Review

The Biology of Australian Weeds
37. *Prosopis* L. species

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Name

Botanical name

The genus *Prosopis* L. (Family Leguminosae) has 44 recognized species (Burkart 1976). They are native to America, from western North America to Patagonia (40 species), and southwest Asia and Africa (four species). According to Perry (1998) the name *Prosopis* is derived from the Greek *pros* (towards) and *Opis* (the Greek goddess of abundance and the wife of Saturn) and was originally used for *Arctium lappa* L. (Asteraceae), an unrelated plant with spiny heads. The genus is a member of the subfamily Mimosoideae and the tribe Mimoseae. In Australia the tribe Mimoseae contains nine native species (Cowan 1998). A further 11 species have become naturalized, of which eight are now weeds (four *Prosopis* spp., three *Mimosa* spp. and *Dichrostachys cinerea* (L.) Wight & Arn.) and a ninth, *Leucaena leucocephala* (Lam.) de Wit, is a fodder tree that has become a weed in some places (Lazarides *et al*. 1997).

The four *Prosopis* species that have naturalized in Australia, (*P. glandulosa* Torr., *P. pallida* (Willd.) Kunth, *P. velutina* Wooton and *P. juliflora* (Sw.) DC.), all belong to the New World Section Algarobia which includes about 29 species (Burkart 1976). One of them, *P. pallida*, belongs to the Pallidae series, whilst the others belong to the Chilensis series (Burkart 1976).

Common name

In Australia *Prosopis* is commonly referred to as mesquite or algaroba. The term mesquite is derived from the Aztec language ‘Nahuatl’, in which the plant was called mizquitl, or ‘bark used for tanning’ (Franco and Aguirre 1996). The Spanish referred to *Prosopis* in South America as algarrobo (*sic*) because it resembled the plant algarrobo (*Ceratonia siliqua* L., the Mediterranean carob) of the Iberian peninsula in its aspect and general uses (D’Antoni and Solbrig 1977).

A large number of common names are used overseas for particular species (see Burkart 1976). Common names that have been used in Australia include Quilpie mesquite, Quilpie algaroba and velvet mesquite (for *P. velutina* × *P. glandulosa* var. *torreyana* and *P. velutina*), honey mesquite (for *P. glandulosa* var. *glandulosa*), hybrid mesquite (for infestations thought to be of hybrids) and Cloncurry prickle bush (for *P. pallida*).

Taxonomy

Species delineation within the section Algarobia is notoriously difficult owing to a paucity of morphological characters, widespread hybridization and introgression (Hunziker *et al.* 1975, 1986) and considerable intra-specific variation (Burkart 1976, Solbrig *et al.* 1977) which is in part environmentally induced (R. Palacios personal communication 1999). The monograph on *Prosopis* taxonomy by Burkart (1976) is currently the most authoritative treatment of the genus, but taxonomic changes, both in species delineation and intra-generic classifications, will undoubtedly occur with further taxonomic studies and the inclusion of non-morphological characters. In addition, the taxonomy of *Prosopis* throughout its introduced range is in urgent need of taxonomic revision (e.g. Fagg and Stewart 1994).

The current consensus among *Prosopis* workers in Australia is that four species have naturalized (*P. pallida, P. glandulosa, P. velutina* and *P. juliflora*) together with various hybrids (Panetta and Carstairs 1989, Csurhes 1996, Perry 1998), although a number of taxonomic issues remain unresolved. Pedley (1977) and Perry (1998) are the only authors to have dealt specifically with the taxonomy of Australian *Prosopis*. Both examined material from only a small proportion of infestations, both relied entirely on morphological characters, neither was familiar with the genus within its native range, and Pedley (1977) was prepared prior to Burkart’s 1976 revision of the genus (Pedley 1977, p. 42). Burkart (1976) and R. Palacios (personal communication 1999) have also identified some Australian material.

Prosopis pallida has been identified from Australia by Burkart (1976) and Perry (1998). This identification was confirmed by R. Palacios (personal communication 1999) and is supported by an isozymic study which found a high degree of similarity between Australian *Prosopis* populations and *P. pallida* from Hawaii (Panetta and Carstairs 1989). Pedley (1977) identified it as *P. limensis* Benth., which was synonymized under *P. pallida* by Burkart (1976) (see also Pedley 1977, p. 42).

Prosopis velutina has been identified from Australia by Burkart (1976), Perry (1998) and R. Palacios (personal communication 1999), although some of the infestations identified as such by Burkart and Perry are likely to be hybrids of *P. velutina* with *P. glandulosa* var. *torreyana* (L.D. Benson) M.C. Johnst. (R. Palacios personal communication 1999). *P. glandulosa* var. *glandulosa* was identified by Burkart (1976), Pedley (1977) and Perry (1998), with evidence of introgression by *P. glandulosa* var. *torreyana* in two specimens from southern Queensland (Perry 1998). *P. glandulosa* var. *torreyana* was identified by Pedley (1977) and R. Palacios (personal communication 1999), although the former identification needs to be confirmed.

There has been considerable dispute as to the species boundaries of *P. juliflora* (Burkart 1976, Pedley 1977). We apply it in the restricted sense of Burkart (1940, 1976). It has also been used as a collective concept which embraced several taxa, including *P. juliflora, P. velutina* and *P. glandulosa.* This has resulted in considerable confusion in the literature (Burkart 1976, Fagg and Stewart 1994), and any reference to *P. juliflora* should be treated with caution. Perry (1998) records *P. juliflora* from two sites and we consider these to be the only confirmed records of this species in Australia. Isozymic studies of representatives from one of these populations (Pallarenda, Queensland) supports this identification (Panetta and Carstairs 1989). Pedley (1977) identified populations in New South Wales as *P. juliflora* but these are probably *P. velutina* and/or *P. velutina* × *P. glandulosa* var. *torreyana.*

Hybrids

The parentage of hybrid mesquite populations in Australia remains poorly understood, and their origins and history are likely to be diverse. On the basis of morphological features they have been identified as *P. juliflora* × *P. velutina* Pedley (1977), *P. glandulosa* × *P. velutina* Perry (1998), and *P. pallida* × *P. glandulosa* var. *torreyana* (R. Palacios personal communication 1999). Some hybrid populations may also contain true species, including *P. glandulosa* (Carnarvon, WA) (Pedley 1977), *P. glandulosa* var. *torreyana* (Carnarvon, WA; Moorooka Station, Qld) and possibly *P. juliflora* (R. Palacios personal communication 1999). At least some of the mesquite infestations are likely to include multiple genotypes.

In central-north Queensland hybrid populations are relatively isolated and are contained within the general distribution of the more widespread *P. pallida*. The few infestations that have been examined taxonomically suggest other genotypes might also be present. On Carrum station individual hybrid plants growing side-by-side with *P. pallida* were identified as *P. pallida* × *P. glandulosa* var. *torreyana* (R. Palacios personal communication 1999), suggesting hybridization may have occurred there. However, an infestation on nearby Rockvale Station has been identified as *P. glandulosa* × *P. velutina* (Perry 1998), and the absence of *P. pallida* introgression in this population is supported by isozyme work (Panetta and Carstairs 1989). Different samples from the largest hybrid infestation in central-north Queensland (on Moorooka Station near McKinlay) have been identified as *P. glandulosa* × *P. velutina* by Perry (1998) and *P. glandulosa* var. *torreyana* by R. Palacios (personal communication 1999).

In Western Australia hybrid populations are widespread, and distinct morphotypes frequently co-occur. On Mardie Station samples have been identified as *P. glandulosa* × *P. velutina* (Perry 1998), ?*P. juliflora* and *P. pallida* × *P. glandulosa* var. *torreyana* (R. Palacios personal communication 1999). The introgression of *P. pallida* into at least some morphotypes is supported by isozyme analyses (Panetta and Carstairs 1989). Similar morphotypes are present in and around Carnarvon and have been identified as *P. glandulosa* × *P. velutina* (Perry 1998), *P. glandulosa* × *P. juliflora*, *P. glandulosa* var. *glandulosa* (Pedley 1977), *P. glandulosa* var. *torreyana* and *P. pallida* × *P. glandulosa* var. *torreyana* (R. Palacios 1999 personal communication).

Elsewhere, *P. velutina* × *P. glandulosa* var. *torreyana* hybrids have been identified in Queensland (Comongin Station) and South Australia (Port Augusta) (R. Palacios personal communication 1999). The infestation on Comongin Station (south-western Queensland) has previously been identified as *P. velutina* by Burkart (1976) and Perry (1998), and as *P. flexuosa* by Pedley (1977, p. 42). An infestation near Broken Hill in New South Wales had leaves similar to *P. velutina*, but fruits resembled those of some hybrids of *P. velutina* × *P. glandulosa* var. *torreyana* seen in Arizona, USA (R. Palacios personal communication 1999).

Further study, using a range of techniques, is required to document the variation present both within and between hybrid populations and to identify component species. Different populations may have different histories: some appear to be monotypic and may have been introduced as such (e.g. Comongin Station, Queensland), while others contain multiple genotypes and may be dynamic (e.g. Mardie Station and Carnarvon, Western Australia).

Figure 1. *Prosopis pallida* tree, Barkly Tablelands, Northern Territory.

Description

The following description of *Prosopis* taxa that have naturalized in Australia was compiled from Burkart (1976), Parsons and Cuthbertson (1992), Jeffrey and March (1995), Perry (1998) and personal observations.

General description

The various *Prosopis* taxa are shrubs or trees which typically grow to about 3–15 m tall. They can either have a single main stem and spreading canopy (Figure 1) or be multi-stemmed and shrubby (Figure 2). Older bark can be rough or smooth and grey or brown. Small branches have smooth dark red or green bark, and have a characteristic zigzag form. Plants can appear rather untidy overall with individual branches protruding beyond the canopy (Figures 1, 2). Spines are solitary or paired, sometimes absent. They range in length from 4 mm to more than 75 mm long. Leaves are bipinnate with 1–4 pairs of pinnae and 7–21 pairs of small, opposite pinnules (leaflets) (Figure 3a). The foliage is usually dark green but can be bluish green. Flowers are greenish cream to yellow, small, regular, on short stalks and grouped in dense spike-like inflorescences, which are axillary and 5–12 cm long (Figure 3a). The calyx is bell-shaped and five-lobed, while the petals can be either united at the base or free. The 10 stamens are free and exserted, and the anthers are tipped with a deciduous gland. The pollen grains are shed singly. Seed pods are 5–20 cm long, compressed, straight to slightly curved, smooth, with slight constrictions between the seeds (Figure 3b). When ripe, the indehiscent pods are straw-coloured, or purplish in some taxa, and usually have a sweet and palatable pulp surrounding the seeds. Each pod contains between five and 20 hard seeds, which are ovate or elliptical, 2.5–7 mm long and 2–5 mm wide.

Figure 2. *Prosopis velutina* × *P. glandulosa* var. *torreyana* shrub, north-western New South Wales.

Distinguishing Australian Prosopis taxa

The four *Prosopis* species in Australia are morphologically quite similar and at times can all be confused with hybrid morphotypes, not all of which have been documented. Identifications must therefore be confirmed by specialists.

