Chapter 15
Wild Genetic Resources of Minor Oil and Rubber Crops

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Abstract Jojoba (*Simmondsia chinensis* (Link) C. K. Schneid), lesquerella (*Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz), and guayule (*Parthenium argentatum* A. Gray) originate from semiarid climate zones of North America; meadowfoam (*Limnanthes alba* Hartw. ex Benth., *Limnanthes bakeri* J. T. Howell, *Limnanthes douglasii* R. Br.) is endemic to the western part of California, Oregon, and Southern Canada and grows around vernal pools and seasonally wet areas. This chapter discusses historic and current uses, domestication efforts, breeding, and cultivation challenges and describes the conservation status of the crops' genetic resources. Meadowfoam and guayule are already cultivated on a limited industrial scale. Jojoba and lesquerella are not grown commercially in North America but are economically important in countries beyond the Americas and are of particular interest to nations with extensive areas of arid lands. North America is an important source of wild genetic resources for these crops, and further efforts are needed to ensure their conservation.

Keywords Oil crops · *Limnanthes* · *Lesquerella* · *Simmondsia* · Rubber crop · *Parthenium*

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15.1 Introduction

Jojoba (*Simmondsia chinensis* (Link) C. K. Schneid), meadowfoam (*Limnanthes alba* Hartw. ex Benth., *Limnanthes bakeri* J. T. Howell, *Limnanthes douglasii* R. Br.), lesquerella (*Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz), and guayule (*Parthenium argentatum* A. Gray) are defined as "new crops" despite the discovery of their potential economic value in the early 1900s for guayule and 1950s for jojoba, meadowfoam, and lesquerella. While their seeds (oil crops) or plants (guayule) contain a high quality and quantity of oil or rubber, cultivation is currently highly limited. The type of oil and rubber that can be produced with these plant materials has many applications as biodegradable lubricants, biofuels, cosmetics, pharmaceuticals, dietetic products (oil crops), and industrial products such as rubber, resin, and bagasse (guayule). The meal can also be used in animal feed and for soil augmentation. All described species have antimicrobial characteristics and might be useful biocides. Wild forms of all of these crops occur in North America.

This chapter describes the historic uses of the wild populations by people living nearby the natural plant populations, as well as contemporary utilization of the wild plants in initial research in cultivar development. Discussed are cultivation efforts and challenges of these crops, the wild habitats and geographic ranges that the wild species occupy, germplasm, improvement status, and characteristics to be improved to make the crops profitable to growers. The current state of the species' taxonomy and past struggles of scientific determination is also reported. Due to vanishing habitat, some meadowfoam and lesquerella species are on US federal or state plant protection listings. Unfortunately, jojoba and guayule wild populations are not currently protected.

15.2 Jojoba: A Species with Uncommon Liquid Wax

Jojoba (*Simmondsia chinensis* (Link) C. K. Schneid) is reported as "one of the most unusual and unique plants of the North American deserts" and "the only known plant in the world to produce liquid wax" (Green et al. 1936; Princen 1979; Sherbrooke and Haase 1974). The scientific name for jojoba is *Simmondsia chinensis* (Link) C. K. Schneid, and *S. californica* Nutt. is a synonym (Carlquist 1982; USDA ARS 2017b). In some countries, jojoba is domesticated and cultivated as a crop due to its tolerance to drought. It is an evergreen desert shrub with thick, leathery bluish-green leaves different in size, shape, color, and pubescence; the shrub may reach a height of 0.2–5 m and live over 200 years (Benzioni and Dunstone 1986; Gentry 1958; Hamerlynck and Huxman 2009; Khan et al. 2017; Wisniak 1994; Yermanos 1979). The species is dioecious (hermaphroditic individuals may rarely occur) and wind-pollinated (Buchmann 1987; Gentry 1958). The fruit is a dehiscent capsule containing one to three seeds. Jojoba tolerates temperatures ranging from −1.1 °C (mature shrubs may endure −9.4 °C) to 46.1 °C (Gentry 1958; Yermanos 1974). Due to its botanical and physiological nature and high adaptability, jojoba is a suitable crop for marginal lands in desert conditions (McKell 1983), and it does not compete for land with food crops. Because of its oil characteristics and potential economic value, jojoba is of interest to countries with vast desert areas (Sidibé et al. 2010; Sukkasi et al. 2010).

15.2.1 Crop Origin and History of Use Worldwide

The name jojoba was adapted by Spaniards from the Tohono O'odham Indian name "hohowi"; the species is also known as hohwi, hohovai, bucknut, bushnut, jobe, jojove, pignut, goatberry, goat nut, deer nut, wild hazel, quine nut, coffeeberry, coffeebush, gray box nut, quinine nut, sheepnut, and wild hazelnut (Castetter and Underhill 1935; Daugherty et al. 1958; Felger and Rutman 2016; Sherbrooke and Haase 1974). The species might be a remnant from a prehistoric era of an ecosystem that does not exist today (Gentry 1972); however, the origin of jojoba is not known (Stebbins and Major 1965). Jojoba nuts and their oil were used by native populations of Baja California for medicinal purposes, as cooking oil and were consumed as roasted seed (Sherbrooke and Haase 1974). The first report on using jojoba was described by Francesco Saverio Clavigero, a Mexican Jesuit in 1789 (Clavigero 1789). In 1925, the Boyce Thompson Southwestern Arboretum in Superior, Arizona, planted experimental plots of jojoba (Nagavi and Ting 1990). In the 1950s and 1960s, jojoba oil was thought as a substitute for sperm whale oil due to their chemical similarities and was hoped to be a source of income for Native Americans residing in semiarid regions of the United States (Benzioni 1995; Miller et al. 1979). However, cultivation of unimproved wild material without any agronomic knowledge resulted in low seed yield (300–400 kg/ha) and did not prove to be economical (Shani 1995; Wisniak 1977; Yermanos 1974). In the 1970s, there was a renewed interest in jojoba due to an oil embargo, subsequent price increases, and oil shortages. Additionally, sperm and other whale species were identified as endangered species, and their harvest restricted. In 1976, jojoba fields were established in Arizona and California (Palzkill and Hogan 1983); however, other authors reported 1978 as the beginning of jojoba cultivation in the United States, reaching its largest acreage of 16,000 ha in 1985 and declining after (Harington 1987). The majority of plantings were abandoned due to yield fluctuations, lack of knowledge of agronomic procedures, and unavailability of high seed-yielding cultivars (Harington 1987; McKay 1987).

More recently, jojoba cultivation, material improvement, and research are of interest in countries with semiarid environments: in Africa, Kenya (Inoti et al. 2015, Inoti 2016), Morocco (Berrichi et al. 2010), Sudan (Nimir and Ali-Dinar 1989) and South Africa (Nimir and Ali-Dinar 1989); in the Americas, Argentina (Tobares et al. 2004), Chile (Botti et al. 1998; Cappillino et al. 2003), Mexico (Foster et al. 1983; Franco-Viziano and Khattack 1990; Godoy 2011), Peru (Kolodziejczyk et al. 2000), and the United States (Palzkill and Hogan 1983; Purcell and Purcell 1988;

Purcell et al. 2000; Yermanos 1978); and in Asia, China (Li et al. 2007), India (Bhatnagar et al. 1991), Iran (Jahromi and Fard 2013), Israel (Dunstone et al. 1984), Jordan (Al-Hamamre 2013), Saudi Arabia (Al-Soqeer 2010; Osman and Hassan 2000; Osman and Abohassan 2013), and Yemen (Eed and Burgoyne 2015). Also it is of interest in Australia (Dunstone and Begg 1983) and Turkey (Ayanoğlu 2000; Ülger et al. 2002).

15.2.2 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Stress

The glassy-winged sharpshooter (*Homalodisca vitripennis* Germar) was observed on jojoba plants in California (Wistorm et al. 2010) and scale (*Aspidiotus nerii* Bouché) in Israel (Berlinger et al. 1999), and several sucking insects were reported in Chile (Quiroga et al. 1991). Several fungal diseases were reported on jojoba. *Verticillium dahliae* Kleb. was noticed in California (Orum et al. 1981; Orum et al. 1983). Seed fungi taxa (*Aspergillus flavus*, Link, *A. niger* Teigh., *Fusarium pallido-roseum* (Cookie) Sacc.) (Sharma and Champawat 2000), *Rhizoctonia solani* J.G. Kühn, and various species of *Fusarium* were reported in the Indian desert (Saroj and Kumar 1983; Champawat et al. 2003). A bacterial disease on leaves was observed in Australia (Cother et al. 2004). The shrub is generally considered to be salt tolerant (Hussain et al. 2011; Tal et al. 1979); however, Hassan and Ali (2014) reported membrane damage, decreased plant height, and lower number of leaves and branches under salinity stress. Its adaptation to arid and warm environments is well known, and genetic diversity in adaptation for saline conditions undoubtedly exists, considering the species' broad range in the Sonoran desert.

15.2.3 Functional Use

Seeds of jojoba contain liquid wax that is not found in any other plant species (Gentry 1958; Princen 1979). Commonly, jojoba waxes are referred to as jojoba oil. The oil content in seeds is between 48% and 65% (Busson-Breysse et al. 1994; Green et al. 1936; Jenderek and Dierig 2008; Salgin et al. 2004). The oil is odorless and light yellow, has a high normal boiling point and low chemical reactivity, and is very stable at temperatures <120 °C (Tobares et al. 2004; Torres et al. 2006). The properties of the oil and its content in seeds stay unchanged during storage over several years (Daugherty et al. 1958). The oil characteristics were summarized by McKell (1983) as being molecularly simple, unsaturated, stable under high temperature and pressure, and not prone to rancidity in storage. Mirov (1952) described the liquid wax as a composition of one long-chain alcohol molecule coupled with one molecule of fatty acid, whereas fats are comprised of a glycerine molecule with three fatty acid molecules attached. The wax composition was reported by Miwa (1971) and later by

Benzioni (1978). Analysis of the liquid jojoba wax showed that the wax is a mixture of esters (docosenyl eicosenoate 41.4%, eicosenyl eicosenoate 28.0%, eicosenyl docosanoate 10.3%, tetracosenyl eicosenoate 6.8%, and eicosenyl oleate 5.7%), triacylglycerols (eicos-11-enoic 76.7%, docos-13-enoic 12.1%, oleic 9.3%), free fatty alcohols (eicos-11-enol 52.3%, docos-13-enol 38.4%, octadec-9-enol 5.3%, and tetracos-15-enol 4.0%), and sterols (sitosterol 69.9, campesterol 16.9%, and stigmasterol 6.7%) (Busson-Breysse et al. 1994; Van Boven et al. 1997).

Jojoba oil is used as unmodified and modified derivatives to produce cosmetics (hair and skin products), pharmaceuticals, dietetic foods, lubricants, polishing products, surfactants, antifoam, resins, and coatings and as a material for production of biodiesel. The plants themselves are used in landscapes and soil conservation around desert cities and as dust protection along roadsides (Ahmed et al. 2015; Al-Hamamre and Al-Salaymeh 2014; Canoira et al. 2006; Harry-O'kuru et al. 2005; Karmakar et al. 2010; Le Dréau et al. 2009; McKell 1983; Mirov 1952; Miwa 1984; Nassar et al. 2015; Khan et al. 2017; Patel et al. 2015; Salgin 2007; Sanchez et al. 2016; Sivasankaran et al. 1988). Several oil extraction methods, oil modifications, and oil uses have been patented (Brieva et al. 1999; Brown et al. 2004; Dresdner et al. 1994; Goedde et al. 1998; Lambert and Johnson 1999; Taygi and Granica 2015). In animal models, jojoba wax showed anti-inflammatory effects (Habashy et al. 2005). Jojoba meal contains up to 15% protein. Aspartic and glutamic acids are the most abundant, which makes the meal suitable for animal feed after the toxic effects of simmondsin and simmondsin 2′-ferulate are neutralized (Verbiscar and Banigan 1978; Yermanos 1974). Stephens (1994) reported 20–30% protein content in oilless meal and suggested using it as feed supplements. Jojoba meal had an inhibitory effect on food intake in rats. The meal has antifungal, insecticidal, and feeding inhibitor properties (Abbassy et al. 2007; Ismail et al. 2009).

15.2.4 Crop Wild Relatives

Simmondsia chinensis belongs to the Simmondsiaceae family and is the only species in the family (Felger and Rutman 2016); Van Tieghem (1898), a Belgian botanist, was the first to postulate placing jojoba in its own family. Shrubs of this species are still abundant in nature and proliferate easily by seeds; as such they are not subject to plant genetic resources conservation.

15.2.5 Distribution, Habitat, and Abundance

Simmondsia chinensis is endemic to the Sonoran Desert and grows in Southwestern Arizona and California and Northwestern Mexico (Al-Ani et al. 1972; Benzioni 1995; Brooks 1978; Princen 1979) (Fig. 15.1). It grows at sea level up to 1500 m altitude. It is found on light- and medium-textured, coarse, and drained soils and

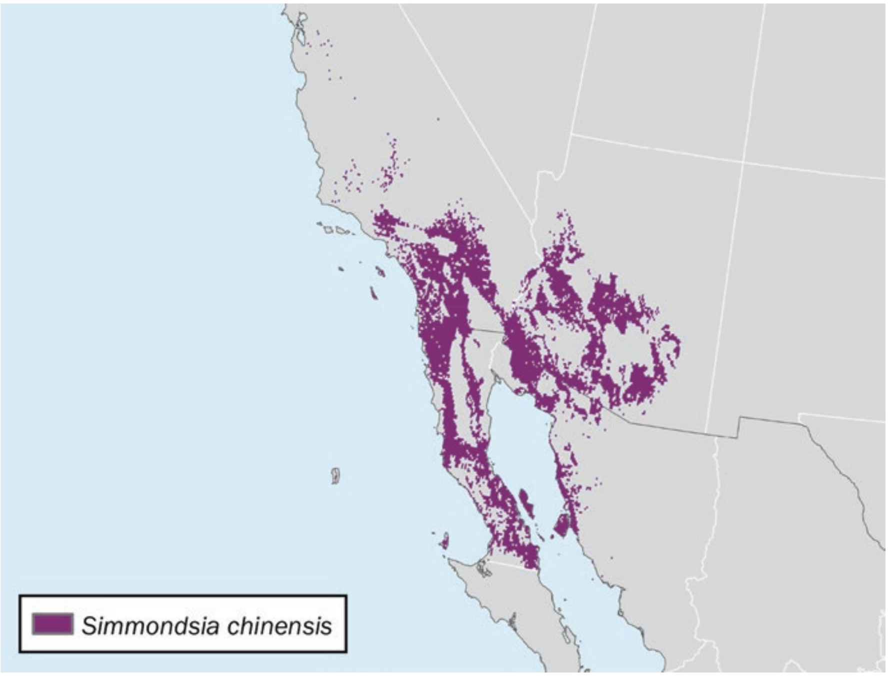

Fig. 15.1 Geographic distribution of jojoba (*Simmondsia chinensis* (Link) C. K. Schneid) based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

frequently on barren slopes. The shrub habit and height depend on environmental conditions; rainfall level of ca. 76–450 mm was reported optimal for the shrub's growth and fruiting. In cultivation, established jojoba stands require 500–600 mm of water (Benzioni and Nerd 1985; Gentry 1958; Yermanos 1974; Undersander et al. 1990; Yermanos 1978). NatureServe (2017) describes the species as secure globally, since it can be commonly local in its distribution range. Beauchamp (1986) reported the species being common in San Diego County.

