Biology and Impacts of Pacific Island Invasive Species. 6. *Prosopis pallida* and *Prosopis juliflora* (Algarroba, Mesquite, *Kiawe*) (Fabaceae)[1]

Timothy Gallaher[2,3] *and Mark Merlin*[2]

Abstract: *Prosopis pallida* and *P. juliflora* (commonly referred to as algarroba, mesquite, or *kiawe*) were introduced from South America to areas in Oceania, Asia, and Africa during the early nineteenth century. In many cases, they naturalized and became widespread. In some places, alien *Prosopis* species are highly valued for the products and services that they can provide such as shade, cattle fodder, wood for fuel and fence posts, and nectar for honey production. In Australia, four *Prosopis* species including *P. pallida*, *P. juliflora*, *P. glandulosa*, *P. velutina*, and their hybrids are considered invasive and are subject to control efforts. After its introduction to Hawai'i in 1828, *P. pallida* became a dominant tree in arid areas of the main Hawaiian Islands, replacing the native lowland dry forest species that had been decimated by human activity, particularly by the introductions of goats and cattle. *Prosopis pallida* also has become an important economic species in Hawai'i. *Prosopis juliflora*, a more recent introduction to Hawai'i, is now spreading and is considered to be a noxious weed. Competition between *Prosopis* and native species as well as negative impacts of *Prosopis* on soil and local hydrology have been reported; however in some cases *Prosopis* species are characterized as midsuccessional species that rehabilitate degraded soils, eventually facilitating later-successional woodland. This provides a potential opportunity to use these species in reforestation efforts. Management decisions regarding these species should include a consideration of both their positive and negative ecological roles. If control or eradication is desired, a number of methods have been employed with various degrees of success.

Prosopis L. is a genus of medium-sized trees and shrubs in the family Fabaceae (Leguminosae), subfamily Mimosoideae, with species occurring naturally in Africa, Asia, and in North and South America. The most recent authoritative work on the taxonomy of the genus was conducted by Burkart (1976), who recognized 44 species in five sections. Phylogeny within the genus has been revisited recently, and changes to subgeneric relationships have been proposed (Hunziker et al. 1986, Bessega et al. 2006, Burghardt and Espert 2007).

Well-known species of *Prosopis* include *P. glandulosa* Torr. (honey mesquite) and *P. velutina* Woot. (velvet mesquite), which are both native to areas of the southwestern United States and Mexico, and *P. pallida* (Humboldt & Bonpland ex Willd.) Kunth and *P. juliflora* (Sw.) DC. from western South America. *Prosopis pallida* and *P. juliflora* are among the most notable invasive species in several arid and semiarid areas of the world. Although these two species are morphologically similar and have in the past been treated together as a complex, these apparent similarities may mask important ecological differences (Burkart 1976, Pasiecznik et al. 2001, Burghardt and Espert 2007).

NAMES

Within their native ranges, numerous indigenous names are applied to species of *Prosopis*.

Mesquite is a common name that originally applied to the North American *P. glandulosa* and *P. velutina*, and the name algaroba is generally used to refer to South American species of *Prosopis* (D'Antoni and Solbrig 1977, Felger 1977). In many places where they have been introduced, both names are commonly applied to all *Prosopis* species. In Australia, all species of *Prosopis* are referred to as mesquite and also as prickle bushes. In Hawai'i, most people today know *Prosopis* as *kiawe*, which according to one definition means, "to stream gracefully, as rain in the wind; to sway, as branches" (Pukui and Elbert 1986:146). The origins and context of the Hawaiian name are not known (Yzendoorn 1911).

Prosopis pallida

Synonyms of *P. pallida* include *Acacia pallida* Humboldt & Bonpland ex Willdenow, *Mimosa pallida* (Willdenow) Poiret, and *Prosopis limensis* Bentham (Pasiecznik et al. 2001). *Prosopis pallida* has been misidentified in the Pa-

cific and elsewhere as *P. chilensis, P. juliflora,* and *P. dulcis*. In Hawai'i, this species was also sometimes referred to as algarrobo or algaroba.

Prosopis juliflora

Synonyms of *P. juliflora* include *Mimosa juliflora* Swartz, *Prosopis pallida* forma *annularis* Ferreyra, *Prosopis inermis* H.B.K., and *Prosopis horrida* Kunth. For a complete list of synonyms for this and other *Prosopis* species see Pasiecznik et al. (2001). *Prosopis juliflora* is commonly referred to as long-thorned *kiawe* in Hawai'i.

DESCRIPTION AND ACCOUNT OF VARIATION

Species Description

Prosopis pallida often grows as a tree with a straight trunk with a diameter of up to 1 m and occasionally reaching heights over 20 m (Figure 1). Tree form may be erect, flat-topped, or decumbent with branches touch-

FIGURE 1. Growth form of *Prosopis pallida*. This tree is growing at a park in leeward O'ahu, Hawai'i.

FIGURE 2. Growth form of *Prosopis juliflora*. This shrub is growing at a park in leeward Oʻahu, Hawaiʻi. A meter stick is present in the image for scale.

ing the ground. *Prosopis pallida* may also grow as a shrub with numerous branches forking just above ground level; in such cases, otherwise tall or erect individuals may assume a shrubby form due to moisture deficit, wind, salt spray, frost damage, browsing, insect infestations, or cutting (Pasiecznik et al. 2001). *Prosopis juliflora* tends to grow as a shrub or small tree rarely reaching heights over 10 m (Figure 2). Both species reach maximum height and productivity in riparian zones with access to shallow groundwater (Schade et al. 2003), and both will also produce extensive coppice growth when cut above ground level. The outer bark of both species is rough, fissured, ropelike, and light gray to dark brown, and the heartwood is dark brown to red and very hard due to the abundance of resin. On older stems, short shoots called brachyblasts develop at the nodes of both species, producing a cluster of 1–10 leaves, inflorescences, and thorns. Thorns may be over 60 mm long on either

species, although typically less than 40 mm in *P. pallida*. In both species, thorns are occasionally small or absent, particularly on upper-canopy branches of mature individuals. Thorns on older branches are incorporated into the secondary growth.

Plants in the genus *Prosopis* are phreatophytes (literally, groundwater-loving plants), referring to their root system, which is capable of accessing relatively deep groundwater sources. *Prosopis* is described as having two complementary root systems: a taproot system and a lateral root system. The taproot system is made up of one to three thickened taproots that grow quickly, rarely branch until a water table is reached, and often reach a depth of 20–25 m (Havard 1884, Heitschmidt et al. 1988, Pasiecznik et al. 2001). In Arizona, roots believed to be from a species of *Prosopis* were found at a depth of 175 feet (53 m), among the deepest roots ever observed (Phillips 1963, Solbrig and Cantino 1975). The second root system comprises a

series of lateral roots that form a dense mat near the soil surface to take advantage of available near-surface water during infrequent rainfall events (Pasiecznik et al. 2001). Lateral roots of *Prosopis* can spread 18 m or more from the base of the tree (Mooney et al. 1977).

Leaves of *Prosopis* are bipinnately compound and have an alternate arrangement on the stem. The length of the compound leaf of *P. pallida* and *P. juliflora* is between 5 and 20 cm. Each leaf is made up of one to five pairs of opposite pinnae, and each pinna has between 6 and 29 pairs of oblong, opposite leaflets 2.5–23 mm long and 1.5–5.5 mm wide (Pasiecznik et al. 2004).

Inflorescences are axillary, spikelike, cylindrical racemes up to 15 cm long. Each is made up of several hundred yellow flowers 0.5 cm long. Namba (1956) found 250–525 flowers per raceme and approximately 100 florets per inch (2.54 cm) on *P. pallida*. The flower is connected to the rachis by a short pedicel. The calyx and corolla both have five lobes, and sepals tend to be fused and petals free; each flower has 10 stamens and a single carpel.

Flower maturation of *Prosopis* begins with a closed bud from which the style protrudes. As the flower bud opens, the anthers dehisce and the stigma becomes receptive. If pollination does not occur the entire flower will fall from the inflorescence (Genise et al. 1990). The fruit (pods) of *Prosopis* are indehiscent (Burkart 1976). They are green when immature and become yellow to dark brown and up to 25 cm long at maturity. Pods may be straight to slightly curved, occasionally appearing coiled. A hard, segmented, water-impervious endocarp surrounds each seed (Solbrig and Cantino 1975). Each fruit contains 10–40 seeds. Seeds are tan, shiny, flattened, oval-round, and approximately 5 mm in diameter. In Hawai'i, *P. juliflora* often forms a greater number of fruit per inflorescence than *P. pallida*, and the rachis of *P. juliflora* tends to become woody with secondary growth to support the numerous developing fruit (T.G., pers. obs.).

Prosopis pallida is diploid ($2n = 28$), as are most members of the genus. Hybridization with *P. juliflora*, the only known tetraploid ($2n = 56$) in the genus, is known to occur and appears to result in individuals that are intermediate in form between the parent species (Harris et al. 2003, Trenchard et al. 2008; T.G., pers. obs.). Hybridization is also frequent between other species of *Prosopis*, particularly among species of sect. *Algarobia*. In some cases, hybrids may be more suitably adapted to particular environments than parental types due to higher intraindividual variability (Vega and Hernandez 2005).

Distinguishing Features

Prosopis may be distinguished from other mimosoid legumes such as *Acacia* species by the combination of cylindrical inflorescences, indehiscent pods, and the absence of phyllodes (Figure 3). Within the genus *Prosopis*, considerable overlap in morphological characteristics between *P. pallida* and *P. juliflora* has resulted in frequent misidentification. A guide to help distinguish between these species is available (see Pasiecznik et al. 2004). In that analysis, the number of interfoliar glands (referring to glands between leaflet pairs) was the most reliable morphological characteristic to distinguish between *P. pallida* and *P. juliflora* (Harris et al. 2003, Pasiecznik et al. 2004). That guide indicates that if there are six or more glands per rachis, 16 or more pairs of leaflets per rachis, or leaflet length greater than 10 mm, then the sample can be identified as *P. juliflora* (Pasiecznik et al. 2004). Observations made on O'ahu (Table 1) found that other characteristics such as growth form, pod color, leaflet spacing, pigmentation, pinnae length, and the ratio between the length of the outermost to innermost pinnae may also be useful distinguishing characteristics (T.G., pers. obs.).