Prosopis glandulosa is a shrub with characteristically long (seven or more times as long as wide) and widely spaced (internodes of the pinnae axes 8–14 mm) pinnules on one, occasionally two, pairs of pinnae (Figure 3d). The two *P. glandulosa* varieties can be distinguished by leaf characters. *P. glandulosa* var. *glandulosa* has 6–13 pairs of pinnules per pinnae, each 30–45 mm long, while *P. glandulosa* var. *torreyana* has 15–25 pairs of pinnules, each 15–25 mm long. The remaining three species have relatively stout and closely spaced pinnules. *P. pallida* is most easily

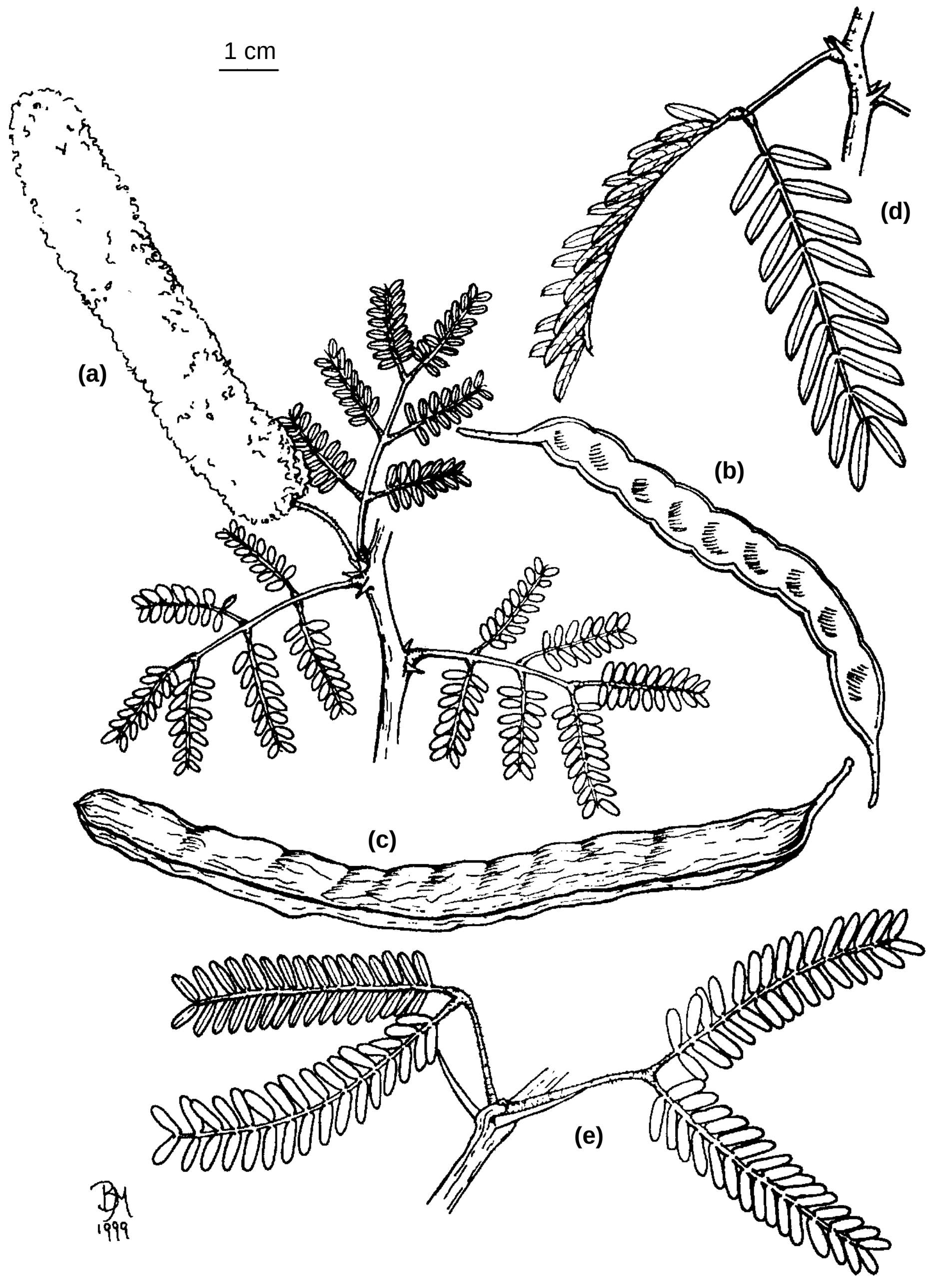

Figure 3. ***Prosopis pallida*****: (a) branch with inflorescence; (b) immature pod; (c) mature pod; (d)** ***P. glandulosa*** **var.** ***glandulosa*** **branch; (e)** ***P. velutina*** **branch.**

characterized by the presence of 2–4 pairs of pinnae (rarely some leaves with one pair) (Figure 3a). In addition, *P. pallida* plants are often single-stemmed (Figure 1), and can grow to a tree up to 20 m tall with a wide girth, while the remaining taxa tend to be multi-stemmed shrubs, although they can grow over 10 m high and wide girths can be attained. Armature is variable on *P. pallida*, from short or no thorns to thorns more than 60 mm long.

Prosopis velutina and *P. juliflora* have two (sometimes one or three) pairs of pinnae (Figure 3e). Perry (1998) states *P. juliflora* can be distinguished as 'having soft, herbaceous leaflets which appear somewhat curled or corrugated when dry' and *P. velutina* as 'having hairy pods'. The latter character is unreliable as it can vary depending on environmental conditions (R. Palacios personal communication 1999).

Distinguishing Prosopis from other Australian taxa

Mesquite can be confused with prickly acacia (*Acacia nilotica* (L.) Del.), mimosa bush (*A. farnesiana* (L.) Willd.) and parkinsonia (*Parkinsonia aculeata* L.), with which it frequently co-occurs. All four taxa produce spines, yellow flowers and bean-like seed pods, and are sometimes collectively referred to as 'prickle bushes'. Mesquite can be most readily distinguished by its spike-like inflorescences, its long pods which are straight or slightly curved and which have only slight constrictions between seeds, and the often untidy appearance of the plant resulting from individual zigzagged branches protruding beyond the main canopy (see also Mackey 1998).

History

Prosopis has been spread around the world as a beneficial plant since at least the early 1800s. Since then there have been many large scale, co-ordinated introductions into many arid regions of the world, as well as innumerable *ad hoc* introductions (Felker and Moss 1996). There have undoubtedly been multiple introductions of mesquite into Australia. However, there is little documentation of their origin and nature.

The potential benefits for Australia of several *Prosopis* species was already being promoted to the Victorian State Parliament by 1871 (von Mueller 1876). However, the first recorded plants are a *P. pallida* tree in the Brisbane Botanic Gardens that was planted in the early 1880s, and a *Prosopis* specimen in the Royal Botanic Gardens Herbarium (Melbourne) that had been collected from the Northern Territory between North MacDonnell Ranges and Lake Nash Station in 1886. The latter must have been planted soon after the first introduction of cattle into the area in 1866 (Mitchell 1978).

In 1895 *P. pallida* seeds, probably of a thorny variety, and originating in Honolulu, were propagated at Kamerunga State Nursery in northern Queensland (Brooks 1900, 1901). Plants first bore fruit in 1899/1900 and the potential value of the tree to pastoralists was promoted in the Queensland Agricultural Journal. As a result, 140 requests for seeds were received from all over the state and 100 shipments made within the first year alone. 'Thornless' types of *P. pallida* were also imported into Australia from Hawaii (Degener 1937), although their fate is unknown. An Hawaiian source for *P. pallida* populations in Western Australia and Queensland is supported by isozymic comparisons of the three populations (Panetta and Carstairs 1989). Seeds were originally introduced into Hawaii in 1828 from a Chilean tree growing in Paris (Degener 1937).

Mesquite seeds, reputedly of a spineless type, were introduced into Western Australia and distributed around the northwest in about 1921, and probably prior to that as well. They were planted in a number of north-western towns and on many station properties to provide shade and shelter, and in the case of pastoralist stations, nutritious pods for livestock (Meadly 1956, 1962). *Prosopis velutina* and/or *P. velutina* × *P. glandulosa* var. *torreyana* (as '*P. juliflora*') was introduced into New South Wales 'some years' prior to 1923 by the New South Wales Department of Agriculture. It was promoted as a fodder plant for cattle but it was 'never taken on among farmers' (Breakwell 1923). One infestation in Victoria (near Charlton) was reputedly the result of an introduction by a landholder as a fodder source, probably from the United States, although it is not known when (K. Harrison personal communication 1999).

By the 1920s or 1930s *Prosopis* was widely planted in Queensland (White 1921, Herron 1986, Jeffrey and March 1995) and Western Australia (Meadly 1956, 1962). It was probably primarily distributed among homesteads and towns by the community as hardy ornamental and shade trees (Mears 1966, Dodd and Madin 1986, Herron 1986, Jeffrey and March 1995, Michelmore 1995, p. 7). It may also have been disseminated through nurseries, from where it was still available in the 1960s (Mears 1966). In western New South Wales mesquite was planted around the Broken Hill area to revegetate dust hazard areas in about 1940 (Milthorpe 1975), possibly by the Zinc Corporation (Eardley 1945). A private citizen also distributed pods aerially over an extensive area on at least one occasion (Condon and Alchin 1979, E. McCormick personal communication 1998). However, it is not clear whether either redistribution effort contributed to the current distribution in western New South Wales. Mesquite was also used as a soil stabilizer in Cloncurry (Jeffrey and March 1995) and is still valued for dust abatement around aboriginal communities in central Australia (S. Wingrave personal communication 2000). It has recently been recommended for permaculture in Australia (Mollison 1994), although we are unaware of it being used in practice.

Most, if not all, of the significant *Prosopis* infestations in Australia were derived from a small number of the planted trees. The infestation on Mardie Station (Western Australia), which is the largest infestation in Australia, originated from a few trees at the homestead and some plantings at mills (Meadly 1956). The infestation on Comongin station (south-western Queensland) reportedly began from two plants near the homestead in the 1930s (Herron 1986, Jones 1992), and has since spread onto neighbouring properties. The majority of infestations in the Northern Territory, New South Wales, north-western Queensland and South Australia probably originated in a similar manner.

Distribution

Native

All four *Prosopis* species thought to have naturalized in Australia are neotropical in origin. *P. velutina* and *P. glandulosa* (var. *glandulosa* and var. *torreyana*) are both from Mexico and southern USA, where they have partially overlapping distributions (Burkart 1976, Johnson and Mayeux 1990) and appear to hybridize naturally (Solbrig *et al.* 1977). *P. pallida* is native to the northwest of South America (Peru, Colombia and Ecuador) where it occurs along the Pacific coast and in the drier parts of the interior (Burkart 1976). *P. juliflora* is a neotropical coastal species native to northern South America (including Venezuela, Colombia, Peru, Ecuador and Montserrat), Central America (Panama to Mexico, including Curacao), and possibly the Greater Antilles (Cuba) although it may have been introduced there (Burkart 1976).

Introduced – worldwide

The identification of *Prosopis* throughout its introduced range is unresolved and the following distribution records should therefore be treated with caution. *P. glandulosa* var. *glandulosa* has been introduced to Asia (Saudi Arabia, Burma, India, Pakistan), the Greater Antilles (Puerto Rico), southern Africa (Harding 1987) and Australia. *P. glandulosa* var. *torreyana* and *P. velutina* have been introduced into South Africa (Harding 1987) and Australia. *P. pallida* has been introduced into Puerto Rico, Brazil, the Hawaiian and Marquesas Islands, Australia and India (Burkart 1976). *P. juliflora* has been introduced into the Greater Antilles (Jamaica, Cuba), northern Brazil, Asia (Iraq, Kuwait, Vietnam, India, Sri Lanka, the Philippines), Africa (Nigeria, Sudan, Senegal, southern Africa) (Burkart 1976, Harding 1987), Ascension Island (S.V. Fowler, unpublished 1998) and Australia, and is now naturalized in arid and semi-arid areas throughout the tropics (Fagg and Stewart 1994). It is not known whether the Australian hybrids are introduced or endemic (see hybrid section).

