# Chapter 10
# *Spondias*

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## 10.1 Introduction

The independent origins of agriculture in at least seven regions of the world ("centers of domestication") have produced a great variety of crops, many of which have become global staples that are cultivated well beyond their original distributions (e.g., banana, cassava, corn, mango, rice, wheat) (Vavilov 1992). In addition, in each of the centers of agricultural origins exists a plethora of cultivated plants that have not become global staples. These "companion" crop species play a crucial role in their native areas, contributing to both regional food security and economic stability (Tuxill 1999).

One of the centers of domestication is Mesoamerica (Mexico and Central America). The diverse flora of this region has contributed several globally important species to agriculture, including agaves (*Agave* spp.), avocados (*Persea americana* Mill), corn (*Zea mays* ssp. *mays*), cotton (*Gossypium hirsutum*), beans (*Phaseolus* spp.), and squashes (*Cucurbita* spp.). Significant components of the companion crop species of Mesoamerica are the cultivated fruit trees. In Mexico and Central America, several native fruit trees have been taken into cultivation including anona (*Anona cherimola*), avocado (*Persea americana*), cas (*Psidium friedrichsthalianum*), jocote (*Spondias purpurea*), nance (*Byrsonima crassifolia*), sapodilla (*Manilkara achras*), sapote (*Pouteria sapota*), and possibly guava (*Psidium guavaja*) and papaya (*Carica papaya*) (Rehm and Espig 1991). Today these fruits are sold in local markets and are consumed widely in the region, although the bulk of cultivation comes from backyard gardens and small multicrop farms. Large-scale production from trees planted in orchards, historically rare, is becoming more common.

The gene pool of a crop species comprises the cultivated populations (landraces, varieties, cultivars), as well as the wild (uncultivated) populations and close relatives. It has been estimated that in recent times (the last 100 years), the diversity within crop species and their wild relatives has declined by as much as 80% (Nabhan 1992; Tanksley and McCouch 1997). Native forests harboring the ancestors of cultivated plants have been lost, and more formal, centralized agriculture has promoted the adoption of a few high-yielding uniform cultivars over broad areas resulting in the abandonment of genetically variable indigenous varieties by subsistence farmers (Altieri and Merrick 1988).

Companion crops that are grown in their native ranges are occasionally cultivated in fields and orchards but are more commonly found in informal agricultural habitats, such as small multicrop farms, backyard gardens, and living fences. In addition, the wild relatives of the crops (individuals that are not cultivated and have not been domesticated) are generally found in these areas as well. Classical studies have demonstrated that traditional (informal) forms of agriculture nurture a diversity of cultivated varieties in a small area (e.g., Anderson 1952). Considering that the informally cultivated populations may be functioning as reservoirs of genetic diversity for these locally important species, and that extant native populations occur in the area, understanding the geographic distribution of genetic diversity both in wild populations and in informal agricultural habitats is vital to the sustainability of local agriculture and the conservation of crop genetic resources.

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## 10.2 Basic Botany of the Genus

*S. purpurea* (Anacardiaceae) is a small fruit tree (2–10 m in height) native to Mexico and Central America. In this region, both native populations as well as domesticated populations are found. *S. purpurea* trees produce plum-like fruits, some of which are eaten fresh, sold in local markets, and made into jams and beverages throughout the Neotropics (Mandujano et al. 1994; Avitia-García 1997; Baraona-Cockrell 2000; Mitchell 2000; Pimienta-Barrios and Ramirez-Hernandez 2003). Like plums, *S. purpurea* fruits have a single stone surrounded by a fleshy layer (mesocarp) and a thin skin, which varies widely in color.

### 10.2.1 Taxonomic and Morphological Framework

*Spondias* L. was described as a monotypic genus by Linnaeus (1753). Subsequent revisions delimited ~17 species (Table 10.1) including seven taxa in the Neotropics (Mexico–Brazil) and ~10 species in the Asian tropics (Linnaeus 1762; Airy Shaw and Forman 1967; Ding Hou 1978; Kostermans 1991; D Daly and JD Mitchell personal communication). *Spondias* is one of the basal-most genera in the Anacardiaceae, although neither the relationship of *Spondias* to closely allied genera, nor the relationships among the species of *Spondias* are well understood (Pell 2004). At least six *Spondias* species have been taken into cultivation: three Asian species (*S. borbonica, S. cytherea*, and *S. pinnata*) and three American species (*S. mombin, S. purpurea,* and *S. tuberosa*) (Table 10.1). This chapter focuses on the wild populations of the cultivated species *S. purpurea* and its sympatric congeners.

