoding 510 amino acids. Recently, the cDNA of the chloroplast-targeted allene oxide synthase from *P. edulis* (Pf-AOS), which is one of the components of the jasmonate pathway, was isolated. The coding region of Pf-AOS contains 1,512 nucleotides and encodes a protein of 504 amino-acids flanked by a 50-UTR of 155 nucleotides and a 30-UTR of 116 nucleotides (Siqueira et al. 2008). This study indicates that PfAOS may play an important role in systemic wound response against chewing insect attack (Siqueira et al. 2008).

7.7.3 Complete Genome Sequences

So far, no genome sequence is available from any *Passiflora* species. Instead, the genome of three pathogenic virus affecting *Passiflora* species has been totally sequenced (Iwai et al. 2006b; Song et al. 2006; Spiegel et al. 2007). The full maracuja mosaic tobamovirus (MarMV) genome consists of 6,794 nucleotides and contains four open reading frames (ORFs) coding for proteins (Song et al. 2006). The genome of carlavirus *Passiflora* latent virus (PLV) isolated from *P. edulis* plants measures 8,386 nucleotides and contains six ORFs (Spiegel et al. 2007). The genomic RNA of East Asian *Passiflora* virus (EAPV) isolated from *P. edulis* is composed of 10,046 nucleotides and contains a single ORF encoding a polyprotein of 3,220 amino acids (Iwai et al. 2006a). The availability of complete genome sequences of *Passiflora* virus will permit to understand better the mechanisms used by the pathogen to generate the disease in the host-plant. The continuous development of the molecular techniques will permit to obtain hopefully the first complete genome sequence of a *Passiflora* species.

7.8 Scope for Domestication and Commercialization

7.8.1 Wild Species as Resistant Rootstock

In passionflower, grafting appears to be a good and more immediate solution than breeding to reduce the heavy impact of soil pathogens. In French Guiana, Delanoë (1992) tested nine species as potential rootstocks for *P. edulis* f. *flavicarpa*. None showed incompatibility, but grafting success varied from 40 to 60% for *P. coccinea*, *P. glandulosa* and *P. garckei*, to 60–80% for *P. nitida*, *P. laurifolia* and *P. cirrhiflora*, or more than 80% for *P. serrato-digitata*, *P. fuchsiiflora* and *P. candida*. However, the plants grafted on *P. fuchsiiflora* and *P. candida* died after 17 months. In terms of quality and development of the rootstock and the scion, the best results were obtained with *P. coccinea*, *P. glandulosa* and *P. laurifolia*, followed by *P. nitida* and *P. garckei*. Junqueira et al. (2005) reported similar grafting experiments using *P. nitida* or a *P. edulis* f. *flavicarpa* × *P. setacea* hybrid as rootstock. The grafted materials yielded as much as seedlings of yellow maracuja, but only half of its production in cuttings. Grafted plants were effectively protected from soil pathogen attacks. However, the economic application of grafting is an issue because of the low availability of wild species germplasm, their erratic seed germination, and the elevated maintenance cost of a crop with short cycle (less than 3 years) (Meletti et al. 2005). In Colombia, Campos (1992) successfully used *P. manicata* as a rootstock for adapting *P. tripartita* var. *mollissima* to lower altitudes and dry conditions. However, the impact on economic parameters has not yet been tested.

7.8.2 New Commercial Fruit Crops

Among the very high diversity of *Passiflora* species producing an edible fruit, there are many potential candidates for developing new fruit crops. However, a more realistic approach would be giving priority to those species that have been partially domesticated, and thus rescuing their cultivated germplasm. These crops include *P. incarnata*, for temperate climates, species of series *Laurifoliae* such as *P. maliformis* and *P. nitida*, species of series *Tiliifoliae* such as *P. platyloba* and species of supersection *Tacsonia* such as *P. cumbalensis*, *P. pinnatistipula* and *P. antioquiensis* for tropical highlands. The gene pools for these species have been briefly presented in Sect. 7.4.

McGuire (1999) proposed to develop the maypop, *P. incarnata* into a fruit crop. This fruit was "abundant in Indian gardens" since its archeological remains are common in the southeast of the United States. However, the level of domestication reached in that time is uncertain (Gremillion 1989). The fruits of *P. incarnata* are good sources of vitamin A and niacin (Martin and Nakasone 1970).

The reputation of *Passiflora maliformis* suffers from its vernacular name of "stone granadilla." However, the epicarp solidity is present only in part of its germplasm and the fruits are sold well on regional markets in Colombia. Some germplasm of this species shares interesting traits with the purple form of *P. edulis*. Indeed, the resemblance is such that they have received the same vernacular names of *gulupa* or *chulupa*. They share a yellow and highly aromatic pulp, similar fruit size and a deep red shell. But *P. maliformis* is superior to *P. edulis* in two aspects: the fruit shell does not wrinkle at maturity keeping its smooth appearance, and it is considered generally resistant or tolerant to most passionfruit pathogens. These interesting traits, found also in the closely related *P. serrulata* and *P. multiformis*, could make *P. maliformis* a strong competitor in the passionfruit market. Lowland species of series *Tiliifoliae* are already cultivated on a very small scale in forest regions of western Colombia. Their fruits could benefit from their resemblance with those of *P. ligularis*, which are appreciated in the national market. But their potential is wider since their fruits could be produced in many other rain forests. As for the highland sweet granadilla, their smooth and brittle epicarp makes them both attractive and easy to consume. The cultivated populations could currently provide an excellent basis for the commercial development of these species.

Species of the series *Laurifoliae* offer similar or even better perspectives. The genetic improvement should aim at equilibrating their resource allocation between generative and vegetative parts in order to reduce the overall development and promote a longer harvesting season. Breeding should easily maintain the general quality of the sweet and aromatic pulp, aril size, and fruit coloration, while the reduction of the fruit mesocarp would enhance pulp proportion.

The rosy passionfruit, *P. cumbalensis*, is cultivated only around Bogota, and this crop will certainly get lost in very near future if no particular attention is paid to it; this species is simply being forgotten. Indeed, it is very similar to its cousin *P. tripartita* var. *mollissima*, with which it shares the large and abundant orange arils of excellent flavor and aroma. The fruit is generally bright red, although some types give yellow fruits, and the plant seems less affected by anthracnose than *P. tripartita* var. *mollissima*. An effort should be done to promote the two fruits on the same market. The botanical varieties of supersection *Tacsonia* found from Colombia to Peru constitute a wide gene pool for the sustainable future of this potential crop (Holm-Nielsen et al. 1988). A similar case of a species that is becoming rare in home gardens is *P. antioquiensis*. Its germplasm is in high danger of extinction while it is still present in the wild. In cultivated materials, the flavor of the cream orange fruit pulp is a special and highly aromatic blend, matching the best fruits of supersections *Passiflora* and *Tacsonia*. But its fruiting may not be abundant enough for commercial production. The species should be restored not only as fruit but also as garden ornamental because of the exceptional beauty of its carmine and fusiform flowers hanging from 30 to 60 cm peduncles. *Passiflora pinnatistipula* is a very particular species of supersection *Tacsonia* because of its round fruits and its flowers, which have a relatively short hypanthium and a filamentose corona. The whitish pulp is extremely sweet; however, the seeds are relatively large, round and hard, so breeding could help to solve this problem. Another potential problem is that the species hybridizes very easily with *P. tripartita* var. *mollissima*, giving sterile hybrids (*P.* × *rosea*) that are difficult to distinguish from *P. pinnatistipula* until they flower. Therefore, these two species cannot be closely cultivated. *Passiflora pinnatistipula* may be grown at higher latitudes (up to 4,000 m), allowing fruit production in cold mountain climates.

7.8.3 Source of Therapeutic Compounds

Since prehistoric periods, *Passiflora* species have been used for therapeutic purposes (Dhawan et al. 2004). Although one species, *P. incarnata*, is the mostly recognized in pharmaceutics, many species have been used in traditional folk medicine in several countries (Table 7.3). After an exhaustive review, Dhawan et al. (2004) concluded: “This genus is a boon and blessing and a panacea for the ailing masses”. The medicinal properties of passionflowers are consequence of their diversity in phyto-constituents among which are flavonoids, glycosides, alkaloids and phenol compounds.

Several experimental studies performed in mice or rats give evidence of the anxyolitic, sedative, antioxidant and anti-inflammatory properties of *Passiflora* extracts such as *P. incarnata, P. edulis, P. alata, P. quadrangularis* extracts (Wolfman et al. 1993, 1994; Soulimani et al. 1997; Zanoli et al. 2000; Petry et al. 2001; Dhawan et al. 2003; Frode et al. 2004, 2005; Rudnicki et al. 2004; Santos et al. 2005; Bezerra et al. 2006; Garros et al. 2006; Gomes et al. 2006; Oliveira et al. 2006; Reginatto et al. 2006; Silva et al. 2006; Beninca et al. 2007; Castro et al. 2007; Montanher et al. 2007; Rudnicki et al. 2007; Vargas et al. 2007; Barbosa et al. 2008; Lorencini et al. 2008). Most of the studies have also shown an absence of secondary adverse effects of *Passiflora* extracts. No adverse effect of *P. incarnata* doses was found in female pregnant mice or their litter during gestational, fetal and post-natal periods (Mello et al. 2007). One experimental research in humans compared the effect of an oral dose of 500 mg of *P. incarnata* (Passipy™ IranDarouk) in a group of 30 patients with pre-operatory anxiety versus the effect of an oral dose of placebo in other 30 patients (Movafegh et al. 2008). The results show that anxiety was significantly lower in patients that took the *Passiflora* dose and the recovery of psychomotor function was comparable in both the groups. This study would support the efficacy of *P. incarnata* extracts as a remedy against anxiety. Other *Passiflora* medicinal uses are as antidote to counteract the venom of the scorpion *Heterometrus laoticus* (Uawonggul et al. 2006), and antimicrobial activity (Bendini et al. 2006).