Introduced – Australia

Distributional data for Australia was obtained from herbarium records (from all Australian herbaria), the scientific literature, State Government employees, State Department files, and from our own field records.

Prosopis pallida is widely distributed across northern Australia (Figure 4). In Queensland it is the most widespread *Prosopis* species. Before control measures were carried out, the largest infestations occurred in north-western Queensland at Cloncurry (about 5000 ha dense), Hughenden (21 000 ha of varying density), near Kynuna (2000 ha dense, 18 000 ha scattered) and Karumba (200 ha medium to high density, 1000 ha isolated to light density) (N. March, personal communication 1999). In addition, scattered infestations are present through much of north-western and central-western Queensland. A total of 8–37% of properties contacted at random reported mesquite (mostly light infestations of *P. pallida*) in the Flinders, Richmond, Cloncurry and McKinlay Shires (N. March, unpublished 1995). In central western Queensland, it was present on 22% of the 315 properties surveyed by questionnaires (Reynolds and Carter 1993). Individual plants or isolated clumps of plants have also been recorded across south-eastern Queensland. In the Northern Territory it is largely confined to isolated infestations of less than a few hundred mature trees on pastoral properties on the Barkly Tablelands, mostly around homesteads, bores and along water courses. In Western Australia *P. pallida* is sparsely distributed on two properties near Onslow (Ritchie 1983b).

Prosopis velutina and the *P. velutina* × *P. glandulosa* var. *torreyana* hybrid are restricted to south-eastern Australia (Figure 5), with the exception of a single record from Alice Springs (Perry 1998). Relatively few infestations have been identified authoritatively. The largest infestation (identified as *P. velutina* × *P. glandulosa* var. *torreyana* by R. Palacios personal communication 1999) is near Quilpie, in south-western Queensland. Prior to control work which commenced in 1992, there was about 4000 ha of dense infestations and 8800 ha of scattered infestations on two properties, and isolated plants extending south to Toompine. In New South Wales most infestations occur in the far west on at least 43 pastoral properties (Alchin and Condon 1983), including two properties with mesquite scattered over more than 1000 ha (Condon and Alchin 1979). These infestations include both *P. velutina* and *P. velutina* × *P. glandulosa* var. *torreyana*. Isolated plants have also been recorded from parts of the

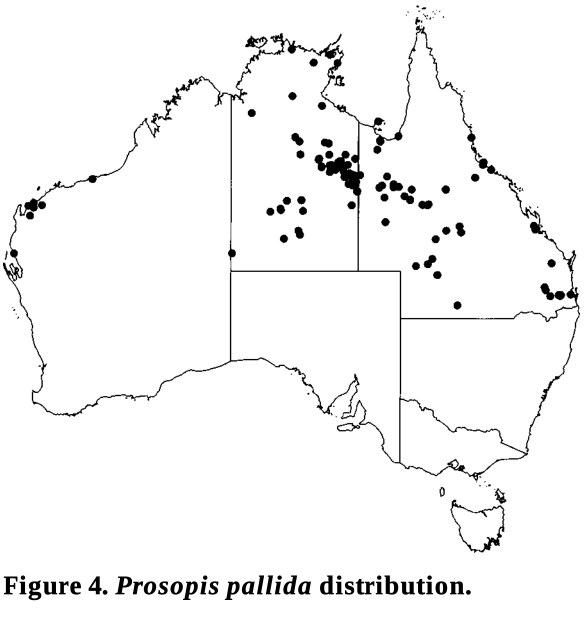

Figure 4. *Prosopis pallida* distribution.

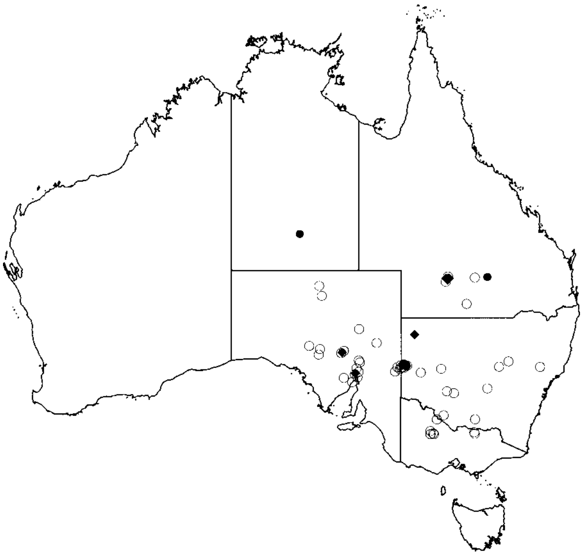

Figure 5. ***Prosopis velutina*** **(●),** ***P. glandulosa*** **var.** ***torreyana*** **×** ***P. velutina*** **hybrid (◆), and unidentified** ***P. velutina*** **or** ***P. velutina*** **hybrid (○) distribution.**

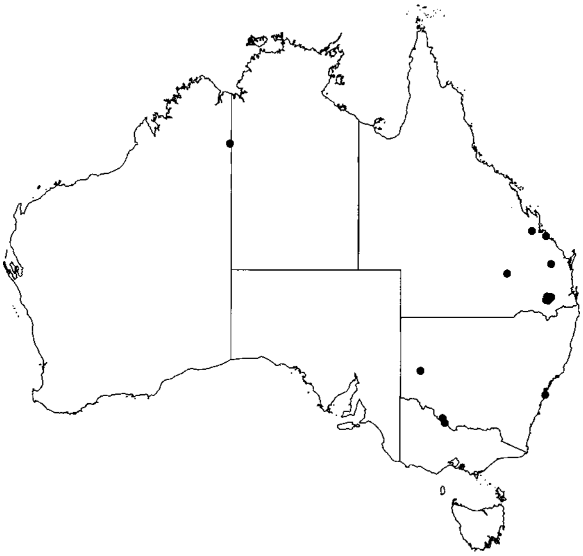

Figure 6. ***Prosopis glandulosa*** **var.** ***glandulosa*** **distribution.**

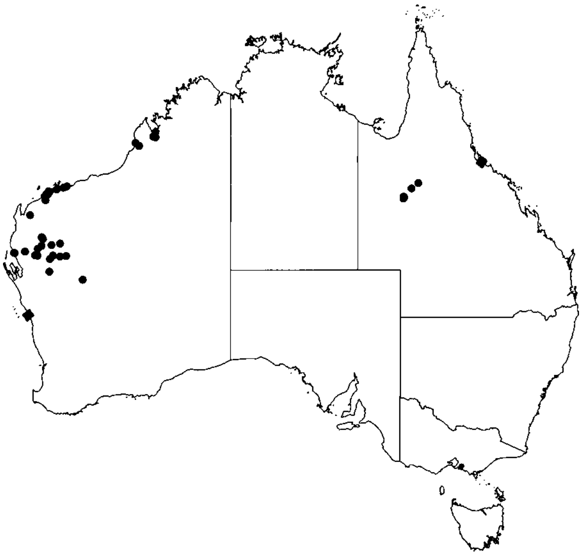

Figure 7. ***Prosopis juliflora*** **(◆) and** ***P.*** **'hybrid' distribution (●).**

south-western Riverina and on the north-western slopes and plains at Gilgandra and Coonamble. In South Australia the largest infestations prior to control work were at Woomera (over 1000 plants associated with surface water, drains and creeks) and adjacent to Lake Torrens (over 200 plants associated with a dune-swale system) (Michelmore 1995). Ongoing control work means that only isolated plants remain, including in and around Port Augusta (identified as *P. velutina* × *P. glandulosa* var. *torreyana* by R. Palacios personal communication 1999) and Woomera. Mesquite infestations reported in Victoria have not been identified by specialists. Two infestations have been reported, one of a few hundred plants near Swan Hill, which was discovered in 1985 (K. Harrison personal communication 1999), and one in a single paddock (about 16 ha) near Wangaratta, which was located in 1995 (P. Goodman personal communication 1999). Isolated plants have also been recorded near Swan Hill (Parsons and Cuthbertson 1992, Entwisle *et al.* 1996).

Small, isolated infestations of *P. glandulosa* var. *glandulosa* occur in New South Wales (Milthorpe and Dellow 1983) and south-eastern Queensland (Kleinschmidt and Johnson 1977, Stanley and Ross 1983, Csurhes 1996) (Figure 6). The only significant infestation is about 1000 ha of scattered plants on a single station in the East Kimberley region (Western Australia) (Hussey *et al.* 1997, R. Watkins personal communication 1999). *P. juliflora* has been recorded from only two localities, from Geraldton in Western Australia and Cape Pallarenda in Townsville (Perry 1998) (Figure 7). The latter has been eradicated.

The so-called 'hybrid' infestations occur in central-north Queensland and Western Australia (Figure 7). In Queensland they are sympatric with *P. pallida*. The largest infestations prior to recent control work were surrounding McKinlay (about 10 000 ha) and on Rockvale Station near Nelia (100 ha) (Csurhes 1996). Infestations include *P. glandulosa* var. *torreyana* × *P. pallida* hybrids and *P. glandulosa* var. *torreyana*, or a mixture of both (R. Palacios personal communication 1999). In Western Australia 'hybrid' infestations are widely distributed, mostly as isolated or sparse trees with occasional small thickets. The single largest infestation is on Mardie station where there is 30 000 ha of dense mesquite and a further 120 000 ha of scattered mesquite (R. Parr and R. van Klinken, unpublished 1999). In the northwest an infestation on Yeeda Station at the lower reaches of Fitzroy River had trees scattered over about 12 000 ha and isolated thickets of less than 1 ha in size prior to control work (M. Everett personal communication 1999). A property near Broome has about 400 ha of scattered plants (R. Watkins personal communication 1999). In the Murchison and Gascoyne Junction Districts over 200 km of water courses have patches of mesquite, and isolated plants have been found throughout. Western Australian 'hybrid infestations' are likely to include *P. pallida* × *P. glandulosa* var. *torreyana*, *P. glandulosa* var. *torreyana* and possibly *P. juliflora* (R. Palacios personal communication 1999).

Habitat

In Australia, significant mesquite infestations occur in climatically diverse regions, from areas with annual mean daily temperatures of 10–15°C in the south to over 25°C in the north, and median annual rainfalls from about 150 mm to about 1200 mm. Mesquite appears to grow well on all soil types (Jeffrey and March 1995), including scalded soils on which little or no native vegetation will grow, cracking clay soils and iron stone where few native trees or shrubs occur, and dune systems. In general, soil moisture rather than soil type seems to determine mesquite distribution, since mesquite tends to establish most successfully on clay soils and alluvial soils which have good moisture retention (Barker *et al.* 1996), and less well where barriers to root penetration are shallow (Loomis 1989). However, roots can grow upwards to take advantage of small precipitation events and penetrate to great depths to access water (Gile *et al.* 1997). Mesquite infestations in Australia occur primarily in pastoral regions, and are associated with diverse vegetation types. These include hummock grassland, chenopod low shrubland, tall shrubland and *Astrebla* (Mitchell grass) grassland.

Mesquite in Australia is still in the early stages of establishment and its current distribution is therefore probably more a reflection of historical patterns of introduction than of habitat requirements. A better idea of habitat requirements can be obtained from observations overseas, although good data comparing mesquite taxa are generally lacking and are obscured by taxonomic impediments.