Intraspecific Variation

Fosberg (1966) recognized two forms of *P. pallida* in Hawai'i, forma *pallida* and forma *armata*. These differ only in that thorns are present in forma *armata* and absent in forma *pallida*. Ferreyra (1987) agreed with the two forms described by Fosberg and also de-

FIGURE 3. *Prosopis* morphology. *Top left:* Leaves and stems of *Prosopis juliflora* (*left*) and *P. pallida* (*right*); *top right:* thorns of *P. juliflora; center:* inflorescence and leaves of *P. pallida; bottom left:* stems, leaves, and pods of *P. pallida* (*left*) and *P. juliflora* (*right*); *bottom right:* a cut stump of *P. pallida* showing coppice regrowth. All photos taken on Oʻahu, Hawaiʻi, by Timothy Gallaher.

scribed two new forms, forma *decumbens* and forma *annularis;* however these taxa have not received widespread support (Pasiecznik et al. 2001). Native populations matching the description of *P. pallida* forma *pallida* are found in southern coastal Peru, and *P. pallida* forma *armata* occurs in coastal Ecuador and northern Peru sympatric with varieties of *P.*

TABLE 1

Observable Characters Used to Distinguish between *Prosopis pallida* and *P. juliflora* (Based on Observations Made in Hawai'i 2008–2009)

Distinguishing Character	*Prosopis pallida*	*Prosopis juliflora*
Growth form	Single stemmed or branching above ground level	Branching at or just above ground level
Thorn length	0–14 mm (reported up to 60 mm)	11–41 mm (reported up to 75 mm)
Pod color	Yellow	Brown
Leaflets per rachis	9–13	10–14
Leaflet length	4–10 mm	8–23 mm
Leaflet width	1.0–3.5 mm	2–6 mm
Leaflet spacing	2.5–4.0 mm	5.0–9.0 mm
Pigmentation at pinnae joints and nectaries	Red pigmentation frequent	Pigmentation absent
Number of pinnae pairs per leaf	2–5	1–3
Pinnae length	13–57 mm	41–113 mm
Ratio of outermost pinnae length to innermost pinnae length	1.17–3.00 (outermost pinnae longer than innermost pinnae)	0.68–1.14 (outermost pinnae slightly greater than, equal to, or less than innermost pinnae)

juliflora (Pasiecznik et al. 2001). In Hawai'i, both forms typically coexist within a population, although *Prosopis pallida* forma *pallida* was less common, comprising between 21% and 44% of individuals in three populations examined by Fosberg (1966).

Burkart (1976) described three varieties of *P. juliflora*. *Prosopis juliflora* var. *juliflora* is described as the typical variety. *Prosopis juliflora* var. *inermis*, found primarily in Guayaquil, Ecuador, is thornless and has pubescent rather than glabrous leaves. *Prosopis juliflora* var. *horrida* has thorns up to 75 mm long. *Prosopis juliflora* var. *inermis* and var. *horrida* are found in coastal Ecuador, and var. *juliflora* is found elsewhere within the native range of the species (Pasiecznik et al. 2001). Specimens in Hawai'i most closely match the description of *Prosopis juliflora* var. *juliflora* (T.G., pers. obs.).

ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACT

Detrimental

Prosopis spp., particularly thorn-bearing varieties, can be a nuisance to both people and cattle. Long-thorned individuals can pierce automobile and bicycle tires. The *Prosopis* inflorescences shed large amounts of pollen,

which has been cited as a major cause of hay fever (Simpson et al. 1977). In Niger, roots of *Prosopis* in the Lake Chad area impede waterways; similar problems have been reported in Yemen (Landeras et al. 2006). Introduced *Prosopis* spp. may reduce habitat for native species, and even within their native range a change in ecological constraints may allow *Prosopis* spp. to develop into monotypic stands such as with *P. glandulosa* in the southwestern United States (Weltzin et al. 1997). In Hawai'i, destruction of native plant populations in dry leeward areas can be mainly attributed to human activities including browsing and grazing by introduced ungulates such as goats and cattle along with repeated burning; the resulting extensive cover of *Prosopis* however may have limited or prevented the subsequent regeneration of native vegetation (Richmond and Mueller-Dombois 1972). Nakano et al. (2003) found that leachate from leaves of *P. juliflora* contains a number of allelopathic substances including L-tryptophan, syringin, and (−)-lariciresinol. A number of alkaloids that inhibit plant growth have also been isolated from extracts of *P. juliflora* leaves (Nakano et al. 2004). These substances may have negative effects on the germination or growth of other species that would otherwise establish under the shaded environments of *Prosopis* canopies.

Negative effects of *Prosopis* on local hydrology are also suspected. For example, the deep taproot system has been implicated in lowering groundwater tables in Hawai'i and elsewhere (Richmond and Mueller-Dombois 1972). On the island of Kaho'olawe, Stearns (1940) found that a decline in the groundwater level coincided with the spread of *P. pallida*. Zones (1961) speculated that *Prosopis* was a major factor in local water budgets and that transpiration from *Prosopis* was responsible for an observed daily rise and fall of the groundwater level on O'ahu. Such reports are anecdotal, and further work is needed to understand the effect that *Prosopis* spp. have on hydrology within different environments, particularly within different climate regimes (Pasiecznik et al. 2001).

In Australia, four *Prosopis* species, *P. pallida*, *P. juliflora*, *P. velutina*, and *P. glandulosa*, and their putative hybrids (*P. juliflora* × *P. velutina* Pedley, *P. glandulosa* × *P. velutina* Perry, *P. pallida* × *P. glandulosa* var. *torreyana*) are naturalized and considered highly invasive (van Klinken and Campbell 2001). Thorns of these species, reported to be up to 60 mm long in the case of *P. pallida*, are said to cause damage to animal hooves and vehicle tires. In addition, dense populations are believed to reduce habitat for native species and cause declines in grassland cover, thus reducing feed available to cattle and potentially contributing to erosion through loss of grass cover (van Klinken and Campbell 2001, Osmond 2003). These species grow in areas of Australia with rainfall between 150 and 1,200 mm, and average temperature between 10° and 25°C, typically north of 28° South latitude (van Klinken and Campbell 2001). *Prosopis* seeds are dispersed in Australia by a number of animals including cattle, horses, pigs, goats, sheep, emus, and kangaroos. Recruitment of seedlings is usually associated with high-rainfall events and flooding. This has resulted in widespread cohorts of same-aged individuals. It has been estimated that 70% of the Australian mainland is climatically suitable for *Prosopis* and that scattered infestations will continue to spread if control efforts under way are not successful (Osmond 2003).

Beneficial

Many studies refer to the positive effects of *Prosopis* on certain ecosystems; indeed the modern, widespread intentional introduction of *Prosopis* was prompted by reports of the ecological benefits that these species can provide. *Prosopis* spp. have been found to reduce soil pH in alkaline soils, reduce soil salinity and bulk density, as well as increase soil moisture-holding capacity, soil porosity, organic matter, total N, available P, and exchangeable K, Ca, and Mg (Singh 1995, Bhojvaid et al. 1996, Bhojvaid and Timmer 1998, Maliwal 1999, Andersson 2005). The ability of *Prosopis* to increase soil carbon may lead to substantial carbon sequestration in semiarid lands (Geesing et al. 2000). *Prosopis* litter fall provides a substantial input of organic matter to soils, and symbiotic relationships formed between *Prosopis* roots and nitrogen-fixing bacteria increase available nitrogen in the soil. Both *P. juliflora* and *P. pallida* form associations with mycorrhizal fungi and various strains of nitrogen-fixing bacteria (Sidhu and Behl 1997, Räsänen et al. 2001, Benata et al. 2008).

Prosopis roots may act as conduits for passive flow of water and dissolved nutrients between soil layers, resulting in increased water and nutrient availability to other species. The roots of *Prosopis* have been found to redistribute water from a deep water table to the subsurface during times of dry surface conditions (Nilsen et al. 1983). This natural process may allow subsurface water to be subject to near-surface evaporation, thus reducing overall soil moisture content; however this same process may also facilitate shallow-rooted species or allow for establishment of seedlings in the understory by increasing near-surface moisture and the availability of nutrients such as phosphorus (Geesing et al. 2000, Hultine et al. 2004, Zou et al. 2005). Hydraulic redistribution from the lateral to the deep root system may also potentially make near-surface nutrients and water available to deep taproots (Hultine et al. 2004).

Prosopis stands have also been characterized as having a positive effect on plant and animal diversity in some ecosystems (Mares et al.

Figure 4. Economic uses of *Prosopis*. *Top left: Prosopis* charcoal sold commercially in Hawai'i; *top right: Prosopis pallida* honey production at Puakō, Hawai'i; *bottom left: Prosopis* honey in Peru; *bottom center: Prosopis* posts; *bottom right:* advertisements for Algaroba bean feed for horses and cattle ca. 1913–1920. Photos by Mark Merlin and Timothy Gallaher.

1977). Under some conditions, *Prosopis* has been found to facilitate establishment of other woody and herbaceous plant species. *Prosopis* provides a reliable food source for animals even during drought conditions. Clumps of *Prosopis* affect microclimate and soil properties; they also attract birds that release seeds, and burrowing animals that potentially improve soil conditions (Whittaker et al. 1979). The effect of the *Prosopis* overstory on the understory assemblage may be dependent upon specific environmental conditions; this could determine whether the advantages of an improved microsite outweigh the cost of competition between overstory and understory species (Belsky 1994). *Prosopis pallida* was considered to be the only

species able to colonize and persist on arid land grazed by cattle after the loss of native species in Hawai'i in the early 1900s.

Prosopis pallida and *P. juliflora* are economically valuable species due to their use as food, fuel, fodder, construction materials, weapons, tools, fiber, and medicine in the regions where they are native and occasionally where they have been introduced (Felger 1977) (Figure 4). The high utility of these species prompted their intentional introductions around the world. In addition, their ability to thrive in dry, saline, or otherwise degraded conditions has also motivated their use in ecosystem restoration and soil remediation. These ethnobotanical and ethnoecological uses may be considered as potential resource

applications for *Prosopis* in some of its cultivated and naturalized populations in Hawai'i or elsewhere.

Prosopis pods have been used as a food source by humans for thousands of years, with evidence from the Tehuacán valley in Mexico dating to about 6500 B.C. (Smith 1967 in Beresford-Jones 2004). Human coprolite analysis indicates that *Prosopis* made up a substantial portion of the prehistoric human diet in areas of Peru (Callen 1969). The pods of *Prosopis* contain 30%–75% carbohydrates, 11%–35% crude fiber, 7%–22% protein, 3%–6% ash, and 1%–6% fat (Pasiecznik et al. 2001). No toxic compounds have been isolated from *Prosopis* fruit tissue although toxic phytohemagglutinins, which are eliminated by cooking, are present in the seeds (Choge et al. 2007). Among many indigenous people of southwestern North America, mature pods were commonly eaten directly or toasted and pounded into flour (with seeds, exocarp, and endocarp removed). This product could be stored for long periods of time. Roasted or boiled *Prosopis* flowers were also eaten (Felger 1977). Both sweet and fermented beverages were made from various parts of the pod, sometimes mixed with the processed flour. Mesquite flour has also been used in more recent times to distill liquor.