The principal bioactive compounds described in this genus are the *C*-glycosil flavonoids (vitexin, isovitexin, orientin, isoorientin and apigenin) and β-carbolinic alkaloids (harman, harmin, harmalin, harmol and harmalol). The high concentration of isovitexin in *P. actinia* extracts would produce sedative and anxyolitic effects in animals (Santos et al. 2006). In addition, vitexin from various *Passiflora* species has an antithyroid effect in mice (Dhawan et al. 2004). Another active compound, the monoflavonoid chrysin purified from *P. caerulea* and *P. incarnata,* is possibly responsible for the anxyolitic and anticonvulsive effects on mice (Dhawan et al. 2004; Brown et al. 2007). This flavonoid is a ligand of benzodiazepine receptors and GABA receptors that mediates biochemical processes in the body. *Passiflora incarnata's* chrysin has also been reported to attenuate the suppression of activity of natural killer (NK) cells after a surgery (Beaumont et al. 2008). The NK cells are lymphocytes responsible for killing virus-infected cells and tumor cells during metastasis. Surgical procedures, anesthetics and pre- and post-surgery stress would affect the activity of NK cells. Therefore, *Passiflora*'s chrysin could have an indirect effect against cancer metastasis. Other anti-cancer activity was reported in extracts from *P. edulis* f. *flavicarpa* that influence the death of transformed foci, potential tumor cells (Rowe et al. 2004). In addition, extracts from fruit of *P. edulis* and *P. foetida*

L. var. *albiflora* inhibit the activity of two enzymes, the gelatinase MMP-2 and MMP-9, two metallo-proteases involved in the tumor invasion, metastasis and angiogenesis (Puricelli et al. 2003). Chrysin has also reported to have some negative effects such as hyperalgesia, which is increased sensitivity to pain stimulation (Zhai et al. 2008). Another compound isolated from *P. edulis* is a defense peptide (*Pe*-AFP1) that inhibits the development of filamentous fungi *Trichoderma harzianum*, *Fusarium oxysporum* and *Aspergillus fungigatus*. The discovery of *Pe*-AFP1 could contribute, in a near future, to the development of biotechnological products as antifungal drugs against pathogenic fungi (Pelegrini et al. 2006). Besides, a hemolysin, probably a saponin, was isolated from the leaves of *P. quadrangularis*. Hemolysins are transmembrane receptors and are potential bactericidal and anticancer drugs (Yuldasheva et al. 2005).

The concentration of phytoconstituents in plants apparently depends on their mineral nutrition. The absence of minerals such as potassium, phosphor and nitrogen, in the nutrition of *Passiflora* plants increments their concentration in vitexin (Freitas et al. 2008). Populations of the same species located in different geographical areas would have different profiles in their phytoconstituents. For instance, the concentration of vitexin in *P. foetida* varies among samples collected in different geographical regions (Pongpan et al. 2007).

Despite all the beneficial pharmaceutical effects of passionflowers, precaution is needed about the presence of toxic compounds such as cyanogenic constituents. The plants of *Passiflora* produce secondary metabolites, especially cyanogenic glycosides as protection against herbivores. The unripe fruits of *P. adenopoda* DC. have already caused poisoning due to the presence of HCN (Dhawan et al. 2004). *Passiflora manicata* is called *diablito* (little devil) in Ecuador, for similar reasons.

Although a few studies are based on non-cultivated species, wild *Passiflora* species have been reported to be diverse in their phytoconstituents (Abourashed et al. 2002, 2003). Wild species also produced flavonoids and alkaloids. Sometimes, the concentration of these phytoconstituents is larger in wild species than in pharmaceutical ones. For example, the concentration of vitexin is seven times higher in the wild species *P. holosericea* L. than in *P. incarnata* (Abourashed et al. 2002). Wild species constitute, therefore, an important source of potential therapeutic compounds. Hence, it is necessary to conduct studies in order to detect their pharmaceutical properties and their active compounds.

7.8.4 Psychoactive Drugs

In certain tropical regions of South America, the dried leaves of *P. edulis* f. *flavicarpa* are sometimes smoked in the same way as those of *Cannabis sativa* L. Specialized websites indicate similar uses for *P. incarnata*, although the effect is said to be weaker than that of marijuana. Tea made with dried flowers also has a slight psychotropic effect. Indeed, *P. incarnata* may contain small amounts of harmala alkaloids, which are used in the preparation of a highly psychotropic drink, the ayahuasca (Recreational Drug Information Website 1999). Besides, harmala alkaloids reduce the breakdown of the psychoactive drug DMT (*N*, *N*-dimethyltryptamine) in the digestive system. In traditional medicine, *P. incarnata* has been used for drug deaddiction of morphine, cannabinoids, nicotine and alcohol, which was successfully tested on mice (Dhawan et al. 2004).

7.8.5 Dietary Supplements

Once again, dietary supplements are mainly reported in cultivated species. However, wild passionflowers constitute a latent source of dietary supplements waiting to be explored. The yellow passionfruit rinds, usually discarded after juice production, have been reported to be a source of variable dietary supplements. Firstly, their cell wall material rich in non-starchy polysaccharides constitute a possible source of dietary fiber, which could protect against cardiovascular diseases, diabetes, obesity, colon cancer and diverticular diseases (Yapo and Koffi 2008). Furthermore, yellow passionfruit rinds are also a potential source of pectin, a compound widely used in many foodstuffs as gelling agents (Yapo and Koffi 2006). The pectin isolated from *P. edulis* f. *flavicarpa* is comparable to the commercial citrus low-methoxyl pectin. Finally, the yellow passionfruit rinds have been also reported as a rich source of lycopene that is an antioxidant carotenoid which probably reduces risk of chronic diseases (Mourvaki et al. 2005). Few sources of lycopene are available in diet such as tomatoes.

7.8.6 Other Uses

Passiflora species could be a source of ecofriendly materials. For instance, a new polysaccharide, xiloglucan biopolymer, is extracted from peels of *P. ligularis*. This biopolymer could be used to produce a biodegradable film using the discards of passionfruit industry (Tommonaro et al. 2007). Seeds of *P. edulis* are also a source of vegetable oils useful to produce ecofriendly polymeric material (Lopes et al. 2008). Moreover, *P. incarnata* extracts have been described as useful to develop organic sunscreens with a protective defense against UV radiation. The use of plant compounds would reduce the concentration of chemical UV filters in sunscreens (Velasco et al. 2008). In addition, the enzyme system of *P. edulis* fruit barks has permitted the biotransformation of carbonyl compounds such as ketones and aldehydes (Machado et al. 2008). These compounds used in perfumery and in paints do not degrade quickly over time, hence the utility of passionfruit preparations to reduce compounds produced in the industry. In addition, peels of *P. edulis* have also permitted the reduction of synthetic dyes such as methylene-blue (Pavan et al. 2008).

Among the numerous alkaloids, phenolics, flavonoids and volatiles substances found in passionflowers, kavain, yagonin, dihydromethysticin and coumarin have properties that completely suppress the barnyardgrass growth. Hence, the use of the allelopathic plant *P. edulis* as a natural herbicide would reduce the dependency on synthetic herbicides and other agrochemicals (Khanh et al. 2006, 2008).

7.9 Invasive Species and Weeds

In a general sense, a weed is a native or exotic plant that grows and reproduces aggressively causing nearly always economic, environmental or ecological loss (Randall 2002). Instead, invasive species is an exotic species (e.g., plant or animal) that adversely affects economically, environmentally or ecologically the habitats that it invades. Human activities provoke the transportation of species beyond their native range. The introduced species are sometimes able to establish and spread in a foreign habitat. Among *Passiflora* species, 19 species have been reported as invasive in 37 countries (Table 7.5).

Islands, which usually present a great number of endemic species, are particularly susceptible to invasions because the introduced species lack natural competitors and predators that control populations in their native ecosystems. The probability of successful invasions is also increased in islands because of the availability of unfilled ecological niches. For instance, the entire island chain of Hawaii has been devastated by foreign insects, plants and animals among which 12 *Passiflora* species with two cause a documented impact. The introduced Andean species *P. tarminiana* (banana poka in Polynesian local language; often confused with *P. tripartita* var. *mollissima*) invaded at least 50,000 ha of upper-elevation rainforests of Hawaii (La Rosa 1992; Trujillo et al. 2001; Trujillo 2005), threatening the survival of the native Hawaiian koa (*Acacia koa* A. Gray) and other 20 native endangered Hawaiian plant species (Trujillo et al. 2001). To control this weed, the US government spent $90,000 per year for uprooting plants and $500,000 to find adequate biological control agent against it (Waage et al. 1981; Causton et al. 2000; Causton and Ranget 2002). A fungal pathogen *Septoria passiflorae* (Coelomycetes: Sphaeropsidales), noxious against *P. tarminiana,* was found in the plant native range (Trujillo et al. 1994). Inoculations of this biological agent permitted to eliminate 95% of the biomass of banana poka in 4 years and allowed the revitalization of the high-elevation forests of Kauai, Maui, and Hawaii (Trujillo et al. 2001; Trujillo 2005).

A native species can become a weed by the effects of natural events or human modifications to the habitat. For example, the Brazilian species, *P. alata* also known as maracuja doce, is colonizing unoccupied regions of southern Brazil (Koehler-Santos et al. 2006a, b). The colonization process of *P. alata* may have been facilitated by the presence of dispersion and pollination agents of other *Passiflora* species already present in the colonized area. In addition, high genetic diversity among and within the populations of *P. alata* probably promotes the success of the colonization process. Therefore, *P. alata* can, in these circumstances, be considered a native weed. In addition to

Table 7.5 *Passiflora* invasive species and native weed[a]

Species	Country	Weed type	Character
Invasive			
P. alata	La Réunion (France)		
P. biflora	United States	EW	N
P. caerulea	Australia (continental), Hawaiian Islands, New Zealand, South Africa	NW	C, T, N
P. coccinea	United States		C, T, N
P. edulis	Australia (continental and Pacific offshore islands), Cook Islands, Ecuador (Galápagos Islands), Federated States of Micronesia, Fiji Islands, Hawaiian Islands, La Réunion (France), New Caledonia, New Zealand (Continental and offshore islands), Niue, South Africa, Tonga, United States	EW	C, T, N
P. filamentosa Cav.	Australia (continental)		N
P. foetida	American Samoa, Australia (continental and Indian Ocean offshore islands), Cambodia, Chile, China, Commonwealth of the Northern Mariana Islands (US), Federated States of Micronesia, Fiji Islands, French Polynesia, Guam, Hawaiian Islands, Indonesia, Japan, Kiribati, La Réunion (France), Malaysia, Naurui, Negara Brunei Darussalam, New Caledonia, New Guinea, Niue, Palau, Palau (main island group), Philippines, Seychelles Islands, Singapore, South Africa, Thailand, Tonga, United States, Vietnam, Wallis and Futuna (Horne) Islands, western Samoa Islands	EW	C, T, N
P. incarnata	Fiji Islands, French Polynesia, Hawaiian Islands, New Caledonia, Niue, Tonga, United States, western Samoa Islands		C, T
P. ligularis	Ecuador (Galápagos Islands), Hawaiian Islands, Indonesia, United States, western Samoa Islands	EW	C
P. maliformis	American Samoa, Cook Islands, Fiji Islands, French Polynesia, Hawaiian Islands, New Caledonia, Niue, Pitcairn Islands, Tonga		
P. mixta	New Zealand	EW, QW, NW	C, N
P. morifolia	Australia, United States		C, N
P. pulchella Kunth (*P. bicornis*)	Hawaiian Islands, United States	QW, NW	C, N
P. quadrangularis	Australia, Ecuador (Galápagos Islands), Federated States of Micronesia, Guyana, Hawaiian Islands, United States, western Samoa Islands		C, T, N
P. rubra	Cook Islands	EW	C, T, N
P. suberosa	Australia (continental), Commonwealth of the Northern Mariana Islands (US), Cuba, Fiji Islands, French Polynesia, Guam, Hawaiian Islands, Japan, La Réunion (France), New Caledonia, Palau (main island group), Seychelles Islands, South Africa, Tonga, United States, western Samoa Islands	EW, QW, NW	C, T, N
P. subpeltata	Australia (continental), Hawaiian Islands, Tonga	EW, QW, NW	C, T, N
P. tarminiana (*P. mollissima*)	Australia (continental), Australia (Indian Ocean offshore islands), Hawaiian Islands, New Zealand, New Zealand (offshore islands), South Africa, United States	EW, QW, NW	C, N

(*continued*)

Table 7.5 (continued)

Species	Country	Weed type	Character
Native Weed			
P. alata	Brazil		C, T
P. cincinnata	Brazil		
P. cinnabarina Lindl.	Australia (continental and Indian Ocean offshore islands)		T, N
P. lutea	United States		C

[a]Randall (2002), Koehler-Santos et al. (2006a), US Forest Service (2007). The species accounted as weed and introduced are considered here as invasive species. The type of weed are also signaled (*EW* Environmental Weed, *NW* Noxious Weed, *QW* Quarantine Weed). Few characteristics of each species are also listed, when information is available (*C* Cultivated, *N* Naturalized, *T* Toxic)

P. alata, two other passionflowers are reported to be native weed, *P. cinnabarina* Lindl. in Australia and *P. cincinnata* also in Brazil (Randall 2002).