Species that have naturalized in Australia are universally well adapted to hot, dry conditions and are not dependent on soil type. They do, however, differ in their preferences and tolerances, as might be predicted from differences in their native-range distributions. For example, *P. glandulosa* var. *glandulosa*, *P. velutina* and *P. glandulosa* var. *torreyana* all originate from North America, but are largely parapatric (Johnson and Mayeux 1990). The former grows in eastern North America, where annual rainfall averages between about 200 and 1000 mm, while the latter two grow in the west, where average annual rainfall is typically below 400 mm. *P. glandulosa* var. *torreyana* even grows in regions such as the Death Valley (California) where the annual average rainfall is as low as 50 mm and daily average maximum temperatures for July are close to 45°C (Felker 1979).

Prosopis pallida and *P. juliflora* are particularly hardy and are used in some parts of the world for reclamation of degraded land (Harsh and Tewari 1998). The ecological amplitude of *P. juliflora* is very wide (Harsh and Tewari, 1998). It can grow in all soil types, including the poorest of soils with low organic matter and nutrient status, and waterlogged soils. It flourishes even where rainfall is low and variable, and can tolerate extremely saline (conductivity >44 dSm^{-1}) and alkaline (up to pH 10) conditions (Dagar 1998, Harsh and Tewari 1998, Singh 1996). *P. pallida* is among the most salt tolerant terrestrial plants in the world, and can grow and fix nitrogen in salinities approaching seawater (>18 000 mgL^{-1}) (Felker *et al.* 1981). In contrast, *P. velutina* tolerates salinities of 12 000 mgL^{-1} poorly, while *P. glandulosa* var. *torreyana* is intermediate between *P. velutina* and *P. pallida* in salt tolerance (Felker *et al.* 1981, Jarrell and Virginia, 1990). The salt tolerance of these species correlates with conditions in their native ranges (Felker *et al.* 1981). *P. velutina* grows primarily on rain-fed uplands where salinity is not usually a problem, while *P. glandulosa* var. *torreyana* grows in low-lying portions of water catchment basements in the southern Californian deserts where both water and salt accumulate.

Frost is an important factor restricting the distribution of some *Prosopis* species. *P. juliflora* (Harsh and Tewari 1998) and *P. pallida* are sensitive to frost (Dagar 1998), while *P. glandulosa* var. *torreyana* is frost tolerant (Felker *et al.* 1981).

It is not known how differences in water requirements and tolerances to climatic and soil conditions will limit the potential distribution of each *Prosopis* taxon in Australia.

Growth and development

Currently, there is a scarcity of information on the growth, development and reproduction of mesquite under Australian conditions. Most research has focused on *P. pallida*, the most widespread species in Australia. To overcome this deficiency, overseas literature relating to the species in Australia has been consulted. Most overseas literature comes from the United States and therefore focuses on *P. glandulosa* and *P. velutina* (Schuster 1969). Available data rarely allow proper comparisons between *Prosopis* species. However, they do suggest significant differences in some aspects such as their phenology and physiological tolerances and responses (e.g. Simpson *et al.* 1977, Nilsen *et al.* 1991, Dagar 1998).

Morphology

The root to shoot ratio of seedlings can increase with decreasing soil moisture, allowing for maximum exploitation of available moisture (Glendening and Paulsen 1955, Mooney *et al.* 1977, Brown and Archer 1990). Brown and Archer (1990) found *P. glandulosa* var. *glandulosa* seedlings with one true leaf and cotyledons still attached had tap roots extending beyond 20 cm and an average of six lateral roots, most of which were in the upper 10 cm. Tap roots of four month old seedlings extended beyond 40 cm and had 10 lateral roots. Similarly, *P. velutina* growing under field conditions had a root to shoot ratio of 3.9 after 10 days, 6.0 after two months, and 9.6 after nine months (Glendening and Paulsen 1955). The stem diameter, height and crown diameter of established *P. velutina* plants in Arizona increased linearly over a 21 year period, although smaller trees were quite variable in initial growth rate (Cable and Martin 1973).

A dormant bud zone, extending 15 to 20 cm below ground level, forms at the base of the stem. Branched trunks form following destruction of the main shoot or apical meristem by animals or abiotic processes such as freezing (Fisher 1977), or by attempts at control.

The pervasive root system of mesquite has undoubtedly aided its successful establishment in diverse habitats. Although mesquites are generally considered to be phreatophytes that access a significant fraction of water requirements from the unsaturated soil fringe above the phreatic zone (Jarrell and Virginia 1990), this is not always the case (Johnson and Mayeux 1990). In fact a detailed study of the root system of *P. glandulosa* found roots could adapt to a wide variety of soils and soil conditions, and could access available water at all depths (Gile *et al.* 1997). Roots could proliferate greatly while spreading laterally over long distances; could grow upwards and take advantage of small precipitation events that wet the soil to depths of only a few centimetres; and could descend to great depths along cracks and other openings in the soil, down which soil water also penetrates. The deepest recorded *Prosopis* roots are of *P. flexuosa* at 80 m (Vervoorst 1954, in Solbrig and Cantino 1975). *P. velutina* roots have been found over 52 m deep (Phillips 1963), and can extend laterally more than 30 m (McGinnies 1972). *P. glandulosa* roots can extend more than 15 m deep (Scifres *et al*. 1973) and at least 18 m laterally (Fisher *et al.* 1959), while the principal *P. pallida* roots grow 20 m or more (Ferreyra 1981).

Perennation

Mesquite is a long lived perennial. A single *P. pallida* plant growing in the Brisbane Botanical Gardens is more than 115 years old, and large *P. pallida* trees growing in Hughenden (northern Queensland) have been there for at least 40 years according to some long term residents (B. Dowling personal communication 1999). *P. velutina* can grow to at least 80 years old (Cable and Martin 1973). Archer (1989) used models to estimate that *P. glandulosa* trees within his study area averaged between 33 and 44 years old, with some trees over 172 years old. In southern New Mexico, growth rings were used to estimate that a 90 cm diameter *P. glandulosa* plant was about 30 years old (Gile *et al.* 1997).

Physiology

In general, *Prosopis* species are regarded as extravagant users of readily available water (Haas and Dodd 1972, Felker 1979, Leakey and Last 1980). For example, water use efficiency for *P. velutina* was estimated to be 1730 kg water kg^{-1} DM, although there is likely to be considerable genotypic and phenotypic variation (Felker 1979). *Prosopis* plants do, however, have physiological capabilities which enable them to withstand prolonged hot, dry conditions.

Several studies have been conducted on water use by *P. glandulosa*. Like desert xerophytes, it can acquire soil water which is held with high matrix forces. Individuals have been recorded to: extract soil water as low as -1.5 MPa at depths to at least 150 cm (Haas and Dodd 1972); survive under soil water potentials as low as -3.0 MPa (Fisher *et al*. 1972, Wan and Sosebee 1991); and actively photosynthesize at water potentials less than -4.0 MPa (Strain 1970). Mechanisms for minimizing water loss include reducing stomatal conductance, changing leaf orientation, increasing wax accumulation and pubescence, increasing leaf thickness, decreasing leaf size, reducing canopy development and shedding leaves (Wan and Sosebee 1991).

Stomatal conductance is very responsive to soil water availability and dryness of the air, with up to six-fold reductions in average daily leaf conductance being observed as a response to reduced soil water availability (Wan and Sosebee 1991). Small leaf size allows greater conduction of heat when stomatal closure prevents evaporative loss (Mooney *et al.* 1977). However, leaf temperatures remain close to ambient, rather than several degrees cooler like some desert species, further conserving water (Wan and Sosebee 1991). *P. glandulosa* also stores a considerable amount of non-structural carbohydrates in roots and stems, which buffers the plant against environmental stresses, and serves as a carbohydrate source for new leaf growth following defoliation (Cralle and Bovey 1996).

Phenology

Leaf loss and subsequent dormancy may occur in late autumn and early winter. A combination of low soil moisture, prior drought, cold temperatures, and shortening day length contribute to the timing of leaf drop of *P. glandulosa* (Mooney *et al.* 1977). Leaf development or budbreak usually recommences in spring as temperatures (and photoperiod) increase, and is independent of rainfall for most species, including *P. velutina* and *P. glandulosa* (Solbrig and Cantino 1975, Mooney *et al.* 1977, Nilsen *et al.* 1991). Winter defoliation rarely occurs under Australian conditions, although it has been observed in some years in New South Wales and south-western Queensland. In northern parts of Australia, where winter temperatures are higher, plants may continue to develop slowly through the winter period (Parsons and Cuthbertson 1992). Some genetically based variation in the timing of leaf bud burst and leaf drop has been observed in populations of *P. glandulosa* (Peacock and McMillan 1965).

Flowering of mesquite occurs predominantly in spring and early summer, with pods taking two to three months to mature and falling in late summer. Flowering can occur over a long period, an average of 105 days for *P. velutina* in one study in the Sonoran Desert (Arizona), although this may vary between species (Simpson 1977). Plants generally produce a single crop of seeds per season, although four crops in one year have been recorded on *P. glandulosa* (Mooney *et al.* 1977).

Mycorrhizae and nodules

Reports on nodulation of mesquite by mycorrhizae are often contradictory. Screenings for nodulating ability under controlled conditions have routinely yielded positive results for the genus, but efforts to recover nodules from the roots of mesquite trees in the field have been much less successful (Allen and Allen 1982, Johnson and Mayeux 1990). Johnson and Mayeux (1990) found nodules on *P. glandulosa* var. *glandulosa* throughout the soil profiles at some sites, and suggested a significant role for biological fixation in the nitrogen and vegetation dynamics of *Prosopis*-dominated ecosystems.

Reproduction

Floral biology

Field observations in Australia suggest that plants generally produce their first flowers and seeds when they are between two and five years of age, although pod production within one year has been observed under ideal conditions on Mardie Station (Western Australia) (R. Parr personal communication 1999). *P. pallida* probably takes longer than three years to reach reproductive maturity under average rainfall conditions. Over a three-year field study of *P. pallida* in northern Queensland only one of the 12 300 young plants observed for three years following germination reached reproductive maturity, and it was growing in a more favourable location than most (A.C. Grice, unpublished 1999).

Mature trees of mesquite have been reported to produce as many as 10 000 inflorescences per year, with *P. velutina* averaging 6000 per year (Simpson *et al.* 1977). Each inflorescence typically averages between 200 and about 350 individual flowers for the Australian *Prosopis* species (Burkart 1976, Simpson *et al.* 1977, Oliveira and Pires 1988), but numbers can vary with environmental conditions (Lee and Felker 1992). *P. velutina* flowers mature from the base of the inflorescence to the tip, requiring 3–7 days from appearance of the first stigma to drying of the last flower, with each individual flower being fully open only for one day (Simpson *et al.* 1977).

The primary mode of pollination is likely to be by invertebrates. There is a large amount of nectar available and an abundance of insect visitors (Simpson 1977, Simpson *et al.* 1977). Inflorescences contain between 4 and 13 mg of sugar and between 9 and 27 mg of pollen. Diptera, Coleoptera, Lepidoptera and Hymenoptera have all been identified as major flower visitors. Several species of section Algarobia (including *P. velutina*) are self incompatible, and this is likely to be the case for all species (Simpson 1977, Hunziker *et al.* 1986). This may explain field observations made at certain locations in Queensland where mature, isolated mesquite plants do not appear to have produced any seedlings (Csurhes 1996).

Only a small fraction of flowers initiate fruit and subsequently produce mature pods. A single *P. velutina* flower spike can produce from 1 to 30 fruits, but many produce none (DeLoach 1988). In one study only 2–3 flowers in every 1000 initiated fruit and approximately 1 in 10 000 flowers resulted in mature fruit (DeLoach 1988). Other studies have reported higher success rates, with 6.5 mature pods resulting from every 1000 flowers in one study (Solbrig and Cantino 1975) and eight mature pods (at an average of 2.15 pods per inflorescence) in another (Simpson *et al.* 1977). The number of seeds per pod is variable: 5–18 for *P. glandulosa*, up to 25 for *P. juliflora*, 10–17 for *P. velutina* and up to 30 for *P. pallida* (Burkart 1976).