In South America, human consumption of *Prosopis* seeds, including *P. pallida*, has had a long history. *Prosopis* wood and pods have been excavated from archaeological sites in Peru dating to about 2,500 years B.C. (Beresford-Jones 2004). As in North American cultures, *Prosopis* pods were eaten raw and processed into flour, bread, porridge, and sweet or fermented beverages by these people in South America (Havard 1884, Pasiecznik et al. 2001, Choge et al. 2007). Certain species, varieties, or individual trees were recognized as having particularly sweet pods and were preferred for human consumption, and bitter or astringent pods were used for animal feed. Many of these traditional products continue to be produced and in some cases sold commercially (Pasiecznik et al. 2001). To this day, *Prosopis* pods in some areas of South America such as Peru are boiled to make a concentrated sweet syrup called *algarrobina*, which is also used as an ingredient in the cocktail *pisco* sour (Felker 2005). In recent times, toasted pods were mixed with water to make a coffee substitute. There has been recent renewed interest in *Prosopis* pods as a source of food for human consumption and for other economic uses. Modern milling technology can produce a number of economic products from *Prosopis* pods (Saunders and Becker 1989). In trials, people in the Lake Chad area of Niger found that products made from 10% *Prosopis* mesocarp flour was as good as or preferable to traditional products made with millet, maize, or sorghum (Kaka 2001). Recent innovations include products such as bread, chips, and breakfast cereals. *Prosopis* flour is described as having a "cinnamon-mocha aroma and flavor" and is typically used at no more than 20% mixed with wheat flour due to its structural properties (Felker 2005); a sugar extract and alcohol can also be produced along with flour production. Endocarp hulls can be used as a low-quality cattle food or as fuel. Seed coat and endosperm can be used to produce galactomannan gum, a product used in pharmaceuticals, and as a food stabilizer and fat substitute (Stanton et al. 2001). Seed cotyledons, which are high in protein and fat, can be used to produce a protein concentrate (similar to soy protein). The high (13%–44%) sugar content of *Prosopis* pods has attracted attention for the use of *Prosopis* in the production of ethanol, particularly on lands where traditional crops are unsuited (Felker et al. 1982).

There are also many documented traditional nonfood uses of *Prosopis*. These include cordage made from *Prosopis* roots, twine from the inner bark, and cloth from softened bark (Felger 1977). *Prosopis* litter fall called *poño* is still used in Peru as a soil additive (Alzamora 1988 in Pasiecznik et al. 2001, Beresford-Jones 2004). Medicines used to treat various conditions were produced by Native Americans from various parts of *Prosopis* including leaves and gum, black pitch or flux, roots, and bark. Other uses derived from *Prosopis* include hair dye, face paints, dye from gum

and pitch, charcoal for tattooing, and tannins from the bark, wood, and fruit to prepare animal skins, particularly cattle hides (Felger 1977).

Prosopis wood is a high-quality fuel source, with a calorific value of approximately 4,200–4,800 kcal/kg for *P. juliflora* (Pasiecznik et al. 2001). Green or dried stems and even roots, which may be more extensive than aboveground parts, are also used for firewood or processed into charcoal (Havard 1884). *Prosopis* wood burns slowly and emits a great amount of heat without producing much smoke. *Prosopis* wood is the most desired for fuel source in Hawaiian earth ovens (*imu*) as well as in other cooking units such as barbeque grills and hibachi.

Prosopis wood is hard and has high dimensional stability and tensile strength and tends to be resistant to rot (Weldon 1986). *Prosopis* wood was used in the construction of housing, pilings, ships, and a number of household items, tools, and toys (Felger 1977, Pasiecznik et al. 2001). *Prosopis* timber continues to have a minor use in construction and furniture manufacture (Pasiecznik et al. 2001); for example, furniture made from native *Prosopis* was offered for sale in Mendoza, Argentina, in 2005 (M.M., pers. obs.), and there has been recent interest in producing *kiawe* furniture in Hawai‘i (Gordon 2008). *Prosopis* gum, which is produced by both *Prosopis* pods and bark, is of a sufficient quality to be used by industry as an emulsifier and thickener in the production of adhesives, pharmaceuticals, and processed food products (Pasiecznik et al. 2001).

Regulatory Aspects

Prosopis pallida appears on the United States federal noxious weed list along with 24 other taxa of *Prosopis* (U.S. Department of Agriculture 2006). *Prosopis pallida* is also listed as a noxious weed or prohibited for import into eight U.S. states. Although it does not appear on the U.S. federal list, *P. juliflora* is considered an invasive species and a noxious weed in Hawai‘i (State of Hawai‘i 2003).

In Australia, *Prosopis* was first considered to be a pest on grazing lands in the 1930s and in 1951 was declared a noxious weed in Western Australia. Currently in Australia, all species of *Prosopis* are considered to be noxious weeds and are listed as "weeds of national significance" (Lynes and Campbell 2000). The current goal of the national strategy in Australia is to confine and eradicate all populations of *Prosopis*, and all *Prosopis* species are currently prohibited from importation into Australia (Agriculture and Resource Management Council of Australia and New Zealand 2000). A manual for identifying and controlling *Prosopis* in Australia is available on the Internet at www.weeds.org.au/wons/mesquite (Osmond 2003).

GEOGRAPHIC DISTRIBUTION

Native populations of *P. pallida* extend from Peru to Ecuador and Colombia (Diaz Celis 1995, Pasiecznik et al. 2001). *Prosopis juliflora* has a wider native distribution including arid areas of Venezuela, Colombia, and Ecuador in South America, extending through Panama up into Mexico in Central America (Burkart 1976). In addition, *P. juliflora* is indigenous or has become naturalized prehistorically throughout the Caribbean and reportedly in the tropical Pacific in the Galápagos Islands where *P. pallida* may also be present as a native or introduced tree (Wiggins and Porter 1971, McMullen 1999). Some populations of *P. pallida* are threatened by deforestation in their native range (Pasiecznik et al. 2004). In Argentina, the natural coverage of *Prosopis* forests was reduced to between one-quarter and one-half of its original area between 1500 and 1975 (D'Antoni and Solbrig 1977, Beresford-Jones 2004).

Prosopis pallida and *P. juliflora* have been intentionally introduced throughout many arid areas of the tropics including approximately 50 countries worldwide. In the Indo-Pacific region, *P. pallida* has been identified from up to 12 island groups and has become naturalized in Australia (Perry 1998), as well as in the Philippines (Baguinon et al. 2005) and the main islands of Hawai‘i (Wagner et al. 1999) (Table 2). *Prosopis juliflora* has been identified from five island groups in the Pacific and four island groups in the Indian Ocean and from several countries in Asia. In

TABLE 2

Distribution of *Prosopis* spp. in the Indo-Pacific

Location	*Prosopis juliflora*	*Prosopis pallida*	Absent	No Info	Notes
Pacific and East Asia					
American Samoa			X		Presumed absent. Not listed by Space and Flynn (2000)
Australia	X	X			Both species are naturalized and invasive; however *P. juliflora* is restricted to a few localities. (Also present: *P. glandulosa, P. glandulosa × velutina,* and *P. velutina*) (Perry 1998)
Brunei	X (?)	X (?)			Particular species not mentioned (Pasiecznik et al. 2001)
Cambodia	X (?)	X (?)			Particular species not mentioned (Pasiecznik et al. 2001)
China	X (?)				*Prosopis* present but not common (Delin and Nielsen 2010)
Cook Islands			X		Presumed absent. Not listed by Space and Flynn (2002*b*)
Easter Island (Rapa Nui)			X		Presumed absent. Not listed by Meyer (2008)
Federated States of Micronesia			X		Presumed absent. Not listed by Fosberg et al. (1979)
Fiji		X (?)			*Prosopis* sp. (likely *P. pallida*) first collected in 1939 on Tovu Island, Viti Levu; introduced in 1918. Possibly only one plant or no longer present (Smith 1985)
French Polynesia					
Austral Islands				X	
Marquesas Islands		X			*Prosopis pallida* present in at least two locations on Ua Huka (Wagner and Lorence 2008); introduced from Hawai'i. Not reproducing in 1964. (Herbarium specimen [BISH 155529] collected by Decker no. 1908 in 1964)
Tuamotu Islands				X	
Society Islands	X (?)	X (?)			*Prosopis* spp. on Tahiti (Fosberg 1997, Florence et al. 2007)
Galápagos Islands	X	X (?)			Native. Individuals representing both *P. juliflora* and *P. pallida* may be present (Wiggins and Porter 1971)
Hawai'i	X	X			*Prosopis pallida* present on all the main islands and Midway Atoll (Wood and Legrande 2006). *Prosopis juliflora* found on Kaua'i, O'ahu, Moloka'i, and Lana'i
Indonesia	X				Cultivated in Java (Nielsen 1992)
Japan			X		Not listed by Ohwi (1965) or Walker (1976)
Johnston Atoll		X			"*Prosopis juliflora*" (likely *P. pallida*) rare in cultivation (BISH 155530) (Fosberg 1949). Only seeds were found in 1976 (Amerson and Shelton 1976)
Kiribati					
Gilbert Islands		X			One tree noted from Tarawa Atoll (Fosberg and Sachet 1987). Not seen in 2003 (Space and Imada 2004)
Phoenix Islands		X			One individual of *P. chilensis* (likely a misidentification of *P. pallida*) in cultivation on Canton Island in 1958 (Degener and Degener 1959)
Line Islands			X		Presumed absent. Not listed by St. John (1974), Wester (1985), or Clapp and Sibley (1971)

TABLE 2 (continued)

Location	*Prosopis juliflora*	*Prosopis pallida*	Absent	No Info	Notes
Mariana Islands (including Guam)		X			Present in Guam (Fosberg et al. 1979)
Marshall Islands (including Wake)			X		Presumed absent. Not listed by Fosberg et al. (1979), Fosberg (1988), or Vandervelde (2003)
Myanmar	X				Cultivated (U.S. National Herbarium 2003)
Nauru			X		Presumed absent. Not listed by Thaman et al. (1994)
New Caledonia		X			Not mentioned in Nielsen (1983). *Prosopis pallida* is present but not naturalized (Meyer et al. 2006)
New Zealand			X		Presumed absent. Not listed by Webb et al. (1988)
Niue			X		Presumed absent. Not listed by Space et al. (2004)
Palau			X		Presumed absent. Not listed by Space et al. (2003, 2009)
Papua New Guinea	X	X			Verdcourt (1979), Nielsen (1992)
Philippines	X				Collected 1902 (RBG Kew HerbCat database) (Royal Botanic Garden Kew 1999). *Prosopis vidaliana* (syn. of *P. juliflora*) forms dense thickets at the back of the beach at Manila Bay. Introduced from Mexico (Merrill 1923, University of the Philippines Science Education Center 1971, Nielsen 1992, Baguinon et al. 2005)
Pitcairn Islands			X		Presumed absent. Not listed by Kingston and Waldren (2003)
Samoa			X		Presumed absent. Not listed by Space and Flynn (2002*a*)
Solomon Islands				X	
Taiwan			X		Presumed absent. Not listed in Huang and Hiroyoshi (1993)
Thailand	X (?)	X (?)			Particular species not mentioned (Pasiecznik et al. 2001)
Tokelau			X		Not listed in Whistler (1987) or Whistler et al. (2008)
Tonga			X		Presumed absent. Not listed in Space and Flynn (2001)
Tuvalu				X	
Vanuatu				X	
Vietnam	X (?)				Burkart (1976)
Wallis and Futuna			X		Presumed absent. Not listed by Meyer (2007)
Indian Ocean					
Mascarene Islands	X				Invasive on Réunion Island (Kueffer et al. 2004)
Mauritius	X				In cultivation (Jean-Yves Meyer, 2009, pers. comm.)
Seychelles				X	
Madagascar	X				Cultivated and naturalized in southern Madagascar (DuPay et al. 2002, eFloras 2008)
Maldives				X	
Chagos Archipelago				X	
Sri Lanka	X				Spreading rapidly in the coastal belts of southern and western provinces (Weerawardane and Dissanayake 2005)

Hawai'i, *P. juliflora* was first identified from O'ahu in 1979 (Wagner et al. 1999). This species has subsequently been reported from Kaua'i (Imada et al. 2000), Moloka'i (Starr et al. 2005), and Lāna'i (Oppenheimer 2007). *Prosopis juliflora* × *P. pallida* hybrids can be found at several locations on O'ahu (T.G., pers. obs.).