15.2.6 Breeding Efforts on Wild Utilized Germplasm

All cultivated and promising selections were made from wild-growing shrubs (Fig. 15.2); but very few seed-derived plants produce an economic yield (Purcell and Purcell 1988). Seeds from endemic jojoba populations were the main source of material for research and processing (Yermanos 1974, 1977; Purcell et al. 2000). Wild populations are highly variable in seed weight and size, oil and protein content, and botanical characteristics (Clarke and Yermanos 1980; Amarger and Mercier 1996; Bhardwaj et al. 2010; Benzioni et al. 1999; Heikrujam et al. 2015; Naqavi et al. 1990; Nagavi and Ting 1990; Reddy and Chikara 2010; Tobares et al. 2004). Hence, breeding and selection of improved material are highly feasible (Ray et al. 2005; Tobares et al. 2004; Yermanos and Duncan 1976). Important characteristics for developing high-performing cultivars are high oil content, large seeds, flowers at each node, early flowering, flower frost tolerance, and erect shrub habit. Also desired is seed production beginning earlier than five years after stand establishment (Yermanos 1979). Selection in Israel was focused on characteristics promoting yield potential and reproductive traits (rapid growth, branching ability, node density, survival rate, flower density, fruit set, seed wax content, earliness that was indicated by flowering in early years of cultivation, and flower density) (Benzioni et al. 1999). Coates et al. (2006) suggested jojoba seed yield might be increased by artificial pollen distribution. For breeding and propagation purposes, early distinction between female and male plants has a practical importance. Several molecular markers, such as male-specific touchdown PCR marker JM900 (Ince et al. 2010), CAPS assay marker (Ince and Karaca 2011), and STS (Heikrujam et al. 2014), ISSR, and RAPD markers (Sharma et al. 2008, 2009), were reported to be applicable in determining plant sex.

The first selected cultivar was 'Vista' (Sherbrooke and Haase 1974); other reported cultivars are 'Keiko' averaging 1176 g/tree (Purcell and Purcell 1988) and 'Mirov' (Yermanos et al. 1968).

The most well-known progress on jojoba cultivation improvement was made in Israel; during a 25-year-long research effort, seed yield improved to 3000–3500 kg/ha, harvest mechanization and agronomic practices were developed, and several clones were selected (Shani 1995; Benzioni 1995). Evaluation of 30 jojoba clones in Israel showed differences in yield, chilling requirements, and morphology (Benzioni et al. 1999).

Jojoba does not transplant well (Gentry 1958). Originally it was cultivated from field-planted seeds. Later, selected clones were propagated through semi-hardwood cuttings (Eed and Burgoyne 2015; Palzkill and Feldman 1993; Prat et al. 1998), grafting (Yoffe 1980), and in vitro shoots (Agrawal et al. 2002; Andressen et al. 2009; Chaturvedi and Sharma 1989; Hegazi et al. 2014; Mohasseb et al. 2009; Singh et al. 2008).

15.2.7 Conservation Status

15.2.7.1 In Situ

Shrubs of this species are still abundant in nature and proliferate easily by seeds. It seems establishing protection on state or federal levels is not needed since wild jojoba stands are not excessively exploited or damaged, and the species has a high resilience to survive in natural conditions. Reports on in situ conservation efforts of *Simmondsia chinensis* in Arizona, California, or Mexico were not found.

15.2.7.2 Ex Situ

In the United States, the USDA-ARS National Arid Land Plant Genetic Resources Unit maintains and distributes 324 accessions as seeds or cuttings for research and cultivar improvement purposes (USDA ARS 2017a). The species is a priority industrial species in Mexico's National Plan of Action for the Conservation of Plant Genetic Resources for Food and Agriculture and 237 accessions, which include 122 wild accessions, are held in the Mexico Conservation Centers Network ex situ collection (see de la Torres et al., Chap. 3, this volume). Botanical gardens in Santa Barbara, CA; San Diego, CA; and the Boyce Thompson Arboretum, AZ, list *S. chinensis* in their planting catalogs (BTA 2017; SBBG 2017; SDBG 2017), and the Botanical Gardens Conservation International database lists 85 accessions (BGCI 2017). Midterm preservation efforts of jojoba using tissue culture were reported (Bekheet et al. 2016; Tyagi and Prakash 2004), but reports of in vitro maintained jojoba collections are not known. In vitro methods have been reported for germplasm distribution (Kumar et al. 2010, 2012). The ex situ germplasm collection of the United States is currently the only source where improved germplasm in the public domain and wild-collected accessions can be obtained. Because of the current interest in using and improving jojoba by many countries having arid land areas, maintaining a diverse collection of jojoba genetic resources is warranted.

15.3 Meadowfoam: A Genus with Unique Oil

15.3.1 Crop Origin and History of Use Worldwide

Meadowfoam (*Limnanthes* sp.) plants got the name from their spectacular appearance during full bloom resembling white-light cream foam. In the 1820s, David Douglas, a Scottish explorer and botanist, collected meadowfoam (*L. douglasii*) during his expedition to Northwestern Pacific regions of America and introduced it as an ornamental to England (Douglas 1836; Gentry and Miller 1965; Purdy and Craig 1987). The species collected by Douglas is still grown in European gardens as an ornamental (Gentry and Miller 1965).

In the 1960s, meadowfoam emerged as a potential new industrial crop as USDA-ARS scientists searched for renewable oil sources in wild, native plant populations in the United States (Earle et al. 1959; Gentry and Miller 1965; Miller et al. 1964; Smith et al. 1960). Seeds of *Limnanthes* plants contain unsaturated long-chain fatty acids ($C_{20–22}$), holding a high level of Δ5 double bonds; those fatty acids have a high oxidative stability which makes meadowfoam oil applicable in industrial products including lubricants, rubber additives, plasticizers, and cosmetics and in production of biodiesel (Cermak et al. 2013; Isbell et al. 1999; Lardans and Trémoliérs 1991; Miller et al. 1964; Moreau et al. 1981; Moser et al. 2010; Phillips et al. 1971; Purdy and Craig 1987; Smith et al. 1960). Meadowfoam has no known nutritional value for humans.

The total oil content in dry seeds varies from 27 to 35 wt. %, and the oil has more long-chain fatty acids than that of rapeseed (*Brassica napus*) and crambe (*Crambe* sp.) (Pollard and Stumpf 1980). Four long-chain fatty acids *cis*-5-eicosenoic (20:1), *cis*-5-docosenoic (22:1), *cis*-13-docosenoic (erucic acid, 22:1), and *cis*-5-*cis*-13-docosadienoic (22:2) make up almost 95% of the total meadowfoam oil (Smith et al. 1960; Bagby et al. 1961). *Limnanthes* oil may be converted to solid waxes with a high melting point similar to carnauba (*Copernicia prunifera*) and candelilla (*Euphorbia* sp.) and to a liquid wax similar to jojoba (*Simmondsia chinensis*) (Gentry and Miller 1965; Miwa and Wolf 1962). Beyond the United States, meadowfoam industrial oil and its oil-derived products are of interest in New Zealand, Europe (Metzger 2009), Japan (Cheng and Gordon 2000; Knapp and Crane 1999; McKenzie et al. 2011; Van Soest 1993; Wynn-Williams and Logan 1985), and Canada (Small 1995). Meadowfoam oil is currently used only in personal care products (Gunestone 2009; Isbell and Cermak 2001). Processing of several meadowfoam oil derivatives is patented (e.g., Erickson et al. 1990; O'Lenick 1997, 1998, 2001; O'Lenick and Wohlman 2001). Meadowfoam seed meal might be suitable for animal feed (Throckmorton et al. 1981). The seed meal also has phytotoxic characteristics making it applicable as bioherbicide (Intanon et al. 2014; Vaughn et al. 1996; Zasada et al. 2012) and potentially as bioinsecticide due to the presence of ecdysteroid glycosides (Bartlet and Mikolajczak 1989; Stevens et al. 2008; Velasco et al. 2011). Added to soil, it contributes to the soil nutrient profile and influences the microbial biome (Intanon et al. 2015). Meadowfoam flower petals and leaves *(L. douglasii)* contain flavonoids (Parker and Bohm 1975) that might be used as natural additives to nutraceutical and pharmaceutical products. Some species are used as ornamentals. Despite the oil's outstanding characteristics and many research reports on successful production of its useful derivatives, *Limnanthes* still belongs to the "promising new species" oil plant group (Zanetti et al. 2013).

Meadowfoams are winter-spring annual plants that are most productive when sown in fall as a winter crop; temperatures ≥16 °C inhibit seed germination, and temperatures ≤5 °C are detrimental to the plants which shorten the available sowing window (Cole 1974; Ehrensing et al. 1997; Nyunt and Grabe 1987; Toy and Willingham 1966). During hot weather, seed matures almost immediately (Higgins et al. 1971) which might prevent full seed development. The best growing areas are in valleys with abundant rain precipitation. The main meadowfoam cultivation area is in Willamette Valley, Oregon; however, agronomic trials have been performed in California, Maryland, and Alaska (Higgins et al. 1971). In Oregon, cultivation of meadowfoam is rotated with grass seed production (Jolliff and Hoffman 2002), but *Limnanthes* may also be double cropped with rice (Jain et al. 1977). The cultivation acreage varied with years; in 2012, 2200 acres of meadowfoam were grown in the Willamette Valley (Knapp and Crane 1999; Sparling 2015). According to the Agricultural Marketing Resource Center (2012), the largest acreage was planted in 2006–5000 acres; however, Isbell and Cermak (2001) reported a cultivation area of 8000 acres for 1997.

Limnanthes domestication and cultivar development have almost a 50-year history. All cultivars known in the United States have been developed from *L. alba* and released by Oregon State University; these are 'Foamore', 'Knowles', 'Mermaid', 'OMF64', 'Ross', 'Floral', and 'Wheeler' (Calhoun and Crane 1975; Calhoun and Crane 1984; Crane and Knapp 2002; Jolliff et al. 1984; Knapp et al. 2005). 'Moginie' is an open-pollinated meadowfoam selection reportedly being used in New Zealand seed trials (Cheng and Gordon 2000). Overproduction of seeds in 1997 that were not purchased by the industry set back meadowfoam cultivation for a few years; also the price of meadowfoam oil is too high to be used in the manufacturing of other cosmetic products (Isbell and Cermak 2001). One of the main factors contributing to the high oil price is the necessity to use bees for pollination. Reported seed yields for experimental settings varied depending on location. Yields up to 1700 kg/ha were reported for California, Maryland, and Oregon when cultivated as a winter-sown annual crop, much less for Alaska where meadowfoam was grown as a spring-sown crop (Higgins et al. 1971; Krebs and Jain 1985). In New Zealand, seed yield varied from 0.6 to 1.6 t/ha depending on the cultivation sites (McKenzie et al. 2011). In production fields, the seed yields are lower. Increasing meadowfoam oil supply will require development of new, improved cultivars with high seed yield, good seed retention, high oil content, self-pollination, and resistance to logging and fruit fly (*Scaptomyza apicalis* Hardy) (Jain and Abuelgasim 1981; Jolliff and Hoffman 2002; Knapp and Crane 1999; Meyers et al. 2010). Cultivars already developed are cross-pollinated and require the use of bees for pollination; in an experimental setting, cross-pollinated cultivars produced higher seed yields than self-pollinated cultivars (Jolliff and Hoffman 2002; Meyers et al. 2010). High-performing cultivars might lower the production costs and make the oil price competitive with fossil materials currently used by the industry.

Limnanthes plants do not have a lot of adversaries. The most serious is a fruit fly (*S. apicalis*) (Knapp and Crane 1999; Panasahatham 2000), also called a meadowfoam fly (*S. apicalis*) (Whaley 2016) that affects buds and crowns causing seed yield reduction. Some tolerance to the insect has been found in breeding material at Oregon State University, but the genetics of the tolerance is not known. A powdery mildew (*Oidium limnanthis*) was observed on potted plants of *L. alba* but was not found in production fields (Putnam and Glawe 2007). Meadowfoam grows well on many types of soil including soils deficiently drained. Temperatures above 16 °C induces secondary seed dormancy (Cole 1974; Ehrensing et al. 1997; Toy and Willingham 1966); hence, warming temperatures will force meadowfoam cultivation to cooler areas. Such changes may also lead to the need for irrigation, as warming is projected to alter precipitation patterns and deplete surface and soil water availability for vernal pools and seepages that are the natural habitats for *Limnanthes* vegetation (Bliss and Zedler 1998; Brooks 2009; Erwin 2009; Pyke 2004).

15.3.2 Crop Wild Relatives, Genepool Classification, Distribution and Habitat, Breeding, and Relative Importance

In natural habitats, meadowfoam plants are low-growing annual herbs, with glabrous to hairy leaves and stems; white, light pinkish, yellow, or a combination of these colors flower petals; and rose or brown anthers and veins, often growing in masses forming dense colorful rings around vernal pools or patches in wet meadows. *Limnanthe*s plants were described by numerous botanists and explorers (Brown 1833; Bayer and Appel 2003; Mason 1952; Ornduff 1969; Ornduff and Crovello 1968). Flowers of all species are hermaphroditic and self-compatible (Kesseli and Jain 1985), and their sexual breeding pattern includes cleistogamy and chasmogamy (Kesseli and Jain 1984; Mason 1952; McNeill and Jain 1983; Ornduff and Crovello 1968).