*Spondias* species are trees (rarely vines) ranging from 2 to 35 m in height. Their floral structure is characterized by having stamens that are twice the number of the petals. The carpels are united and range in number from 1 to 12 (usually 4–5), with terminal styles. The ovules are pendulous from an apical funicle. The primary synapomorphies for *Spondias* are an endocarp that is completely surrounded by a capsule of strong, intertwined longitudinal fibers, and leaflets with a marginal vein (Kostermans 1991). Variable breeding systems are common in the Anacardiaceae. In *Spondias*, several species are known to exhibit unisexual flowers (e.g., *S. purpurea*), bisexual flowers (e.g., *S. mombin*), or both (e.g., *S. bipinnata*, *S. mombin*, *S. pinnata*, and *S. purpurea*) (Kostermans 1991).

**Table 10.1** *Spondias* species and their geographic distributions (Williams 1930; Airy Shaw and Forman 1967; Cavalcante 1976; Popenoe 1979; Brücher 1989; Kostermans 1991; D Daly, personal communication)

| Species | Native range |
|---|---|
| *S. acida* Bl. | Malay Penninsula |
| *S. acuminata* Roxb. | India, Burma, Thailand |
| *S. bipinnata* Airy Shaw & Forman | Thailand (limestone hills) |
| *S. bivenomarginalis* K.M. Feng & P.Y. Mao & P. Me. | Yunnan, China |
| *S. dulcis* Parkinson | Asian; Cult. In New World, Brazil, Caribbean |
| *S. macrocarpa* Engl. | Eastern Brazil |
| *S. malayana* Kosterm. | Malesia, Philippines |
| *S. mombin* L. var. *mombin* | Mexico to Bolivia and eastern Brazil, Central America, Brazil |
| *S. mombin* L. var. *globosa* | Colombia, Venezuela, Ecuador, Peru, Bolivia |
| *S. novoguineensis* Kosterm. | New Guinea, Solomon Islands, etc. |
| *S. pinnata* (Koenig ex Linn. F.) Kurz | India, Himalayas, Burma, Sri Lanka |
| *S. purpurea* L. | Mexico – Central America, Ecuador |
| *S. radlkoferi Donn. Sm.* | Mexico, Central America, NW Venezuela, W. Ecuador |
| *S. testudinis* J.D. Mitch & Daly | SW Amazonia |
| *S. tuberosa* Arruda | NE Brazil |
| *S. venulosa* Mart. ex Engl. | E. Brazil |
| *S. tonkinensis* Kosterm. | Tonkin, Langson Province |
| *S. xerophila* Kosterm. | Sri Lanka |

In the Neotropics, six *Spondias* taxa are recognized: *S. macrocarpa* Engl., *S. mombin* L. var. *mombin*, *S. mombin* L. var. *globosa*, *S. purpurea* L., *S. radlkoferi* Donn. Smith, *S. testudinis* J.D. Mitch. & Daly, and *S. tuberosa* Arruda (D Daly, personal communication). Of these, three occur naturally in Mexico and Central America: *S. mombin* var. *mombin*, *S. purpurea*, and *S. radlkoferi*. *S. mombin* var. *mombin* and *S. radlkoferi* share many similarities; both are large trees ($\leq$35 m) that are found primarily in tropical wet forests. Inflorescences of large hanging panicles carry numerous small, cream-colored, white, yellow, or greenish, primarily hermaphroditic, outcrossing flowers (Stacy et al. 1996). *S. mombin* is distinguished from *S. radlkoferi* by its fruits. The fruits of *S. mombin* are yellow–orange spheres, while those of *S. radlkoferi* are more oblong in shape, and are green at maturity. In addition, the leaves of *S. radlkoferi* are pubescent with stellate hairs. Croat (1974) observed that the species flower at different times.