HABITAT

Climatic Requirements and Limitations

Natural populations of *Prosopis* grow in areas with an annual rainfall between 250 and 1,250 mm (National Academy of Sciences 1983). Optimum temperatures for growth are within the range of 20°–30°C. *Prosopis juliflora* is able to survive in areas with daytime shade temperatures over 50°C and soil temperatures as high as 70°C. Temperature appears to be an important factor influencing germination. Seeds of *P. juliflora* achieve the highest levels and rates of germination at approximately 30°C, decreasing significantly at temperatures below 20°C and above 40°C (Solbrig and Cantino 1975, Teketay 1996). Most species of *Prosopis* are tolerant of frost, although this is not the case for *P. pallida* or *P. juliflora*, which are killed at temperatures at or below −6°C; however, mature individuals of *P. juliflora* are somewhat more tolerant of short periods of frost than those of *P. pallida* (Felker et al. 1984). *Prosopis* spp. are highly successful in arid environments and in areas with seasonal or periodic drought due to a number of drought-avoidance and drought-tolerance characteristics (Nilsen et al. 1983, Nilsen et al. 1984). However, water availability limits germination and successful establishment of seedlings (Mooney et al. 1977, Vilela and Ravetta 2001). López et al. (2005) found that recruitment of *P. pallida* in northwestern Peru was positively correlated with annual rainfall, with recruitment being nearly twice as high during ENSO (El Niño–Southern Oscillation) years than during non-ENSO years.

Habitat and Resource Requirements and Limitations

Modern invasions of *Prosopis* species have been facilitated by their intentional introduction and in most cases by cultivation. Their success in new habitats is likely highly influenced by climatic factors. Areas without arid or subarid habitats are unlikely to experience an invasion of these species. The subsequent naturalization and spread of *Prosopis juliflora* and *P. pallida* has been prompted by the pres-ence of adequate dispersal agents and by mechanical soil disturbance to scarify seeds within the seed bank.

Prosopis pods are dispersed by animals, streams, ocean currents, or overland water flow (Baes et al. 2001). Ingestion by animals or the abrasion of the pods against rocks and sand as they move through a stream or along a coast act to remove the seeds from the indehiscent pods and scarify the seed coat. If the seeds are not removed from the fruit by mechanical means, natural decomposition of the pod is necessary before germination can take place (Baes et al. 2001). Ingestion may also kill seed-eating insects (Pasiecznik et al. 2001); however, Solbrig and Cantino (1975) observed living bruchids on pods recently removed from goat excrement.

Modern dispersers of *Prosopis* include cattle, horses, goats, camels, deer, sheep, warthogs, feral pigs, and rodents (Lynes and Campbell 2000, Kneuper et al. 2003, Shiferaw et al. 2004). Some species, such as the kangaroo rat *Dipodomys merriami*, consume *Prosopis* pods and in the process destroy the seeds; however they may also cache pods, some of which are likely to be forgotten and may be in a position to germinate (Mares et al. 1977).

It is commonly reported that seeds of *Prosopis* spp. require mechanical, chemical, or thermal scarification to break seed dormancy (Baes et al. 2002, van Klinken et al. 2006). Shiferaw et al. (2004) reported germination rates for *P. juliflora* of 100% with mechanical scarification, 97%–99% germination with sulfuric acid, 37% after passage through goats, 47% through warthogs, 15% through camels, 4% through cattle, and 21% with no treatment. Solbrig and Cantino (1975) found less than 1% germination if the endocarp remained intact and 25%–55% germination for most species of *Prosopis* following scarification. However, in some cases, high levels of germination (>80%) have been observed in unscarified seeds (El-Keblawy and Al-Rawai 2005). Similar results were reported in Hawai'i by Judd (1920) for seeds presumed to be *P. pallida*. Newly harvested seeds, whose seed coats have not fully developed, may also exhibit high levels of germination without scarification (Ffolliot and Thames 1983).

FIGURE 5. *Prosopis pallida* growing from a crack in bare *pāhoehoe* lava, North Kona, Hawai'i.

Germination can occur in as little as 6 hr after exposure to moisture (Glendening and Paulsen 1955).

Prosopis spp. are capable of germination in a wide variety of soils including pure beach sand, soils with high levels of clay, stony substrates, and in debris that collects in cracks on bare lava (Morris 1899, Pasiecznik et al. 2001; M.M., pers. obs.) (Figure 5). Germination success is increased if seeds are buried under 1–2 cm of soil or other material such as dung (Havard 1884, Mooney et al. 1977). *Prosopis* spp. typically have a high level of seed dormancy and are generally believed to remain viable in the soil, particularly in dry conditions (Pasiecznik et al. 2001).

A map of the total potential extent, assuming no limitations to its spread, of *Prosopis* in Hawai'i was developed using spatial climate data including average monthly minimum and maximum temperatures and precipitation (Figure 6). Based on our observations of the extent and limit of *Prosopis* populations on the major islands of Hawai'i, optimal *Prosopis* habitat was defined as any area in Hawai'i with any substrate type found within the "Arid" and "Very Dry" moisture zones (Price et al. 2007) that in any month does not have an average temperature that reaches below freezing and achieves an average high temperature above 20°C in at least 1 month out of the year. The "Arid" zone in this model was defined by Price et al. (2007) as any area with a moisture availability index (MAI) below −689 and the "Very Dry" zone" as any area with a MAI value between −389 and −689. MAI is calculated by subtracting potential evapotranspiration for an area from its median annual precipitation. These criteria identified 341,800 ha of optimal *Prosopis* habitat on the main Hawaiian Islands.

Marginal *Prosopis* habitat includes any areas in the "Moderately Dry" moisture zones (MAI between 0 and −389) restricted to the same average monthly temperature criteria as
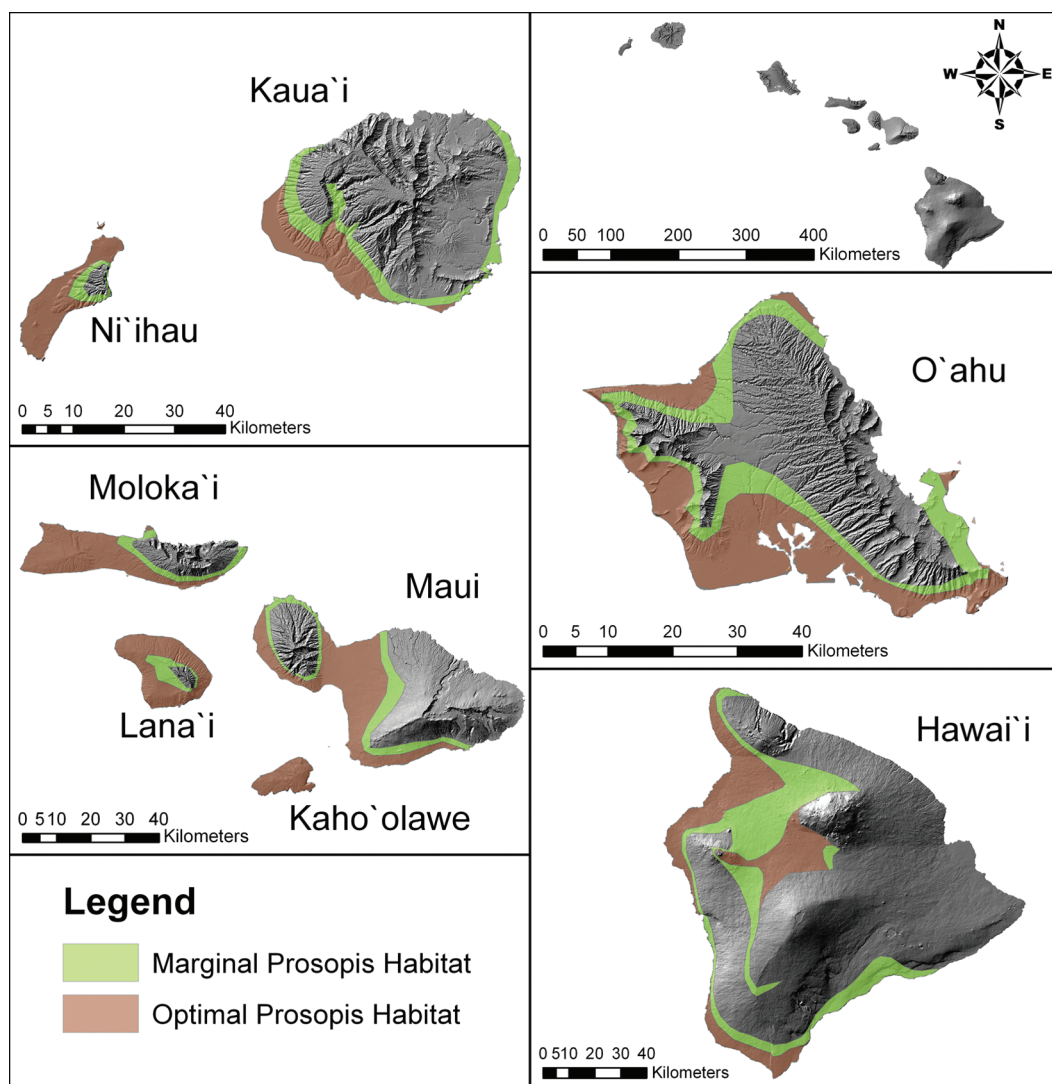
FIGURE 6. Map of the potential *Prosopis* distribution in Hawai'i. Optimal *Prosopis* habitat includes any area found within the "Arid" and "Very Dry" moisture zones (Price et al. 2007) and in any month does not have an average temperature that reaches below freezing and achieves an average high temperature above 20°C in at least 1 month out of the year. Marginal *Prosopis* habitat includes any areas in the "Moderately Dry" moisture zones restricted to the same average monthly temperature criteria. Data included in this model include combined minimum and maximum average monthly temperature data for 1971–2000 from the PRISM climate group, Oregon State University (Daly and Halbleib 2006), and moisture zone data from Price et al. (2007). The base map is a digital elevation model derived from U.S. Geological Survey 7.5′ quads. Projection NAD83 UTM Zone 4.

in the "Arid" and "Very Dry" zones. Marginal *Prosopis* habitat includes areas within the physiological tolerances of the species; however, in these areas it is expected that other species will outcompete *Prosopis* in most cases. The criteria for marginal *Prosopis* habitat identified 152,000 ha. Together the optimal and marginal potential *Prosopis* habitat comprises 34% of the total land area of the main Hawaiian Islands.