Weed and invasive species can be a threat for human health if the species are toxic. For instance, the weed *P. alata* induces occupational respiratory allergic disease (Giavina-Bianchi et al. 1997), and should be considered a risk because it could induce allergic problems in new colonized areas. Ten weedy *Passiflora* are also accounted as toxic (Table 7.5). Programs for the identification of *Passiflora* weeds and prevention of dispersal of these plants are essential to maintain the equilibrium of ecosystems.

7.10 Conclusion

Wild *Passiflora* species constitute a large source of genetic resource for the improvement of cultivated species and the introduction of new fruit crops and tropical garden ornamentals. Moreover, new pharmaceutical, organic and ecofriendly products can be developed from these wild passionflowers. Although the majority of studies have been conducted on cultivated species, in particular in *P. edulis*, they constitute a useful reference to conduct similar studies in wild species

The fragmentation and loss of habitat caused by human activities endanger many tropical plants, such as wild *Passiflora* species. Many passionflowers are endemic and certainly threatened; thus it is indispensable to ensure their conservation. The determination of their geographical distribution is required to further develop in situ conservation programs. In addition, ex situ *Passiflora* germplasm collections should be increased in number of species and individuals to ensure the conservation of a great range of the genetic variability of wild species and its economic valorization.

Acknowledgments We thank Sophie Nadot and Pablo Arbelaez for their useful comments on the manuscript.

References

Abourashed EA, Vanderplank JR, Khan IA (2002) High-speed extraction and HPLC fingerprinting of medicinal plants – I. Application to Passiflora flavonoids. Pharm Biol 40:81–91

Abourashed EA, Vanderplank J, Khan IA (2003) High-speed extraction and HPLC fingerprinting of medicinal plants – II. Application to harman alkaloids of genus Passiflora. Pharm Biol 41:100–106

Abreu EFM, Aragao FJL (2007) Isolation and characterization of a myo-inositol-1-phosphate synthase gene from yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) expressed during seed development and environmental stress. Ann Bot 99:285–292

Abreu PP, Souza MM, Santos EA, Pires MV, Pires MM, de Almeida AAF (2009) Passion flower hybrids and their use in the ornamental plant market: perspectives for sustainable development with emphasis on Brazil. Euphytica 166:307–315

Anderson A (1976) A comparison of two species of *Passiflora*. Dissert Abstr Int 36:4267B

Apple JL, Feener DH (2001) Ant visitation of extrafloral nectaries of *Passiflora*: the effects of nectary attributes and ant behavior on patterns in facultative ant-plant mutualisms. Oecologia 127:409–416

Arjona HE, Matta FB (1991) Postharvest quality of passion fruit as influenced by harvest time and ethylene treatment. HortScience 26:1297–1298

Aukar AP, Lemos EG, Oliveira JC (2002) Genetic variations among passion fruit species using RAPD markers. Rev Bras Frutic 24:738–740

Azevedo MAM (2008) Three new species of *Passiflora* subgenus *Decaloba* (Passifloraceae) from Brazil. Brittonia 60:310–317

Baker CA, Jones L (2007) A new potyvirus found in *Passiflora incence* in Florida. Plant Dis 91:227

Baldwin JT (1949) Polyploidy in Passiflora lutea. Rhodora 51:29

Barbosa LV, Vieira MLC (1997) Meiotic behavior of passion fruit somatic hybrids, Passiflora edulis f. flavicarpa Degener plus P. amethystina Mikan. Euphytica 98:121–127

Barbosa PR, Valvassori SS, Bordignon CL, Kappel VD, Martins MR, Gavioli EC, Quevedo J, Reginatto FH (2008) The aqueous extracts of *Passiflora alata* and *Passiflora edulis* reduce anxiety-related behaviors without affecting memory process in rats. J Med Food 11:282–288

Beal PR (1969a) Cytology of the native Australian *Passiflora* species. 1. Chromosome number and horticultural value. Queensl J Agric Anim Sci 26:75–81

Beal PR (1969b) Chromosome numbers of the exotic *Passiflora* species in Australia. Queensl J Agric Anim Sci 26:407–421

Beal PR (1971) Chromosome numbers in some recently introduced species of *Passiflora* in Australia. Queensland J Agric Anim Sci 28:179–180

Beal PR (1972) Two new interspecific hybrids in the genus *Passiflora*. Sabrao Newslett 4:113–115

Beal PR (1973) Cytology of the native Australian and several exotic *Passiflora* species. 2. Chromosome morphology. Queensl J Agric Anim Sci 30:17–18

Beal PR (1975) Hybridization of *Passiflora edulis* Sims and *P. edulis* Sims f. *flavicarpa* Degener. Queensl J Agric Anim Sci 32:101–111

Beaumont DM, Mark TM, Hills R, Dixon P, Veit B, Garrett N (2008) The effects of chrysin, a *Passiflora incarnata* extract, on natural killer cell activity in male Sprague-Dawley rats undergoing abdominal surgery. Aana J 76:113–117

Beckett KA (1960) A hybrid passion flower. J R Hortic Soc 85:184–186

Bellon G, Faleiro FG, Junqueira KP, Junqueira NTV, dos Santos EC, Braga MF, Guimaraes CT (2007) Genetic variability of wild and commercial passion fruit (*Passiflora edulis* Sims.) accessions using RAPD markers. Rev Bras Frutic 29:124–127

Bendini A, Cerretani L, Pizzolante L, Toschi TG, Guzzo F, Ceoldo S, Marconi AM, Andreetta F, Levi M (2006) Phenol content related to antioxidant and antimicrobial activities of *Passiflora* spp. extracts. Eur Food Res Technol 223:102–109

Beninca JP, Montanher AB, Zucolotto SM, Schenkel EP, Frode TS (2007) Evaluation of the anti-inflammatory efficacy of *Passiflora edulis*. Food Chem 104:1097–1105

Benson WW (1978) Resource partitioning in passion vine butterflies. Evolution 32:493–518

Benson WW, Brown KS, Gilbert LE (1975) Coevolution of plants and herbivores: passion flower butterflies. Evolution 29:659–680

Berry PE (1987) Chromosome number reports 95. Taxon 36:493

Bezerra JAF, Campos ACL, Vasconcelos PRLd, Nicareta JR, Ribeiro ER, Sebastiao APM, Urdiales AIA, Moreira M, Borges AM (2006) Extract of *Passiflora edulis* in the healing of colonic anastomosis in rats: a tensiometric and morphologic study. Acta Cir Bras 21(Suppl 3):16–25

Biodiversity International (2009) New world fruits database. http://www.bioversityinternational.org/Information_Sources/Species_Databases/New_World_Fruits_Database/. Accessed 13 Feb 2009

Bowden WM (1940) The chromosome complement and its evolutionary relationship to cold resistance in the higher plants. Chron Bot 6:123–125

Bowden WM (1945) A list of chromosome numbers in higher plants. II. Menispermaceae to Verbenaceae. Am J Bot 32:191–201

Braga MF, Junqueira NTV (2000) Uso potencial de outras espécies do gênero *Passiflora*. Informe Agropecuário, Belo Horizonte 21:72–75

Brown EW, Hurd NS, McCall S, Ceremuga TE (2007) Evaluation of the anxiolytic effects of chrysin, a *Passiflora incarnata* extract, in the laboratory rat. Aana J 75:333–337

Bruckner CH, Moraes T, Rêgo MM, Nunes ES (2005) Autoincompatibilidade do maracujá – implicações no melhoramento genético. In: Faleiro FG (ed) Maracujá: germoplasma e melholramiento genético Embrapa Cerrados, Planaltina, Brazil. Embrapa, Planaltina, Brazil, pp 317–338

Brunt AA, Crabtree K, Dallwitz MJ, Gibbs AJ, Watson L, Zurcher EJ (1996) Plant viruses online: Descriptions and lists from the VIDE database. http://image.fs.uidaho.edu/vide/. Accessed 2 Mar 2009

Büchert A (1998) Passionflowers and their birds, bees and butterflies. The ecology and evolution of pollination and herbivory in Passiflora. Department Ecology and Genetics, University of Aarhus, Denmark

Campos TC (1992) El cultivo de la curuba, *Passiflora mollissima* (H.B.K.) Bailey, en Colombia. Acta Hortic 310:215–229

Carneiro MS, Camargo LEA, Coelho ASG, Vencovsky R, Leite RP, Stenzel NMC, Vieira MLC (2002) RAPD-based genetic linkage maps of yellow passion fruit (*Passiflora edulis* Sims. f. *flavicarpa* Deg.). Genome 45:670–678

Castañeda RR (1956) Plantas de valor commercial del género *Passiflora*: granadilla, curuba, badea y otras

Castro PCF, Hoshino A, da Silva JC, Mendes FR (2007) Possible anxiolytic effect of two extracts of *Passiflora quadrangularis* L. in experimental models. Phytother Res 21: 481–484

Causton CE, Ranget AP (2002) Field observations an the biology and behaviour of *Dasiops caustonae* Norrbom and McAlpine (Dipt., Lonchaeidae), as a candidate biocontrol agent of *Passiflora mollissima* in Hawaii. J Appl Entomol 126:169–174

Causton CE, Markin GP, Friesen R (2000) Exploratory survey in Venezuela for biological control agents of *Passiflora mollissima* in Hawaii. Biol Control 18:110–119

Cervi AC (2002) A new species of *Passiflora* (Passifloraceae) from Amazonian Brazil. Brittonia 54:54–56