Although all three Mesomerican *Spondias* species are cultivated to some degree, *S. purpurea* is the most widespread and economically important. In most cases, *S. purpurea* trees are easily distinguished from *S. mombin* var. *mombin* and *S. radlkoferi*. Unlike its sympatric congeners, *S. purpurea* is a small tree (~2–10 m) native to the dry forests (Rzedowski 1978). *S. purpurea* flowers are cauliflorous; the inconspicuous unisexual or hermaphroditic flowers occur in fasicles or small, appressed panicles on the stem, and develop before the leaves appear. Unisexual flowers appear nearly perfect (Avitia-García 1997) or with reduced vestiges of the non-functional sex. The petals are cream to yellow or more commonly reddish-purple in color. The cauliflorous fruits are cylindrical to oblong drupes (2–6 cm in length) that range in color (red, orange, yellow, green, purple), taste (sweet, acidic), and size (3.0–5.5 cm). The leaflets of *S. purpurea* are smaller and more numerous than *S. mombin* var. *mombin* and *S. radlkoferi*.

Native *S. purpurea* populations are dioecious or polygamodioecious, a condition that has been shown to be relatively common in tree species in the dry forests of tropical regions (Bawa 1974; Bawa et al. 1985; Bawa and Opler 1975). Most likely, *S. purpurea* pollination is entomophilous, although the pollination mechanisms in native populations have not been studied. The fruits are usually bright red or yellow, and are smaller and more acidic than the fruits of cultivated *S. purpurea*. The fruits of native *S. purpurea* trees are an important water and food resource for forest animals (Mandujano et al. 1994). In Jalisco, Mexico, seeds of native *S. purpurea* trees are dispersed by coyotes (*Canis latrans*), coati (*Nasua narica*), gray fox (*Urocyon cinereoargenteus*), iguana (*Ctenosaura pectinata*), collared peccary (*Pecari tajacu*), Collie's squirrel (*Sciurus colliaei*), chachalaca (*Ortalis poliocephala*), and white-tailed deer (*Odocoileus virginianus*) (Mandujano et al. 1994). The endocarp must be kept wet or germination is unlikely. Mandujano et al. (1994) observed that only seeds covered with litter germinated, and that endocarps dispersed by iguanas were less likely to produce germinating seedlings than those dispersed by white-tailed deer (35% to 72%, respectively).

### 10.2.2 Distribution and Geographical Locations of Genetic Diversity

Native populations of *S. purpurea* are found in the dry forests along the Pacific side of Mexico and Central America below 1,300 m (Rzedowski 1978; Mandujano et al. 1994; Avitia-García 1997). Cultivated *S. purpurea* trees were grown widely from Mexico to the northern region of South America when the Europeans arrived in Mesoamerica, as recorded by the early chroniclers (Oviedo, Sahagún) (Estrada Lugo 1989; Cuevas 1994). The ancient Council Book of the Quiché Mayans, the *Popul Vuh*, lists *S. purpurea* (common name in Quiché: Q'inom) together with other native fruit trees valued and consumed by the Maya: anonas or cherimoya (*Annona* spp.), cacao (*Theobroma cacao*), matasanos (*Casimiroa edulis*), nance (*Byrsonima crassifolia*), and zapotes (*Manilkara zapota*) (Tedlock 1996). Ethnobotanical studies have shown that *S. purpurea* fruits are known and consumed by most indigenous groups in Mexico and Central America [e.g., the Huichol people of Jalisco and Nayarit, Mexico (Bauml 1994), the Mixteca people of Guerrero (Casas et al. 1994), the Huastec Maya of Veracruz and San Luis Potosi (Alcorn 1984), the Zinacantec Maya of Chiapas (Breedlove and Laughlin 2000)]. There are over 180 common names in more than 20 languages for *S. purpurea* including abal, ciruela mexicana, hog plum, jocote, and purple mombin (Miller 2004). Today, *S. purpurea* trees are grown throughout the Neotropics.