The family Limnanthaceae, containing two genera, *Limnanthes* R. Br. and *Floerkea* Willd., belongs to the order Brassicales (Rodman et al. 1998). Both genera are endemic to North America (Fig. 15.3) and are closely related; *Floerkea* has three-petaled flowers, whereas *Limnanthes* has five-petaled flowers, with one four-petaled species (*L. macounii* Trel.) (Meyers et al. 2010). Taxonomy of the meadowfoams has been debated over years starting with Brown (1833), including a discussion on separating or combining of the two Limnanthaceae genera. Based on molecular phylogenetic studies, Plotkin (1998) proposed to keep the two genera separate. Mason (1952) identified eight *Limnanthes* species and grouped them into two sections based on petal appearance following fertilization: Inflexae (petals surround a developing seed) and Reflexae (petals reflex from a developing seed). Following nomenclatural rules proposed by the International Code of Botanical Nomenclature, the section name Reflexae should be changed to *Limnanthes* (Meyers et al. 2010; McNeill et al. 2006). In 1969, Ornduff identified a new species *L. vinculans* and placed it into the Reflexae section. Meyers et al. (2010) suggested distinguishing only four *Limnanthes* species in the

Fig. 15.2 Ornamental 2-year-old jojoba (*Simmondsia chinensis* (Link) C. K. Schneid)

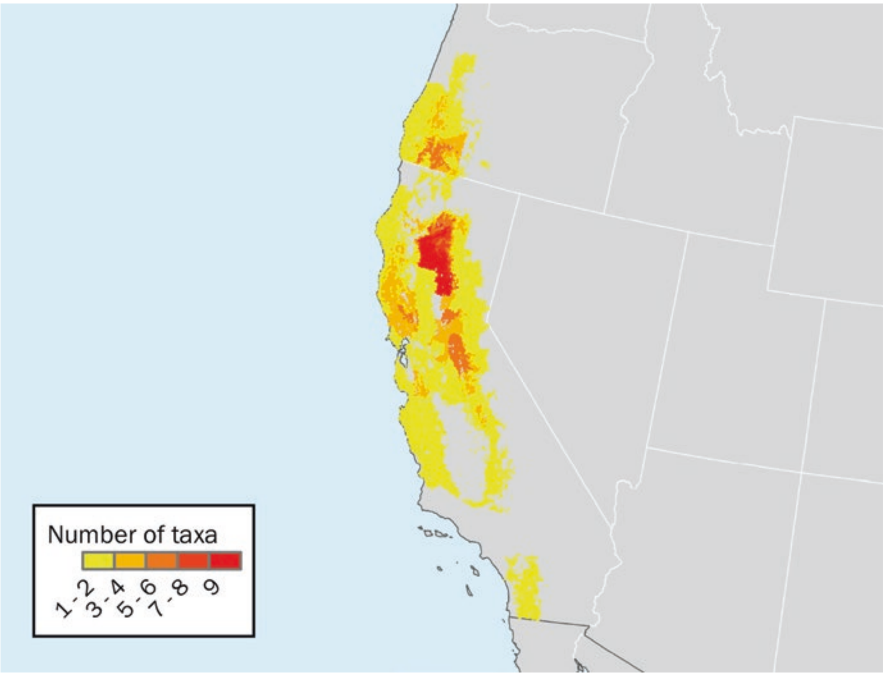

Fig. 15.3 Richness of meadowfoam (Limnanthes R. Br.)

Limnanthaceae genus. Buxton (2013) proposed separating a tetramerous population of *L. douglasii* R. Br. found in San Mateo County, California as a new subspecies *L. d.* subsp. *ornduffii* E. G. (Ornduff's meadowfoam); it is a single population endemic to Moss Beach in San Mateo, California. Buxton claimed that this is an independently occurring relic taxon; the taxon is not yet recognized.

The US National Plant Germplasm System lists ten species including *L.* hybr. which do not have a common name (Table 15.1). Common names of the *Limnanthes* species refer to names of their discoverers, appearance, or location they were found.

Meadowfoam's natural habitats are around vernal pools, seepages, and seasonally wet meadows (Fig. 15.3). In California, they are also found along road edges and occasionally in abandoned agricultural fields (Arroyo 1975). Specific natural *Limnanthes* populations were reported in six locations (Table 15.2). *L. macounii* is the most north-occurring meadowfoam species (Karron 1991).

Wild *Limnanthes* populations have high intra- and interpopulation variability (Kesseli and Jain 1987; Pierce and Jains 1977). Kishore et al. (2004) developed conserved SSR markers that might be useful in genetic conservation, phylogenetics, and ecological studies. Using SSR fingerprints for 61 *Limnanthes* accessions collected in natural habitats in California and Oregon, Donnelley et al. (2008) suggested all

Table 15.1 Scientific and common names of *Limnanthes* species in the National Plant Germplasm System

Scientific name[a]	Common name[b]
The Inflexae section includes	
L. alba Hartw. ex Benth.	White meadowfoam
L. alba subsp. *alba* Hartw. ex Benth.	White meadowfoam
L. alba subsp. *versicolor* (Greene) C.T. Mason	White meadowfoam
L. floccosa Howell	Woolly meadowfoam
L. floccosa subsp. *bellingeriana* (M. Peck) Arroyo	Woolly meadowfoam
L. floccosa subsp. *californica* Arroyo	California meadowfoam
L. floccosa subsp. *floccosa* Howell	Woolly meadowfoam
L. floccosa subsp. *grandiflora* Arroyo[c]	Woolly meadowfoam
L. floccosa subsp. *pumila* (Howell) Arroyo	Woolly meadowfoam
L. gracilis Howell	Slender meadowfoam
L. gracilis subsp. *gracilis*[d] Howell.	Slender meadowfoam
L. gracilis subsp. *parishii* (Jeps.) R. M. Beauch.[e]	Parish's slender meadowfoam
L. montana Jeps.	Mountain meadowfoam
L. vinculans Ornduff	Sebastopol meadowfoam
The Reflexae[f] section comprised of	
L. douglasii R. Br.	Douglas' meadowfoam
L. douglasii subsp. *douglasii* R. Br.	Douglas' meadowfoam
L. douglasii subsp. *nivea* (C.T. Mason) C. T. Mason	Douglas' meadowfoam
L. douglasii subsp. *rosea* (Hartw. ex Benth.) C.T. Mason	Douglas' meadowfoam
L. douglasii subsp. *sulphurea* (C.T. Mason) C. T. Mason	Douglas' meadowfoam
L. striata Jeps.	Foothill meadowfoam
L. bakeri J. T. Howell	Baker's meadowfoam
L. macounii Trel.	Macoun's meadowfoam

[a]US National Plant Germplasm System (USDA ARS 2017b)
[b]Classification of *Limnanthes*; Common Names (USDA Plants 2016)
[c]Also listed as *L. pumila* subsp. *grandiflora* (Arroyo) S.C. Meyers & Chambers (ECOS 2017b, USFW 2017)
[d]Synonymous to *L. alba* Hartweg ex. Bentham subsp. *gracilis* (Howell) Morin; (ITIS report 2017)
[e]Active name: *L. alba* (Jeps.) Morin subsp. *parishii* (Jeps.) Morin (Calflora, Taxon report 4834)
[f]"Reflexae" name should be referred to as *Limnanthes* (McNeill et al. 2006)

Table 15.2 Location of specific natural *Limnanthes* populations

Taxon	Location	Reference
L. alba Hartw. ex Benth.	West of Cascade Mountain ranges, California and Oregon	Arroyo (1975)
L. floccosa Howell	Tehama Co., California and northern part of Jackson Co. Oregon	Arroyo (1975)
L. douglasii R. Br.	Central Valley, California	Runquist (2012)
L. vinculans Ornduff	Laguna de Santa Rosa near Sebastopol, Sonoma Co., California	Ornduff (1969)
L. macounii Trel.	Southeast of Vancouver Island, Canada	Arroyo (1975), Catling and Porebski (1998), Jain (1994), and Ornduff (1969)
L. montana Jeps.	Southwestern USA, California	USDA ARS (2017b)

evaluated accessions contained unique alleles. The highest level of genetic diversity was observed in *L. alba*, *L. floccosa*, and *L. douglasii*. According to Jolliff et al. (1981), those species have the greatest potential for novel cultivar development. Evaluation of seed and selected plant characteristics of 21 *L. alba* accessions collected in California also demonstrated a large diversity within the species (Jenderek and Hannan 2009). Both sets of genetic resources evaluated by Donnelley et al. (2008) and Jenderek and Hannan (2009) are maintained at the National Arid Land Plant Genetic Resources site, USDA-ARS, Parlier, CA (2016).

Wild meadowfoam genotypes are essential for development of cultivars with characteristics desired by growers and the meadowfoam oil industry. They are the potential gene source for increasing seed yield and developing self-pollinating breeding material. Genotypes with upright, short stems and uniform seed maturing time might support the development of cultivars for mechanical seed harvest of the crop. The ability of wild meadowfoam plants to grow on poorly drained soils might give rise to a crop that can be cultivated on marginal semi-marsh lands.

15.3.3 Conservation Status

15.3.3.1 In Situ

L. floccosa subsp. *californica*, *L. floccosa* subsp. *grandiflora* (*L. pumila* subsp. *grandiflora*), and *L. vinculans* are listed as endangered by the US Fish and Wildlife Service (CDFW 2017a, c; USFW 2017). In California, *L. douglasii* subsp. *sulphurea* and *L. alba* subsp. *parishii* are listed as endangered and *L. bakeri* as rare (Calflora 2017; Dole and Sun 1992; Meyers et al. 2010; CDFW 2017a, c); *L. floccosa* subsp. *pumila* is on the Oregon's threatened list (Oregon Department of Agriculture, Dwarf meadowfoam 2017).

Limnanthes taxa listed as "endangered," "threatened," or "rare" on federal or state levels are legally protected in their endemic habitats, and germplasm collection from such populations requires obtaining a collection permit from the CDFW Scientific Collecting Permits (2017b). Conservation of the diversity in these species is dependent on adequate protection of their habitats. In the last 50–100 years, California lost an estimated 88% of vernal pool habitat due to urban sprawl, grazing, and land conversion to cultivation (Barry 1998; Holland 1978; Jensen 2011). Disappearing vernal pools is also reported for Agate Desert, Oregon, the habitat for *L. floccosa* subsp. *grandiflora* (Wille and Petersen 2006). A permanent protection of remaining vernal pools is imperative for conservation of natural *Limnanthes* vegetation environments.

Fragmentation and geographical isolation of populations of many species contribute to low genetic diversity, low heterozygosity, and high fixation indices (Sloop et al. 2011). Increased knowledge of population size, breeding patterns, behavior of pollination vectors, seed dispersal mechanisms, and molecular markers will provide guidelines for conservation and reintroduction of known genotypes into the vanishing plant communities in their habitats. Such recommendations have been reported for the endangered *L. floccosa* subsp. *californica* (Sloop et al. 2011, 2012; Warne and

Sloop 2009) and *L. vinculans* (Ayres et al. 2008; Sloop et al. 2012; Sloop and Ayres 2009). Significant current conservation efforts are also being made by the US and California Fish and Wildlife Departments as well as the US Department of the Interior and the Oregon Fish and Wildlife Office (US Department of the Interior 2017). Scientific information on the natural habitats, plant communities, and conservation needs is published by scientists from the University of California, San Francisco Joint Venture, and others (CDFW 2017a, b; Griggs and Jain 1983; Sloop et al. 2012). Conservation of in situ *Limnanthes* diversity is not easy due to limited resources; open, physically unprotected growing areas; and conflicting interests of urban/demographic/agricultural developments, but maintaining the diversity is necessary for current and future purposes; the beauty and the economic potential of natural meadowfoam populations are irreplaceable. Further, climatic temperature increase may impact wild *Limnanthes* populations by inducing seed dormancy and preventing their germination. Urban development and grazing represent additional real threats to the natural habitats of meadowfoam (Pyke and Marty 2005).

15.3.3.2 Ex Situ

A collection of 78 meadowfoam accessions is preserved in Parlier, CA, at the USDA ARS National Arid Land Plant Genetic Resources Unit (NALPGRU), a genebank of the NPGS (Table 15.3).

Table 15.3 *Limnanthes* taxa and number of accessions preserved in the NPGS collection

Taxon	No. of accessions preserved at NALPGRU, CA
L. alba Hartw. ex Benth	21
L. alba subsp. *alba* Hartw. ex Benth	10
L. alba subsp. *versicolor* (Greene) C.T. Mason	3
L. bakeri J. T. Howell	2
L. douglasii R. Br.	3
L. douglasii subsp. *douglasii* R. Br.	2
L. douglasii subsp. *nivea* (C.T. Mason) C.T. Mason	7
L. douglasii subsp. *rosea* (Hartw. ex Benth.) C.T. Mason	6
L. floccosa Howell	9
L. floccosa subsp. *bellingeriana* (M. Peck) Arroyo	2
L. floccosa subsp. *grandiflora* Arroyo	1
L. floccosa subsp. *pumila* (Howell) Arroyo	2
L. gracilis Howell	2
L. gracilis subsp. *gracilis* Howell	2
L. gracilis subsp. *parishii* (Jeps.) R. M. Beauch	1
L. hybr.	1
L. montana Jeps.	1
L. spp.	1
L. striata Jeps.	2

Regeneration of these accessions is done in isolation cages with and without pollination vectors. The origin of the genetic resources is documented; plants are evaluated and characterized and upon request freely distributed to breeders and researchers. Evaluation data are available through research publications and germplasm characterization documented on the Germplasm Resources Information System (USDA ARS 2017a). Evaluation and characterization of the collection are the bases for informed meadowfoam germplasm utilization. Regenerated seed is backed up at the USDA-ARS, National Laboratory for Genetic Resources Preservation in Fort Collins, CO. Although the USDA collection is considered to be relatively diverse, inclusion of populations from habitats not yet collected would add diversity to the already existing meadowfoam collection and provide a broader gene pool to future users and possible future restoration (Figs. 15.4, 15.5, 15.6, 15.7, 15.8, and 15.9).