Flowering and fruiting can vary dramatically between trees and seasons, even within a population (Glendening and Paulsen 1955, Mooney *et al* 1977). Moisture availability can be important, with drier conditions prior to and during flowering resulting in three to four times more pods being produced in some studies (Nilsen *et al.* 1991, Lee and Felker 1992). Rainfall during the flowering period can result in low fruit production (Mooney *et al.* 1977). Field observations in northern Queensland suggest that this also appears to be the case for *P. pallida* (P. Jeffrey personal communication 1999).

Seed production

All species of mesquite are prodigious seed producers (Kingsolver *et al.* 1977, Brown 1996), although there are limited figures available on seed production and none are available for mesquite in Australia. The most comprehensive estimate is for *P. velutina.* In North America samples of fruits taken over a three year period from 30 young trees with crown diameters of 4 m yielded an average of 0.7 kg dry weight of pods per year per tree. These fruits contained an estimated 5000 seeds (Glendening and Paulsen 1955). Larger mature trees with canopies of about 6 m were estimated to be capable of producing more than 16 kg of fruits per year per tree, or about 140 000 seeds (Kingsolver *et al.* 1977). Seed production can, however, be considerably higher. An 8.5 m high *P. glandulosa* tree yielded 43 kg and 50.9 kg of pods (DW) in two consecutive years (in a region with mean annual rainfall of 100 mm). *P. pallida* has been reported to yield 4000–20 000 kg pods ha^{-1} yr^{-1} in Hawaii (Felker 1979), and a *P. juliflora* tree in Brazil produced an average of 367 kg of pods over three successive years (Silva 1988).

Seed dispersal

The dispersal of mesquite seed occurs at different scales and involves many agents. On a global scale, humans have been the major dispersal agent, transporting seeds to many parts of the world for various purposes. Within Australia most infestations have originated from human dispersal. At a landscape scale, mesquite seed can be transported by floodwaters, run-off and by animals. Dispersal by water is likely to be limited to the movement of mature, intact pods which are generally rare because of predation by vertebrates. Dispersal by floodwaters may contribute to the observed concentration of mesquite plants along water courses and in low lying areas (Csurhes 1996), but such a distribution often also correlates with ideal mesquite habitat and possibly with dispersal by vertebrate herbivores. Mesquite pods are highly attractive to herbivores, probably because of the high sugar (16%) and protein (12%) content of the pods (Kingsolver *et al.* 1977). Numerous domestic, native and feral animals have been identified as dispersers of mesquite seed (Mooney *et al.* 1977, Brown and Archer 1987, Harding 1991, Cox *et al.* 1993, Lynes and Campbell 2000).

Lack of vertebrate herbivores can be the primary limitation to the spread of mesquite (including *P. glandulosa* var. *glandulosa*), and studies in south-western United States suggest cattle might be the major limiting factor there (Brown and Archer 1987). In Australia, cattle, sheep, horses, emus, pigs, macropods, donkeys and feral goats are all known to disperse viable seed. However, the extent to which each is contributing to the spread of mesquite has not been clarified. In north Queensland over 200 *P. pallida* seedlings have been observed emerging from individual cattle dung pats (S.D. Campbell, unpublished 2000), and an average of two viable seeds (0–19 seeds per sample) were retrieved from 38 feral pig dung samples (Lynes and Campbell 2000). The largest infestation in Australia occurs on a property that almost exclusively runs sheep (but also has large populations of macropods and emus), implying that cattle may not be the only effective dispersers.

Vertebrate herbivores not only disperse seeds, but can affect their viability and germinability. Seed viability can be protected if pods are consumed before predatory insects can damage the seeds, but mastication reduces viability. Germinability can increase through scarification, as seeds pass through the digestive system (Haas *et al.* 1973, Mooney *et al.* 1977). Herbivores differ greatly in their effect on seed viability and germinability. In feeding trials with horses, cows and ewes, Fisher *et al.* (1959) found that 91, 76 and 16% respectively of *P. glandulosa* seeds consumed passed through the digestive tract unharmed. Of those, 82, 69 and 25% germinated, compared with 26% for seeds which had not passed through any digestive tract. Harding (1991) also reports relatively low viability after ingestion by sheep (an average of 85% of seeds consumed in whole pods were killed). Estimates of germinability of *P. velutina* seeds following ingestion by cattle and sheep of 3 and 13% respectively (Cox *et al.* 1993) are probably misleading, as seeds rather than pods were fed to them.

Physiology of seeds and germination

Seed dormancy and longevity are two key characteristics that make mesquite species so resilient in the environments in which they grow. The hard seed coat ensures that a large proportion of freshly fallen seed is dormant and capable of remaining viable for many years (Tschirley and Martin 1960). Such dormancy ensures that germination is distributed through time, increasing the chance that some seeds will successfully germinate to complete the life cycle (Teketay 1996). Scarification, either mechanical or chemical (e.g. herbivore digestion or fungal attack), and subsequent wetting of the germplasm is required for germination (Brown 1996).

Optimum germination temperatures have been identified for a number of mesquite species, and generally fall between 20 and 35°C. For *P. glandulosa*, optimum temperatures range between 25 and 30°C (Haas *et al.* 1973), with soil temperatures in excess of 35°C capable of reducing emergence by regulating imbibition (Scrifes and Brock 1969). Similarly, *P. velutina* germinates best between 26 and 31°C (Cox *et al.* 1993). At 16°C *P. velutina* failed to germinate and at 38°C, 65% of the seedlings had stunted radicles and black lesions on the root tip. Germination of *P. juliflora* continued to increase from approximately 20% at 10°C to over 80% at 30°C (Teketay 1996). Less moisture is required for germination at optimal temperatures than at higher or lower temperatures (Scifres and Brock 1971), which may be a mechanism to prevent seeds germinating in winter rains (Mooney *et al.* 1977). However, seedling emergence and survival may still be high even when soil temperatures are supraoptimal and soil water is relatively low (Brown 1996).

The length of time that mesquite seed will remain viable will depend on the conditions to which seeds are exposed. Seeds will remain viable indefinitely if kept free of predators and stored in a dry environment and moderate temperatures (Tschirley and Martin 1960). *P. velutina* seeds stored in a laboratory at the Herbarium of Tuscon, Arizona retained 60% viability for at least 50 years (Glendening and Paulsen 1955). Tschirley and Martin (1960) studied the germination and longevity of *P. velutina* seed buried in the soil over a 10 year period under field conditions. In open soil most emerged after two to three years, but some emerged after six years. In jars placed in the soil to prevent direct access of water 63% of seeds remained intact after two years, 47% after five years and 10% after 10 years, of which 86–89% germinated.

In northern Queensland, a study was undertaken to follow the run down of the seedbank of *P. pallida* (A.C. Grice, unpublished 1999). All emerging *P. pallida* seedlings were counted following rainfall. There was no significant decrease in emergence over the following three wet seasons. In the absence of domestic grazing there are two possible explanations. Firstly, dormancy mechanisms may be controlling the availability of seed to germinate, leading to a staggered pattern of germination and emergence and, secondly, native and feral animals have transported seeds into the clean areas. It is likely that both factors were contributing in this situation.

Seedling establishment

Following seed fall, most mesquite seeds will remain close to the soil surface. A study undertaken in northern Queensland to determine the location of *P. pallida* seed in the soil profile found 97, 2 and 1% of seed at depths of 0, 0–1 and 1–3 cm respectively (B.C. Lynes, unpublished 2000). Emergence of *P. pallida* in a cracking light medium clay was highest for seeds located at 2 cm depth, intermediate if on the soil surface and minimal if buried at 5 cm depth (Barker *et al.* 1996). Cox *et al.* (1993) determined the effects of planting depth and soil texture on emergence and seedling growth of *P. velutina*. Soils compared were silty clay loams and sandy loams, with seeds planted at depths of 0, 1, 2, 4, and 8 cm. Germination of seed placed on the soil surface averaged 95%, but only 20% of *P. velutina* radicles were able to penetrate the surface soil. Seedlings with exposed radicles died in 3–6 days. Emergence was greatest at 1–2 cm in sandy loam soils and decreased with increasing depth thereafter. No emergence occurred in silty clay loam soils once planting depths exceeded 2 cm. These findings suggest that with most seed located on the soil surface, large-scale recruitment will be dependent on prolonged rainfall events that maintain moisture levels on the surface for sufficient time to enable germination to occur and for radicle penetration into the soil. Deposition in faeces could potentially also affect seedling survival, by providing a relatively moist and nutritious microenvironment, at least with herbivores such as cattle, horses and possibly emus and pigs. It may also suppress competition from surrounding herbaceous species (Brown and Archer 1987).

Young seedlings appear to have a marked ability to survive damage from livestock trampling and herbivory by small mammals or insects, provided cotyledons remain intact (Tischler *et al.* 1998). Extensive studies in the United States on *P. glandulosa* var *glandulosa* (Tischler *et al.* 1998) showed that while clipping below cotyledons was lethal, removal of the epicotyl was not, although seedling growth could be restricted. *P. glandulosa* seedlings can survive top-removal within two weeks of emergence (Weltzin 1990), after one year they can survive intense prairie fires (Wright *et al.* 1976).

Full sunlight is necessary for optimal growth of *P. glandulosa*, and a 70% reduction in solar radiation reduces seedling survival and growth (Bogusch 1951). In a glasshouse study of *P. glandulosa* seedlings it was found that reducing sunlight by 48 and 63% had no effect on the rate of leaf appearance, seedling height and shoot/root ratio, but biomass accumulation was reduced by 24 and 38% respectively (Vilela and Ravetta 2000).

Vegetative reproduction

All species are capable of regenerating from basal buds located up to 20 cm below the soil surface. When top growth is removed, subsequent growth can be expressed as either single stemmed trees or multiple stemmed shrubs. New shoots do not develop from the roots (Fisher *et al.* 1959).

Population dynamics

Most mortality occurs in the seedling stage, and population dynamics will be driven by the number of cohorts produced and the proportion of seedlings in each which survives to the more hardy juvenile stage (Brown and Archer 1989). Mature plants tend to be extremely resilient and long lived and consequently only minor reductions occur, unless control techniques are imposed.

Across the current distribution of mesquite, seedling establishment and survival can occur even in years when precipitation is below average (Brown and Archer 1990, Keir *et al.* 1999). In a three year study of seedling dynamics of *P. pallida* in northern Queensland, 11 cohorts were identified according to distinct rainfall events on which they germinated (Keir *et al.* 1999). Seedling density was positively correlated with the density of reproductive trees (Figure 8), and was sometimes massive (over 58 000 seedlings per hectare). Survival of cohorts after 12 months averaged 4%, ranging from 0 to 16% (Figure 9). Cohorts that exhibited high survival tended to receive high initial rainfall and good follow up rainfall soon after germination. Rainfall in each year of the study was, however, below the long-term average of 396 mm, demonstrating the invasive potential of this plant.

Major recruitment events are likely to be episodic, occurring when seed banks are large and when the growing seasons have protracted wet periods (Archer *et al.* 1988, A.C. Grice, unpublished 1999). Anecdotal data in Australia support this pattern. For example, dramatic increases in the size and density of infestations on Mardie Station (Western Australia) and in north-western New South Wales were both associated with above average rainfall years (Meadly 1962, Condon and Alchin 1979). Conditions suitable for recruitment events can be widely spaced. Simulations of precipitation patterns indicated episodic woody plant establishment events have occurred six times in the past 97 years in an approximately 300 mm rainfall region in New South Wales (Harrington 1991). However, the typically long-lived nature of mesquite plants ensures that they can easily bridge periods between major recruitment events.