Analyses of cultivated and native populations based on Geographic Information Systems (GIS) data have revealed significant differences in the environmental attributes that characterize the geographic distributions of native *S. purpurea* populations relative to cultivated *S. purpurea* populations in Mesoamerica (Miller and Knouft 2006). Specifically, the areas inhabited by wild and cultivated *S. purpurea* populations differ significantly in mean diurnal temperature range, annual temperature range, precipitation seasonality, annual precipitation, and precipitation in the driest quarter. Areas where wild *S. purpurea* populations are found are characterized by significantly higher mean diurnal temperature range, higher annual temperature range, higher precipitation seasonality, lower annual precipitation, and lower precipitation in the driest quarter relative to areas in which cultivated *S. purpurea* populations reside. In addition, the variances of these five environmental variables were significantly less for native populations compared to cultivated populations (Miller and Knouft 2006). These data suggest that during the course of domestication, wild *S. purpurea* populations native to the dry forests were preferentially cultivated in regions that were less seasonal, cooler, and wetter relative to the dry forests. Further, these data demonstrate that the geographic distribution of native *S. purpurea* populations is remarkably narrow relative to the geographic range of their cultivated descendants (Miller and Knouft 2006).

### 10.2.3 Reproductive Biology

Native *S. purpurea* populations are dioecious (Mandujano et al. 1994; Avitia-García 1997; AJ Miller, personal observation), although there are some reports of wild populations with hermaphroditic flowers on female trees (Raymundo Ramirez, personal communication). Reproductive structures of the opposite sex are present in unisexual flowers, but are highly reduced and non-functional. In February 2005, the author visited four wild *S. purpurea* populations near Guadalajara, Jalisco (Mexico), and observed that wild populations include mostly male trees. To confirm these observations, the author collected and dissected five flowers per tree for nine wild *S. purpurea* trees. Eleven percent of wild trees surveyed were females (1 of 9 trees). Low numbers of female trees in wild populations may represent a common phenomenon in dioecious species; natural dioecious plant populations generally have male-biased populations (Lloyd and Webb 1977; Delph 1999). A second explanation is that decreased numbers of females in the wild populations may be the result of tree harvesting by humans; *S. purpurea* is readily propagated from large cuttings, and perhaps female trees were preferentially removed from the forest for cultivation.

In striking contrast to male-biased native *S. purpurea* populations, apparently all cultivated *S. purpurea* individuals in this dioecious species produce fruit, indicating a preponderance of flowers with female components in cultivated populations. As part of the study described in the previous section, the author visited five cultivated *S. purpurea* populations near Guadalajara, Jalisco (Mexico), and observed that cultivated populations appeared to be entirely female. To confirm these observations, the author collected and dissected five flowers per tree for ten cultivated *S. purpurea* trees. As expected, 100% of cultivated trees surveyed were females (A Miller, unpublished data). These observations underscore the importance of crop wild relatives as a source of sexual diversity. Many dioecious species have been domesticated for their fruits (Zohary and Spiegel-Roy 1975), and in these species, males are found only in native populations.

Native *S. purpurea* populations reproduce sexually and consist of seedling, sapling, and mature trees. This is not the case for cultivated *S. purpurea* populations, which are propagated exclusively vegetatively. Indeed, field observations and interviews with farmers from seven Mesoamerican countries failed to uncover a single case of *S. purpurea* propagation from seed (Miller 2004). Empirical studies have shown that seeds of cultivated *S. purpurea* trees do not form viable embryos (Juliano 1932; Avitia-García 1997). It appears that native *S. purpurea* populations may be the only remaining populations of *S. purpurea* which are capable of sexual reproduction; it is not clear if cross-pollination between cultivated and native *S. purpurea* results in viable offspring.

Fruits of native *S. purpurea* trees vary geographically. For example, native populations in central western Mexico produce small, bright red fruits before or just as the leaves are emerging in late spring. Native populations in Central America (e.g., Costa Rica, El Salvador) have yellow fruits. Artificial selection focused primarily on fruit production, which led to clear differences in the fruits of cultivated and wild *S. purpurea* trees; cultivated *S. purpurea* fruits are larger than wild fruits, and have a thicker, juicier mesocarp, exhibit a greater range of colors (mature cultivated fruits can be red, orange, yellow, green, or purple; wild fruits are either red or yellow), and are much sweeter than the acidic wild fruits.