Oregon State University, Corvallis, OR, also holds a large breeding and crop wild relative collection of *Limnanthes* (Kling 2017, personal communication). Conservation efforts at Rancho Santa Ana Botanic Gardens, CA include establishment

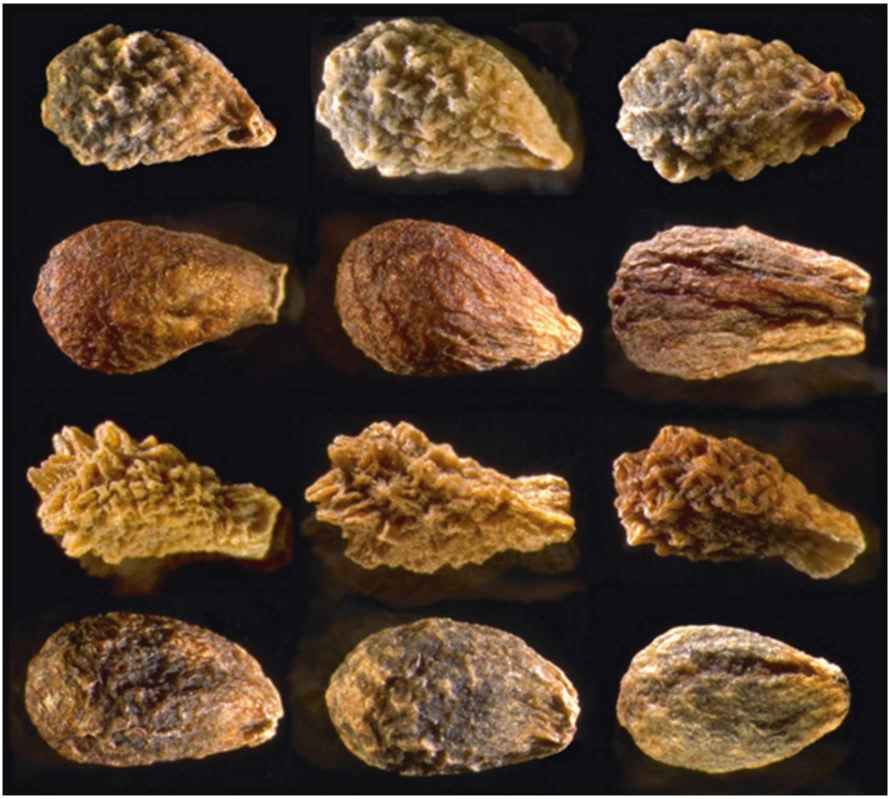

Fig. 15.4 Meadowfoam (*Limnanthes* R. Br.) seed. Top to bottom: *L. alba* Hartw. ex Benth., *L. douglasii* R. Br., *L. floccosa* Howell, and *L. gracilis* Howell (*L. a.* subsp. *gracilis*). (Photo: J. Donald, NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.5 Nuttles *of L. alba* Hartw. ex Benth., PI 374793. (Photo: NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.6 Flower of *L. alba* Hartw. ex Benth., PI 374791. (Photo NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.7 Flowers of *L. striata* Jeps., PI 283728. (Photo, NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.8 Flowers of *L. gracilis* subsp. *gracilis* Howell., PI 283723. (Photo NALPGRU, USDA-ARS, Parlier, CA)

of new vernal pools and inoculation with seeds of tested meadowfoam genotypes similar to the natural ones. Botanical gardens play an important role in meadowfoam conservation by displaying the *Limnanthes* flower beauty to the broad public, maintaining diversity, seed banking, research, and educational activities.

Fig. 15.9 Flower of *L. douglasii* subsp. *rosea*, PI 283716. (Photo NALPGRU, USDA-ARS, Parlier, CA)

15.4 Lesquerella

15.4.1 Origin of the Crop and Brief History of Use Worldwide

Lesquerella [*Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz, synonym *Lesquerella fendleri* (A. Gray) S. Watson], is an oilseed species in the mustard family (Brassicaceae). It is native to the Southwestern United States and Northern Mexico where it is best suited to be integrated into existing crop production systems as a winter annual. The species produces about 30% seed oil with lesquerolic fatty acid predominating and oleic and linolenic acids contributing minor components to its seed oil (Barclay et al. 1962; Dierig et al. 1996a, b; Salywon et al. 2005; Wang et al. 2010). As a source of hydroxy fatty acids, it can provide important raw materials for manufacturing industrial lubricants, plastics, cosmetics, and pharmaceuticals (Roetheli et al. 1991; Isbell et al. 2006). The distinguishing characteristic of this species compared to other taxa in the genus is the more favorable agronomic characteristics and high seed productivity.

Lesquerella is considered a new crop since there is currently no commercial production and as domestication and formal breeding research and development activities started in the 1980s (Van Dyne 1997). The initial utility of lesquerella species was identified in the 1950s during a large national oilseed screening program of over 200 plant families growing in native habitats initiated by the New Crops Research Branch of the US Department of Agriculture (USDA)-Agricultural Research Service (ARS) (Barclay et al. 1962; Dierig et al. 1993). The US Government was interested in finding unusual kinds of oils that would not compete with vegetable oils and finding a domestic species that could be grown locally instead of importing petroleum-based commodities (Jones and Wolff 1960; Princen 1983). Of the many plant species analyzed, species of *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray and *Paysonia* O'Kane & Al-Shehbaz (then all included in *Lesquerella*) received attention due to fatty acid composition that is similar to ricinoleic acid from castor oil but without the highly toxic seed meal. Castor oil is mostly imported to the United States (Brigham 1993). The hydroxy fatty acid present in *Physaria* is lesquerolic acid (14-hydroxy-eicosa-11-enoic, 14-OH-20:1) with densipolic acid (12-hydroxy-octadec-cis-9,15-enoic, 14-OH-18:2) in *Paysonia* and auricolic acid in *Paysonia auriculata* (Engelm. & A. Gray) O'Kane & Al-Shehbaz (14-hydroxy-eicos-cis-11,17-enoic, 14-OH-20:2). The hydroxy fatty acid content in the seed oil of lesquerella and related species is between 45 and 55% (Barclay et al. 1962; Salywon et al. 2005; Dierig and Ray 2009). Lesquerolic acid is two carbons longer than the ricinoleic acid (12-hydroxy-octadeca-9-enoate, 12-OH-18:1) in castor oil, while densipolic and auricolic acids have an additional unit of unsaturation (double bond), and auricolic acid also is two carbons longer (Engeseth and Stymne 1996). The chemical similarity of these fatty acids to ricinoleic acid allows it to be used as replacements for castor oil, while their chemical differences may lead to novel products. To date castor oil has been the major commercial source of hydroxy fatty acids (Smith et al. 1998).

Lesquerella seed oil is suitable for producing triglyceride estolides that have numerous applications in industry and can be used in biodegradable lubricants for superior low-temperature properties (Cermak et al. 2006; Cermak and Evangelista 2013). For example, lesquerella oil additives in ultralow sulfur diesel (ULSD) have been demonstrated to increase lubricity (Moser et al. 2008). Other value-added products from lesquerella seed have also shown potential. The seed gum has applications in the food industry as a thickener (Holser et al. 2000). In addition to having industrial application, the high protein content of lesquerella was found to be a good additive to animal and poultry feed (Carlson et al. 1990). Feeding dehulled lesquerella seed to chickens resulted in a slightly better feed conversion, and the additive had no negative effect (Beier et al. 2014).

There were previously two public crop germplasm improvement programs on *lesquerella* that focused on improving the agronomy and yield of the crop. The first was a program of the University of Arizona under D.D. Rubis which operated from 1966 to 1978 and the second at the USDA-ARS US Water Conservation Laboratory (now USDA-ARS Arid Land Research Center) by A.E. Thompson and D.A. Dierig, from 1984 to 2010 (Thompson and Dierig 1994). Germplasm from Dr. Rubis's program was transferred to the USDA. Currently, there are several advanced germplasm lines developed by the USDA, with improved seed and oil yield as well as abiotic stress tolerance. Plants with 45% oil content have been obtained from breeding activities (Dierig et al. 2006a, b). Small yield trials as well as observations from farmer fields showed that the improved germplasm yields in excess of 2000 kg/ha (Wang et al. 2010). In terms of suitable production areas, the US southwestern region was reported to be where the highest yields of current germplasm were obtained. Agronomic trials have also been conducted in other areas such as Oregon, Northern

Mexico, Canada, Argentina, and parts of Europe (Roseberg 1993; Rodríguez Garcia et al. 2007; Windauer et al. 2004; EuroBioRef 2015). However, the yield and performance of the existing germplasm grown in these environments were poorer. Continued research activities and the development of germplasm lines that are more adapted to these regions will help overcome these problems and establish lesquerella along with other industrial crops that are adapted to broader areas.

As a new crop, lesquerella does not have major issues with diseases and insect pests. One important insect pest in arid land crops, *Lygus hesperus* Knight, which feeds on cotton, alfalfa, and many vegetable species, has been studied for its effect on lesquerella. Naranjo and Stefanek (2012) found that *Lygus* insects did not significantly impact lesquerella agronomic performance. The insects feed mostly on flowers, leaves, and petioles, but the damage is not as much as compared to other new industrial crops (Hagler et al. 2016). Studies to determine potential insect and pest problems on large acreage still need to be conducted. Due to the early-spring flowering season of lesquerella, Naranjo et al. (2011) previously noted it may harbor significant populations of *Lygus* as well as their natural enemies and these may affect the pest dynamics across multiple crops. There were also important fungal pathogens found in lesquerella including *Helminthosporium namum* Nees, *Phoma punctiformis* Desmazières, *Phymatotrichum omnivorum* Duggar, and *Puccinia aristidae* Tracy (Duke 1983).

The influence of warmer temperatures expected with climate change has not been researched within lesquerella. Higher temperatures during the growth period were observed to positively influence root traits (Cruz et al. 2012a), as well as to increase biomass and seed yield (Dierig et al. 2006a). There have been no studies reporting neither the response of lesquerella to other environmental factors such as increased carbon dioxide levels nor the effects of extreme temperature on pollination. Since lesquerella is an outcrossing species with self-incompatibility mechanisms, the abundance of pollinators and pollen viability are critical for successful seed production (Mitchell 1997; Hatfield and Prueger 2015).

15.4.2 Crop Wild Relatives, Genepool Classification, Distribution and Habitat, Breeding, and Relative Importance

Lesquerella is an herbaceous short-lived perennial plant also known as Fendler's bladderpod, yellowtop, desert mustard, and cloth of gold. The wild populations of *P. fendleri* are usually found on limestone outcrops, gravels, sandy washes, rocky slopes, shallow drainage areas, and roadcuts in the plains and desert regions in the US Southwest (Arizona, New Mexico, and Texas) as well as Coahuila, Chihuahua, and Nuevo Leon, Mexico (Rollins 1993) (Fig. 15.10). These populations often depend on soil moisture and are usually found among mixed, sparse vegetation with predominance among creosote habitats (Cabin and Marshall 2000). Plants in native populations were found in areas that range 315–1643 m^2 with plant density of

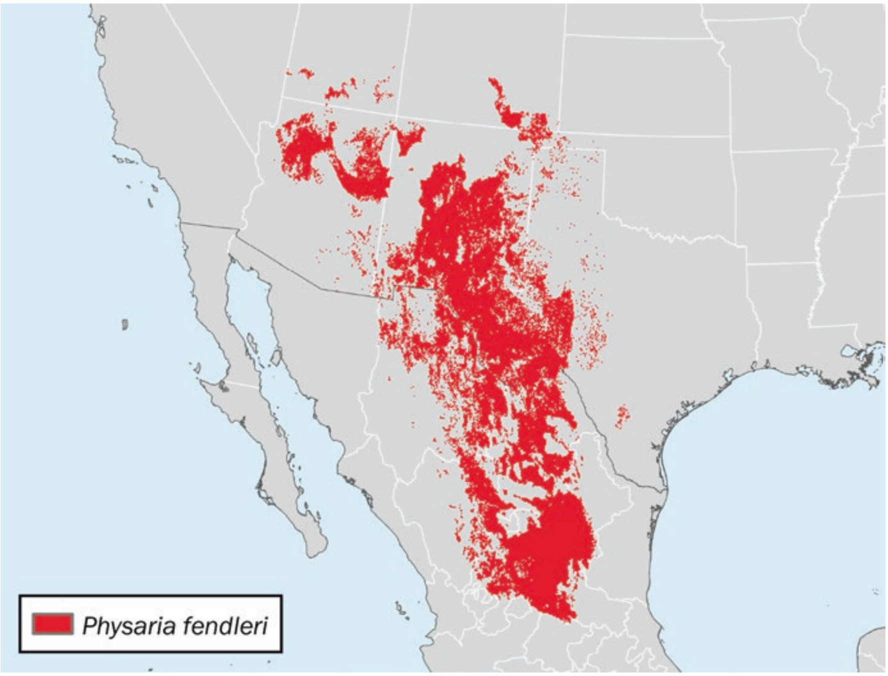

Fig. 15.10 Geographic distribution of lesquerella [*Physaria fendler*i (A. Gray) O'Kane & Al-Shehbaz] based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

1–12 plant/m^2 (Cruz et al. 2013b). The number of plants in native populations varies according to changes in short-term climatic and edaphic factors that may influence seed production and germination. There have been collections of *P. fendleri* germplasm from Arizona, Colorado, New Mexico, Texas, and southern Utah as well as from provinces in Mexico (Rollins and Shaw 1973; Dierig et al. 1996b; Salywon et al. 2005). Currently, there are ~106 *Physaria* species. Among the recently discovered species include the Navajo bladderpod (*P. navajoensis*) (O'Kane) O'Kane & Al-Shehbaz found in New Mexico and *P. scrotiformis* O'Kane which is a high-elevation species in Colorado (O'Kane and Al-Shehbaz 2002; O'Kane 1999, 2007). Since lesquerella is a new crop, the utilization of the other wild relatives has not been fully researched.

Lesquerella flowers between March and May depending on the elevation and also after suitable rain events in the summer and fall. The seed dormancy in wild populations of lesquerella may persist for up to 3 years, allowing individuals from different generations to be represented in the soil seed bank (Cabin et al. 1998). The population genetic structure resulting from this event may change every season, as various seed genotypes are believed to have accumulated in soil seed banks ensuring genetic diversity (Cabin 1996). This seed dormancy in advanced germplasm lines is not as pronounced as in wild populations; however seed pretreatment with gibberellic acid was found desirable to increase germination, eliminate the light requirement, and allow for synchronous germination during plant propagation and field plantings (Cruz et al. 2012b; Puppala and Fowler 2002).

Lesquerella is easily recognized by their glabrous siliques and fused trichomes which set the species apart from other *Physaria*. Plants have an indeterminate growth habit with densely pubescent silvery leaves that grow to about 40 cm high. The yellow flowers of lesquerella have petals that are 8–12 mm long and sometimes observed with orange guidelines (Rollins 1993). The flowers are hermaphroditic and self-incompatible. In natural populations, pollinations are accomplished by a wide array of pollinator generalists that are foraging for nectar and pollen. Successful seed set was found to be related to plant density, with higher densities positively correlated to the number of seeds found per fruit (Roll et al. 1997).