Cervi AC (2006) A new species of *Passiflora* (Passifloraceae) from Minas Gerais, Brazil. Brittonia 58:385–387

Chang CA (1992) Characterization and comparison of passionfruit mottle virus, a newly recognized potyvirus, with passionfruit woodiness virus. Phytopathology 82:1358–1363

Chang CA, Chen CC, Deng TC, Zettler FW (1994) Characterization of passionfruit crinkle potyvirus – a newly found virus. Plant Prot Bull 38:339–354

Cole DL, Hedges TR, Ndowora T (1992) A wilt of passion fruit (*Passiflora edulis* f. *edulis* Sims) caused by *Fusarium solani* and *Phytophthora nicotianae* var. *parasitica*. Int J Pest Manage 38:362–366

Coppens d'Eeckenbrugge G (2003) Exploração da diversidade genética das passifloras. In: Sexto Simpósio Brasileiro sobre a Cultura do Maracujazeiro. 24–27 Nov 2003, Campos de Goytacazes, Brazil

Coppens d'Eeckenbrugge G, Barney VE, Jorgensen PM, MacDougal JM (2001a) *Passiflora tarminiana*, a new cultivated species of *Passiflora* subgenus *Tacsonia* (Passifloraceae). Novon 11:8–15

Coppens d'Eeckenbrugge G, Segura SD, Hodson E, Gongora GA (2001b) Passion Fruits. In: Charrier A, Jacquot M, Hamon S, Nicolas D (eds) Tropical plant breeding. CIRAD, Science, Enfield, NH, USA, pp 381–401

Corriveau JL, Coleman AW (1988) Rapid screening method to detect potential biparental inheritance of plastid DNA and results for over 200 angiosperm species. Am J Bot 75:1443–1458

Crochemore ML, Molinari HBC, Vieira LGE (2003) Genetic diversity in passion fruit (*Passiflora* spp.) evaluated by RAPD markers. Braz Arch Biol Technol 46:521–527

Darlington CD, Janaki Ammal EK (1945) Chromosome atlas of cultivated plants. George Allen and Unwin, London, UK

Davis RI, Thomas JE, McMichael LA, Dietzgen RG, Callaghan B, James AP, Gunua TG, Rahamma S (2002) Plant virus surveys on the island of New Guinea and adjacent regions of northern Australia. Australas Plant Pathol 31:385–390

De Candolle AP (1822) Passifloreae. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 1:435–436

Degener O (1932) *Passiflora edulis*. In: Flora Hawaiiensis family 250. Honolulu, USA

Delanoë O (1991) Etude de la résistance de passiflores de Guyana française vis-à-vis de *Fusarium* pathogènes de la culture des fruits de la passion (*Passiflora edulis* f. *flavicarpa*). Fruits 46:248–255

Delanoë O (1992) Les ressources génétiques des passiflores de Guyane. Amélioratidoen la culture des fruits de la passion (*Passiflora edulis* f. *flavicarpa* Degener, Passifloraceae). University of Montpellier Il, Montpellier, France

Department of Employment Economic Development & Innovation (2005) Growing passionfruit: common questions. http://www2.dpi.qld.gov.au/horticulture/5524.html. Accessed Mar 31 2009

Dhawan K, Kumar S, Sharma A (2003) Evaluation of central nervous system effects of *Passiflora incarnata* in experimental animals. Pharm Biol 41:87–91

Dhawan K, Dhawan S, Sharma A (2004) *Passiflora*: a review update. J Ethnopharmacol 94:1–23

Dianese AC, Costa AM, Dianese JC (2008) A new *Pseudocercospora* species causing a serious leaf spotting and bligh on *Passiflora setacea*. Phytopathology 98:S46

Diers L (1961) Der anteil an polyploiden in den vegetationsgürteln der westkordillere Perus. Z Botanik 49:433

Do YY, Shii CT, Huang PL (1992) Retriction patterns and inheritance of chloroplast DNA in *Passiflora edulis* Sims and its related species. In: Huang SC, Hsieh SC, Dah-Jiang Liu DJ (eds) The impact of biological research on agricultural productivity. Taichung District Agricultural Improvement Station, Taichung, pp 10–13

Endress PK (1994) Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge, UK

Escobar LK (1981) Experimentos preliminares en la hibridación de especies comestibles de *Passiflora*. Actual Biol 14:111–121

Escobar LK (1985) Biologia reproductiva de *Passiflora manicata* e hibridacion con la curuba *Passiflora mollissima*. Actual Biol 14:111–121

Escobar LK (1989) A new subgenus and five new species in *Passiflora* (Passifloraceae) from South-America. Ann MO Bot Gard 76:877–885

Fajardo D, Angel F, Grum M, Tohme J, Lobo M, Roca W, Sánchez I (1998) Genetic variation analysis of the genus *Passiflora* L. using RAPD markers. Euphytica 101:341–347

Ferreira FR (2005) Recursos genéticos de *Passiflora*. In: Faleiro FG (ed) Maracujá: germoplasma e melholramiento genético Embrapa Cerrados, Planaltina, Brazil. Embrapa, Planaltina, pp 41–51

Feuillet C (2002) A new series and three new species of *Passiflora* subgenus *Astrophea* from the Guianas. Brittonia 54:18–29

Feuillet C (2004) *Passiflora phellos*, a new species in subgenus *Passiflora* (Passifloraceae). Novon 14:285–287

Feuillet C, MacDougal JM (2003) A new infrageneric classification of *Passiflora*. Passiflora 13(2):34–35, 37–38

Finkler C, Giacomet C, Muschner VC, Salzano FM, Freitas LB (2005) Molecular investigations of pathogenesis-related Bet v 1 homologues in *Passiflora* (Passifloraceae). Genetica 124:117–125

Fischer E (2004) Hybrids and hybridization. In: Ulmer T, MacDougal J (eds) *Passiflora*. Passionflowers of the world. Timber, Portland, OR, USA, pp 362–376

Fischer IH, Lourenço SA, Martins MC, Kimati H, Amorim L (2005) Seleção de plantas resistentes e de fungicidas para o controle da podridão do colo do maracujazeiro causada por *Nectria haematococca*. Fitopatol Bras 30:250–258

Fore SA, Spira TP (2002) Macrogeographic allozyme variation in *Passiflora incarnata*. J Torr Bot Soc 129:326–330

Fouque A, Fouque R (1980) A few notes on yellow passion fruit, *Passiflora edulis* Sims var *flavicarpa*. Fruits 35:309–312

Freitas DS, Coelho MCF, Souza MT, Marques A, Ribeiro BM (2007) Introduction of the anti-apoptotic baculovirus p35 gene in passion fruit induces herbicide tolerance, reduced bacterial lesions, but does not inhibits passion fruit woodiness disease progress induced by cowpea aphid-borne mosaic virus (CABMV). Biotechnol Lett 29:79–87

Freitas MSM, Monnerat PH, Vieira IJC (2008) Mineral deficiency in *Passiflora alata* Curtis: Vitexin bioproduction. J Plant Nutr 31:1844–1854

Frode TS, Vargas A, Geremias DS, Gossman G, Schenkel E, Medeiros YS, Reginatto FH, Fornari PE, Provensi G (2004) Anti-inflammatory effects of *Passiflora edulis* Sims on the mouse model of pleurisy induced by carrageenan. Clin Chem 50:A36–A37

Frode TS, Vargas A, Pereira RR, Vigil SV (2005) Anti-inflammatory effects of *Tacrolimus* in mouse models of inflammation. Clin Chem 51:A208

Garros IC, Campos ACL, Tambara EM, Tenorio SB, Torres OJM, Agulham MA, Araujo ACF, Santis-Isolan PMB, Oliveira RM, Arruda ECM (2006) Extract from *Passiflora edulis* on the healing of open wounds in rats: morphometric and histological study. Acta Cir Bras 21(Suppl 3):55–65

Giavina-Bianchi PF, Castro FFM, Machado MLS, Duarte AJS (1997) Occupational respiratory allergic disease induced by *Passiflora alata* and *Rhamnus purshiana*. Ann Allergy Asthma Immunol 79:449–454

Gilbert LE (1971) Butterfly-plant coevolution – has *Passiflora adenopoda* won selectional race with Heliconiine butterflies? Science 172:585–586

Gilbert LE (1980) Butterflies and plants. In: Gilbert L, Raven P (eds) Coevolution of animals and plants. University of Texas, Austin, TX, USA, pp 210–240

Gilbert LE (1982) The coevolution of a butterfly and a vine. *Heliconius* butterflies, *Passiflora*. Sci Am 247:110–116, 119–121 illust

Gilbert LE (1983) Coevolution and mimicry. In: Futuyma D, Slatkin M (eds) Coevolution. Sinauer, Sunderland, MA, USA, pp 263–281

Gilbert LE (1998) Ecology, systematics, and evolution of passionvines (Passifloraceae). http://uts.cc.utexas.edu/~gilbert/research/passionvines/index.html. Accessed 13 Feb 2009

Gilbert LE, MacDougal JM (2000) *Passiflora microstipula*, a new species of Passifloraceae from Southeast Mexico. Lundellia 3:1–5

Gill BS, Bir SS, Sikdhu MS (1984) Chomosome number reports LXXXIV. Taxon 33:536–539

Gioria R, Espinha LM, Rezende JAM, Gaspar JO, Kitajima EW (2002) Limited movement of *Cucumber* mosaic virus (CMV) in yellow passion flower in Brazil. Plant Pathol 51:127–133

Girault L (1984) Kallawaya Guérisseurs itinérants des Andes. Recherche sur les pratiques médicales et magiques. ORSTOM, collection Mémoires, Paris, France

Gomes CS, Campos ACL, Torres OJM, Vasconcelos PRLd, Moreira ATR, Tenorio SB, Tambara EM, Sakata K, Moraes Junior H, Ferrer ALS (2006) *Passiflora edulis* extract and the healing of abdominal wall of rats: morphological and tensiometric study. Acta Cir Bras 21(suppl 2):9–16

Gonzalez MS, Suarez Z, Rosales C, Parra D (2000) Collar rot and wilt of yellow passion fruit in Venezuela. Plant Dis 84:103

Grattapaglia D, Sederoff R (1994) Genetic linkage maps of *Eucalyptus grandis* and *Eucalyptus urophylla* using a pseudotestcross: mapping strategy and RAPD markers. Genetics 137:1121–1137

Gremillion KJ (1989) The development of a mutualistic relationship between humans and maypops (*Passiflora incarnata* L). J Ethnobiol 9:135–155

Guerra M (1986) Citogenética de angiospermas coletadas em Pernambuco. Gen Mol Biol 9:21–40

Hansen AK, Gilbert LE, Simpson BB, Downie SR, Cervi AC, Jansen RK (2006) Phylogenetic relationships and chromosome number evolution in *Passiflora*. Syst Bot 31:138–150