### 10.2.4 Agricultural Status

*S. purpurea* trees are cultivated for their fruits, which are eaten fresh, stewed, and made into jams and beverages (Baraona-Cockrell 2000; Pimienta-Barrios and Ramirez-Hernandez 2003). *S. purpurea* trees are cultivated throughout Mexico, Central America, the Caribbean, portions of South America, and the Philippines (Juliano 1932; Kostermans 1991; Macía and Barfod 2000). Fruits of *S. purpurea* are an excellent source of vitamin C (Koziol and Macía 1998). They are eaten fresh, candied, and made into jelly, wine, and vinegar. In Mexico, green fruits are made into a tart sauce. The fresh shoots are eaten raw or cooked as a vegetable (Kostermans 1991). The bulk of propagation occurs in traditional agricultural habitats (e.g., fruits are harvested from wild trees or from trees grown in backyard gardens and living fences). Commercial plantings are relatively uncommon, but have been developed in Mexico, Guatemala, Honduras, Costa Rica, and El Salvador (Kostermans 1991; Cuevas 1994, AJ Miller, personal observation). *S. purpurea* trees are cultivated exclusively vegetatively. Large branch-sized cuttings are used to propagate new trees, which usually set fruit within 2–3 years.

## 10.3 Conservation Initiatives

It has been estimated that less than 2% of the native habitat of *S. purpurea*, the Mesoamerican dry forests, remains (Janzen 1988). Little research has been conducted on specific native taxa in these threatened forests (Sánchez-Azofeifa et al. 2005). Unfortunately, there are no known in situ or ex situ conservation efforts explicitly designed for native *S. purpurea* populations or other *Spondias* species. The conservation of crop genetic resources must include both the wild relatives of the cultivated species (*Spondias* spp.) and the native populations from which the cultivated populations are derived (native, uncultivated *S. purpurea* populations). In addition, although many crop populations are found in modern agricultural environments (e.g., orchards in the case of trees), conservation initiatives must take the cultivated populations found in more traditional agricultural habitats into account (e.g., home gardens, living fences). Because traditional agricultural habitats can include domesticated plants as well as propagules derived directly from wild individuals, it has been suggested that these populations may represent one portion of a continuum of genetic differentiation ranging from wild to domesticated variants (Harris 1989; Tanksley and McCouch 1997; González-Soberanis and Casas 2004; Miller and Schaal 2006).

### 10.3.1 Evaluation of Genetic Erosion

Genetic variation in native *S. purpurea* populations has been quantified using amplified fragment length polymorphism (AFLP) data, chloroplast sequence data, and nuclear sequence data (Miller and Schaal 2005, 2006; Miller 2008). Analyses of chloroplast sequence data based on the spacer region *trnS–trnG* revealed that 71% of total allelic diversity was recovered in native populations, whereas only 53% of the total allelic diversity was recovered in cultivated populations (some alleles were found only in native populations, whereas other alleles were carried exclusively by cultivated individuals) (Miller and Schaal 2005). The extent of genetic erosion in *S. purpurea* was addressed directly in a study that compared native *S. purpurea* populations to cultivated populations collected from three different types of agricultural habitats: orchards, home gardens, and living fences (Miller and Schaal 2006). Thirty-four populations were sampled including 15 native populations, ten backyard populations, five living fence populations, and six orchard populations a total of 216 individuals. DNA was extracted and molecular markers were generated using the dominant AFLP marker technique (Vos et al. 1995). Briefly, the AFLP technique fragments genomic DNA using restriction enzymes; then, two rounds of polymerase chain reaction (PCR) are conducted with (1) pre-selective primers and (2) selective primers to amplify a subset of fragments. The selective primers are fluorescently labeled and resulting fragments are visualized using an automated sequencer. Fragments are sized (in base pairs) and fragments of the same size are scored as present or absent for each individual. In this study, two primer combinations resulted in 200 polymorphic fragments that ranged in size from 40 to 400 bp. Based on these data, population genetic diversity was estimated using standard parameters, percentage of polymorphic sites, Shannon's diversity index, Nei's (1973) gene diversity, and Bayesian methods (e.g., average panmictic heterozygosity). Wilcoxon two-group tests revealed that orchard populations harbored significantly less genetic variation than native populations; however, there were no significant differences between native populations and living fence populations, or between native populations and backyard populations. When native populations were compared to cultivated populations as a group (orchards + living fences + backyards), the cultivated populations were found to harbor significantly less genetic variation than the native populations. In addition to the levels of genetic diversity, the amount of population structuring varies in the different stages of domestication. Estimates of population structure (based on AMOVA and Bayesian estimators of $F_{\mathrm{st}}$) reveal that in wild populations, a smaller proportion of genetic variance is attributed to differences among populations (30.19%, $\phi_{\mathrm{ST}} = 0.302$) than in cultivated populations (39.76%, $\phi_{\mathrm{ST}} = 0.398$). This likely reflects differences in reproduction in *S. purpurea* populations; wild populations reproduce exclusively from seed, while cultivated populations are propagated vegetatively. Populations of backyard trees exhibit only slightly more variation among populations (31.19%, $\phi_{\mathrm{ST}} = 0.311$) than do the wild populations, whereas living fences and orchards harbor greater proportions of genetic variance among populations (48.31%, $\phi_{\mathrm{ST}} = 0.483$; 44.82%, $\phi_{\mathrm{ST}} = 0.448$, respectively) than do the wild and backyard populations. Elevated estimates of population structuring in living fences and orchards as compared with backyard trees and wild populations may reflect greater levels of vegetative propagation in living fences and orchards, human-dispersal of cuttings from backyard trees, or that some gene flow occurs between backyards, or backyards and wild populations, or both.