Several wild *Physaria* species are on the federal and state list of imperiled and vulnerable species, as well as some with habitats protected under the Endangered Species Act (Table 15.4). Only four of these critical species have representative accessions in the NPGS to date. There is limited information on the genepool clas-

Table 15.4 *Physaria* species in decline that may be in danger of extinction. Figure 15.11 shows a map of US NPGS and Mexico lesquerella [*Physaria* (Nutt. ex Torr. & A. Gray) A. Gray] collection sites

Scientific name	Common name	Global rank	State rank	State	NPGS accessions
P. alpina Rollins	Avery Peak twinpod	G2	S2	CO	0
P. aurea (Wooton) O'Kane & Al-Shehbaz	Golden bladderpod	G2	S2	NM	0
P. bellii G. A. Mulligan	Bell's twinpod	G2, G3	S2, S3	CO	0
P. calcicola (Rollins) O'Kane & Al-Shehbaz	Rocky Mountain bladderpod	G3	S3	CO	0
P. congesta (Rollins) O'Kane & Al-Shehbaz	Dudley Bluffs bladderpod	G1	S1	CO	0
P. didymocarpa subsp. *didymocarpa* (Hook.) A. Gray	Common twinpod	G5	S1	WA	0
P. dornii Lichvar	Dorn's twinpod	G1	S1	WY	
P. douglasii subsp. *tuplashensis** (Rollins et al.) O'Kane & Al-Shehbaz	White Bluffs bladderpod	G4	S2	WA	1
*P. filiformis** (Rollins) O'Kane & Al-Shehbaz	Missouri bladderpod	G3	–	AR, MO	0
*P. globosa** (Desv.) O'Kane & Al-Shehbaz	Short's bladderpod	G2	S1	IN, KY, TN	0
P. grahamii C. V. Morton	Graham's twinpod	G1	S1	UT	0
P. iveyana O'Kane, K.N. Sm. & K.A. Arp		G1	S1	NM	0

(continued)

Table 15.4 (continued)

Scientific name	Common name	Global rank	State rank	State	NPGS accessions
P. navajoensis (O'Kane) O'Kane & Al-Shehbaz	Navajo bladderpod	G2	S1	NM	0
*P. obcordata** Rollins	Piceance twinpod	G1, G2	S1, S2	CO	0
P. pallida (Torr. & A. Gray) O'Kane & Al-Shehbaz	White Bladderpod	G1	S1	TX	5
P. parviflora (Rollins) O'Kane & Al-Shehbaz	Piceance bladderpod	G2	S2	CO	0
P. parvula (Greene) O'Kane & Al-Shehbaz	Pygmy bladderpod	G3?	S2	CO	0
P. pruinosa (Greene) O'Kane & Al-Shehbaz	Pagosa bladderpod	G2	S1, S2	CO, NM	0
P. pulvinata O'Kane & Reveal	Cushion bladderpod	G1	S1	CO	0
P. rollinsii G. A. Mulligan	Rollins' twinpod	G1	S1	CO	0
P. scrotiformis O'Kane	West silver bladderpod	G1	S1	CO	0
P. subumbellata (Rollins) O'Kane & Al-Shehbaz	Parasol bladderpod	G3	S2	CO	0
P. thamnophila (Rollins & E. A. Shaw) O'Kane & Al-Shehbaz	Zapata Bladderpod	G1	S1	TX	1
P. vicina J.L. Anderson, Reveal & Rollins	Good- neighbor bladderpod	G2	S2	CO	0
P. stylosa Rollins	Duchesne River twinpod	G1	S1	UT	0
P. tumulosa (Barneby) O'Kane & Al-Shehbaz	Kodachrome bladderpod	G1	S1	UT	0
P. vitulifera Rydb.	Rydberg twinpod	G3	S3	CO	1

Notes: G1/S1, critically imperiled; G2/S2, imperiled; G3/S3, vulnerable; G4/S4, apparently secure; G5/S5, secure Information compiled from CNHP (2017), ECOS (2017a, b), IDNR (2017), NatureServe (2017), TPW (2017), US Fish and Wildlife Service (2015a, b), USDA-ARS (2017a), and WNHP (2015). Asterisks denote species protected under the Endangered Species Act of 1973

sification of *Physaria*. The outcrossing rate in lesquerella is 86–89% (Dierig et al. 1996a). In Colorado, naturally occurring hybrids between the rare *P. bellii* G. A. Mulligan and more common congener *P. vitulifera* Rydb. have been found, which initiated a study to look into the threat of gene swamping (Kothera et al. 2007). Though some groups of *Physaria* can easily cross-pollinate, Dierig and Ray (2009) noted that hybridization among some species found in the Western United States was challenging and necessitated ovule culture and colchicine treatments to overcome the sporophytic incompatibility system. Bud pollination is used in *P. fendleri* to overcome self-incompatibility. It can be speculated that these species comprise those in the secondary genepool. The species of *Paysonia* found in the Eastern United States do not have the same issue, and interspecific hybridization is common. The genus *Paysonia* is sister to *Physaria*, yet DArT (Diversity Arrays Technology) markers only shared about 70% similarity between the genera (Cruz et al. 2013a). Several *Paysonia* species have desirable characters that maybe of interest due to the densipolic type of HFA in their seed oil. Rollins (1988) and Rollins and Solbrig (1973) reported that there was successful interspecies hybrid swarm among *P. stonensis* (Rollins) O'Kane & Al-Shehbaz, *P. densipila* (Rollins) O'Kane & Al-Shehbaz, *P. lescurii* (A. Gray) O'Kane & Al-Shehbaz, *P. lyrata* (Rollins) O'Kane & Al-Shehbaz, and *P. perforata* (Rollins) O'Kane & Al-Shehbaz also called *Lesquerella* 'Kathryn'. The hybrids obtained showed a range of flower color, silique, and trichome characteristics relative to the parents (Rollins and Solbrig 1973). Outcrossing in these auriculate-leaved *Paysonia* species found in Tennessee and Alabama is obligated with the hybrids also exhibiting self-incompatibility (Rollins 1988).

Intergeneric hybridization of lesquerella to *Brassica napus* L. has been investigated by conducting protoplast fusion. Hybrid plants were obtained which were fertile and able to cross-pollinate to *B. napus* (Skarzhinskaya et al. 1996, 1998). In addition, cross-fertilization between *B. napus* and *Physaria fendleri* using the latter as a pollen source resulted in F1s with higher levels of linoleic, linolenic, eicosanoic, and erucic acids than the *B. napus* parents. The wide crosses resulted to chromosome elimination and doubling as well as genomic reorganization in *B. napus* (Du et al. 2008). These results indicate the possible utility of lesquerella to enhance traits in other Brassica oilseeds.

15.4.3 Wild Utilized Species

Introgression of desirable traits from *Physaria* and *Paysonia* species to lesquerella was a focus of the USDA breeding program (Dierig and Ray 2009). Among the important *Physaria* sister species already utilized include *P. lindheimeri* (A. Gray) O'Kane & Al-Shehbaz and *P. gracilis* (Hook.) O'Kane & Al-Shehbaz which were found to have higher lesquerolic acid content with 89% and 60–70%, respectively (Buchanan and Duke 1981; Dierig et al. 1996b; Salywon et al. 2005). These species have the same chromosome number as lesquerella ($2x = 2n = 12$) (Dierig and Ray 2009). Successful production of hybrids from these species as well as *P. pallida* has been reported (Dierig et al. 1996a, b, 2004) with some hybrids, showing elevated levels of lesquerolic acid that were 20% greater than *P. fendleri*. However, most hybrids were sterile or had low seed production and had low seedling vigor.

Two species, *P. pallida* (Torr. & A. Gray) O'Kane & Al-Shehbaz and *P. mcvaughiana* (Rollins) O'Kane & Al-Shehbaz, have been identified to exhibit self-fertility which could increase seed yield under commercial production. Lesquerella seed yield depends on pollinator activity (Roll et al. 1997; Mitchell 1997). With self-fertile germplasm, the requirement for insect pollinators may be circumvented reducing production cost and attaining consistent yield (Dierig and Ray 2009). As pollinators are very important in lesquerella, a detailed study of its floral structure was made to understand floral nectary structure and distribution of gynoecial stomata. Results indicated that the flower morphology ensures insect-assisted cross-pollination and that monitoring these structures for changes during the breeding selection activities was recommended (Kehl and Erickson 1995).

Another important trait that needs study is yield and productivity at colder regions. The importance to derive adaptation when growing the crop at these regions at higher elevations was investigated in Arizona and in Argentina. It was determined that *P. pallida* and *P. angustifolia* (Nutt.) O'Kane & Al-Shehbaz are more productive when planted at higher elevations (Dierig et al. 2006a, b; Ploschuk et al. 2003). *P. angustifolia* was recommended as an alternative crop in the Chubut River Valley, Patagonia, Argentina, where the field testing was conducted. Another species, *P. mendocina*, native to the Patagonia and Monte regions of Argentina was also evaluated for suitability in cold arid growing regions (Ravetta and Soriano 1998; Windauer et al. 2004).

During phenotypic characterization of the *Physaria* and *Paysonia* germplasm collection, several species were identified to have potential to be directly utilized as ornamentals. This germplasm represents *Physaria* species (*P. mcvaughiana*, *P. mexicana* (Rollins) O'Kane & Al-Shehbaz, *P. ovalifolia* (Rydb. ex Britton) O'Kane & Al-Shehbaz, *P. pallida*) and *Paysonia* (*P. perforata*, *P. stonensis*) reported to have plants that show white flowers, as well as plants that show full bloom for a longer period (*Physaria*, *P. argyraea* (A. Gray) O'Kane & Al-Shehbaz; *Paysonia*, *P. grandiflora* (Hook.) O'Kane & Al-Shehbaz, *P. lasiocarpa* (Hook. ex A. Gray) O'Kane & Al-Shehbaz) (Jenderek 2006). As more genetic and genomic information are obtained in *Physaria*, the significance of native genes and genomic sequences should become evident. To date, a *P. fendleri* promoter *LfKCS3* has been identified useful for modifying the levels of saturated fatty acids in cells of biotech canola plants (Gachotte et al. 2014).

15.4.4 Conservation Status

15.4.4.1 In Situ

The federal and state conservation programs include several *Physaria* species as indicated in Table 15.4. Critical habitat areas have been designated by the US Department of the Interior for *P. globosa* (Desv.) O'Kane & Al-Shehbaz and *P. douglasii* subsp. *tuplashensis* (Rollins et al.) O'Kane & Al-Shehbaz in 2014 and 2013, respectively (ECOS 2017a, b). For the other imperiled and endangered species, respective state agencies monitor and track the status of wild populations. Among the major threats to populations in *Physaria* natural habitat include grazing, impact of nonnative species, soil erosion, wildfires, and damage from off-road vehicles (O'Kane 2006). Small fragmented populations are also more susceptible to genetic erosion due to genetic drift. The relative diversity among the species listed in Table 15.4 is not known, but in lesquerella there is substantial genetic diversity being maintained within the soil seed bank. Seed dormancy influences the number of plants that will germinate along with other edaphic factors (Cabin et al. 1998).

In Colorado, best management practices to populations of *P. obcordata* Rollins, *P. congesta* (Rollins) O'Kane & Al-Shehbaz, and *P. bellii* G. A. Mulligan (endemic in the state) have been formulated to reduce the impact of road maintenance and revegetation activities. Special management areas have been created, as well as plans to control noxious weed species that occupy habitat areas of *P. bellii* (Panjabi and Smith 2014). The suggested actions for *P. obcordata* and *P. congesta* conservation included more intensive coordination with private landowners and energy companies, who conduct activities in areas near natural habitats (Panjabi and Neely 2010). In *P. parvula* (Greene) O'Kane & Al-Shehbaz, although no protected federal area has been designated, a technical conservation assessment has been conducted. *P. parvula* has a very limited distribution occupying windswept and barren mountain slopes at elevations of 6000–8900 ft. in Colorado, Wyoming, and Utah (O'Kane 2006). Climate change is hypothesized to impact *Physaria* species in their natural habitat, especially those adapted to colder habitats such as *P. parvula* as not only the temperature and rainfall patterns may change but the timing availability of pollinators may not coincide with plant flowering (Grossman 2004; Scaven and Rafferty 2013).

In Texas, monitoring of habitats of *P. thamnophila* (Rollins & E. A. Shaw) O'Kane & Al-Shehbaz at the Tamaulipan thornscrub near the Rio Grande has been conducted routinely for 6 years to develop a management plan. It was determined that there were more plants on areas that were brush-cut, suggesting that the plant litter helps prevent soil erosion allowing the seedlings of this species to get established (Fowler et al. 2009). A recent review (US Fish and Wildlife Service 2015b) listed ten elements of occurrence of *P. thamnophila* in two counties in Texas. Among the future plans to assist recovery is to conduct public outreach activities to increase awareness on this species, as well as seed collection and subsequent reintroduction to suitable protected habitats creating designated refugia (Fig. 15.11).

15.4.4.2 Ex Situ

Lesquerella germplasm is being conserved in the United States by the NPGS and in the United Kingdom by the Millennium Seed Bank Partnership. A total of 238 accessions of 34 *Physaria* species are under ex situ conservation (Table 15.4) (Genesys 2017). The NPGS has 214 of these accessions available for distribution (USDA ARS 2017b) (Fig. 15.12).

The *Physaria* germplasm and related *Paysonia* species at the NPGS have been fully characterized for oil and fatty acid content (Jenderek et al. 2009) as well as morphological and phenological traits (Salywon et al. 2005; Dierig et al. 1995). These characterization and evaluation data are publically available online at the USDA germplasm database (USDA ARS 2017a). There are a total of 36 descriptors encompassing oil composition, growth, and morphological, phenological, and production traits.