Ecosystem and Community Types Invaded

Recruitment of *Prosopis* is often associated with disturbed and, in particular, heavily grazed lands. *Prosopis* spp. have commonly invaded grasslands and pastures where cattle have been grazed. Native and feral animals also disperse *Prosopis* seeds, carrying them into nonpasture areas. *Prosopis juliflora* and *P. pallida* are well adapted to hot, dry ecosystems, and both of these species are capable of colonizing saline and alkaline soil environments, including coastal environments. Due to coastal drift dispersal, both species are part of the leeward coastal strand community in Hawai'i, and ocean drift spread between islands is suspected (Figure 7).

HISTORY

The first *Prosopis* tree (*P. pallida*) in the insular Pacific region (note that *P. juliflora* is considered by some to be native to the Galápagos Islands [Wiggins and Porter 1971]) was reportedly planted from seed in 1828 in Hawai'i on the island of O'ahu by Father Alexis Bachelot (1796–1837), a French Catholic priest charged with establishing the first Catholic mission in Hawai'i (Wilcox 1910, Birkett 2007). Father Bachelot arrived on the French ship *Comete* in July 1827. Soon after, he organized the construction of a chapel in downtown Honolulu, where he planted the tree. The seed or seeds reportedly originated from a tree planted at the Jardin du Roi in Paris (Wilcox 1910, Judd 1916, Tabrah 1984) however the *Comete* also made stops in Lima and Arequipa Peru before arriving in Hawai'i and these may be more likely sources of the seed(s). In 1832, the first *Prosopis* tree in Honolulu began producing fruit, and subsequently the species quickly spread to other parts of leeward O'ahu (Wilcox 1910, Degener 1933, Skolmen 1997).

By the 1890s, *P. pallida* was widely recognized for its use as cattle feed and fuel wood in Hawai'i. Pods of this species were commonly combined with other fodder to improve the nutritional value of cattle feed (Krauss 1905). *Kiawe* was observed to take over marginal and unproductive lands, even colonizing bare *pāhoehoe* lava, and consequently was referred to as "a blessing of the wastes" (Morris 1899). During the latter part of the nineteenth century and early twentieth century, large commercial operations planted substantial areas of *kiawe* in Hawai'i because of its considerable commercial value (*The Hawaiian Commercial and Sugar Company v. The Waikapu Sugar Company* 1894, Judd 1918).

During that period, *kiawe* spread rapidly throughout the dry leeward lowland areas of O'ahu and the other main islands of Hawai'i, in some cases reaching a reported elevation of 600 to 700 m in the drier uplands of the leeward areas (Dillingham 1904, Hosmer 1904, Tempsky 1904). The spread of *kiawe* was directly linked to its use as feed for the growing cattle industry in Hawai'i. It was recognized early on that germination of *kiawe* may be aided by consumption of the pods by goats or cattle (Hall 1904). In at least one reported case, planting of *kiawe* in Hawai'i was repeatedly unsuccessful until mules fed with *kiawe* pods were turned loose on the land (Judd 1907).

By 1904, the first *P. pallida* tree in Hawai'i, planted 76 years earlier by Father Bachelot in downtown Honolulu, was over 0.5 m in diameter and over 15 m tall. By that time, *kiawe* forest was described as the dominant forest type in dry and lowland areas of the south and west coasts of O'ahu, with an extent estimated at 8,000 ha and another 12,000 ha on the other islands of Hawai'i (Hall 1904, Zon 1910). Populations of the tree were described as growing tall, straight, and dense. Cords of wood (1 cord = 128 cubic feet) for fuel were sold for $9–10 apiece in Honolulu. The wood was also a primary source for fence posts; it was said to last 15–20 years in the ground without rotting (Philipp 1961). *Prosopis pallida* reportedly becomes quickly established in pastures and even in suburban lots. "Within three or four years from the time of cutting the trees again take complete possession of the ground and attain a height of 20 to 25 feet" (Hall 1904:10).

The flowers of *P. pallida* were the most important source of nectar for honey production in Hawai'i during the late nineteenth and early twentieth centuries. By 1906, the Hawai'i honey industry was worth $100,000

FIGURE 7. *Prosopis juliflora* recently established along the coast at Sand Island, O'ahu. Coastal drift dispersal is suspected as a main mechanism for the spread of this species in Hawai'i.

TABLE 3

Introductions of *Prosopis pallida* from Hawai'i to Various Locations Worldwide

Country	Year of Introduction	Source
Australia	1880	Judd (1907), Panetta and Carstairs (1989)
Bahrain	1920–1930	Anon (1931)
China	1915	Judd (1915)
Cuba	Before 1933	Degener (1933)
Fiji	Before 1933	Degener (1933)
Kenya	1973	Choge et al. (2007)
Marquesas	Before 1964	Wagner and Lorence (2008)
South Africa	1897–1916	Zimmermann (1991)

(Hosmer 1907*a*). Honeybees were introduced into Hawai'i in 1857, and within a short time 200 tons of *kiawe* honey were being exported from Hawai'i each year (Little and Skolmen 1989). That number reached an estimated 600 tons in 1907 and 1,000 tons in 1908 (Van Dine 1909*a*, Wilcox 1916).

By 1910, the Hawai'i Agricultural Experiment Station had developed a process to grind the hard-coated *Prosopis* seeds to help make the protein content of the seeds more available to ruminant animals and thus improve the nutritional content of cattle feed. This resulted in a profitable $400,000 annual industry by 1916 (MacCaughey 1916, Wilcox 1916). Collecting *P. pallida* pods became an economic activity involving the general public. It was noted that the pods began to drop just as school vacation was starting. This facilitated the recruitment of schoolchildren and others in the gathering of *kiawe* pods (Boyce 1914). Two companies in Honolulu purchased *P. pallida* pods for $10 a ton (Wilcox 1916), and the resulting "ground *algarroba* bean meal" was sold for approximately $25 a ton (Smith 1919). Approximately 500,000 bags of pods were collected annually and stored as food for cattle and horses (Wilcox 1910). In addition to cattle feed, the *P. pallida* pods were ground, roasted, and caramelized, and the product was briefly marketed as a coffee substitute (Wilcox 1916).

By 1916, an estimated 32,000 ha in Hawai'i were covered in *P. pallida* (Judd 1917). All the major islands of Hawai'i had leeward belts of *P. pallida* forest running from near the shore to 250–300 m elevation (Wilcox

1910). One acre (0.4 ha) of *P. pallida* forest in 1919 was estimated to yield 2 to 10 tons of beans and 1 ton of wood per year (Smith 1919). A mature tree reportedly produced up to 91 kg of pods annually (Degener 1933). One exceptional tree reportedly produced 226 kg of pods in a single season; and the productivity of *P. pallida* earned it international distinction as one of the "king crops of the world" (Smith 1929). The superintendant of forestry for the Territory of Hawai'i claimed that "no introduced tree has been of greater benefit to the islands than the *algarroba*" (Judd 1916:330).

Between the end of the nineteenth century and the first decades of the twentieth century, numerous varieties and species of *Prosopis*, including *P. pubescens* and *P. glandulosa*, which have not naturalized in Hawai'i, were purposefully introduced by the Hawai'i Agricultural Experiment Station and others for the purpose of improving feedstock (Hosmer 1904, Van Dine 1909*b*, Carpenter 1919). Seeds produced in Hawai'i were also used for the introduction of *Prosopis*, especially *P. pallida*, to other parts of the world (see Table 3). The use of *P. pallida* pods as fodder for U. S. Cavalry horses deployed to parts of Asia from Honolulu may also have played a role in its spread (Smith 1929).

The early 1900s also saw an increase in the number of pests of *Prosopis* found in Hawai'i, including a scale insect, a moth, and a number of seed-eating and wood-boring beetles (Van Dine 1909*b*, Fullaway 1912, Carpenter 1919, Delobel et al. 2003). The most destructive of these pests were seed-eating bruchid beetles.

According to Swezey (1926, 1928), the parasitoids *Heterospilus prosopidis, Urosigalphus bruchi, Glyptocolastes bruchivorus* (Hymenoptera: Braconidae), *Lariophagus texanus* (Hymenoptera: Pteromalidea), and *Horismenus* sp. (Hymenoptera: Eulophidae) and the egg parasite *Uscana semifumipennis* (Hymenoptera: Trichogrammatidae) were introduced to Hawai'i between 1910 and 1921 to combat four species of bruchid beetles (Coleoptera, Chrysomelidae, subfamily Bruchinae) including *Algarobius bottimeri, Caryedon serratus, Mimosestes nubigens*, and *Mimosestes amicus*, which had been unintentionally introduced to Hawai'i between 1908 and 1923. By the late 1920s, Swezey (1928:675) indicated that Prosopis pods in Hawai'i were "mostly free from serious injury."

Anacamptodes fragilaria (Geometridae), the "*kiawe* moth," was first collected in Hawai'i in 1944 and was reported to defoliate *P. pallida*. A larval parasite of this moth species, *Apanteles praesens* (Hymenoptera: Braconidae), was introduced in 1946. Although the introduced parasite apparently did not become established, two predatory wasps, *Eumenes latreillei petiolaris* and *E. pyriformis philippinensis* (Hymenoptera: Vespidae), that were probably accidental introductions to Hawai'i were found to control populations of *A. fragilaria* in the Islands (Pemberton 1964). Before 1953, the moth *Ithome concolorella* (Cosmopterigidae), also known as the "*kiawe* flower moth," was accidentally introduced to Hawai'i and resulted in substantial declines in honey production (Namba 1956). In 1965, *Agathis cincta* (Braconidae), a parasitoid wasp, was introduced as a biological control for *I. concolorella* (Funasaki et al. 1988). The monkeypod-*kiawe* caterpillar or cutworm, *Melipotis indomita* (Noctuidae), which is known to cause defoliation of *Prosopis* spp. in the south-western United States, was first collected in Hawai'i in 1969 (Oda and Mau 1974, Cuda et al. 1990); in response, a species of *Eucelatoria* (Diptera, Tachinidae) was released in 1974 as a biocontrol for this alien caterpillar (Funasaki et al. 1988). Another bruchid, *Mimosestes insularis* has been more recently reported from Hawaii (Kingsolver and Johnson 1978).