Invasion of grasslands by mesquite can ultimately result in closed-canopy woodlands. In Texas, invasion by *P. glandulosa* resulted in a linear succession from grassland to a woodland of *P. glandulosa* (Archer *et al.* 1988, Scanlan and Archer 1991). Infestations that consisted of discrete, scattered shrub clusters eventually expanded and coalesced into a closed canopy. Mesquite plants are successful invaders of uplands (Wright *et al.* 1976, Archer *et al.* 1988, Bahre and Shelton 1993), although invasions typically begin along low lying areas, water courses and bore drains.

Importance

Opinions concerning mesquite have changed through time (Schuster 1969). It was first described as a valuable plant. Towards the end of the 1920s and early 1930s it became regarded as a noxious species on grazing lands, and by the late 1930s and early 1940s problems relating to thicket formation were being recognized by conservationists. Since 1950 most publications deal with its undesirable properties and means of control. More recently, research on beneficial properties has been renewed, particularly as a resource for developing countries and as a means of minimizing weediness (Felker and Moss

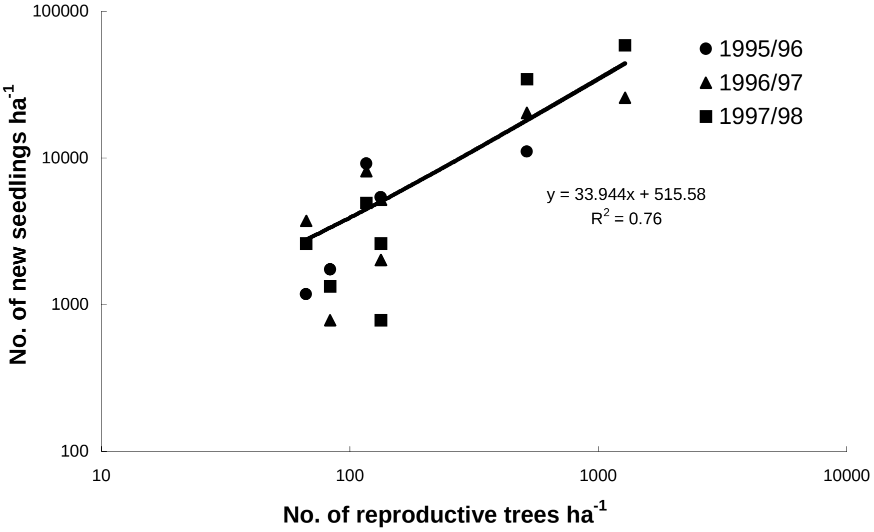

Figure 8. Relationship between seedling emergence and reproductive plant density for different cohorts identified over a three year period (Adapted from Keir *et al.* 1999).

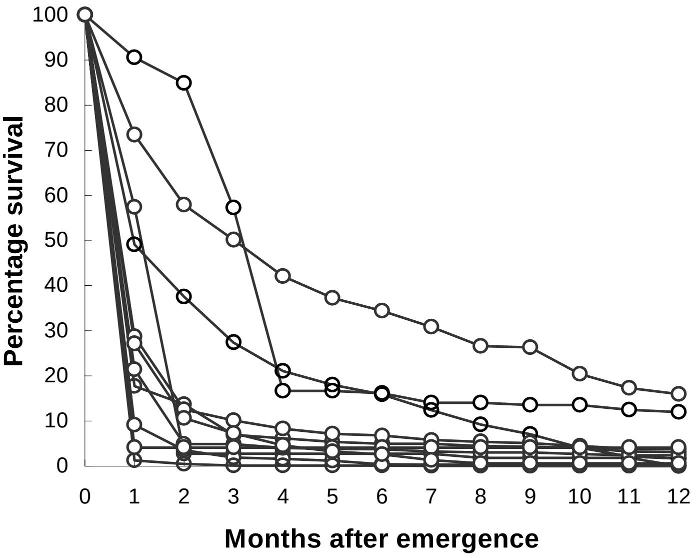

Figure 9. Twelve month survivorship curves for 11 cohorts of *Prosopis pallida* that emerged between October 1995 and April 1998 (Adapted from Keir *et al.* 1999).

1996, Tewari *et al.* 1998). In Australia the actual and potential negative economic and environmental impacts of mesquite are considered to far outweigh any potential benefits (NWS 2000).

Detrimental

The primary problem with mesquite is its ability to rapidly form dense, thorny forests (DeLoach 1985, Harding 1987, Gibbens *et al.* 1992). For the pastoral industry this translates into decreased carrying capacity through loss of grass cover by replacement and by competition for limited soil water (DeLoach 1985). For example, in one study in New Mexico, the carrying capacity of pastures infested by shrubs (mostly mesquite) was reduced by 75% over a 35 year period, while the carrying capacity of mesquite-free pastures remained unchanged (Paulsen and Ares 1961). In arid regions of the United States, grass production is consistently reduced by 50–90% as a result of mesquite (DeLoach 1985). Ultimately, loss in grass cover through mesquite invasion can result in serious erosion and sand dune formation (DeLoach 1985), although mesquite has also been reported to restore degraded soils and prevent dune formation elsewhere in the world (see below). Invasion of rangelands by mesquite also results in problems in stock management, impedes stock access to water, and makes the maintenance of water points difficult. Other effects include thorns injuring the hooves of animals and puncturing vehicle tyres, the poisoning of livestock through excessive feeding on pods (Alder 1949, Dollahite 1964), and serious allergenic problems in humans (DeLoach 1985).

Australian rangelands are of both pastoral and conservation significance. The transformation of open rangelend to closed-canopy thorn-forests (Figure 10), and the associated loss of grass cover and erosion, will therefore have a serious impact not only on the pastoral industry, but also on conservation qualities of the environment. Direct effects include the replacement of native flora and the habitat of native fauna, the provision of refuges and food for feral animal pests such as pigs, and the alteration of soil properties, including the nitrogen balance (Felker 1979, DeLoach 1985). High transpiration rates could also have significant effects on the water economy of arid areas (Leakey and Last 1980), although a study by Dugas and Mayeux (1991) does not support this at one site in Texas. In South Africa *Prosopis* is estimated to reduce the mean annual runoff by approximately 481 million m^3 (Impson *et al.* 1999). However, actual and potential environmental consequences of mesquite in Australia have not been documented beyond obvious structural changes in vegetation, but they could include altered ecosystem properties at several scales (Archer *et al.* 1988, Gordon 1998).

Figure 10. Closed-canopy *Prosopis pallida* thorn-forest near Hughenden (Queensland).

Actual costs to Australia. Infestations in Australia are still in the early stages, with significant losses to livestock production through decreased carrying capacity probably being restricted to parts of one property in Western Australia (hybrid *Prosopis*), one property in south-western Queensland (*P. velutina* × *P. glandulosa* var. *torreyana*), and several properties in northern Queensland (*P. pallida* and hybrid *Prosopis*). Of those, the largest impact is on Mardie Station in Western Australia where dense infestations have resulted in the loss of production on at least 30 000 ha of rich alluvial country. In northern Queensland production losses have been estimated to be about $25 000 per year (M.P. Bolton, unpublished 1989). In addition, increased difficulty in mustering is likely to incur indirect costs on at least some of these properties.

To date, the main costs of *Prosopis* infestations in Australia have been in control and eradication efforts, particularly in New South Wales (Alchin and Condon 1983), Western Australia (Ritchie 1983a,b) and Queensland (March 1996). The largest expense is in Queensland where the Department of Natural Resources allocated about $4 million between 1995 and 1999 to an eradication program (NWS 2000), supplemented by over $614 000 from landholders.

Potential costs to Australia. Although the current extent of mesquite infestations in Australia is limited, there appear to be few climatic or biological limitations to the eventual spread of mesquite over much of semi-arid and arid Australia. Furthermore, all *Prosopis* taxa present in Australia have already demonstrated their ability to rapidly form impenetrable thickets. However, the various *Prosopis* taxa will undoubtedly differ in their potential distribution, based on differences in their biology.

The associated costs to Australia of significant increases in distribution and density of *Prosopis* have not been predicted. However, some indication of the potential magnitude of the problem can be obtained from the United States, where *P. glandulosa* and *P. velutina* infestations are extensive. Direct costs were estimated at $US200–500 million annually, and losses to total economic activity were estimated at approximately three times this amount (DeLoach 1985). However, costs may now be at least partially off-set by recent developments in industries which utilize mesquite as a resource (see later). Potential costs to Australia are likely to differ between *Prosopis* taxa according to their potential distribution and densities and the relative costs of effective management options.

Beneficial

Mesquite species, including those now naturalized in Australia, have been an invaluable resource for indigenous communities from pre-historic times (Felger 1977, D'Antoni and Solbrig 1977, Fagg and Stewart 1994, Franco and Aguirre 1996). Every part of the plant was utilized, serving as a primary resource for food, fuel, housing, weapons, tools, fibre, medicine, religious uses, and other purposes. Their value as shade and wind breaks continues to be appreciated, and industries have developed around mesquite products, including charcoal, timber, honey, flour, supplementary livestock feed, paper, medicines, alcohol, tannins and gums (DeLoach 1985, Zimmermann 1991, Fagg and Stewart 1994, Csurhes 1996, Kanzaria and Varshney 1998). Such industries can help offset detrimental aspects of mesquite through changing landuse (Miller 1996).

Mesquite is currently being promoted as an important contributor towards the development of productive but sustainable agriculture in dryland regions of the world, particularly for economically poor communities (Fagg and Stewart 1994, Sene 1996). Many mesquite species have an extreme resistance to heat, drought, salinity and alkalinity, drifting sand, grazing and repeated cutting (Fagg and Stewart 1994, Tewari *et al.* 1998, p. 3). Not only do they provide resources under inhospitable conditions, but they are valuable for stabilizing land (including sand dunes) and reclaiming degraded soils (assisted by their nitrogen-fixing ability) (Felker 1981, Singh 1996, Ahmad *et al.* 1996, Diagne 1996). However, even under these circumstances the benefits of mesquite are frequently compromised by its weediness (Fagg and Stewart 1994, Kumar *et al.* 1998). New research is aimed towards improving management techniques, developing better cultivars, and the processing, marketing and utilization of potential products (Felker and Moss 1996). In Australia mesquite was introduced for its beneficial aspects, primarily as hardy ornamentals, but occasionally as shade and fodder trees for livestock. They are still appreciated at low densities for shade by some pastoralists, although all 34 landholders randomly surveyed in the McKinlay Shire (north-western Queensland) considered mesquite to be a liability (N. March, unpublished 1995).

Legislation

Prosopis species have been declared as noxious weeds in all mainland states of Australia, and in the Northern Territory. In Western Australia *Prosopis* was first declared in 1951 and is now a declared plant in the eradication category P2 in all parts of the State except on Mardie Station, where the size of the infestation is so great that a P4 (prevention of spread) declaration has applied since 1988. In South Australia all *Prosopis* species are proclaimed plants on Schedule 1, obliging landholders to notify the Animal and Plant Control Commission and their local board of any infestations, and to destroy all plants. In New South Wales *Prosopis* species are declared a W1 in all councils in the far-west eastward to the Newell Highway, obliging landholders to notify government authorities and infestations to be continually suppressed and destroyed. In Queensland *Prosopis* was first declared in 1954 (as *P. juliflora s.l.*). Now *P. pallida* (syn. *P. limensis*) is declared in category P3 (to be reduced), *P. velutina* (formerly known as *P. flexuosa*), *P. glandulosa* and all known *Prosopis* hybrids are declared in category P2 (to be destroyed), and all other *Prosopis* species are declared in categories P1 (introduction prohibited) and P2. In Victoria *Prosopis* is a state-prohibited weed. In the Northern Territory it is not to be introduced, and *P. pallida* is a Class B weed (growth and spread to be controlled).