In addition to morphological characterization, the *Physaria* collection along with a limited number of *Paysonia* germplasm at USDA has been analyzed using molecular markers. Analysis of genetic diversity has been conducted on the collection using 2833 DArT and 27,748 DArT-seq markers (Cruz et al. 2013b). Two distinct genetic

Fig. 15.11 A native population of lesquerella [*Physaria* (Nutt. ex Torr. & A. Gray) A. Gray] found on a roadside to Ft. Davis, Texas

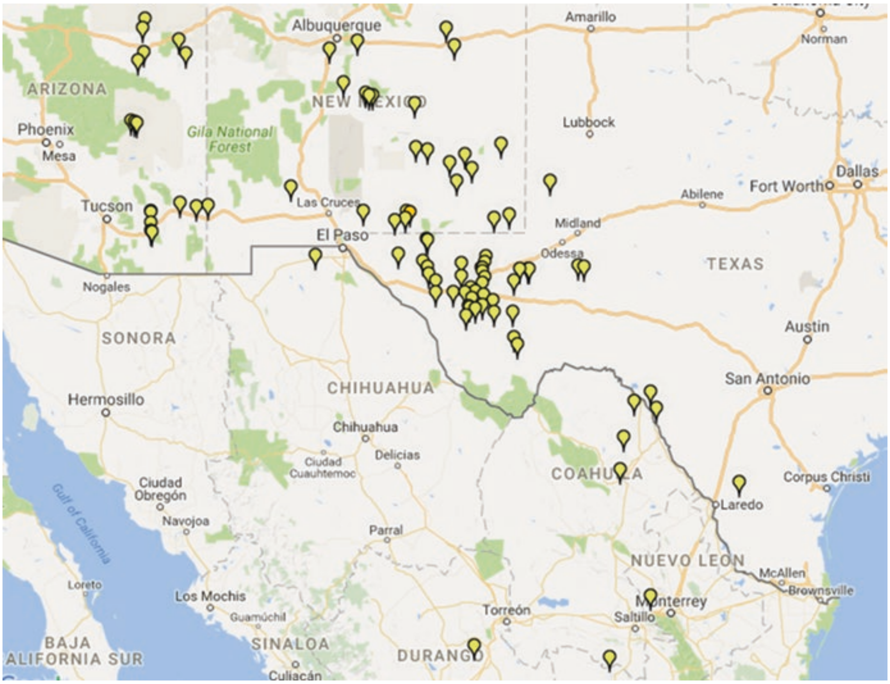

Fig. 15.12 US NPGS collection sites of lesquerella [*Physaria* (Nutt. ex Torr. & A. Gray) A. Gray] across three US states and four provinces in Mexico

clusters in the *P. fendleri* collection were identified separating germplasm from Texas and Mexico. The study also found that there was high genetic similarity among the two *P. pallida* accessions included in the study, suggesting that a follow-up analysis focusing on underrepresented species in the collection might be necessary.

In 2010, several native sites in the US Southwest were revisited to collect seeds (Cruz et al., 2013a) (Fig 15.13). During the collecting trips, several sites in New Mexico and Texas were found to be nonexistent. However, because of highly variable environmental factors, the dynamics of population establishment is expected to change depending on whether the year was favorable for growth or not. In addition to genebank-stored seeds, there are a few *Physaria* species that are being maintained as living collections in botanical gardens. The Denver Botanic Gardens have plants of *P. alpina*, *P. bellii*, *P. eburniflora* Rollins, and *P. subumbellata* (Denver Botanic Garden 2017). The Desert Botanical Garden in Phoenix, AZ, also has accessions of *P. fendleri*, *P. gordonii* (A. Gray) O'Kane & Al-Shehbaz, and *P. tenella* (A. Nelson) O'Kane & Al-Shehbaz stored as seeds with some plants grown in the gardens in the past (Desert Botanical Garden 2017). Continued utilization of germplasm as well as sustained efforts to commercialize *P. fendleri* and the other promising *Physaria* species will help ensure a sustainable source of domestic raw material (Table 15.5).

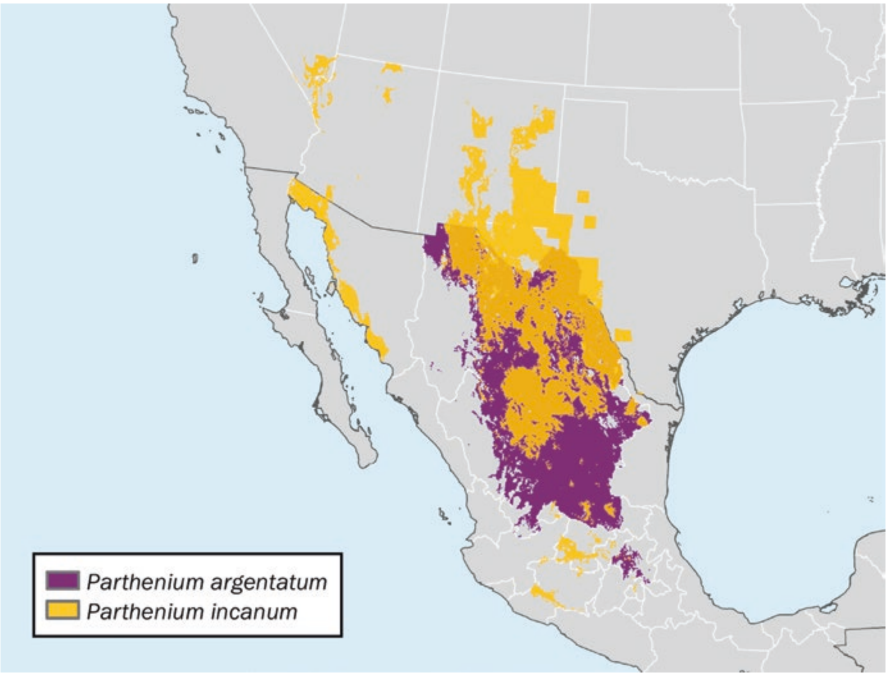

Fig. 15.13 Geographic distribution of guayule (*Parthenium argentatum* A. Gray) and mariola (*Parthenium incanum* Kunth) based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Table 15.5 Number of germplasm accessions of *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray and holding institutes

Millennium Seed Bank Partnership, Royal Botanic Gardens, Kew		**USDA-ARS Western Regional Plant Introduction Station, Pullman, WA**	
P. acutifolia Rydb.	1	*P. acutifolia* Rydb.	2
P. chambersii Rollins	1	*P. chambersii* Rollins	1
P. rollinsii G. A. Mulligan	1	*P. gordonii* (A. Gray) O'Kane & Al-Shehbaz	1
P. vitulifera Rydb.	1	*P. macrocarpa* (A. Nelson) O'Kane & Al-Shehbaz	1
		P. rollinsii G. A. Mulligan	1
		P. tenella (A. Nelson) O'Kane & Al-Shehbaz	2
		P. vitulifera Rydb.	2
USDA-ARS National Arid Land Plant Genetic Resources Unit, Parlier, CA			
P. acutifolia Rydb.	1	*P. mcvaughiana* (Rollins) O'Kane & Al-Shehbaz	1
P. angustifolia (Nutt.) O'Kane & Al-Shehbaz	4	*P. mexicana* (Rollins) O'Kane & Al-Shehbaz	2
P. argyraea (A. Gray) O'Kane & Al-Shehbaz	11	*P. montana* (A. Gray) Greene	2
P. arizonica (S. Watson) O'Kane & Al-Shehbaz	1	*P. multiceps* (Maguire) O'Kane & Al-Shehbaz	1
P. bellii G. A. Mulligan	1	*P. ovalifolia* (Rydb. ex Britton) O'Kane & Al-Shehbaz	5
P. chambersii Rollins	2	*P. pallida* (Torr. & A. Gray) O'Kane & Al-Shehbaz	6
P. cinerea (S. Watson) O'Kane & Al-Shehbaz	1	*P. palmeri* (S. Watson) O'Kane & Al-Shehbaz	3
P. densiflora (A. Gray) O'Kane & Al-Shehbaz	1	*P. pinetorum* (Wooton & Standl.) O'Kane & Al-Shehbaz	2
P. douglasii (S. Watson) O'Kane & Al-Shehbaz	3	*P. rectipes* (Wooton & Standl.) O'Kane & Al-Shehbaz	4
P. fendleri (A. Gray) O'Kane & Al-Shehbaz	119	*P. recurvata* (Engelm. ex A. Gray) O'Kane & Al-Shehbaz	2
P. gordonii (A. Gray) O'Kane & Al-Shehbaz	30	*P. reediana* O'Kane & Al-Shehbaz	1
P. gracilis (Hook.) O'Kane & Al-Shehbaz	2	*P. rollinsii* G. A. Mulligan	1
P. intermedia (S. Watson) O'Kane & Al-Shehbaz	4	*P. schaffneri* (S. Watson) O'Kane & Al-Shehbaz	1
P. kingii (S. Watson) O'Kane & Al-Shehbaz	3	*P. sessilis* (S. Watson) O'Kane & Al-Shehbaz	1
P. lindheimeri (A. Gray) O'Kane & Al-Shehbaz	1	*P. tenella* (A. Nelson) O'Kane & Al-Shehbaz	2
P. ludoviciana (Nutt.) O'Kane & Al-Shehbaz	2	*P. thamnophila* (Rollins & E. A. Shaw) O'Kane & Al-Shehbaz	1
USDA-ARS National Laboratory for Genetic Resources Preservation, Fort Collins, CO			
P. fendleri (A. Gray) O'Kane & Al-Shehbaz	3		

15.5 Guayule

15.5.1 Origin of the Crop and Brief History of Use Worldwide

Guayule, *Parthenium argentatum* A. Gray, is a source of natural rubber suitable for production in arid and semiarid regions of the world. This xerophytic, perennial shrub species is the only member of the *Parthenium* L. genus producing significant quantities of natural rubber to be economically useful. Guayule is a member of the family Compositae (Asteraceae) and is native to the desert regions of the Southwestern United States and Northern Mexico (Chihuahuan desert region) (Fig. 15.13). The wild relatives of guayule are native to a more expansive region covering North and South America.

Aztec Indians in Mesoamerica knew of the rubber-containing plant and made balls for sporting events long before this. Rubber was extracted by communal mastication of the bark for recreational use (Wilcox 1991; Haury 1937). Rubber balls from prehistoric times have been discovered in the Southwestern United States and verified by archeologists at the US National Park Service as guayule rubber.

Guayule was first discovered for scientific purposes in Texas by Dr. J. M. Bigelow as part of the Mexican boundary survey in 1852. The collected shrub specimen was from near Escondido Creek, Texas (on the border of the United States and Mexico), and sent to Professor Asa Gray of Harvard University who named *Parthenium argentatum* with A. Gray as the naming authority (McGinnies and Haase 1975). The first commercial use of guayule natural rubber was made by the New York Belting and Packing Company which imported 22,000 kg of guayule shrub in 1880 and extracted the rubber by immersing it in hot water (McGinnies and Haase 1975). In 1904, 22 kg of rubber was shipped from Mexico by the Continental Mexican Rubber Company who adopted the most successful extraction method using pebble mill and water floatation (McGinnies and Haase 1975). The rubber was sent to the Manhattan Rubber Company in New York where it was found to be equivalent to the rubber from the *Hevea* Aubl. rubber tree grown in the tropics. In 1910, it made up 24% of the rubber imported to the United States. The shrub was also an excellent smelter fuel and burned in large mining smelters. The bagasse (what is left of the ground shrub after rubber and resin are extracted) was used as a fuel in extraction factories in Mexico (McGinnies and Haase 1975). An extraction plant was also built in the United States in Marathon, Texas, where surveys showed there was an estimated 2500 tons of shrub in this general area (McGinnies and Haase 1975). Native stands were apparently harvested for rubber extraction without concern for replenishment of the genetic resources during this period and perhaps a reason for the scarcity of stands present in Texas today. It was reported that only tetraploid stands were found in Texas when surveyed during the Emergency Rubber Project (ERP) (Hammond and Polhamus 1965). At this time it was estimated that there were 254,000 metric tons of shrub available in Mexico in the states of Chihuahua, Coahuila, Durango, Nuevo Leon, San Luis Potosi, and Zacatecas. In 1942, four guayule mills were consuming180 metric tons of shrub for a 24-h day (McGinnies and Haase 1975).

There is a documentation of guayule being cultivated on private farms especially when Continental Rubber Co. moved to the United States and became the Intercontinental Rubber Co. around 1910. They planted 3240 ha of guayule selections/strains, indicating that some breeding and selection were occurring. However, it was not known at that time that reproduction of most guayule germplasm occurred by facultative apomixis and was a reason for the lack of improvement. This was not discovered until later (Esau 1944, 1946). Research fields to explore cultivation practices increased, and production fields developed during this time (McGinnies and Haase 1975).

Many of the native guayule stands in Texas and Mexico were used to feed extraction facilities during the beginning of the rubber industry. The shrub was pulled by hand and thrown into large carts, then towed by small crawler tractors to collecting locations, and there baled by the contractor (Bonner 1975). The current practice of cutting plants at ground level and allowing regrowth was not practiced until the ERP era. Seed sources from known localities from that time no longer exist.

Guayule has a history of association with wartime needs in both Mexico and the United States. In 1930 the War Department (precursor to the US Department of Defense) studied guayule production to lessen dependence on Southeast Asia and as a source of domestic jobs. Legislation provided for a takeover of the Intercontinental Rubber Company by the US Government and for the EPA to be the sole guayule grower in the United States, with company land holdings including a 26 ha nursery and 567 ha plantation. The physical inventory included the Spence Mill for extraction of rubber, about 10,432 kg of seed, 14,000 nursery seedlings, and 273 ha of shrub plantations. The legislation signed by President Roosevelt in 1942 was supported by the General Tire and Rubber Company, the Goodrich Company, the Goodyear Tire and Rubber Company, and the Firestone Tire and Rubber Company (now Bridgestone Corporation) (McGinnies and Haase 1975).

A reconnaissance survey of some 13 million ha of land was made and the classification of over 2 million ha for guayule culture. Land acquisition work was intensified and some 25,000 ha were leased. Because of later curtailment of the project, the planting goal was never reached, with only 13,000 ha being planted during the life of the ERP.

Research and development came to a halt at the end of the ERP in the early 1950s although informally continued until 1959 (Hammond and Polhamus 1965). One explanation for the end of the project besides the end of the war was the promise of synthetic rubber replacing natural rubber which has never been achieved. Today synthetic rubber comprises much of requirements for passenger car tires; however, larger tires for trucks, agriculture equipment, and aircraft require natural rubber. In the late 1970s with the US Congressional Action, research was revived. This time it was a petroleum crisis that made many countries aware of their dependence on uncertain geopolitical rubber sources (Nakayama 2005). The National Academy of Science recommended in 1977 the need to increase research on guayule. The Native Latex Act of 1978 followed, and as petroleum prices continued to rise, the US Congress enacted the Critical Agricultural Materials Act in 1984 to replace the Native Latex Act. This project was terminated with the stabilization of the source and price of petroleum and the subsequent decrease in the price of *Hevea* rubber. During that time, a solvent extraction processing plant was built in Sacaton, Arizona, and commercial fields nearby planted and managed by the Gila River Indian Community. The variety of guayule that was planted was Gila 1, a naturally occurring interspecific hybrid between guayule and *P. tomentosum* var. *stramonium* (Greene) Rollins. Later this was confirmed to be the same as line AZ 101 from the University of Arizona (D.T. Ray, personal comm.). Although the shrub grew quickly, it had very little rubber yield. Both Goodyear Tire Company and Firestone Tire and Rubber Company (now Bridgestone Corp.) had roles in that project producing various types of tires.