Hansen AK, Escobar LK, Gilbert LE, Jansen RK (2007) Paternal, maternal, and biparental inheritance of the chloroplast genome in *Passiflora* (Passifloraceae): implications for phylogenetic studies. Am J Bot 94:42–46

Harms (1923) Beiträge zur Kenntnis der amerikanischen Passifloraceen – I. Fed. Repert. Sp Nov Regni Veg 19:58

Harms (1925) *Passiflora*. In: Engler A, Prantl K (eds) Die natürlichen pflanzenfamilien. Wilhelm Engelmann, Leipzig, Germany, pp 470–507

Harris SA, Ingram R (1991) Chloroplast DNA and biosystematics: the effects of intraspecific diversity and plastid transmission. Taxon 40:393–412

Harvey MJ (1966) IOPB chromosome number reports VII. Taxon 15:155–163

Heenan PB, Sykes WR (2003) *Passiflora* (Passifloraceae) in New Zealand: a revised key with notes on distribution. NZ J Bot 41:217–221

Heiser CB (1963) Numeración cromosómica de plantas ecuatorianas. Cienc Nat 6:2–6

Heitz E (1926) Der Nachweis der Chromosomen. Vergleichende Studien über ihre Zahl, Grösse und Form im Pflazenreich. I. Z Bot 18:625–681

Hiscock SJ, Tabah DA (2003) The different mechanisms of sporophytic self-incompatibility. Philos Trans R Soc Lond B Biol Sci 358:1037–1045

Holm-Nielsen LB, Møller-Jørgensen P, Lawesson JE (1988) Passifloraceae 126. In: Harling G, Andersson L (eds) Flora of Ecuador. University of Göterborg, Riksmuseum; Pontificia Universidad Católica del Ecuador, Göteborg; Stockholm; Quito Ecuador, pp 1–130

Houel C (2009) Collection Nationale de passiflores de Christian Houel et Daniel Hermelin. http://www.passiflorae.fr/. Accessed 29 Mar 2009

Howell CW (1989) Major fruit varieties of *Passiflora*. Trop Fruit News 23:73–75

Ito PJ (1978) 'Noel's Special' passion fruit. HortScience 13:197

Iwai H, Terahara R, Yamashita Y, Ueda S, Nakamura M (2006a) Complete nucleotide sequence of the genomic RNA of an Amami-O-shima strain of East Asian *Passiflora* potyvirus. Arch Virol 151:1457–1460

Iwai H, Yamashita Y, Nishi N, Nakamura M (2006b) The potyvirus associated with the dappled fruit of *Passiflora edulis* in Kagoshima prefecture, Japan is the third strain of the proposed new species East Asian *Passiflora* virus (EAPV) phylogenetically distinguished from strains of passion fruit woodiness virus. Arch Virol 151:811–818

Jankovics T, Bai Y, Kovacs GM, Bardin A, Nicot PC, Toyoda H, Matsuda Y, Niks RE, Kiss L (2008) *Oidium neolycopersici*: Intraspecific variability inferred from amplified fragment length polymorphism analysis and relationship with closely related powdery mildew fungi infecting various plant species. Phytopathology 98:529–540

Jaramillo A (1957) Primeros resultados de un ensayo sobre el cultivo de la curuba (*Passiflora* spp.). Agric Trop 13:301–308

Jørgensen PM (2004) Three new species of *Passiflora* subgenus *Decaloba* (Passifloraceae) from Ecuador. Nord J Bot 23:11–19

Jørgensen PM (2009) Preliminary conservation status of accepted species in *Passiflora* subg. *Decaloba:* http://www.mobot.org/mobot/research/passiflora/conservation_status_accepted_species.shtml. Accessed 29 Mar 2009

Jørgensen PM, Weigend M (2004) *Passiflora inca*, a new species of Passifloraceae from Peru and Bolivia. Novon 14:79–83

Jørgensen PM, Sheth S, Consiglio T, Jiménez I (2009) Assessing conservation status of *Passiflora*. http://www.mobot.org/mobot/research/passiflora/conservation.shtml. Accessed 13 Feb 2009

Junqueira NTV, dos Anjos JRN, Silva APD, Chaves RD, Gomes EAC (2003) Reaction to diseases and yield of eleven cultivars of sour-passion fruit cultivated with no pesticides. Pesqui Agropecu Bras 38:1005–1010

Junqueira NTV, Braga MF, Faleiro FG, Peixoto JR, Bernacci LC (2005) Potencial de espécies silvestres de maracujazeiro como fonte de resistência a doenças. In: Faleiro FG (ed) Maracujá: germoplasma e melholramiento genético Embrapa Cerrados, Planaltina, Brazil. Embrapa, Planaltina, pp 81–108

Junqueira KP, Faleiro FG, Ramos JD, Bellon G, Junqueira NTV, Braga MF (2007) Genetic variability of wild passion fruit determined by molecular markers. Rev Bras Frutic 29:571–575

Junqueira KP, Faleiro FG, Junqueira NTV, Bellon G, Ramos JD, Braga MF, de Souza LS (2008) Confirmation of interspecific hybrids in *Passiflora* using molecular markers. Rev Bras Frutic 30:191–196

Jussieu AL (1805a) Premier Mémoire. Sur quelques espèces du genre *Passiflora*, et sur la nécessité d'établir une famille des passifloracées. Ann Mus Hist Nat 102–116

Jussieu AL (1805b) Second mémoire. Sur la famille des passifloracées, et particulièrement sur quelques espèces nouvelle du genre *Tacsonia*. Ann Mus Hist Nat 389–396

Kajewski SF (1941) Cross breeding experiments in the Bowen district. Queensl Agric J 56:473–476

Kavati R, Coppens d'Eeckenbrugge G, Ferreira FR (1998) Sweet maracuja, a promising newcomer. Fruitrop 43:20–21

Kay E (2001) Observations on the pollination of *Passiflora penduliflora*. Biotropica 33:709–713

Kay E (2003) Floral evolutionary ecology of *Passiflora* (Passifloraceae); subgenera Murucuia, Pseudomurucuja and Astephia. Saint Louis University, Saint Louis, MI, USA

Khanh TD, Chung IM, Tawata S, Xuan TD (2006) Weed suppression by *Passiflora edulis* and its potential allelochemicals. Weed Res 46:296–303

Khanh TD, Xuan TD, Linh LH, Chung IM (2008) Allelopathic plants: 18. Passion fruit (*Passiflora* spp.). Allelopath J 21:199–206

Killip EW (1938) The American species of Passifloraceae. Field Museum of Natural History, Chicago, IL, USA

Knight RJ (1972) The potential for Florida of hybrids between the purple and yellow passionfruit. FL Stat Hortic Soc 85:288–292

Knight RJ (1991) Development of tetraploid hybrid passion fruit clones with potential for the North temperate zone. HortScience 26:1541–1543

Knight RJ, Payne JA, Schnell RJ, Amis AA (1995) Byron-Beauty, an ornamental passion vine for the temperate zone. HortScience 30:1112

Koehler-Santos P, Lorenz-Lemke AP, Muschner VC, Bonatto SL, Salzano FM, Freitas LB (2006a) Molecular genetic variation in *Passiflora alata* (Passifloraceae), an invasive species in southern Brazil. Biol J Linn Soc 88:611–630

Koehler-Santos P, Lorenz-Lemke AP, Salzano FM, Freitas LB (2006b) Ecological evolutionary relationships in *Passiflora alata* from Rio Grande do Sul, Brazil. Braz J Biol 66:809–816

Krosnick SE (2005) *Passiflora xishuangbannaensis* (Passifloraceae): a new Chinese endemic. Novon 15:160–163

Krosnick SE, Freudenstein JV (2005) Monophyly and floral character homology of old world *Passiflora* (Subgenus *Decaloba*: Supersection *Disemma*). Syst Bot 30:139–152

Krosnick SE, Harris EM, Freudenstein JV (2006) Patterns of anomalous floral development in the Asian *Passiflora* (subgenus *Decaloba*: supersection *Disemma*). Am J Bot 93:620–636

La Cour LF (1951) Annual Report. John Innes Hortic Inst 41:23

La Rosa AM (1992) The status of banana poka in Hawai´i. In: Stone CP, Smith CW, Tunison JT (eds) Alien plant invasions in native ecosystems of Hawai'i: management and research. University of Hawaii Press, Honolulu, HI, USA, pp 271–299

Leal IR, Fischer E, Kost C, Tabarelli M, Wirth R (2006) Ant protection against herbivores and nectar thieves in *Passiflora coccinea* flowers. Ecoscience 13:431–438

Lepper L, Duharte Gongora M (1988) Beitrage zur chromosomen-dokumentation cubanischer pflanzensippen: 5. *Passiflora santiagana* (Killip) Borhidi und *P. cubensis* Urb. Wissenschaftliche Zeitscrift der Friedrich-Schiller, Universität Jena, Thüringen. Math-Natur Beitrag Okol Land 37:165–168

Liberato JR (2006) Powdery mildew on *Passiflora* in Australia. Australas Plant Pathol 35:73–75

Lindberg AB, Olesen JM (2001) The fragility of extreme specialization: *Passiflora mixta* and its pollinating hummingbird *Ensifera ensifera*. J Trop Ecol 17:323–329

Linden UM (2007) The passionfruit market – Is it controllable? Fruit Process Jan-Feb:6–9

Linnaeus C (1745) Dissertation botanica de *Passiflora*, qua cum consensu amplis. Uppsala University, Uppsala, Sweden

Linnaeus C (1753) Species Plantarum. Stockholm, Sweden

Lloyd RM (1963) Tetraploid *Passiflora incarnata* in North Carolina. Rhodora 65:79–80

Lopes R, Lopes MTG, Carneiro MS, Matta FD, Carnargo LEA, Vieira MLC (2006) Linkage and mapping of resistance genes to *Xanthomonas axonopodis* pv. *passiflorae* in yellow passion fruit. Genome 49:17–29

Lopes RVV, Loureiro NPD, Fonseca PS, Macedo JL, Santos ML, Sales MJ (2008) Study of the thermal polymerization of linseed and passion fruit oils. AIP Conf Proc 1042: 339–341

Lorencini M, Hurtado SP, Moreira PL, Martinelli M, Delarcina S, Sa-Rocha VM, Gesztesi J (2008) Flavonoids-rich *Passiflora alata* extract is effective to reduce skin micro-inflammation process in aging. J Invest Dermatol 128:S42

Lorenz-Lemke AP, Muschner VC, Bonatto SL, Cervi AC, Salzano FM, Freitas LB (2005) Phylogeographic inferences concerning evolution of Brazilian *Passiflora actinia* and *P. elegans* (Passifloraceae) based on ITS (nrDNA) variation. Ann Bot 95:799–806

MacDougal JM (1983) Revision of *Passiflora* L. section *Pseudodysosmia* (Harms) Killip emend. J. MacDougal, the hooked trichome group (Passifloraceae). Departmen of Botany, Duke University, Durham, NC, USA