During the second half of the nineteenth and early part of the twentieth centuries, the value of *Prosopis* trees in land remediation was recognized; as a result, recommendations were made for reforestation projects using *P. pallida* on lowland areas denuded of native vegetation (Hosmer 1907*a,b*). *Prosopis pallida* was also used for attempted reforestation of Kaho'olawe Island (Hosmer 1904), where it is currently a dominant woody species along with *Leucaena leucocephala* (M.M., pers. obs.).

On 23 October 1919, the 91-yr-old *Prosopis* tree planted by Father Bachelot, which by then had a diameter at breast height of nearly 1 m, was removed to make way for improvements at the church property (Thurm 1919). Upon the occasion, an obituary was recorded that attests to the importance of *P. pallida* during that time in Hawai'i's history: "Perhaps no other tree in the world has had such a remarkable history or has been responsible for greater benefits than this original *algarroba* from which there have been established on the shores throughout these islands forests which cover approximately 90,000 acres now producing an annual crop of about 30,000 cores of excellent fuel, over \$100,000 worth of honey and an enormous yield of beans which furnish a valuable fattening food for stock at a time when the long dry summer has exhausted the grass supply" (Judd 1919:309).

On the other hand, the reputation of *Prosopis* was not always held in high regard. With the decline of cattle on O'ahu in the 1920s, the spread of *P. pallida* was reduced. Further reductions of cattle ranching eventually followed on the other islands. On Moloka'i, pods of *P. pallida* were blamed for a nerve disease responsible for cattle deaths, and this species was believed to be encroaching upon more valuable feedstock (Carlson 1952). In addition, it had been reported that *Prosopis* pods gave an undesirable flavor to milk when fed to dairy cows (Havard 1884, Wilcox 1910). Cattle operations began to clear *Prosopis* and plant grass instead (Carlson 1952). Moreover, rising incomes in Hawai'i made collection and processing of *Prosopis* pods economically unfeasible (Smith 1950, Esbenshade 1981), and increasing human popula-

tions necessitated clearing of large areas of *Prosopis* for houses and development, particularly in leeward Oʻahu, an area formerly dominated by a large contiguous band of *kiawe* forests.

Today, the remnants of over 12,000 ha of *P. pallida* forest outline the developments and suburbs of leeward Oʻahu. Large stands of *P. pallida* remain on all the main islands of Hawaiʻi, particularly on Hawaiʻi Island, Molokaʻi, and Niʻihau, where cattle ranching persists and where development is limited. The Hawaiʻi GAP Analysis Program, using Thematic Mapper satellite data from 1999 to 2004, estimated the total area of "kiawe forest and scrubland" in Hawaiʻi at 58,766 ha or 3.55% of the total land area of the state (Gon et al. 2006). This figure, which also includes lands dominated by *Leucaena leucocephala*, is similar to the 60,702 ha of *Prosopis* in Hawaiʻi estimated by Nelson (1967).

Few people in Hawaiʻi today are aware of the important role that *P. pallida* has played in the history of Hawaiʻi. Most know the plant by its nuisance thorns or by its use in the production of charcoal, honey, and fuel wood for *imu* (underground earth ovens), which continue to be important economic resources associated with the species.

Prosopis juliflora is a more recent introduction to Hawaiʻi than *P. pallida*, with the first specimen recorded on Oʻahu in 1978 (Wagner et al. 1999). *Prosopis juliflora* is generally much less valued in Hawaiʻi because of its shrubby form and is considered a noxious weed due to its long thorns. *Prosopis juliflora* is currently spreading throughout coastal areas of Oʻahu and Kauaʻi, and small populations have been subject to control efforts on Molokaʻi, Kauaʻi, and Lānaʻi. This species appears to be more productive than *P. pallida* near coastal areas, possibly due to a higher tolerance for saline ocean spray. Its high productivity in close proximity to the coast may allow *P. juliflora* to utilize coastal waterways more often for dispersal.

As early as the 1870s, *Prosopis* was being promoted for introduction to Australia (Mueller 1871). *Prosopis pallida* was the first of four species of *Prosopis* to be introduced (van Klinken and Campbell 2001). A single *P. pal-*

lida tree was planted in the Brisbane Botanical Garden in the 1880s, possibly from seeds imported from Hawaiʻi. Widespread populations of *P. pallida* in Western Australia and Queensland today likely also originated from material sent from Hawaiʻi (Panetta and Carstairs 1989).

Prosopis pallida is widely distributed throughout northern Australia and northwestern Queensland. At its greatest extent *P. pallida* covered over 47,000 ha in northern Australia and 500,000 ha of grazing land in northwestern Queensland; however, control efforts have likely reduced the extent of these invasions (Campbell and Setter 2002). *Prosopis velutina* and *P. glandulosa* var. *torreyana* are found in southeastern Australia, with 4,000 ha of dense infestation and 8,000 ha of scattered infestation, although control measures have likely also reduced the distribution of these species (van Klinken and Campbell 2001). *Prosopis glandulosa* var. *glandulosa* is scattered in New South Wales and southeastern Queensland. *Prosopis juliflora* has been identified from two locations, Geraldton in Western Australia and Cape Pallarenda in Townsville where it has likely been eradicated. Populations consisting of *Prosopis* hybrids occur in central-north Queensland and the Pilbara region of Western Australia. These hybrids are typically sympatric with *P. pallida* (van Klinken and Campbell 2001). Most infestations consist of isolated trees and clumps; however dense stands up to 30,000 ha have been reported at Mardie Station in Pilbara (Osmond et al. 2003*a*).

PHYSIOLOGY

The roots of some *Prosopis* species are adapted to low-moisture environments and can absorb water held in the soil at high matric forces that are unavailable to most other species (Haas and Dodd 1972, Nilsen et al. 1983). After germination, taproots grow quickly, reaching a depth of up to 40 cm in 8 weeks (Pasiecznik et al. 2001). In some cases, survival during long periods of drought is dependent upon root position relative to underground water tables. Once the roots of *Prosopis* have reached a ground-

water supply, the tree will maintain its leaves and even flower and fruit during extended drought. The lateral root system is capable of utilizing near-surface water from discreet and often brief precipitation events. Low stem and root resistance to water flow allows water to be redistributed efficiently between the aboveground portions of the plant and both root systems (Nilsen et al. 1983). Some *Prosopis* spp. are able to tolerate water stress through osmotic adjustments that maintain turgor pressure, allowing stomata to remain open until reaching very low leaf-water potentials. Stomata respond to high vapor pressure deficits by closing stomata, which stops transpiration and photosynthesis (Elfadl and Luukkanen 2006). The small leaflets of *Prosopis* allow the leaves to cool more rapidly once transpiration has stopped. Response by the pulvinus to water deficit can cause the leaflets to fold, reducing exposed leaf area and protecting stomata on the upper leaf surfaces from water loss (Pasiecznik et al. 2001). Adaptive features of *Prosopis* leaflets include their sunken stomata, with more located on adaxial than on abaxial surfaces, a thick and waxy cuticle, and the presence of mucilaginous cells that store water (Vilela and Palacios 1997).

Prosopis pallida and *P. juliflora* are highly tolerant of salinity, as are many members of the genus. In one study, total germination was the same among *P. juliflora* seeds soaked in tap water or in 10%, 20%, or 30% diluted seawater solution. In the same study, the height of 65-day-old seedlings irrigated with up to 30% seawater plus added nutrients was statistically similar although a declining trend was observed and seedlings irrigated with 20% and 30% seawater solution had significantly fewer leaves (Khan et al. 1987). Another study found that germination of *P. juliflora* seeds was consistently high at NaCl concentrations between 0 and 400 mM at a temperature of between 15° and 25°C (El-Keblawy and Al-Rawai 2005). *Prosopis pallida* showed no decrease in growth during a salinity tolerance study on rooted cuttings consisting of 18,000 mg/liter NaCl. The cuttings in that study continued to grow, although at a reduced rate, at 36,000 mg/liter NaCl, the

equivalent of seawater (Felker et al. 1981). In an assessment of 31 tree species irrigated with saline water (electrical conductivity 8.5–10 dS/m), *P. juliflora* performed well in terms of survivorship (94% after 8 yr), gain in height (>1 m/yr), rate of biomass increase, improvement of soil organic carbon, and water use efficiency (37 kg/cm) (Tomar et al. 2003). *Prosopis pallida* appears to be somewhat less tolerant of persistent saltwater spray than *P. juliflora*. On Oʻahu, it has been observed that in areas where exposure to salt spray or salt-laden ocean breeze is high, individuals of *P. pallida* often appear stunted and defoliated with little to no flowering or fruiting relative to nearby, apparently healthy and reproductive *P. juliflora* (T.G., pers. obs.).

REPRODUCTION

Natural reproduction in *Prosopis* occurs primarily through seeds. Treated stem cuttings will develop roots although results are variable (Lima 1988*b*). Natural vegetative reproduction through root suckers is rare for *P. pallida* but has been reported to occur in about 5% of individuals of *P. juliflora* (Goel and Behl 1992). Fallen main stems of *P. pallida* that maintain connectivity with the root system will occasionally produce adventitious roots along points of contact with the ground and send up multiple new erect shoots along the length of the stem (T.G., pers. obs.).

Prosopis will typically begin flowering 2–5 yr after germination (Lima 1988*a*, Pasiecznik et al. 2001). In a few documented cases, flowering has been observed in individuals 3–5 months old (Pasiecznik et al. 2006). When conditions are optimal, *Prosopis* may flower year-round, although two seasons of abundant flowering are typically observed. In Hawaiʻi, two flowering seasons, January through March and September through October, have been reported for *P. pallida* (Skolmen 1997).

Flowers within a *Prosopis* inflorescence mature in clusters over the course of a few days, and the pollen they produce reflects ultraviolet light and is highly visible to insects (Simpson et al. 1977). The flowers also exude a sweet odor, and the anthers produce a protein-carbohydrate exudate upon which

insects feed (Chaudry and Vijayaraghavan 1992). Major floral visitors include species of Diptera, Coleoptera, Lepidoptera, and Hymenoptera (Simpson et al. 1977).

Genise et al. (1990) found that nectar is not present before anther dehiscence and the stigmatic surface is dry, indicating that the flowers are not protogynous as suggested by other workers (Burkart 1976, Hunziker et al. 1986, Goel and Behl 1995). Goel and Behl (1996) found *P. juliflora* pollen viability to be between 79% and 96%.