15.5.2 Modern Day Use

Unlike past government driven efforts, the current era is being driven by a consortium of industry that will profit from utilization of all plant products (rubber, resin, bagasse). Crop improvement utilizing modern breeding tools is being applied as well as better agronomic management including seed establishment and rate, irrigation efficiency, pesticide registrations, and harvesting equipment led by industry with government support.

Guayule is either solvent extracted for solid rubber (tire) use or water extraction for latex products. There are a growing number of industrial companies in the early stages of development occurring in the Southwestern United States, Mexico, and parts of Europe. Guayule has a resin coproduct composed of fatty acid triglycerides and complex mixtures of terpene and sesquiterpenoid compounds (Schloman et al. 1983). Resins make up around 8–10% of the shrub's biomass. The chemical composition of the resin and rubber has been used as a tool toward developing taxonomic relationships and evolution of *Parthenium* species (Nakayama 2005; Hashemi et al. 1986) since it's the only species of the taxon with any substantial quantities of rubber and resin. The resin has recently been demonstrated to have utility as a recycling agent in hot asphalt mixes (Lusher and Richardson 2015).

In addition to the rubber and resin, the guayule bagasse is a critical component of the economics of the crop. This could be used as a high-energy-value fuel pellet or as a biofuel (Nakayama 2005). When unprocessed wood or flake boards were impregnated with guayule resin or the bagasse with residual resin, they were made resistant to termite and wood-rot attack (Nakayama 2005).

15.5.3 Challenges in Cultivation

Commercial guayule cultivation is very limited. However, industry is pursuing a sustainable effort to supplement the supply of natural rubber from *Hevea*. Most planted fields are less than 40 ha in size and are for research or scale-up purposes. Guayule is still in the research and development stage and not commercially available for most markets. Commercial production areas will likely include the Southwestern United States and Mexico. We do not know the extent of pests and diseases affecting guayule until more acreage and more geographic areas are planted. Areas suitable for production may be discounted due to disease and insect pressure (Tysdal and Rands 1952).

Guayule is a perennial crop that needs to be grown for at least 2 years to optimize rubber yield. It can be harvested by cutting at ground level and allowed to regenerate from the roots which adds another growing cycle and ties up land for an additional 2 or more years. Most farmers grow annual crops, so a crop like guayule may pose some challenges. Direct seeding has now replaced transplanting at a significant savings in production costs. An insect encountered is the flea beetle (*Systena blanda*) that feeds on the newly emerged seedling; however, transplants are not affected. Seedlings from direct seeding are also more sensitive to herbicides.

There are a number of literature reports identifying pathogenicity and other pests in guayule. For the purposes of this chapter, we will not review this literature but only note that sources of resistance are present within *P. argentatum*. Other wild relatives used to cross with *P. argentatum* to confer resistance or increased biomass are found in the NPGS. Cal 1 and Cal 2 are interspecific hybrids between *P. argentatum* x *P. tomentosum* DC. and *P. argentatum* x *P. fruticosum* Less., respectively. Both are identified in GRIN as resistant to *Verticillium albo-atrum* Reinke & Berthe. to have higher biomass but diluted in rubber content, as a result of *P. tomentosum*. The University of Arizona tested lines of *P. argentatum* with the same disease resistance. Those lines have not been released but indicate that resistance is available within species.

15.5.4 Anticipating Climate Change

Other species of *Parthenium* have a wider range of geographic distribution than *P. argentatum* and found at high elevations and colder climates. These species may be valuable for adaptation of guayule. The challenge is that other *Parthenium* species do not contain rubber. Collections of *P. incanum* Kunth are limited compared to historical sites at higher elevations, so new collection efforts would be needed if this were the choice for introgression. It is likely that variation for cold tolerance can be found within *P. argentatum* (Mitchell 1944). In the past, 11,591 plants (accession PI 478640) were planted in Texas, and some plants survived extreme cold conditions during those experiments (Foster et al. 2011). Reports from the ERP indicated that some plants survived in Texas at −15 °C, so some plants appear to have tolerance, at least for a short exposure time. Mitchell (1944) reported that outdoor plants adapted much better to low temperatures compared to plants grown first in the greenhouse and allowed to develop more lush, succulent growth. It was also shown that seedlings that were unhardened could withstand long exposures of −4° C, while unhardened potted plants 15–18 months withstood exposure to −7 °C. Roots were sensitive in these experiments, and when exposed to soil temperatures of −3° C plants for 8–10 h, plants were subject to injury. When plants were hardened, the stems of transplants withstood repeated and prolonged exposures to −15 °C. An accession named A5058 (no longer available from USDA) showed more tolerance than others indicating there is room for selection within the germplasm pool.

15.5.5 Crop Wild Relatives

15.5.5.1 Crop Wild Relatives and Their Genepool Classifications

Table 15.6 lists accepted named species of *Parthenium*. These all occur in the Western Hemisphere; however, Mexico is the primary center of diversity. Species are both annuals and perennials that include herbaceous plants, woody shrubs, and small trees.

Table 15.6 List of 14 accepted names of *Parthenium* species from The Plant List (www.theplantlist.org)

Species	2*n* count if available	Miscellaneous notes on origin
P. alpinum (Nutt.) Torr. & A. Gray	72	NM, CO, WY
P. argentatum A. Gray	36 + polyploids	TX and Mexico
P. bipinnatifidum (Ortega) Rollins	24	
P. cinereum Rollins		Bolivia, Paraguay
P. confertum A. Gray	34 / 68	AZ, NM, TX, N. Mexico
P. fruticosum Less. ex Schltdl. & Cham.	36	Tamaulipas to Chiapas, Mexico
P. hysterophorus L.	34	Aggressive weed N. and S. America
P. *incanum* Kunth	36 + polyploidy	Nearest relative of *P. argentatum*; NV, UT, AZ, NM, TX, N. Mexico
P. integrifolium L.	72	Perennial herb, Eastern United States; TX to MA + MN
P. ligulatum (M.E. Jones) Barneby	36	CO, UT
P. parviceps S.F.Blake		
P. rollinsianum Rzed.		San Luis Potosi, Mexico
P. schottii Greenm. ex Millsp. & Chase	36	Yucatan, Mexico
P. tomentosum DC.	36	Oaxaca and Puebla, Mexico

Rollins (1950) reports that the genus *Parthenium* does not appear to be closely related to any other genus in the Compositae family. In his publication he describes the morphological characteristics distinguishing species and subspecies. The taxonomic key to the species of *Parthenium* by Rollins lists 16 species. A more updated list is found on the Plant List website with 14 accepted species (Table 15.6). There are 42 accessions of guayule in the NPGS collection based on the recent genotyping study by Ilut et al. (2017). Two accessions (AZ-2 and AZ-3) released by Ray et al. (2005) that were thought to be guayule were found to be interspecific hybrids of guayule and another species (possibly *P. tomentosum*) (Ilut et al. 2017). AZ-2 is the primary germplasm line used by private companies trying to commercialize guayule due to many desirable traits such as more vigorous seedlings and plant growth and high biomass. The biomass production of this germplasm line accounts for the high rubber yield/ha compared to other lines in the USDA collection. This shows promise for utilization of other species in a breeding program. *P. incanum* (mariola) is the only species beside guayule to have a slight amount of rubber/latex. This species is also apomictic with a polyploid series somewhat similar to *P. argentatum*. The two species are known to naturally hybridize in the wild. *P. incanum* compared to other species may have some utility in a breeding program because it has a wider geographic distribution and adaptability to colder areas than *P. argentatum* (Fig. 15.13). There is always the possibility when more is known about the metabolic components involved in rubber production in a shrub; other species with faster growth, such as *P. schottii* Greenm. ex Millsp. & Chase, *P. tomentosum*, or *P. fruticosum*, could be candidates for genetic modification and contribute to increased biomass.

15.5.5.2 Distribution, Habitat, and Abundance of *P. argentatum* and *P. incanum*

15.5.5.2.1 *P. argentatum*

The guayule in Mexico is localized in six states, three of them bordered by the United States and the rest in neighboring states (Fig. 15.13). In the United States, it is only found in the state of Texas in the Big Bend area. The Mexican state of Coahuila has the largest concentration of wild sites (total of 27), which are distributed from the north to the southeast of the state, followed by the state of Durango with 19 sites in the northeast and central east region, and Zacatecas with 16 sites located in the northern region. Twelve sites were identified in the Southwestern Nuevo Leon, nine sites in the north region of San Luis Potosi, and six sites in the east and south portion of Chihuahua. In addition, two sites were identified in the Northwestern Hidalgo. The map of the guayule region (Fig. 15.13) was drawn with revised information from the databases of herbarium specimen collections of Universidad Autónoma Agraria Antonio Narro (ANSM) from collections carried out during the period of 1964–2015, as well as of the University of Texas (TEX) and Arizona State University (ASU) database. Guayule is native to North-Central Mexico, in the states of Coahuila, Chihuahua, Durango, Zacatecas, San Luis Potosi, Nuevo Leon, and Southwestern United States in the Big Bend area of Texas (Rollins 1950). It is largely restricted to outwash slopes of calcareous soils in regions having an annual rainfall of 10–15 inches (McGinnies and Haase 1975). Some of these native sites have plants sparsely scattered in small areas, while others are many acres in size. Plants are often found growing sympatrically with lesquerella (*Physaria fendleri*) throughout North-Central Mexico. The distribution shown from Fig. 15.13 and Table 15.7 reveals that climatic (temperature, precipitation) conditions of the Mexican desert, as well as the different soil types and pH, favor the natural development of the guayule (Angulo-Sánchez et al. 2002).

Table 15.7 Herbarium information of Mexican collections of *P. argentatum* A. Gray (guayule)

State	City	Region	Site description and associated plants
Coahuila	Saltillo	Southeast	Microphyllous desert scrubland associated with *Viguiera brevifolia* Greene.; *Parthenium incanum* Kunth; *Larrea tridentata* (DC.) Coville; *Flourensia cernua* DC.
Coahuila	Parras de la Fuente	Southeast	Microphyllous scrubland of *Agave lecheguilla* Torr.; rosetophile scrubland of *Dasylirion cedrosanum* Trel; *Mortonia palmeri* Hemsl.; *Quercus intricata* Trel.; *Q. saltillensis* Trel.; *Yucca carnerosana* (Trel.) McKelvey
Coahuila	Torreón	Laguna	Scrubland of *Acacia* Mill.; *Yucca* L.; *Opuntia* Mill; *Mortonia* A. Gray; *Rhus* L.; *Fouquieria* Kunth; *Agave* L.; *Cercocarpus* Kunth; *Senegalia crassifolia* (A. Gray) Britton & Rose (syn. *Acacia crassifolia* A. Gray); *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.); *Lindleya mespiloides* Kunth; *Cercocarpus mojadensis* C.K. Schneid.; *Vauquelinia californica* (Torr.) Sarg.
Coahuila	Ocampo	Center-Desert	Scrubland of *Vachellia constricta* (Benth.) Seigler & Ebinger (syn. *Acacia constricta* Benth.)*; Flourensia cernua* DC. and *Prosopis glandulosa* Torr.; microphyllous scrubland with *Parthenium argentatum* A. Gray and *Agave lecheguilla* Torr.; *Yucca* L. sp.; *Vachellia constricta* (Benth.) Seigler & Ebinger (syn. *Acacia constricta* Benth.); *Aristida* L.; *Stipa* L.; *Acourtia* D. Don; *Koeberlinia* Zucc.; scrubland of *Larrea tridentata* (DC.) Coville, *Senegalia berlandieri* (Benth.) Britton & Rose, *Fouquieria splendens* Engelm., *Dasylirion* Zucc. sp. *Lycium berlandieri* Dunal.
Coahuila	Sierra Mojada	Center-Desert	Scrubland of *Larrea tridentata* (DC.) Coville, *Agave* L., *Opuntia imbricata* (Haw.) DC., *Prosopis glandulosa* Torr., and *Vachellia farnesiana* (L.) Wight & Arn. (syn. *Acacia farnesiana* (L.) Wild. Saline soil
Nuevo León	Doctor Arroyo Municipality	South	Desert scrubland Limestone hillside (abundance-excess)

(continued)

Table 15.7 (continued)

State	City	Region	Site description and associated plants
Zacatecas	Mazapil Municipality	North	Rosetophile scrubland of *Agave lechuguilla* Torr., *Larrea tridentata* (DC.) Coville, *Parthenium incanum* Kunth, *Pinus pinceana* Gordon & Glend., *Yucca carnerosana* (Trel.) McKelvey, *Rhus virens* Lindh. ex A. Gray, *Sophora secundiflora* (Ortega) Lag. ex DC.
Zacatecas	Norias de Guadalupe	North	Scrubland of *Flourensia cernua* DC. and *Chenopodium* L.
Durango	Mapimi West	Northeast	*Agave lechuguilla* Torr.; *Yucca carnerosana* (Trel.) McKelvey; *Parthenium incanum* Kunth
Durango	Cuencame	Central east	*Larrea tridentata* (DC.) Coville; *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley); *Cordia parvifolia* A.DC.
San Luis Potosí	Charcas	North	*P. argentatum* A. Gray, 15–40-cm-high microphyllous scrubland, rosetophile scrubland with *Yucca decipiens* Trel., *Berberis trifoliolata* Moric., *Rhus microphylla* Engelm., and *Agave salmiana* Otto ex Salm-Dyck
Hidalgo	Highway Mexico-Pachuca	Southwest	Sharp slopes. Stony limestone soil. Hills with desert scrubland

15.5.5.2.2 *P. incanum*

Mariola (*Parthenium incanum*) is native to Mexico and the Southwestern United States (Rollins 1950) (Fig. 15.13). It is a perennial, small (10 cm high), aromatic, spreading, and very branched shrub with grayish bark below and tender and small leaves (Rollins 1950). It is a facultative apomictic plant with a natural ploidy series ranging from triploid to pentaploid (Sanchez et al. 2014). Mariola is considered the closest related taxon of guayule as it coexists with guayule in the wild (Rollins 1945). Interspecific hybrids between guayule and Mariola have been detected in the wild and have been produced by controlled crosses in order to extend the genetic base of guayule (Rollins 1945). Several accessions in the NPGS collection identified as guayule were found to be guayule and mariola hybrids based on SNP markers. There are 15 mariola collections from Arizona and Texas in the NPGS collection.