Weed management

History

Mesquite was recognized as a threat to the Australian pastoral industry by 1944 (White 1944), although control programs were not initiated until the 1950s. Since then eradication programs have been commenced in Western Australia, Queensland, New South Wales and South Australia. In Victoria naturalized mesquite was first reported in the 1980s, and infestations are eradicated on discovery. A brief overview of how mesquite control has been tackled in each state serves to illustrate the diversity of approaches that have been taken, and the difficulties encountered.

Western Australia was the first state to initiate control programs, with major control trials beginning on Mardie Station in 1954 (Meadly 1956, 1962). By 1962 control efforts by local authorities, pastoralists and town residents had resulted in a marked reduction in the number of trees on other stations and in coastal towns, and the return of cleared areas on Mardie Station to useful herbage (Meadly 1962). Control efforts were continued throughout the 1960s and early 1970s but *Prosopis* still spread, as the cost of control exceeded resources of individual landholders (Ritchie 1983a). From 1976 funds, obtained through a rate on pastoral leases and a government contribution, allowed for a more active approach to mesquite control, as did contributions from the Commonwealth government work training program (Ritchie 1983b), and resulted in significant reductions in many infestations through the late 1970s and 1980s. However, very little control work has been done in Western Australia since the early 1990s and many infestations are returning. Exceptions include an eradication program on Yeeda Station, where patrols are conducted annually by helicopter for mesquite regrowth (M. Everett personal communication 1999), and the 1 km wide buffer zone placed around Mardie station in 1991, which is patrolled annually by quad-bike (R. Parr personal communication 1998). The Pilbara Mesquite Management Committee has recently (April 2000) been initiated to contain and manage the infestation on Mardie Station, and is represented by private and government stakeholders.

The Queensland Government commenced control work in 1978. Initial work (using basal-bark spray techniques) focused on the infestation in south-western Queensland and continued through until 1989, resulting in a reduction of the initial dense infestation from 4000 to 3000 ha and the removal of much of the sparser outlying infestations. Responsibility for control was then passed to landholders, but they were unable to keep up with control strategies, and re-establishment occurred. In northern Queensland extensive survey work and research to develop control techniques was conducted by the State Government between 1986 and 1992. It was concluded that eradication was feasible. A state-wide mesquite eradication program was initiated in 1992 and is continuing. Outcomes have been dramatic, with dense infestation in the southwest being reduced to approximately 500 ha and a reduction of infestations in the north from 100 000 to 40 000 ha.

In New South Wales mesquite was formally acknowledged as a potential problem by the Western Land Commission in 1967 and some landholders commenced treatment at their own cost (Alchin and Condon 1983). By 1969 it became apparent that control was beyond the capacity of the individual and in 1970 State Government funds were given to the Western Lands Commission to initiate a control program with the aim of eradicating all mesquite from the Western Division (Condon and Alchin 1979, Alchin and Condon 1983). This program was controlled and funded by government agencies through until 1992 (E. McCormick personal communication). By 1983 205 000 plants had been killed (96.6% by the Western Lands Commission) and only 15 of the original 43 properties with infestations were still ‘active’, of which two (White Leeds and One Tree stations) were considered potentially serious (Alchin and Condon 1983). By 1992 no known mesquite plants remained on One Tree or White Leeds, and few or none elsewhere (E. McCormick personal communication 1998), and the responsibility for eradication was transferred to the landholders. Virtually no control work was done between 1992 and 1997, which resulted in the return of significant infestations on White Leeds and One Tree and reports of mesquite on a further 20 properties near Milparinka and Broken Hill (P. Walker personal communication 1997). Government subsidies commenced in 1997, resulting in control work by landholders on 20 stations but this support ceased after the 1999/2000 season (P. Gray personal communication 2000).

In South Australia *Prosopis* was first acknowledged as a potential threat in the late 1960s and control work was being conducted by 1970. A concerted effort to eradicate mesquite from the state has been overseen by the Animal and Plant Control Commission since at least the mid-1980s. Infestations at Cockburn, Malkorky (Radium Hill) and Whyalla were considered eradicated by 1991 (Michelmore, unpublished 1991), but follow up surveys have not been done at Cockburn or Malkorky. Isolated trees remain in and around Woomera, in Port Augusta and the surrounding sandhills, and on Wallerberdinna (Lake Torrens). These are treated when found (30–40 plants were treated around Port Augusta since 1995; more than 20 plants around Woomera in 1998) (N. Secomb personal communication 1998).

The success of eradication (and control) programs is difficult to assess, as long-term monitoring of infestations to detect post-control regrowth is rarely conducted. However, it is apparent that although there has been a reduction in size of many of the larger infestations only relatively few, minor, infestations have been successfully eradicated. In most instances eradication efforts have been thwarted by difficulties in locating plants at low densities, long-lived seed banks, the withdrawal of resources before eradication is achieved, and by disagreement between landholder and government agencies regarding responsibility for control work. A nationally coordinated management strategy which aims to confine and eventually eradicate mesquite from Australia was developed for mesquite in 2000 (NWS 2000).

Available control techniques

There is a range of control techniques available for mesquite. However, the most appropriate option will depend primarily on which particular species is to be treated and the location, density, size and situation (e.g. uplands or along watercourses) of the infestation. The main options available to landholders in Queensland have been outlined elsewhere (Jeffrey and March 1995, Csurhes 1996). Extensive management techniques for *P. glandulosa* var. *glandulosa* have been developed in Texas (Scifres *et al.* 1985, Hamilton *et al.* 1989). It is generally concluded that a combination of techniques is necessary before the required control is achieved. Follow up control work can be essential to avoid the regrowth of multi-stemmed trees, which can exacerbate impact on surrounding vegetation and can make subsequent treatment more difficult (Archer 1989, Brown 1996).

Herbicides

Prior to it being no longer produced 2,4,5-T was the most widely used chemical for controlling mesquite in Australia (Milthorpe 1975, Condon and Alchin 1979) and overseas (Jacoby *et al.* 1981, Jacoby and Meadors 1983, Meyer and Bovey 1985). Today, there are a limited number of registered chemicals available for the control of mesquite species in Australia, and a range of application methods: basal bark spraying, cut stump technique and foliar spraying. Recommended application rates are currently the same for all species. However, recent work suggests significant interspecific differences in responses (Sparkes and Panetta 1999). They compared responses of *P. pallida* and *P. velutina* to foliar applications of metsulfuron methyl at 1:200, fluroxypyr at 1:800, glyphosate at 1:267, triclopyr / picloram at 1:800, triclopyr ester at 1:800 and clopyralid at 1:800. The treatments applied had different effects on the two species, with mortalities from metsulfuron, fluroxypyr and triclopyr showing the greatest interspecific differences. *P. velutina* consistently showed less response to these herbicides at the tested dosages. Further research is currently underway to develop more appropriate chemical options for particular species. However, because of the relatively small areas occupied, it may not be considered an economic proposition for chemical companies to seek and obtain registration for individual species.

In Australia the basal bark and cut stump techniques using either triclopyr or triclopyr / picloram (triclopyr present as the butoxyethyl ester and picloram present as the isooctyl ester) are the recommended options for treating established plants, and result in kills of >97% if properly applied (Jeffrey and March 1995). Best results using basal bark application are achieved when the plants are actively growing, whilst the cut stump technique can be undertaken at any time of the year (Jeffrey and March 1995, Csurhes 1996). Costs become prohibitive at higher densities. Initial treatment of dense *P. velutina* × *P. glandulosa* var. *torreyana* in south-western Queensland cost approximately \$583 ha^{-1}, with a further \$150–200 ha^{-1} needed for follow-up (R. Cobon personal communication 2000).

Triclopyr / picloram (triclopyr present as the butoxyethel ester and picloram present as the hexyloxypropylamine salt) is registered as a foliar application, preferably for young plants under 1.5 m in height. This is an effective option (>90% kill) for dense thickets of seedlings, provided a wetting agent is added to the mixture (Jeffrey and March 1995). The risk of reduced efficacy if rainfall occurs soon after application appears to be minimal if results on *P. glandulosa* are indicative of *Prosopis* generally. Bovey *et al.* (1990) tested a range of foliar chemicals (including triclopyr and picloram), and concluded that even if rainfall occurred within 15 minutes of application, mortality of *P. glandulosa* was generally unaffected.

No chemical is currently registered for aerial application in Australia, although the McKinlay Landcare Group in northern Queensland undertook a demonstration trial using different rates (3, 4 and 6 L ha^{-1}) of triclopyr / picloram. When applied from a helicopter, this treatment cost between \$250–280 ha^{-1} with efficacy greater than 85%.

Soil applied herbicides, such as hexazinone and tebuthiuron, have been tested in Australia with mixed results (P. Jeffrey personal communication 2000). Generally poor efficacy combined with application difficulties in dense thickets, cost, and lack of selectivity has resulted in their non-registration in Australia. Studies on tebuthiuron in the United States concluded that it was ineffective against *P. glandulosa* (Meyer and Bovey 1985).

Extensive research into the development of herbicides for mesquite control has been undertaken in the United States, particularly in Texas (Jacoby *et al.* 1981, Jacoby and Meadors 1983, Meyer and Bovey 1985). Most of this research has been on *P. glandulosa* and has resulted in a wide selection of chemicals and application techniques being made available to land managers. These include triclopyr ester, 2,4-D amine, hexazinone, dicamba, clopyralid, picloram, dicamba / 2,4-D and 2,4-D / picloram (Welch 1995). Numerous mixtures have also been developed for use in specific situations and locations (Welch 1995). Despite this wide choice, recent extension efforts have concentrated on the promotion of two easy-to-use individual plant treatments known to result in high levels of mortality (Ueckert *et al.* 1999). These are the foliar spray containing 0.5% clopyralid monoethanolamine salt + 0.5% triclopyr butoxyethyl ester applied in a 5% diesel fuel / 95% water emulsion or in water containing 0.25% surfactant, and basal bark application to the lower 30 cm of all stems of 15 to 25% triclopyr butoxyethyl ester in a diesel fuel carrier. Foliar spray is recommended for use in the spring and summer once leaves have turned dark green and the soil temperature at 30 cm is at least 24°C. Both treatments result in average kills of 80%. Aerial applications of clopyralid + triclopyr at 0.28 + 0.28 kg ha^{-1} produce an average kill of 70%, although there is a wide range in efficacy (15–92%). Economic data based on costs for treating a range of infestation densities using these techniques have been compiled (Figure 11).

The expense of chemical control in rangeland situations in Australia, relative to economic benefits, is a major limitation to their use. Consequently herbicides are generally used by landholders only as a spot spraying treatment to control seedlings and / or light infestations of established plants. So far there are no effective and affordable chemical treatments for control of large and dense infestations.

Mechanical options

Mechanical control is likely to be most effective in early spring, when root reserves are low and not being replenished (Parsons and Cuthbertson 1992). Mechanical techniques used for mesquite in Australia include grubbing, blade ploughing and chaining. The efficacy of these is dependent on the species being treated and the size and density of the infestation. For scattered infestations, grubber attachments on bulldozers and tractors can prove effective, as long as the size of the equipment is matched to the size of plants to be treated. Csurhes (1996) reported that trials on grubbing of *P. velutina* were effective, with best results achieved in late winter and autumn in a year with a normal wet season. The success of this technique is dependent on cutting the root system below the ground surface (approximately 30 cm) to reduce the risk of reshooting. Multi-stemmed plants have a tendency to reshoot if they are broken off at ground level. The mostly single stemmed *P. pallida*, on the other hand, is relatively easy to kill, with a 99% mortality recorded following bulldozing (Campbell *et al.* 1996).