MacDougal JM (1994) Revision of *Passiflora* subgenus *Decaloba* section *Pseudodysosmia* (Passifloraceae). Syst Bot Mon 41:1–146

MacDougal JM (2001) Two new species of passionflower (*Passiflora*, Passifloraceae) from southwestern Mexico. Novon 11:69–75

MacDougal JM (2003) *Passiflora boenderi* (Passifloraceae), a new egg-mimic passionflower from Costa Rica. Novon 13:454–458

MacDougal JM (2004) Six new taxa of *Passiflora* (Passifloraceae), with nomenclatural notes on the genus in Mesoamerica. Novon 14:444–462

MacDougal JM (2006) *Passiflora sandrae* (Passifloraceae), a new species from Panama. Novon 16:85–88

MacDougal JM, Feuillet C (2004) Systematics. In: Ulmer T, MacDougal JM (eds) *Passiflora*, passionflowers of the world. Timber, Portland, OR, USA, pp 27–31

MacDougal JM, Hansen AK (2003) A new section of *Passiflora*, subgenus *Decaloba* (Passifloraceae), from Central America, with two new species. Novon 13:459–466

Machado LL, Monte FJQ, de Oliveira MDF, de Maltos MC, Lemos TLG, Gotor-Fernandez V, de Gonzalo G, Gotor V (2008) Bioreduction of aromatic aldehydes and ketones by fruits' barks of *Passiflora edulis*. J Mol Catal 54:130–133

Maluf WR, Silva JR, Grattapaglia D, Tomabraghini M, Corte RD, Machado MA, Caldas LS (1989) Genetic gains via clonal selection in passion fruit *Passiflora edulis* Sims. Rev Bras Gen 12:833–841

Martin FW, Nakasone HY (1970) The edible species of *Passiflora*. Econ Bot 24:333

Martins I, Peixoto JR, Junqueira NVT, De Mello SCM (2008) Reaction of sour passionfruit genotypes to *Colletotrichum gloeosporioides*. Rev Bras Frutic 30:639–643

McGuire CM (1999) *Passiflora incarnata* (Passifloraceae): a new fruit crop. Econ Bot 53:161–176

Meletti LMM (1998) Caracterização agronômica de progênies de maracujá amarelo (*Passiflora edulis* Sims f. *flavicarpa* Deg). Univ de São Paulo, Brazil

Meletti LMM, Santos RR, Minami K (2000) Melhoramento do maracujazeiro-amarelo: obtenção do cultivar Composto IAC-27. Sci Agric 57:491–498

Meletti LMM, Soares-Scott MD, Bernacci LC, Silva IRP (2005) Melhoramento genético do maracujá: passado e futuro. In: Faleiro FG (ed) Maracujá: germoplasma e melholramiento genético Embrapa Cerrados, Planaltina, Brazil. Embrapa, Planaltina, Brazil, pp 55–78

Mello FB, Langeloh A, de Mello JRB (2007) Study of the toxicity and efficacy in Wistar rats of a phytoterapic used as sedative and/or hypnotic. Lat Am J Pharmacy 26:38–44

Melo NF, Guerra M (2003) Variability of the 5S and 45S rDNA sites in *Passiflora* L. species with distinct base chromosome numbers. Ann Bot 92:309–316

Melo NF, Cervi AC, Guerra M (2001) Karyology and cytotaxonomy of the genus *Passiflora* L. (Passifloraceae). Plant Syst Evol 226:69–84

Mita S, Kawamura S, Yamawaki K, Nakamura K, Hyodo H (1998) Differential expression of genes involved in the biosynthesis and perception of ethylene during ripening of passion fruit (*Passiflora edulis* Sims). Plant Cell Physiol 39:1209–1217

Mita S, Kawamura S, Asai T (2002) Regulation of the expression of a putative ethylene receptor, PeERS2, during the development of passion fruit (*Passiflora edulis*). Physiol Plant 114:271–280

Mitter C, Brooks DR (1983) Phylogenetics aspects of coevolution. In: Futuyma DJ, Slatkin M (eds) Evolutionary interactions among herbivorous insects and plants. Sinauer, Sunderland, MA, USA, pp 65–99

Montanher AB, Zucolotto SM, Schenkel EP, Frode TS (2007) Evidence of anti-inflammatory effects of *Passiflora edulis* in an inflammation model. J Ethnopharmacol 109:281–288

Moraes MC (2005) Mapas de ligação e mapeamento de QTL ("quantitative trait loci") em maracujá-amarelo (*Passiflora edulis* Sims f. *flavicarpa* Deg.). University of Saõ Paulo, Escola Superior de Agricultura "Luiz de Queiroz", Piracicaba, Brazil

Moraes MC, Geraldi IO, Matta FD, Vieira MLC (2005) Genetic and phenotypic parameter estimates for yield and fruit quality traits from a single wide cross in yellow passion fruit. HortScience 40:1978–1981

Morales FJ, Lozano I, Castano M, Arroyave J, Velasco AC, Varon F (2002) Partial characterization of a tymovirus infecting passion fruit in Colombia. South Am J Phytopathol 150:292–296

Morton JF (1967) Yellow passionfruit ideal for Florida home gardens. FL Stat Hortic Soc 80:320–330

Mourvaki E, Stefania G, Rossi R, Rufini S (2005) Passionflower fruit – a "new" source of lycopene? J Med Food 8:104–106

Movafegh A, Alizadeh R, Hajimohamadi F, Esfehani F, Nejatfar M (2008) Preoperative oral *Passiflora incarnata* reduces anxiety in ambulatory surgery patients: a double-blind, placebo-controlled study. Anesth Analg 106:1728–1732

Mrácek J (2005) Investigation of interspecific genome-plastome incompatibility in *Oenothera* and *Passiflora*. Biology der Ludwig-Maximilians. Universität München, München, Germany

Muschner VC, Lorenz AP, Cervi AC, Bonatto SL, Souza-Chies TI, Salzano FM, Freitas LB (2003) A first molecular phylogenetic analysis of *Passiflora* (Passifloraceae). Am J Bot 90:1229–1238

Muschner VC, Lorenz-Lemke AP, Vecchia M, Bonatto SL, Salzano FM, Freitas LB (2006) Differential organellar inheritance in *Passiflora*'s (Passifloraceae) subgenera. Genetica 128:449–453

Nakajima G (1931) The chromosome numbers in cultivated and wild angiosperms. Bot Mag Tokyo 45:7–11

Nakasone HY, Hirano R, Ito P (1967) Preliminary observations on the inheritance of several factors in the passion fruit *Passiflora edulis* and forma *flavicarpa*. Hawaii Agric Exp Stat Tech Progr Rep 161:3–11

Nascimento AVS, Santana EN, Braz ASK, Alfenas PF, Pio-Ribeiro G, Andrade GP, de Carvalho MG, Zerbini FM (2006) Cowpea aphid-borne mosaic virus (CABMV) is widespread in passionfruit in Brazil and causes passionfruit woodiness disease. Arch Virol 151:1797–1809

NCBI (2009) National Center for Biotechnology Information. http://www.ncbi.nlm.nih.gov. Accessed 3 Mar 2009

Nishiyama I, Kondo N (1942) Report of the Kihara Institute for Biological Research 1:29

Obando J, Fernandez-Trujillo JP, Martinez JA, Alarcon AL, Eduardo I, Arus P, Monforte AJ (2008) Identification of melon fruit quality quantitative trait loci using near-isogenic lines. J Am Soc for Hortic Sci 133:139–151

Ocampo J, Coppens G, Restrepo M, Jarvis A, Salazar M, Caetano C (2007) Diversity of Colombian Passifloraceae: biogeography and an updated list for conservation. Biota Colomb 8:1–45

Olaya CA (2002) Primer estudio de la meiosis en *Passiflora tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen, *Passiflora tarminiana* Coppens & Barney, *Passiflora mixta* L. y tres de sus híbridos. University of Caldas, Manizales, Colombia

Olaya Arias CA, Caetano CM, Coppens d'Eeckenbrugge G, Serna AL (2002) Chromosome number, meiotic behavior and pollen fertility of *Passiflora tarminiana* Coppens &

Barney, a new species of *Passiflora* (Subgenus *Tacsonia*). Nucleus 45:96–102

Oliveira AMA, Coleman JR (1996) Estudos citogene´ticos de espe´cies do ge´nero Passiflora (Passifloraceae). Braz J Genet (Suppl) 19:134

Oliveira VR, Oliveira JC, Tihohod D, Tomioka EH (1996) Reação de *Passiflora alata* Dryander e *Passiflora macrocarpa* Mast a *Metodologyne incognita* raça 1. Científica, São Paulo 224:363–369

Oliveira EJ, Padua JG, Zucchi MI, Camargo LEA, Fungaro MHP, Vieira MLC (2005) Development and characterization of microsatellite markers from the yellow passion fruit (*Passiflora edulis* f. *flavicarpa*). Mol Ecol Notes 5:331–333

Oliveira RMW, Lolli LF, Santos CA (2006) Possible involvement of GABAA-benzo-diazepine receptor in the anxiolytic-like effect induced by *Passiflora actinia* extracts in mice. Eur Neuropsychopharmacol 16:S254

Oliveira EJ, Vieira MLC, Garcia AAF, Munhoz CF, Margarido GRA, Consoli L, Matta FP, Moraes MC, Zucchi MI, Fungaro MHP (2008) An integrated molecular map of yellow passion fruit based on simultaneous maximum-likelihood estimation of linkage and linkage phases. J Am Soc for Hortic Sci 133:35–41

Otoni WC, Blackhall NW, Vaz FBD, Casali VW, Power JB, Davey MR (1995) Somatic hybridization of the *Passiflora* species, *Passiflora edulis* f. *flavicarpa* Degener and *P. incarnata* L. J Exp Bot 46:777–785

Padua JG, Oliveira EJ, Zucchi MI, Oliveira GCX, Camargo LEA, Vieira MLC (2005) Isolation and characterization of microsatellite markers from the sweet passion fruit (*Passiflora alata* Curtis: Passifloraceae). Mol Ecol Notes 5:863–865

Pares RD, Gunn LV, Keskula EN, Martin AB, Teakle DS (1997) Occurrence of *Passiflora* latent carlavirus in cultivated and wild *Passiflora* species in Australia. Plant Dis 81:348–350

Parrella G, Castellano MA (2002) Passiflora chlorotic spot a disease caused by a strain of bean yellow mosaic virus in *Passiflora coerulea* in Italy. J Plant Pathol 84:139

Parry JN, Davis RI, Thomas JE (2004) *Passiflora* virus Y, a novel virus infecting *Passiflora* spp. in Australia and the Indonesian Province of Papua. Aust Plant Pathol 33:423–427

Passiflora Society International (2008) *Passiflora* Society International. http://www.passiflora.org. Accessed 13 Feb 2009