## 10.4 Role in Elucidation of Origin and Evolution of Allied Crop Species

Historically, circumscription of the *Spondias* lineage has proved difficult. In 1952, in his book *Plants, Man, and Life*, Edgar Anderson addressed the genus *Spondias* (mombins) in Mesoamerica:

> It is a little hard to talk about the mombins because they have so many different names, none of which are really widely used. They are popular fruits in various parts of the tropics, and are about the size of plums. In Latin America they are frequently called the "ciruela" that being the common Spanish name for the European plum. Botanically they go in the genus *Spondias*, and are not at all closely related to plums, though like that fruit they are more or less acid and have a large central stone. Some are red, some are yellow, some red with a flush of yellow. Most Europeans do not consider them much of a delicacy, but to the Indian populations they are one of the pleasures of life. One sees baskets and piles of them in every native market. Indians coming into town with bundles of produce on their heads munch them as they hurry along at a half trot, and when they are in season towns like Antigua have a superficial paving on mombin pits on top of the old cobblestones. How many species of mombin are there, and where do they come from? . . ."Who knows? There may be two kinds; there may be fifty. The Indians have been gathering them and spitting them out again for we don't know how long. They have been planting selected forms in their native gardens and these native gardens have reverted to woodland. How are we ever going to know where they all came from?" (Anderson 1952, pp 91–92).

Recent studies have focused on identifying the lineage to which cultivated *S. purpurea* populations belong (Miller 2008), and on identifying the geographic origins of cultivated *S. puprurea* populations in Mesoamerica (Miller and Schaal 2005, 2006). In addition to *S. purpurea* accessions, these studies included samples of other congeneric taxa including *S. mombin* var. *mombin*, *S. mombin* var. *globosa*, *S. radlkoferi*, and *S. testudinus*.

### *10.4.1 Relationships Between* S. purpurea *and Related Species*

A thorough molecular phylogenetic analysis of *Spondias* is lacking. Evolutionary analyses based on molecular data to date have included only a subset of species in the genus (Miller and Schaal 2005; Miller 2008;

Santos and de Oliveira 2008), consequently providing limited insight into relationships between *S. purpurea* other *Spondias* species. Distance-based analyses of AFLP data revealed that *S. purpurea* is genetically more similar to *S. mombin* than to *S. tuberosa* or *S. cytherea* (Santos and de Oliveira 2008). Chloroplast haplotype data demonstrated that in some Central American populations, three *trnS–G* alleles are shared by both *S. purpurea* and *S. mombin* var. *mombin*, and one *trnS–G* allele is shared by both *S. purpurea* and *S. radlkoferi* (Miller and Schaal 2005). Haplotype sharing can indicate shared evolutionary history; alternatively, it can result from gene flow between two distinct lineages. In the chloroplast data set, the situation is further complicated by the mutational relationships among additional alleles carried by other *Spondias* species. For example, aside from the shared alleles described above, the *trnS–G* alleles carried by *S. purpurea* trees are most closely related to alleles recovered in *S. testudinus* and *S. mombin* var. *globosa* populations collected in Brazil. Network analyses of nuclear sequence data from the fourth intron of the gene encoding phosphoenolpyruvate carboxylase (*Pepc*) yielded no shared haplotypes between *S. purpurea* and *S. mombin* (Miller 2008).