Solbrig and Cantino (1975) found that only approximately seven out of 10,000 flowers in *P. flexuosa* and one in 10,000 flowers of *P. chilensis* developed into mature fruit. Simpson et al. (1977) found that an average of two fruit develop per inflorescence although up to 30 fruit (species not given) have been observed from a single inflorescence. This low fruiting efficiency may be a result of pollen limitation, sterile flowers, or fruit abortion. Flowers that develop fruit typically have between 50% and 100% of their ovules develop into seed, and between 7.1% and 24.9% of seeds collected from mature pods of 15 American species were underdeveloped (Solbrig and Cantino 1975).

It was initially believed that all *Prosopis* species were obligate outcrossers; however individuals of some species are partially self-compatible (Alban et al. 2002). According to Bessega et al. (2006), selfing occurs in some species of *Prosopis*, with rates as high as 29% observed in *P. alba*. Limited self-compatibility, approximately 4%, has been observed in *P. juliflora* after bagging and hand pollination (Sareen and Yadav 1987). Hoc et al. (1994) suggested that these species exhibit a gametophytic self-incompatibility system.

POPULATION DYNAMICS

Mature individuals of *Prosopis* have very low mortality rates. A recent study in Australia reported adult and postseedling juvenile mortality rates of less than 2% per year, even during periods of very low (<220 mm) annual rainfall (van Klinken et al. 2006). Individuals may live for up to 150 yr or more.

A very old individual of *P. pallida* near the town of Palpa in Peru known locally as "*el huarango milenario*" has a trunk diameter of 4.6 m and is estimated to be over 1,000 yr old based on a ring count from a damaged main stem (Beresford-Jones 2004).

A mature *Prosopis* tree can produce 20–100 kg of pods per year (Pasiecznik et al. 2004). This results in an estimated 19,000 to 142,000 seeds per year from a mature plant (Solbrig and Cantino 1975, Kingsolver et al. 1977). Fruit and seed production may be lower in dense stands (van Klinken et al. 2006). *Prosopis juliflora* typically produces many more fruit per individual than *P. pallida* (Lima 1988a; T.G., pers. obs.). Shiferaw et al. (2004) found an average seed density of *P. juliflora* within the soil seed bank of 1,932 seeds/m² (307 SE) in Ethiopia and speculated that some seeds may be capable of germination immediately whereas others are more likely to remain dormant after maturity. Van Klinken and White (2009) found less than 40 seeds/m² in the soil under *Prosopis* canopies in Australia.

Successful germination of seeds is dependent upon a number of interrelated factors. Within its native range fruit maturation of *Prosopis* has been observed to occur during the rainy season when soil moisture will provide the highest chance of germination and seedling success (Mooney et al. 1977). *Prosopis* seeds can remain dormant in the soil for many years, particularly in arid conditions, until conditions are right for germination (van Klinken and Campbell 2001). In some cases, *Prosopis* seedlings fail to establish under a *Prosopis* canopy, possibly due to shading, lack of scarification, or higher predation rates by seed-eating insects (Mooney et al. 1977, Bush and Van Auken 1990, Pasiecznik et al. 2001). In Australia, however, van Klinken et al. (2006) found that seedlings and juveniles of *P. pallida* were more abundant under dense canopies, but these were observed to be in a quiescent stage with no evidence of recent growth. In the United Arab Emirates, El-Keblawy and Al-Rawai (2007) also found higher density of *P. juliflora* seedlings under, rather than away from, the canopy of mature individuals. Autoallelopathy has been pro-

posed as a mechanism reducing germination and seedling success under the parent canopy of *Prosopis*. Chemical extracts from both pod pericarps and mature leaves were found to decrease total germination and seedling growth in *P. juliflora* (Warrag 1994, 1995). Vilela and Ravetta (2001) found that successful germination of five species of *Prosopis* was significantly higher in commercial soil media than in soil taken from below the canopy of *P. velutina*, or in that same soil with added fertilizer (NPK 14:14:14), although the mechanism limiting seedling development was not investigated.

In Australia a hybrid swarm of *Prosopis* covering 150,000 ha was observed to be much denser than observed in native *Prosopis* populations, resulting in the exclusion of the herbaceous layer or the establishment of other species in the understory. El-Keblawy and Al-Rawai (2007) found that understory species richness, evenness, and density were greater outside compared with under the canopy of *P. juliflora* in the United Arab Emirates. Further, they found that dense stands of *P. juliflora* reduced understory species richness, evenness, and density both below the canopy and outside the canopy. Hughes et al. (2006) found that in North-central Texas, understory herbaceous biomass increased with *Prosopis glandulosa* biomass in shallow clays, but an inverse relationship was observed on clay loam soil, indicating that soil type or perhaps broader environmental factors may influence the relationship between *Prosopis* spp. and the establishment of understory plant species. In the Sonoran Desert, Schade et al. (2003) found that herbaceous biomass was significantly higher under canopies of *Prosopis velutina* than in open patches. According to those authors, this was likely due to increased soil moisture under *Prosopis* canopies.

Some have observed that seedlings of *Prosopis* spp. do not compete well against grasses or other woody trees and shrubs (Egler 1947, van Auken 2000, Vilela and Ravetta 2001); however, Brown and Archer (1999) found that experimental density reduction of grass had little effect on the emergence or subsequent growth of *P. glandulosa* seedlings.

RESPONSE TO MANAGEMENT

Methods for *Prosopis* control include mechanical removal, herbicidal application, fire, biological controls, and restriction of dispersal. Control methods have been employed in Hawai'i, Australia, South Africa, and elsewhere with various degrees of success. Extensive and intensive harvesting of *Prosopis* has more recently been suggested as a way to control population sizes. A combination of control methods will most likely result in the greatest chance of achieving population management goals (Pasiecznik et al. 2001).

The most successful mechanical methods of eradication require cutting the stem or root at least 10–20 cm below ground to remove dormant buds (Osmond et al. 2003*a*, Shiferaw et al. 2004, van Klinken et al. 2006). Some mechanical techniques that have been employed successfully in Australia include blade plowing, chain pulling, bulldozing, and stick raking. These treatments vary in cost and effectiveness depending upon the density of the population and tree form. Up to 95% mortality has been achieved with these methods (Osmond et al. 2003*b*).

Blade plowing, which consists of a blade plow attached to a tractor or bulldozer, cuts the stem below ground level, preventing or at least reducing coppice regrowth. This method has been most successful with shrubby forms, but large single-stemmed tree forms may damage equipment. Chain pulling requires the use of two bulldozers that pull a chain near ground level. This method is used to pull down dense infestations of trees and requires follow up with control by burning to induce mortality of the root stock. Bulldozers may also be directly used to push over individual trees at or slightly below ground level. The stick-raking method uses cutter bars attached to a bulldozer; these cut stems below ground level (Osmond et al. 2003*b*). After mechanical control of mature individuals, seedlings may be controlled through fire or the use of a foliar herbicide such as triclopyr or picloram (Osmond et al. 2003*b*, Geesing et al. 2004, van Klinken et al. 2006).

Foliar application of herbicides (triclopyr plus picloram [salt] in water) in Australia has

been used on individuals smaller than 1.5 m, achieving mortality rates greater than 90% (van Klinken and Campbell 2001, Osmond 2003). Basal bark application of a mix of these herbicides in diesel applied to the lower 30 cm of stem has resulted in mortality of up to 97% of individuals and is effective in all size classes (Osmond et al. 2003b, van Klinken et al. 2006). Basal bark and cut-stump application of triclopyr and picloram have also been employed in Australia. Although this method works well for isolated individuals, it is both cost- and time-prohibitive for dense stands (Osmond et al. 2003b).

At Volcanoes National Park on the island of Hawai'i, P. pallida was controlled through individually cutting mature stumps and applying 100% Roundup and 5% Garlon 4 in diesel fuel, with seedlings being uprooted manually. This treatment was partially effective in eradicating P. pallida (Tunison and Zimmer 1992). Motooka et al. (2003) reported that P. pallida saplings are sensitive to basal bark applications of 2,4-D and triclopyr at 2% in diesel or crop oil or triclopyr ester at 5% product in diesel oil, and that P. juliflora individuals under 1.5 m on Kaua'i were successfully killed by foliar drizzle application of triclopyr ester at 15% in crop oil.

Prosopis can also be controlled with fire. One study recorded up to 95% mortality of P. pallida for all size classes in a 2-yr field trial (Campbell and Setter 2002). Burning also reduces postfire recruitment through direct mortality of the seeds on or near the surface (Smith and Tunison 1992, Campbell and Setter 2002). McLaughlin and Bowers (1982) reported up to 50% mortality of P. juliflora after a particularly hot fire in the Sonoran Desert. Other Prosopis species are reportedly much more fire tolerant (van Klinken and Campbell 2001, Campbell and Setter 2002); however, for those individuals that survive, fire may result in death of the upper canopy, which may reduce or eliminate seed set for a number of years. The use of fire as a control agent may be cost-prohibitive in areas where fuel is scarce and may promote invasion by other fire-tolerant invasive species. In a study conducted in Hawai'i, fire resulted in a 20% recovery rate for Prosopis and led to increased

cover of grass, including Cenchrus ciliaris, and other more fire-tolerant, persistently invasive woody legumes such as Leucaena leucocephala (Smith and Tunison 1992). A fire in the dry coastal lowland at Puakō, Hawai'i, in 2007 destroyed a portion of an extensive P. pallida forest; however, that burned-over area has shown vigorous regeneration from the seed bank, likely facilitated by subsequent mechanical disturbance of the soil by bulldozers and other heavy equipment (Neil Logan, 2009, pers. comm.).

A number of insects have been used as biological controls for Prosopis. In Australia, a sap-sucking psyllid, Prosopidopsylla flava (Hemiptera: Psyllidae), was released in 1998; however this species failed to establish (van Klinken et al. 2009). A leaf-tying moth (Evippe sp. [Gelechiidae]) was also released in Australia in 1998. Heavy defoliation (up to 100%) resulting in lower growth rates and seed production due to the moth has been reported for P. pallida populations; however significant differences between sites and among species have been reported (van Klinken and White 2009). The effect of P. flava on Prosopis in Australia has not been reported (van Klinken et al. 2006). Another psyllid, Heteropsylla texana (Psyllidae), has been successfully tested for host specificity for three species of Prosopis in Australia; however this species has not yet been released (Donnelly 2002, van Klinken et al. 2009). Two bruchid beetles, Algarobius prosopis and A. bottimeri, were also introduced in 1996 and 1997 to Australia as a Prosopis biocontrol (van Klinken and White 2009). Only A. prosopis was observed emerging from pods in a recent study, suggesting that A. bottimeri may be either rare or extirpated in Australia (van Klinken and White 2009). These two bruchid species were released in South Africa between 1987 and 1990 to control invasive Prosopis populations in that country. Initial observations found that only A. prosopis had become established and that this species destroyed up to 92% of the seeds sampled (Zimmermann 1991). Another bruchid, Neltumius arizonensis, was released in South Africa in 1993 and 1994 and subsequently became established, although this species accounted for only a small

fraction of seed mortality compared with *A. prosopis* (Coetzer and Hoffmann 1997). *Algarobius prosopis* and *N. arizonensis* were introduced in 1997 to Ascension Island in the Atlantic Ocean to control dense populations of *P. juliflora* that had been introduced there in the 1970s or 1980s and that became established partly due to dispersal by feral donkeys. Observations indicate that *A. prosopis* has become widespread, but *N. arizonensis* failed to persist. The effect of these releases on *Prosopis* on Ascension has not been reported (Cheesman 2006).