Mariola is one of the most abundant forages in the Northeast Coahuila, Mexico. It is used as part of goat diets throughout the year in rural communities (Mellado et al. 2007). The low-molecular-weight latex from mariola, named "tsacurra" by the Huicholes (indigenous people living in the state of Nayarit, Mexico), has been empirically used to cure stomach and throat ailments (Casillas Romo 1990). It has been reported that the Kickapoo Indians, who live in Northern Coahuila, use the tea of the mariola leaves to heal wounds (Latorre 1977).

Mariola has a wide distribution in Mexico and is reported in 14 states and in Texas, New Mexico, and Arizona in the United States. The largest number of wild sites occurs in the state of Coahuila (total of 23), from the US border to the southern tip of the state. In Chihuahua 13 sites are reported: San Luis Potosí with 11 sites and Nuevo León, Guanajuato, and Zacatecas eight, six and four sites reported, respectively. Durango and Querétaro were reported with four sites for each state. Also, Sonora and Hidalgo had two sites identified in each state. Finally, in Jalisco, Michoacán, Tamaulipas, and Guerrero had one site reported for each state. The map of mariola region (Fig. 15.13) was drawn with revised information from the databases of herbarium specimen collections of Universidad Autónoma Agraria Antonio Narro (ANSM) from collections carried out during the period of 1972–2015 as well as from the University of Texas (TEX) and Arizona State University (ASU) database (Native Plants 1981).

The wide geographic distribution of mariola in Mexico (Fig. 15.13) shows that this plant is able to adapt to a diversity of climates that arises from the North to Central and Western Mexico (Angulo-Sánchez et al. 2002). Information on associated vegetation with guayule and mariola in some documented native sites in Mexico is shown in Tables 15.7 and 15.8.

15.5.6 Conservation Status

None of the *Parthenium* species are listed as threatened or endangered. Guayule germplasm has been on the decline in the United States. Many historical sites in Texas listed in herbarium records are no longer present based on the collection attempt in Texas in 2005 and 2008 by Drs. M. Foster and T. Coffelt. Only three accessions of guayule were obtained in 2005 and two accessions in 2008. Figure 15.13 is a model-generated richness map that offers potential areas of distribution based on historical collection sites for both species. Although guayule has never been documented in the warmer climates about the western coast in Sonora (see yellow area), it's an area similar to Arizona where guayule is not native but grows very well for production.

One barrier is that some native collections occur on National Park Service lands which make it very difficult for the USDA to collect seed from another agency's jurisdiction due to differing objectives. The legal process to collect in Mexico is prohibitive due to International treaties. Few new collections have gone into the NPGS since the 1980s from Mexico. Some previous collections made by J. Tipton or R. Rollins are no longer viable. The NPGS curates guayule and its relatives at NALPGRU in Parlier, CA. Germplasm from this area appears to offer distinct diversity from the remainder of the public collection (Ilut et al. 2017).

The largest research effort on guayule occurred in the 1940s during the US Government's ERP. The breeding effort that took place included many collections and characterization of germplasm. The documentation of their work was a lasting contribution. Unfortunately, many of the fields were destroyed, and a relatively small amount of the germplasm was conserved in long-term seed storage. When there was a resurgence in guayule research in the late 1970s, there were a number of public projects working on plant improvement. Again, when some of these projects

Table 15.8 Herbarium information on Mexican collections of *P. incanum* Kunth (mariola)

State	City	Region	Site description and associated plants
Coahuila	Saltillo	Southeast	Rosetophile scrubland of *Agave lecheguilla* Torr. with *Opuntia microdasys* (Lehm.) Pfeiff. and *Dasylirion cedrosanum* Trel; abundant herbaceous stratum with *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult.; *Bouteloua gracilis* (Kunth) Lag. ex Griffiths; *Rhus virens* Lindh. ex A. Gray; *Yucca carnerosana* (Trel.) McKelvey; *Ephedra aspera* Engelm. ex S. Watson; *Flourensia cernua* DC.; and *Prosopis glandulosa* Torr. Stony soil. Microphyllous desert scrubland of *Viguiera greggii* (A. Gray) S.F. Blake isolated shrubs of *Larrea tridentata* (DC.) Coville; isolated trees of *Pinus pinceana* Gordon & Glend.; temperate zone. Scrubland of *Ziziphus obtusifolia* (Hook. ex Torr. & A. Gray) A. Gray; *Aristida* L. sp.; *Erionerum* Nash; and *Stipa* L. Submontane scrubland of *Purshia plicata* (D. Don) Henrickson; *Lindleya mespiloides* Kunth; *Mimosa biuncifera* Benth. with *Zinnia acerosa* (DC.) A. Gray; *Cyphomeris crassifolia* (Standl.) Standl. Scrubland of *Condalia warnockii* M.C. Johnst.; *C. spathulata* A. Gray
	Parras de la Fuente	Southeast	Microphyllous scrubland of *Agave lecheguilla* Torr; *Brickellia laciniata* A. Gray; *Larrea tridentata* (DC.) Coville; *Sericodes greggii* A. Gray; *Yucca carnerosana* (Trel.) McKelvey; *Berberis trifoliolata* Moric.; *Purshia plicata* (D. Don) Henrickson; *Agave falcata* Engelm.; *Pinus pinceana* Gordon & Glend.; *Juniperus saltillensis* M.T. Hall; *Quercus pringlei* Seemen General Cepeda: *Pinus pinceana* Gordon & Glend; *Zexmenia brevifolia* A. Gray; *Bouteloua curtipendula* (Michx.) Torr.; stony hillsides with vegetation of desert material; *Parthenium incanum* Kunth very abundant
	Ramos Arizpe	Southeast	Microphyllous desert scrubland of *Larrea tridentata* (DC.) Coville; *Parthenium argentatum* A. Gray; *P. incanum* Kunth. Plants of *Vachellia rigidula* (Benth.) Seigler & Ebinger (syn. *Acacia rigidula* Benth.), *Rhus virens* Lindh. ex A. Gray., *Pistacia mexicana* Kunth, and *Fraxinus greggii* A. Gray. Limestone hillside very stony; scrubland of *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.); *P. glandulosa* Torr.
	Torreón	Laguna	Scrubland of *Agave* L.; *Yucca* L.; *Rhus* L.; *Mortonia* A. Gray; *Cercocarpus* Kunth; *Senegalia crassifolia* (A. Gray) Britton & Rose (syn. *Acacia crassifolia* A. Gray); *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.); *Lindleya mespiloides* Kunth; *Cercocarpus mojadensis* C.K. Schneid.
	San Buenaventura	Center-Desert	Grazing land with *Hymenoxys odorata* DC.; *Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz; *Acoutia parryi* (A. Gray) Reveal & R.M. King

	Cuatro Ciénegas	Center-Desert	*Agave lechuguilla* Torr.; *Senegalia greggii* (A. Gray) Britton & Rose (syn. *Acacia greggii* A. Gray); *Larrea tridentata* (DC.) Coville; *Viguiera stenoloba* S.F. Blake; regosol and lithosol soils. Microphyllous scrubland of *Larrea tridentata* (DC.) Coville, *Flourensia cernua* DC., *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley), *Prosopis glandulosa* Torr.
	Candela	Center	Chaparral of *Vachellia rigidula* (Benth.) Seigler & Ebinger (syn. *Acacia rigidula* Benth.), *Leucophyllum frutescens* (Berland.) I.M. Johnst., *Mortonia greggii* A. Gray, *Cercocarpus* Kunth, *Senegalia crassifolia* (A. Gray) Britton & Rose (syn. *Acacia crassifolia* A. Gray), *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *A. berlandieri* Benth.), *Prosopis* L., *Lippia* L., *Mimosa* L., *Opuntia* Mill., *Bouteloua* Lag., *Heteropogon* Pers., *Agave lecheguilla* Torr., *Chamaecrista greggii* (A. Gray) Pollard ex A. Heller, *Neopringlea integrifolia* (Hemsl.) S. Watson.
	Ocampo	Center-Desert	*Agave lecheguilla* Torr.; *Larrea tridentata* (Cav.) Coville; *Flourensia cernua* DC.; *Opuntia* Mill.s; *Bouteloua* Lag.; *Prosopis glandulosa* Torr.; *Dasylirion* Zucc.; *Acourtia* D. Don.; *Koeberlinia* Zucc; *Andropogon spadiceus* Swallen; *Celtis pallida* Torr.; *Flourensia cernua* DC.; *Bouteloua hirsuta* Lag.; *Lippia graveolens* Kunth; *Jatropha dioica* Sessé; *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley); *Opuntia leptocaulis* DC. Halophyte grazing land of *Sporobolus airoides* (Torr.) Torr., *Yucca* L., *Bouteloua curtipendula* (Michx.) Torr., *Aristida* L.
	Sierra Mojada	Center-Desert	Xerophilic scrubland of *Larrea* Cav., *Flourensia* DC., *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.), *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *A. neovernicosa* Isley), and *Agave lecheguilla* Torr.
	Progreso	North	Mezquital of *Prosopis glandulosa* Torr.; shrub stratum composed of *Celis pallida* Torr., *Aloysia gratissima* (Gillies & Hook.) Tronc., and *Baccharis glutinosa* Pers.
Nuevo León	Doctor Arroyo	South	Chaparral with *Larrea* Cav. and *Yucca* L.
	Galeana	South	*Larrea* Cav. and *Yucca* L.
	Aramberri	South	Limestone hillside with *Agave lecheguilla* Torr.
	Monterrey	Center	Arborescent plants, disturbance zones
Durango	San Juan de Guadalupe		Xerophilic scrubland with dominant *Larrea* Cav., *Prosopis* L., *Flourensia* DC. desert, rocky hillside
	Cuencame	Central east	Scrubland of *Larrea* Cav., *Acacia* Mill., *Prosopis* L., and *Flourensia* DC. Microphyllous scrubland of *Larrea tridentata* (DC.) Coville, *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley), *Prosopis laevigata* (Humb. & Bonpl. ex Willd) M.C. Johnst., and *Cordia parvifolia* A.DC.
	Ceballos	Northeast	Xerophilic scrubland
	Mapimi	Northeast	Xerophilic scrubland; secondary vegetation; scarce shrub

(continued)

Table 15.8 Continued

State	City	Region	Site description and associated plants
Zacatecas	La Pardita	North	Shallow soil
San Luis Potosí	Guadalcazar	North	Scrubland of *Agave striata* Zucc., *Rhus virens* Lindh. ex A. Gray, *Pinus pinceana* Gordon & Glend., and *Quercus* L.
	Villa de Santo Domingo	Northeast	Association zacaton-gobernadora (*Larrea tridentata* (DC.) Coville)
	Matehuala	North	Deep soil-sand-clay
	Charcas	North	Microphyllous scrubland with *Larrea tridentata* (DC.) Coville, *Yucca decipiens* Trel., *Opuntia* Mill., and *Agave salmiana* Otto ex Salm-Dyck. Alluvial limestone scrubland
	Moctezuma Train Station	Center	Shrubs about 60 cm high, abundant greenish yellow inflorescence. Microphyllous desert scrubland
	Venado	Center	Crassicaule scrubland with *Prosopis* L. and *Dalea* L. Deep soil very shepherded, shrubs from 30 to 70 cm high
Tamaulipas	Tula	Southwest	Xerophilic scrubland with *Crasirroso*. Limestone low hills, shrubs of regular abundance
Guanajuato	San Luis de la Paz	Northeast	Grazing land. Plain terrain
	La Aurora Mine		Submontane scrubland on hillside, shrubs 1 m
Chihuahua	Manuel Benavides	East	Forest of pine-oak
	Rancho El 45		Microphyllous desert scrubland
Querétaro	Pinal de Amoles	North	Xerophilic scrubland, in hillside, suffruticose herbaceous plants from 40 to 50 cm high
	Vizarrón Municipality of Cadereyta	East	Microphyllous scrubland of *Larrea tridentata* (DC.) Coville
	San Pablo Tolimán	West center	Crassicaule scrubland of *Lama oreocereus*

ended, the germplasm did not always get deposited into a long-term seed storage facility such as the USDA, National Laboratory for Genetic Resources Preservation at Fort Collins, Colorado. The Crop Germplasm Committees (CGC) are trying to help this situation. Guayule is part of the New Crops Crop Germplasm Committee which started in 1991.

An obvious gap in the USDA collection is the lack of sexually reproduced diploids. Only two accessions (W6-429 and Cal 3) are available, and they are genetically highly similar. Very little breeding work has been done with diploids even though they have the most potential for improvement. It is not known if the current USDA germplasm collection adequately represents what is available in the wild. The USDA accessions have only recently been genotyped and phylogenetic relationships proposed based on SNP markers (Ilut et al. 2017). Thompson and Ray (1988) described the source of 23 of the 26 USDA cultivars and germplasm lines as originating from two collections of five bulk plants each. One resulted in the diploid accession W6-429, and the other resulted in 22 polyploid apomictic accessions. Molecular markers for genotypic analyses have been identified since (Estilai et al. 1990; Brown et al. 2008), but more recent analyses provided a comprehensive look at the phylogenetic relationships among germplasm using SSRs and SNPs (Cruz et al. 2015) and genotyping by sequencing (GBS) (Ilut et al. 2015, 2017). The results provide great insights into the relationships of accessions when combined with collection and breeding records. Ilut et al. (2015, 2017) were able to group accessions into four distinct clades and trace the heritage of collections. However, existing information still shows the need for more genotyping to determine intra-accession variation, along with phenotypic characterization of the entire collection.

To improve conservation, it is important that what is available in Texas and in the six states of Mexico be preserved both in situ and ex situ. The public USDA collection is very small in comparison to other crops. Acquisition of more germplasm may be helpful; however, the current collection needs to be better characterized to be useful to breeding programs. A descriptor list for guayule was previously proposed by Coffelt and Johnson (2011) which could be utilized and further refined. More information must be obtained through genetic analysis to determine phylogenetic relationships, increase understanding of traits through analysis of gene regulation and expression patterns, and exploit what diversity is currently available. Hopefully we are at a historical time when guayule has a good chance to become what was dreamt for the past 100 years of becoming a viable crop for arid climates. The key to this success is the available germplasm (Fig. 15.13).

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