### 10.4.2 *Relationships Between Cultivated* **S. purpurea** *Populations and Their Wild (Native) Ancestors*

Cultivated and native *S. purpurea* populations share several features that distinguish the species from others in the genus: flowers unisexual (occasionally hermaphroditic) cauliflorous, developing before the leaves appear, usually purple (but occasionally yellowish-white), fruits cylindrical to oblong drupes, fruit color variable, and leaflets small and numerous (see Sect. 2.1). On the basis of these morphological characters, as well as chloroplast and nuclear sequence data, cultivated and native *S. purpurea* populations form a monophyletic group (Miller and Schaal 2005; Miller 2008).

Native populations of *S. purpurea*, in conjunction with cultivated *S. purpurea* populations, have been the subjects of two distinct statistical analyses designed to investigate the geographic origins of cultivated *S. purpurea* populations. First, chloroplast sequence data were employed in a nested clade analysis (Miller and Schaal 2005). In this approach, mutational relationships among alleles were used to construct a haplotype network. Haplotypes within the network were grouped into nested clades (smaller clades are nested in larger clades); at each level of nesting, the null hypothesis was no association between geographical locations of individuals and the clades in which the alleles they carry are found (Templeton and Sing 1993; Templeton 1998). In the *Spondias* study, sequences of the chloroplast spacer *trnS–trnG* were used to construct a haplotype network and to identify clades. The null hypothesis of no association between geography and genealogical lineage was rejected for four clades; two clades consisted of alleles carried by individuals collected in southern Mexico and Central America (in the southern portion of the range of *S. purpurea*) and two clades included alleles carried by individuals in western central Mexico (the northern portion of the *S. purpurea* range). These results provide statistical support for two distinct groups of *S. purpurea* alleles, a southern group and a northern group. Because each group includes haplotypes recovered in both native populations and in cultivated populations, these results suggest that alleles recovered in cultivated populations in the southern portion of the range were derived native trees in the southern portion of the range, whereas alleles recovered in cultivated populations in the northern portion of the range were derived from native trees in the northern portion of the range. This phylogeographical analysis provides statistical support for two genetically and geographically distinct native *S. purpurea* gene pools, each of which gave rise to cultivated populations.

The second investigation of the origins of *S. purpurea* populations was based on AFLP data (200 fragments) generated for 13 native populations (85 individuals) and 21 cultivated populations (131 individuals) collected in Mexico and Central America (Miller and Schaal 2006; described in Sect. 3.1). Variation in the AFLP dataset was summarized using a principal components analysis. Analyses of the first three principal components indicated that trees from native populations cluster in two distinct groups (1) a southern group and (2) a northern group, and that trees from cultivated populations cluster geographically as well. Further analyses provided statistical support for the two groups of wild trees and the two groups of cultivated trees (Miller and Schaal 2006). The AFLP dataset corroborates the results of the phylogeographic study based on chloroplast sequence data, providing further support for geographically and genetically distinct native *S. purpurea* populations from which cultivated *S. purpurea* populations were derived in at least two independent domestication events (Miller and Schaal 2005, 2006).