Patiño VM (1963) Plantas cultivadas y animales domesticos en América equinoccial. Tomo *1*. Frutales. Imprenta Departamental, Cali, Colombia, 547 p

Pavan FA, Mazzocato AC, Gushikem Y (2008) Removal of methylene blue dye from aqueous solutions by adsorption using yellow passion fruit peel as adsorbent. Bioresour Technol 99:3162–3165

Payan FR, Martin FW (1975) Barriers to hybridization of *Passiflora* species. Euphytica 24:709–716

Pegg KG, Willingham SL, O'Brien RG, Cooke AW, Coates LM (2002) Base rot of golden passionfruit caused by a homothallic strain of *Fusarium solani*. Aust Plant Pathol 31:305–306

Peixoto M (2005) Problemas e perspectivas do maracujá ornamental. In: Faleiro FG (ed) Maracujá: germoplasma e melholramiento genético Embrapa Cerrados, Planaltina, Brazil. Embrapa, Planaltina, pp 457–463

Pelegrini PB, Noronha EF, Muniz MAR, Vasconcelos IM, Chiarello MD, Oliveira JTA, Franco OL (2006) An antifungal peptide from passion fruit (*Passiflora edulis*) seeds with similarities to 2S albumin proteins. BBA Proteins Proteom 1764:1141–1146

Petry RD, Reginatto F, de-Paris F, Gosmann G, Salgueiro JB, Quevedo J, Kapczinski F, Ortega GG, Schenkel EP (2001) Comparative pharmacological study of hydroethanol extracts of *Passiflora alata* and *Passiflora edulis* leaves. Phytother Res 15:162–164

Ploetz RC (1991) Sudden wilt of passion fruit in Southern Florida caused by *Nectria haematococca*. Plant Dis 75:1071–1073

Ploetz RC (2006) *Fusarium* induced diseases of tropical, perennial crops. Phytopathology 96:648–652

Pongpan N, Luanratana O, Suntornsuk L (2007) Rapid reversed-phase high performance liquid chromatography for vitexin analysis and fingerprint of *Passiflora foetida*. Curr Sci 93:378–382

Porter-Utley KE (2007) *Passiflora tacanensis*, a new species of *Passiflora* subgenus *Decaloba* supersection *Cieca* from Mexico. Brittonia 59:25–28

Primot S, d'Eeckenbrugge GC, Rioux V, Pérez JAO, Garcin F (2005) Variación morfológica de tres especies de curubas (*Passiflora tripartita* var. *mollissima*, *P. tarminiana* y *P. mixta*) y sus híbridos en el Valle del Cauca (Colombia). Rev Bras Frutic 27:467–471

Puricelli L, Dell'Aica I, Sartor L, Garbisa S, Caniato R (2003) Preliminary evaluation of inhibition of matrix-metalloprotease MMP-2 and MMP-9 by *Passiflora edulis* and *P. foetida* aqueous extracts. Fitoterapia 74:302–304

Randall RP (2002) A global compedium of weeds. R.G. and F.J. Richardson, Melbourne

Recreational Drug Information Website (1999) Passion flower (*Passiflora incarnata*). http://www.a1b2c3.com/drugs/var027.htm. Accessed 2 Apr 2009

Reginatto FH, De-Paris F, Petry RD, Quevedo J, Ortega GG, Gosmann G, Schenkel EP (2006) Evaluation of anxiolytic activity of spray dried powders of two south Brazilian *Passiflora* species. Phytother Res 20:348–351

Rego MM, Bruckner CH, da Silva EAM, Finger FL, de Siqueira DL, Fernandes AA (1999) Self incompatibility in passion fruit: evidence of two locus genetic control. Theor Appl Genet 98:564–568

Rego MM, Rego ER, Bruckner CH, Da Silva EAM, Finger FL, Pereira KJC (2000) Pollen tube behavior in yellow passion fruit following compatible and incompatible crosses. Theor Appl Genet 101:685–689

Roemer MJ (1846) *Familiarum naturalium regni vegetabilis synopses monographicae*. Landes-Industrie-Comptoir, Weimar

Rowe CA, Nantz MP, DeNiera C, Green K, Talcott ST, Percival SS (2004) Inhibition of neoplastic transformation of benzo alpha pyrene-treated BALB/c 3T3 murine cells by a phytochemical extract of passionfruit juice. J Med Food 7:402–407

Ruberté-Torres R, Martin FW (1974) First generation hybrids of edible passion fruit species. Euphytica 23:61–70

Rudnicki M, Silveira MM, Pereira TV, Romanelli A, Oliveira MR, Reginatto FH, Dal-Pizzol F, Moreira JCF (2004) Antioxidant activity of *Passiflora alata* extract against carbon tetrachloride-induced oxidative damage in rats. Free Radical Biol Med 36:S131

Rudnicki M, Silveira MM, Pereira TV, Oliveira MR, Reginatto FH, Dal-Pizzol F, Moreira JCF (2007) Protective effects of *Passiflora alata* extract pretreatment on carbon tetrachloride induced oxidative damage in rats. Food Chem Toxicol 45:656–661

Sanchez I, Angel F, Grum M, Duque MC, Lobo M, Tohme J, Roca W (1999) Variability of chloroplast DNA in the genus *Passiflora* L. Euphytica 106:15–26

Santos KC, Santos CAM, Oliveira RMW (2005) *Passiflora actinia* Hooker extracts and fractions induce catalepsy in mice. J Ethnopharmacol 100:306–309

Santos KC, Kurtz S, Muller SD, Biavatti MW, Oliveira R, Santos CAD (2006) Sedative and anxiolytic effects of methanolic extract from the leaves of *Passiflora actinia*. Braz Arch Biol Technol 49:565–573

Santos CEM, Pissioni LLM, Morgado MAD, Cruz CD, Bruckner CH (2008) Strategies of selection in yellow passion fruit progenies for vigor and scab incidence. Rev Bras Frutic 30:444–449

Schoeniger G (1986) La curuba: técnicas para el mejoramiento de su cultivo. Editora Guadalupe, Bogotá, Colombia

Segura SD, Coppens G, Ollitrault P (1998) Isozyme variation in five species of *Passiflora* subgenus *Tacsonia* and *P. manicata*. P Inteamer Soc Trop Hortic 42:260–266

Segura S, d'Eeckenbrugge GC, Bohorquez A, Ollitrault P, Tohme J (2002) An AFLP diversity study of the genus *Passiflora* focusing on subgenus *Tacsonia*. Genet Resour Crop Evol 49:111–123

Segura S, d'Eeckenbrugge GC, Lopez L, Grum M, Guarino L (2003a) Mapping the potential distribution of five species of *Passiflora* in Andean countries. Genet Resour Crop Evol 50:555–566

Segura SD, d'Eeckenbrugge GC, Ocampo CH, Ollitrault P (2003b) Isozyme variation in *Passiflora* subgenera *Tacsonia* and *Manicata*. Relationships between cultivated and wild species. Genet Resour Crop Evol 50:417–427

Segura SD, d'Eeckenbrugge GC, Ocampo CH, Ollitrault P (2005) Isozyme variation in *Passiflora* subgenus *Tacsonia*: geographic and interspecific differentiation among the three most common species. Genet Resour Crop Evol 52:455–463

Senter SD, Payne JA, Knight RJ, Amis AA (1993) Yield and quality of juice from passion fruit (*Passiflora edulis*), Maypops (*P. incarnata*) and tetraploid passion fruit hybrids (*P. edulis* × *P. incarnata*). J Sci Food Agric 62:67–70

Shiomi S, Kubo Y, Wamocho LS, Koaze H, Nakamura R, Inaba A (1996) Postharvest ripening and ethylene biosynthesis in purple passion fruit. Postharvest Biol Technnol 8:199–207

Silva JRSd, Campos ACL, Ferreira LM, Aranha Junior AA, Thiede A, Zago Filho LA, Bertoli LC, Ferreira M, Trubian PS, Freitas ACTd (2006) Extract of *Passiflora edulis* in the healing process of gastric sutures in rats: a morphological and tensiometric study. Acta Cir Bras 21(Suppl 2):52–60

Simmonds N (1954) Chromosome behaviour in some tropical plants. Heredity 8:139–146

Simonet M, Miedzyrzecki C (1932) Etude caryologique de quelques espèces arborescentes ou sarmenteases d'ornement. CR Hebd Acad Sci 40:969–973

Siqueira CL, Jardim BC, Umenyi TP, Vicente ACP, Hansen E, Otsuki K, da Cunha M, Madureira HC, de Carvalho DR, Jacinto T (2008) Wound response in passion fruit (*Passiflora* f. *edulis flavicarpa*) plants: gene characterization of a novel chloroplast-targeted allene oxide synthase up-regulated by mechanical injury and methyl jasmonate. Plant Cell Rep 27:387–397

Smiley J (1986) Ant constancy at *Passiflora* extrafloral nectaries – effects on caterpillar survival. Ecology 67:516–521

Snow N, Macdougal JM (1993) New chromosome reports in *Passiflora* (Passifloraceae). Syst Bot 18:261–273

Snow DW, Snow BK (1980) Relationships between hummmingbirds and flowers in the Andes of Colombia. Bull Br Mus Nat Hist (Zool) 38:105–139

Soares-Scott MD (1998) Caracterização citogenética de algumas espécies e híbridos interespecíficos de *Passiflora*. Universidade Estadual de Campinas, Campinas, Brazil

Soares-Scott MD, Meletti LM, Recco-Pimentel SM (2003) Meiotic behaviour and pollen fertility in sexual and somatic hybrids of *Passiflora* species. Caryologia 56:129–137

Soares-Scott MD, Meletti LM, Bernacci LC, Passos IR (2005) Citogenética clássica e molecular em passifloras. In: Faleiro FG (ed) Maracujá: germoplasma e melholramiento genético Embrapa Cerrados, Planaltina. Embrapa, Planaltina, Brazil, pp 213–240

Soengas P, Hand P, Vicente JG, Pole JM, Pink DAC (2007) Identification of quantitative trait loci for resistance to *Xanthomonas campestris* pv. *campestris* in *Brassica rapa*. Theor Appl Genet 114:637–645

Song YS, Min BE, Hong JS, Rhie MJ, Kim MJ, Ryu KH (2006) Molecular evidence supporting the confirmation of Maracuja mosaic virus as a species of the genus *Tobamovirus* and production of an infectious cDNA transcript. Arch Virol 151:2337–2348

Soulimani R, Younos C, Jarmouni S, Bousta D, Misslin R, Mortier F (1997) Behavioural effects of *Passiflora incarnata* L and its indole alkaloid and flavonoid derivatives and maltol in the mouse. J Ethnopharmacol 57:11–20

Souza MM (2002) Estudos genômico e reprodutivo em espécies de *Passiflora*. Universidades Estadual do Norte Fluminenses, Campos dos Goytacazes, Brazil