Management of cattle and other potential seed dispersers may effectively control the spread of *Prosopis*. Fencing has been promoted to prevent seed dispersal by livestock or feral ungulates; however this may not stop small native and introduced animals from dispersing seeds (Lynes and Campbell 2000). The absence of effective seed dispersal agents in parts of Hawai'i now free of cattle and goats, together with the activity of seed and seedling predators, appears to have arrested the spread of *P. pallida*.

Recently, harvesting and use of *Prosopis*, particularly for fresh-cut fuel wood and charcoal as well as for nontimber products, has been advocated as a means to control invasive populations both in its native range and where it is introduced (Pasiecznik et al. 2001, Geesing et al. 2004, Logan 2007). Programs in Kenya, India, and elsewhere have promoted intensive use of the species as part of an overall control strategy (Berhanu and Tesfaye 2006, Choge et al. 2007). This alternative, however, may not be sufficient to arrest the spread of *Prosopis*, particularly when wild animals act as effective seed dispersers (van Klinken et al. 2006).

NATURAL ENEMIES

Over their total geographic range, *Prosopis* spp. are a resource for a wide variety of vertebrate and invertebrate herbivores including over 945 phytophagous insects (van Klinken et al. 2006). A number of species of Lepidoptera, Hemiptera, Heteroptera, Homoptera, and Orthoptera preferentially feed on flowers and leaves of *Prosopis*. For example, the leaf-tying moth *Evippe* sp. is responsible for large-scale defoliation of *Prosopis* in Australia, where it was introduced as a *Prosopis* biological control (van Klinken and Campbell 2001). Some species of beetles (Melyridae, Tenebrionidae, and Carabaeidae), Hemiptera, and larvae of Lepidoptera feed on flowers and immature *Prosopis* pods, resulting in aborted seeds and up to 30% loss of whole pods (Kingsolver et al. 1977, Simpson et al. 1977, Johnson 1983). Leaf-cutting ants may harvest entire inflorescences of *Prosopis* (Simpson et al. 1977), and ants have also been observed carrying and consuming segments of pods or seeds (Milesi and de Casanave 2004). Other insects that affect *Prosopis* spp. include thrips, which are known to attack inflorescences (Simpson et al. 1977), and a cerambycid borer that causes substantial mortality of *P. pallida* seedlings in North Queensland (van Klinken and Campbell 2001).

In the discussion here describing alien insect impact on *Prosopis* in Hawai'i, we noted that some of the most destructive pests of *Prosopis* are species of bruchid beetles that feed upon developing and mature seeds. Species from 10 genera of Bruchinae feed on *Prosopis* seeds, along with other species of Coleoptera, Diptera, Heteroptera, and Lepidoptera (Johnson 1983, Pasiecznik et al. 2001). Predation rates by seed predators can be high, with typically over 25% of seeds destroyed (Pasiecznik et al. 2001). Bruchids lay their eggs on mature or developing pods (Southgate 1979). Hatching larvae enter the pod and may feed first on the pod mesocarp before entering the seed to complete their maturation, consuming the embryo in the process (Bridwell 1920). Distinct endocarp segments between seeds act to discourage larvae from spreading between seeds during development; however some bruchids may consume multiple seeds before reaching maturity (Kingsolver et al. 1977).

Adult bruchids typically emerge after 4–6 weeks but may remain in the pod for up to 130 days (Bridwell 1919). Adults emerge through a large exit hole and may begin to deposit eggs soon after emergence. Bruchid adults may consume pollen and nectar from their host tree and will typically mate in

Prosopis inflorescences (Simpson et al. 1977, Southgate 1979). Between 1.5% and 24.2% of seeds are affected by bruchid beetle predation while pods are still on the tree. Newly emerged adults may continue to reinfect seeds in cases where the pods are being stored for human or animal use (Southgate 1979). Johnson (1983) noted that some bruchids such as *Algarobius prosopis* can lay numerous eggs many times per year resulting in three or more generations per year. Where bruchids are abundant, nearly all seeds left below the *Prosopis* canopy may be destroyed; for example, destruction of between 15% and 99% of seeds has been reported for fallen pods (Solbrig and Cantino 1975, Southgate 1979, Zimmermann 1991, Baes et al. 2001). Therefore, dispersal of pods away from parent populations can greatly improve seed survival (Solbrig and Cantino 1975, Mooney et al. 1977).

In some cases where bruchids are considered a pest, biocontrols have been used to reduce their populations. Hymenoptera and one family of Diptera include parasitoids of bruchid beetles; and high levels of bruchid mortality have been observed when parasitoids are present (Southgate 1979). However, when the number of host plants is limited, or when pods are only available seasonally, bruchids may not reach population sizes large enough to support stable populations of parasitoids (Bridwell 1919).

Small mammals and birds may destroy *Prosopis* seedlings (Weltzin et al. 1997). In feeding trials in Hawai'i, the alien black rat (*Rattus rattus*) was capable of removing seeds of *P. pallida* from mature pods, directly consuming nearly all seeds (Aaron Shiels, 2009, pers. comm.). Rodents have also been observed consuming considerable quantities of seeds from immature pods on O'ahu (T.G., pers. obs.). Foxes, armadillos, skunks, rabbits, coyotes, wolves, kangaroo rats, wood rats, and prairie dogs consume *Prosopis* fruit and likely destroy some seeds. Eradication of prairie dog populations in the southwestern United States in the early 1900s may have removed a limiting factor to the growth of *P. glandulosa* populations in that region, resulting in the encroachment of *Prosopis* populations into grasslands (Weltzin et al. 1997).

Some birds, including parrots, winged doves, ravens, and quail species, have also been observed feeding on *Prosopis* seeds and although these primarily represent seed predation, some may play a limited role in dispersal (Solbrig and Cantino 1975). A number of seed-eating birds including the Red-masked Parakeet (*Aratinga erythrogenys*), the Rose-ringed Parakeet (*Psittacula krameri*), the Northern Cardinal (*Cardinalis cardinalis*), and the House Finch (*Carpodacus mexicanus*) are also known to cause considerable damage to the immature pods of *P. pallida* on O'ahu (Nicholas Kalodimos, unpubl. data).

PROGNOSIS

The establishment of new populations and new patches of *Prosopis* within an ecosystem is highly dependent upon adequate dispersal vectors. Germination is also greatly improved by mechanical disturbance that removes seeds from their endocarp and scarifies the seed coat. In areas where animals or running water provide adequate dispersal (and scarification), *Prosopis* populations will continue to expand at a rapid rate. In the absence of adequate dispersal, and particularly when bruchid beetles, birds, or rodents result in substantial seed mortality, population growth may be more readily controlled (see Table 4).

In 1947, Egler predicted that populations of *P. pallida* in leeward O'ahu would slowly decline after the removal of cattle. In areas near the sites where Egler made his prediction, aerial photography and direct observations indicate that *P. pallida* canopy cover has become reduced in extent and that little or no recent recruitment has occurred in the area (Wester et al. 2006; T.G., pers. obs.). In 2008 and 2009, we investigated numerous populations in leeward O'ahu and could find only limited recent recruitment of *P. pallida*, although we did observe active recruitment of *P. pallida* at Puakō on Hawai'i Island in areas affected by a recent fire and subsequent bulldozing. Active recruitment of *P. juliflora* appears to be occurring in coastal areas of leeward O'ahu and Kaua'i. Although we attribute the decline of some populations of *P. pallida*, as did Egler, to the loss of adequate

TABLE 4

Factors Influencing *Prosopis* Establishment and Spread

Promotes *Prosopis*	May Limit *Prosopis*
Arid habitat	Small mammal seed predators (e.g., rodents)
Large mammal dispersers	Seed-eating birds
Access to rivers, streams, and coastal waterways for dispersal	Bruchid beetles
Access to groundwater	Leaf-tying moth (*Evippe* sp.)
Mechanical soil disturbances	Wood and pod harvest (?)
	Absence of promoting factors

dispersal, the mechanism preventing population growth may include a combination of seed predation, lack of seed scarification, or possibly changes in local hydrology under *Prosopis* stands caused by these phreatophytic species. Additional work is needed to confirm observations of the decline of *P. pallida* in Hawai'i and to determine the degree to which each of the above factors influences population dynamics.

Further work is needed to understand the interactions of populations of *Prosopis* species with competitors, dispersal agents, and seed predators and their parasites. Where multiple *Prosopis* species are sympatric, research is needed to understand how these species partition the environment and how hybridization and introgression affects their invasive tendencies.

The behavior of *Prosopis* species in particular environments seems to be highly context specific. In some cases *Prosopis* may facilitate the establishment of more-diverse later successional woodland that may actually restrict further *Prosopis* recruitment (Scanlan and Archer 1991, Archer 1995). Elsewhere, observations suggest that *Prosopis* may strongly compete with native species, resulting in monotypic *Prosopis* stands. The latter condition appears to have occurred in Hawai'i before the removal of effective ungulate dispersal agents and continues to occur in Australia, India, and elsewhere prompting control efforts.

In some cases, however, populations of alien *Prosopis* thrive in habitats degraded by cattle and other direct or indirect actions of humans, where native species are no longer capable of establishing themselves. The invasive characteristic of *Prosopis* in such areas may be an indication of poor land-use strategies, and consequently native species may not be able to reclaim such degraded areas without improvements in soil quality or the establishment of certain microsite conditions (Fisher 1990, Bhojvaid and Timmer 1998). In some cases *Prosopis* may be used as an agent of ecosystem restoration (Esbenshade 1981, Logan 2007). At Puakō on the Big Island of Hawai'i, efforts are under way to determine whether native species can be reestablished under a thinned canopy of *P. pallida* (Neil Logan, 2009, pers. comm.; T.G. and M.M., pers. obs.). Despite their invasive tendencies, *Prosopis* spp. continue to be highly valued resources around the world. In some cases a balance may be struck between population control and sustainable use of these species (Alban et al. 2002, Laxén 2007).

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