## 10.5 Role in Classical and Molecular Genetic Studies

Recently, molecular genetic techniques such as DNA sequence data and AFLPs have been applied to elucidate the evolutionary history of *S. purpurea* (Miller and Schaal 2005, 2006; Miller 2008). Although these studies have advanced the general understanding of domestication processes in trees, there have been no known studies applying classical genetic techniques in *Spondias*. Several aspects of the basic biology of trees complicate classical genetics initiatives (see Petit and Hampe 2006; Savolainen et al. 2007 for reviews). For example, trees are long-lived organisms that can take decades to reach maturity. Experimental crosses cannot be evaluated until offspring reach maturity, which can be several years at best. Trees are primarily outcrossers and while variants resulting from genetic exchange provide a wealth of options on which natural selection can act in wild populations, extensive variation impedes efforts to improve tree crops. Classical genetics is hindered further by self-incompatibility in many native tree populations. In the case of *S. purpurea*, although chloroplast and nuclear sequence data suggest that gene flow between *S. purpurea* and *S. mombin* is possible (Miller and Schaal 2005; Miller 2008), however, classical genetic approaches may be difficult due to low levels of viability observed in *S. purpurea* seeds (Juliano 1932), as well as the time to maturity.

## 10.6 Role in Crop Improvement Through Traditional and Advanced Tools

The success of traditional breeding efforts is evidenced by the abundance of fruit shapes, sizes, and colors in cultivated *S. purpurea* populations, and by the number of local names available for *Spondias*. Interviews with local residents and farmers during field studies in Mexico and including Central America uncovered about 100 unique names for native Mesoamerican *Spondias* species, 89 names for *S. purpurea*, and seven names for *S. mombin*. Data from field collections were combined with names obtained from literature sources to produce a comprehensive list of 247 common names for *Spondias* in Mesoamerica (Miller 2004). On the basis of this information, 183 names are used for *S. purpurea* and 64 common names have been applied to *S. mombin*.

Potential for crop improvement through modern breeding efforts with wild populations (native *S. purpurea* populations) or other closely related species (e.g., *S. mombin*) has not been thoroughly explored. The application of modern breeding techniques to *S. purpurea* may be met with limited success because (1) *S. purpurea* have relatively long juvenile phases (see discussion in Sect. 5); and (2) cultivated *S. purpurea* populations may have lost the ability to reproduce sexually (Sect. 2.3).

During the course of the domestication of many tree species, humans propagated desirable individuals through cloning (Zohary and Spiegel-Roy 1975; Ladizinsky 1998; Zohary 2004). In these species, the original cultivars were derived from their wild ancestors in two possible ways (1) cuttings of the wild trees were removed directly from native forests and placed in human-managed environments, or (2) an assortment of wild seeds were transferred from the forests to cultivated habitats. Once established in cultivated habitats, individuals were propagated vegetatively. New individuals were simply clonal reproductions of the most attractive individuals that were initially removed from the wild populations for cultivation (Zohary and Spiegel-Roy 1975; Zohary 2004). Additionally, it is likely that new genotypes were introduced periodically from local native populations.

Many of the world's oldest and most well-known fruit trees are propagated vegetatively, including almonds, olives, figs, breadfruit, and dates (Casas et al. 1999; Sonnante et al. 2002; Lumaret et al. 2004; Zerega et al. 2004; Bender and Whiley 2002; Morton 1987; Zohary and Spiegel-Roy 1975 respectively). The shift from sexually reproducing wild populations to vegetatively propagated cultivated populations has led to a suite of morphological changes that characterize the evolution of cultivated trees. These changes include, in self-incompatible wild populations, a shift to self-compatible cultivated populations, and in dioecious wild progenitors, a shift to cultivated populations with hermaphroditic flowers (e.g., grapes), or with only female trees that produce fruit parthenocarpically (without fertilization) (e.g., figs) (Zohary and Spiegel-Roy 1975; Zohary and Hopf 2000; Zohary 2004). In the case of *S. purpurea*, cultivated trees are grown exclusively from cuttings, and seeds do not appear to form viable embryos (Juliano 1932; Avitia-García 1997; Miller 2004).

While traditional breeding alone may not be practical in *S. purpurea*, crop improvement may be a feasible option with the application of molecular genetic tools. To date, two studies have applied AFLP data to characterize diversity in *S. purpurea* and its relatives (Miller and Schaal 2006; Santos and de Oliveira 2008). AFLP markers can be used to generate molecular maps that, in concert with phenotypic data, can be used to identify markers associated with phenotypic traits of interest (e.g., Skøt et al. 2005). In the case of *S. purpurea*, the AFLP markers could be applied in marker-assisted selection programs designed to identify individuals with traits of agronomic importance.

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