Souza MM, Pereira TNS, Silva LC, Reis DSS, Sudré CP (2003a) Karyotype of six *Passiflora* species collected in the State of Rio de Janeiro. Cytologia 68:165–171

Souza MM, Pereira TNS, Viana AP, Pereira MG, Bernacci LC, Sudre CP, Silva LD (2003b) Meiotic irregularities and pollen viability in *Passiflora edmundoi* Sacco (Passifloraceae). Caryologia 56:161–169

Souza MM, Palomino G, Pereira TNS, Pereira MG, Viana AP (2004) Flow cytometric analysis of genome size variation in some *Passiflora* species. Hereditas 141:31–38

Souza MM, Pereira TNS, Dias AJB, Ribeiro BF, Viana AP (2006) Structural, hystochemical and cytochemical characteristics of the stigma and style in *Passiflora edulis* f. *flavicarpa* (Passifloraceae). Braz Arch Biol Technol 49:93–98

Souza MM, Pereira TNS, Vieira MLC (2008) Cytogenetic studies in some species of *Passiflora* L. (Passifloraceae): a review emphasizing Brazilian species. Braz Arch Biol Technol 51:247–258

Spencer KC (1988) Chemical mediation of coevolution in the *Passiflora-Heliconius* interaction. In: Spencer KC (ed) Chemical mediation of coevolution. Academic, Chicago, IL, USA, pp 167–240

Spiegel S, Zeidan M, Sobolev I, Beckelman Y, Holdengreber V, Tam Y, Bar Joseph M, Lipsker Z, Gera A (2007) The complete nucleotide sequence of *Passiflora* latent virus and its phylogenetic relationship to other carlaviruses. Arch Virol 152:181–189

Storey WB (1950) Chromosome numbers of some species of *Passiflora* occurring in Hawaii. Pac Sci 4:37–42

Studer B, Boller B, Herrmann D, Bauer E, Posselt UK, Widmer F, Koelliker R (2006) Genetic mapping reveals a single major QTL for bacterial wilt resistance in Italian ryegrass (*Lolium multiflorum* Lam.). Theor Appl Genet 113:661–671

Suassuna TDF, Bruckner CH, de Carvalho CR, Borem A (2003) Self-incompatibility in passionfruit: evidence of gametophytic-sporophytic control. Theor Appl Genet 106:298–302

Tague RT, Fore SA (2005) Analysis of the spatial genetic structure of *Passiflora incarnata* in recently disturbed sites. Can J Bot 83:420–426

Tang J, Clover GRG, Alexander BJR, Quinn BD (2008) First report of *Passiflora* latent virus in banana passionfruit (*Passiflora tarminiana*) in New Zealand. Plant Dis 92:486

Tommonaro G, Rodriguez CSS, Santillana M, Immirzi B, De Prisco R, Nicolaus B, Poli A (2007) Chemical composition and biotechnological properties of a polysaccharide from the peels and antioxidative content from the pulp of *Passiflora ligularis* fruits. J Agric Food Chem 55:7427–7433

Torres R, Giacometti D (1963) Comportamiento del "Maracuya" (*Passiflora edulis* var. *flavicarpa*, Degener) bajo las condiciones del Valle del Cauca. Agric Trop (Colomb) 22:247–254

Trevisan F, Mendes BMJ, Maciel SC, Rezende JAM, Vieira MLC, Meletti LMM (2007) Resistance to passion fruit woodiness virus in transgenic plants of the yellow passion fruit expressing the viral coat protein gene. In: Proceedings of international symposium on biotechnology of temperate fruit crops and tropical species, Daytona Beach, FL, USA, March 2007, pp 495–499

Trujillo EE (2005) History and success of plant pathogens for biological control of introduced weeds in Hawaii. Biol Control 33:113–122

Trujillo EE, Norman DJ, Killgore EM (1994) Septoria leaf-spot, a potential biologica control for banana poka vine in forests of Hawaii. Plant Dis 78:883–885

Trujillo EE, Kadooka C, Tanimoto V, Bergfeld S, Shishido G, Kawakami G (2001) Effective biomass reduction of the invasive weed species banana poka by *Septoria* leaf spot. Plant Dis 85:357–361

Turner BL, Zhao Z (1992) Documented chromosome numbers 1992: 2. Miscellaneous U.S.A. and Mexican species, mostly Asteraceae. Sida 15:147–150

Uawonggul N, Chaveerach A, Thammasirirak S, Arkaravichien T, Chuachan C, Daduang S (2006) Screening of plants acting against *Heterometrus laoticus* scorpion venom activity on fibroblast cell lysis. J Ethnopharmacol 103:201–207

Uphof JCT (1968) Dictionary of Economic plants. Cramer, Stechert-Hafner, Wiirzburg, Germany

US Forest Service (2007) Pacific Island ecosystems at risk (PIER). http://www.hear.org/pier/. Accessed 6 Mar 2009

USDA (2010) National Plant Germplasm System. http://www.ars-grin.gov/npgs/. Accessed 25 Mar 2010

Vanderplanck J (1991) Passion flowers and passion fruit. Cassel, London, UK

Vanderplanck J (2000) Passion flowers. MIT Press, Cambridge, MA, USA

Vargas AJ, Geremias DS, Provensi G, Fornari PE, Reginatto FH, Gosmann G, Schenkel EP, Frode TS (2007) *Passiflora alata* and *Passiflora edulis* spray-dried aqueous extracts inhibit inflammation in mouse model of pleurisy. Fitoterapia 78:112–119

Vásquez R (1998) Las especies de *Passiflora* subgénero *Granadilla* serie *Laurifoliae* (Passifloraceae) en Bolivia. Rev Soc Boliviana de Bot 2:36–45

Vásquez R, Delanoy M, Scheldeman X, Van Damme P, Beck S (2007) *Passiflora venusta*, a new species of *Passiflora* series *Laurifoliae* (Passifloraceae) from Bolivia. Novon 17:120–124

Velasco MVR, Sarruf FD, Salgado-Santos IMN, Haroutiounian-Filho CA, Kaneko TM, Baby AR (2008) Broad spectrum bioactive sunscreens. Int J Pharm 363:50–57

Viana AP, Pereira TNS, Pereira MG, Souza MMd, Maldonado JFM, Amaral Júnior ATd (2003) Diversidade genética entre genótipos comerciais de maracujazeiro-amarelo (*Passiflora edulis* f. *flavicarpa*) e entre espécies de passifloras nativas determinada por marcadores RAPD. Rev Bras Frutic 25:489–493

Vieira MLC, Carneiro MS (2004) *Passiflora* ssp. Passion fruit. In: Litz RE (ed) Biotechnology of fruits and nuts crops. CABI, Wallingford, Oxon, UK, pp 436–453

Villacis LA, Vega J, Grum M, Coppens d'Eeckenbrugge G (1998) Morphological characterization of Andean passifloras (*Passiflora* spp.) from Ecuador. Plant Genet Resour Newsl 115:51–55

Villalobos W, Moreira L, Rivera C, Lee I-M (2009) First report of new phytoplasma diseases associated with soybean, sweet pepper, and passion fruit in Costa Rica. Plant Dis 93:201

Vitta FA, Bernacci LC (2004) A new species of *Passiflora* in section *Tetrastylis* (Passifloraceae) and two overlooked species of *Passiflora* from Brazil. Brittonia 56:89–95

Waage JK, Smiley JT, Gilbert LE (1981) The *Passiflora* problem in Hawaii – prospects and problems of controlling the forest weed *Passiflora mollissima* Passifloraceae with Heliconiine Butterflies. Entomophaga 26:275–284

Waterhouse DF (1994) Biological control of weeds: Southeast Asian prospects. ACIAR, Canberra

Webster CG, Coutts BA, Jones RAC, Jones MGK, Wylie SJ (2007) Virus impact at the interface of an ancient ecosystem and a recent agroecosystem: studies on three legume-infecting potyviruses in the southwest Australian floristic region. Plant Pathol 56:729–742

Winks CW, Menzel CM, Simpson DR (1988) Passionfruit in Queensland. 2. Botany and cultivars. Queensl Agric J 114:217–224

Wolcan S, Larran S (2000) First report of anthracnose caused by *Glomerella cingulata* on passion fruit in Argentina. Plant Dis 84:706

Wolfman C, Viola H, Paladini A, Dajas F, Medina J (1993) Anxiolytic effects of chrysin, a central benzodiazepine receptor-ligand isolated from *Passiflora coerulea*. J Neurochem 61:S77

Wolfman C, Viola H, Paladini A, Dajas F, Medina JH (1994) Possible anxiolytic effects of chrysin, a central benzodiazepine receptor-ligand isolated from *Passiflora coerulea*. Pharmacol Biochem Behav 47:1–4

Wu R, Ma CX, Painter I, Zeng Z-B (2002) Simultaneous maximum likelihood estimation of linkage and linkage phases in outcrossing species. Theor Popul Biol 61:349–363

Yapo BM, Koffi KL (2006) Yellow passion fruit rind – a potential source of low-methoxyl pectin. J Agric Food Chem 54:2738–2744

Yapo BM, Koffi KL (2008) Dietary fiber components in yellow passion fruit rind – a potential fiber source. J Agric Food Chem 56:5880–5883

Yockteng R (2003) Phylogénies: outils pour l'étude de l'histoire évolutive des organismes. L'exemple des pensées (genre *Viola* L.) et des passiflores (genre *Passiflora* L.). Biology Univ Paris Sud-XI, Orsay, France

Yockteng R, Nadot S (2004a) Phylogenetic relationships among *Passiflora* species based on the glutamine synthetase nuclear gene expressed in chloroplast (ncpGS). Mol Phylogenet Evol 31:379–396

Yockteng R, Nadot S (2004b) Infrageneric phylogenies: a comparison of chloroplast-expressed glutamine synthetase, cytosol-expressed glutamine synthetase and cpDNA maturase K in *Passiflora*. Mol Phylogenet Evol 31:397–402

Yuan XJ, Pan JS, Cai R, Guan Y, Liu LZ, Zhang WW, Li Z, He HL, Zhang C, Si LT, Zhu LH (2008) Genetic mapping and QTL analysis of fruit and flower related traits in cucumber (*Cucumis sativus* L.) using recombinant inbred lines. Euphytica 164:473–491

Yuldasheva LN, Carvalho EB, Catanho M, Krasilnikov OV (2005) Cholesterol-dependent hemolytic activity of *Passiflora quadrangularis* leaves. Braz J Med Biol Res 38:1061–1070

Zanoli P, Avallone R, Baraldi M (2000) Behavioral characterisation of the flavonoids apigenin and chrysin. Fitoterapia 71:S117–S123

Zhai K, Hu L, Chen J, Fu CY, Chen Q (2008) Chrysin in mice induces hyperalgesia via the GABA(A) receptor. Planta Med 74:1229–1234

Zonneveld BJM, Leitch IJ, Bennett MD (2005) First nuclear DNA amounts in more than 300 Angiosperms. Ann Bot 96:229–244