The use of grubbing and bulldozing is cost effective at low densities but becomes relatively expensive and impractical at high densities. For example, bulldozing a dense *P. pallida* infestation can cost over \$200 ha^{-1}. Consequently, these techniques are only appropriate for treating light infestations or perhaps small areas of thick infestations (Campbell *et al.* 1996). However, P. Jeffrey (personal communication 2000) suggests that other options such as stick-raking may be more cost effective and should be investigated further.

For denser infestations covering large areas, more cost effective treatments are needed. Blade ploughing has been used as part of control efforts on both *P. velutina* (Csurhes 1996) and the hybrid infestation at McKinlay (S.D. Campbell, unpublished 2000). In both instances, control of existing plants was excellent, but heavy rain soon after treatment resulted in substantial seedling recruitment. In the case of *P. velutina*, some 1100 seedlings ha^{-1} were recorded more than a year after treatment. Provided follow up control is implemented before seedling regrowth becomes reproductive, promotion of seedling germination may be an advantage, as the seed bank will be depleted faster. A desirable feature of blade ploughing dense infestations of mesquite is the subsequent increased pasture growth that occurs after treatment, especially if the area is reseeded. This improved pasture growth often offsets the cost of the operation (Csurhes 1996). Conversely, if mesquite is treated in 'grassy' areas, substantial mortality of grasses may occur and subsequent pasture recovery may be slow (S.D. Campbell, unpublished 2000).

Costs of treating a *P. velutina* infestation in 1992 using a 4 m Homan blade plough pulled by a D-9 Dozer was \$A148 per hour, with approximately 1.14 ha covered per hour (Csurhes 1996). The cost of treating a hybrid infestation at McKinlay, northern Queensland, using a 3.5 m front mounted Ellrott blade plough attached to a D-6 Dozer, was determined for a range of densities in 1997 (Figure 12). Costs ranged from \$A29 ha^{-1} (or 53c tree^{-1}) at the lowest density to \$A107 ha^{-1} (or 20c tree^{-1}) at the highest density (Figure 12).

Chain pulling is by far the cheapest mechanical option but it is often relatively ineffective on mesquite. Single and double chain pulling of *P. pallida* produced 60 and 80% mortality, respectively (Campbell *et al.* 1996). Less than 10% of hybrid mesquite plants were killed following single chaining (S.D. Campbell, unpublished 2000). Csurhes (1996) suggests that this would also be the situation with *P. velutina*, because of the plant's robust nature and potential for regrowth from basal buds. Experimental chaining of *P. pallida* cost about \$A25–54 ha^{-1} for single and double chaining, respectively (Campbell *et al.* 1996). On a larger commercial scale these costs would probably be lower.

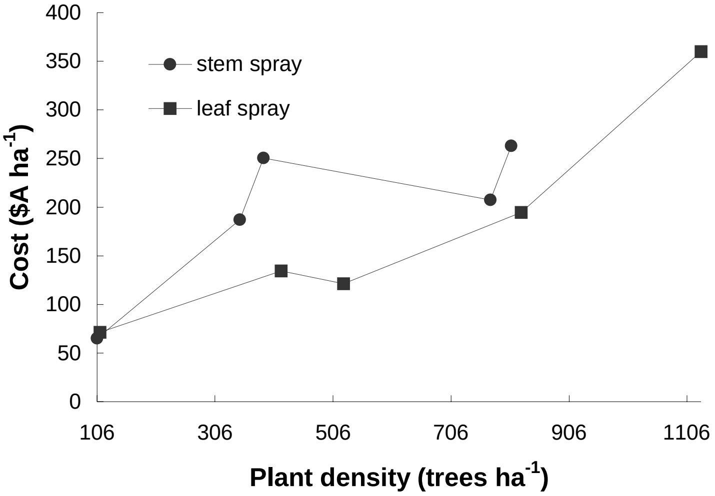

Figure 11. Total cost in \$A per hectare for the Brush Busters foliar spray and basal bark treatment as related to *Prosopis glandulosa* density. Aerial application costs remained at a constant \$A255 ha^{-1} irrespective of density (Adapted from Ueckart 1999).

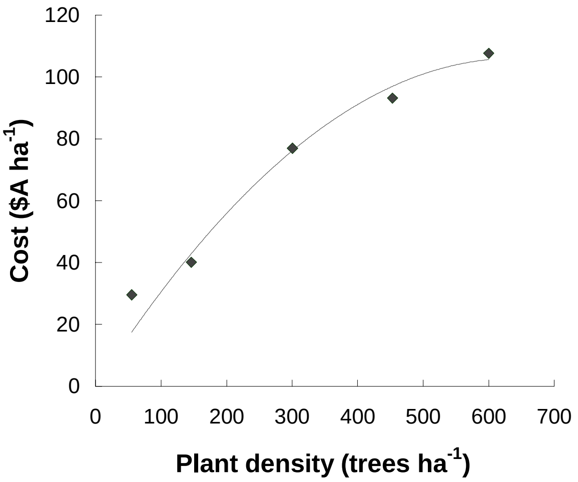

Figure 12. Relationship between cost of treatment and tree density for hybrid mesquite infestation (McKinlay, northern Queensland) using a 3.5 m front mounted 'Ellrott' blade plough (S.D. Campbell, unpublished 2000).

Fire

Recent studies undertaken in northern Queensland have found *P. pallida* to be extremely sensitive to fire. Changes in plant density and total stem basal area of *P. pallida* were compared between burnt and unburnt plots over a two year period following a single fire (Campbell and Setter 1999). Burning significantly decreased the density and total stem basal area of the initial *P. pallida* infestation. Three months after burning only 8% of the original 1760 plants ha^{-1} remained alive, compared with 100% survival in control plots. Over the ensuing 18 months, a further 2.5 and 21% of the original plants died in burnt and control plots, respectively. Ninety percent of control plants that died were young, less than 0.5 m in height (S.D. Campbell, unpublished 2000). Burning also reduced recruitment of *P. pallida* during the two post-fire years. The decrease in the first year was probably associated with a reduction in the size of the seed bank through fire-induced seed mortality. Differences in the second year, on the other hand, were attributed to fewer reproductive trees contributing to the seed bank in burnt plots. *P. pallida* seeds located on the soil surface are also susceptible during burning (B.C. Lynes, unpublished 2000). The number of viable seeds of *P. pallida* on the soil surface was reduced from 82 seeds m^{-2} before the fire to 6 seeds m^{-2} after the fire. There was no difference in viable seed numbers of pre- and post-burn samples of buried seeds.

Preliminary data from burning on Mardie Station (Western Australia) suggests mesquite taxa present there are also susceptible to fire (R.D. van Klinken, unpublished 2000). Mortality in April 2000 from a hot fire in the previous November averaged 88% (n = 99), with mortalities of 60% or more in all size classes. A further 9% of trees were top-killed and no seedlings were found, despite being common in nearby unburnt areas.

Data from overseas suggest that the other *Prosopis* species present in Australia are relatively fire tolerant. Seedlings and juveniles are typically most sensitive, but most older plants regenerate from bud zones (Hamilton and Scifres 1982, Martin 1983, Bock and Bock 1992). Wright *et al.*

(1976) reported that *P. glandulosa* trees up to 1.5 years of age were readily killed by fire, severely harmed at 2.5 years of age, but were very tolerant of fire after 3.5 years. They concluded that trees older than 3 years were difficult to kill unless they had been previously top-killed by a herbicide treatment. *P. velutina* is also relatively fire-resistant. Only 60% of trees less than 1.25 cm diameter were completely killed and less than 20% of trees >2.5 cm were killed (Glendening and Paulsen 1955). Low mortality rates were recorded in other fire trials with *P. velutina* (Reynolds and Bohning 1956). Even seedlings are fire-tolerant, with only 67% of *P. velutina* plants 10–15 cm high and up to one year old killed by fire in one study, with the remainder resprouting, despite being top-killed (Cable 1961). McLaughlin and Bowers (1982) reported 50% mortality of *P. juliflora* in the Sonoran desert following a wildfire, but suggested that there was an unusually high fuel load because the previous two winters had been exceptionally wet. Fire can, however, impact on the seedbank of these species. For example, all seed of *P. velutina* failed to germinate if located on the soil surface, whilst at 2 cm it was unaffected (Cox *et al.* 1993).

If effective, using fire as a control technique for invasive woody weeds, such as mesquite, offers some advantages over other available methods. In particular, it is relatively inexpensive (Burgess 1987, Hodgkinson and Beeston 1995) compared with chemical and mechanical control techniques and, furthermore, it can be applied over large areas. Even if trees are not killed by fire, top-kill can occur, which eliminates seed production for a number of years (Grice 1997) and causes a temporary reduction in woody cover, which may assist other control techniques and increase grass production. Effectiveness of the treatment depends on how long it takes for plants to return to their pre-burn size. Removal of the surface seed bank through fire can also be advantageous. Hodgkinson and Beeston (1995) quoted costs of \$A0.50–1.20 ha^{-1} for burning of rangelands dominated by *Eremophila mitchellii* Benth. in Australia. Teague *et al.* (1997) estimated that burning for *P. glandulosa* control in Texas would cost around \$US2.50 acre^{-1} (equates to \$A10.60 ha^{-1} based on current conversion rate of \$US0.58 per \$A1.00) for properties using a rotational grazing system and \$US5.00 acre^{-1} (\$A21.20 ha^{-1}) for those using continuous grazing, as additional costs for pre- and post fire grazing deferment have to be included.

A major constraint to using fire is fuel availability and, in pastoral areas, any destocking period required to facilitate the accumulation of fuel will impose an economic cost (Grice 1997). Fuel availability can, however, be increased by integration with other techniques, such as selective mechanical control (S.D. Campbell, unpublished 2000). Kill rates can be affected by timing of the burn, size of tree, heat of burn (fuel, weather conditions, moisture) and location.

Grazing management systems

Cattle are an important dispersal agent for mesquite (Brown and Archer 1987), and their management can therefore help in slowing the invasion process. The increase in density of existing infestations within paddocks can be minimized by preventing access by cattle to infested areas during pod drop. The risk of movement of seed into clean paddocks or properties (e.g. through livestock transport) can be minimized by confining livestock suspected of coming from infested areas to a holding area which is free of seed-producing mesquite for sufficient time to enable the gut to be completely cleared of seeds. No information is available for gut-passage times of mesquite seeds, but *Acacia nilotica* (L.) Del. can take over six days (Mackey 1998). Vendor declarations are being considered as a means to prevent movement of infected cattle between properties.

Grazing management has been recognized for its contribution in regulating the number of seedlings that will survive in grasslands and their relative growth rates, although there are conflicting opinions as to the extent of this occurrence. In some instances, stands of grasses have been reported to reduce seed germination and establishment (Glendening and Paulsen 1955, Bush and van Auken 1995), whilst in other situations, mesquite seeds germinate and seedlings survive in grass stands, even those long protected from grazing by livestock (Brown and Archer 1989). Bush and van Auken (1995) investigated the effect of grass competition on the establishment of *P. glandulosa*. They concluded that seedling growth of *P. glandulosa* in a C4 grassland would be very limited, with successful establishment possible only through gap formation. In contrast, Brown and Archer (1990) concluded that competition from pasture was minimized by the rapid development of roots of *Prosopis* seedlings during their first year of growth, enabling them to access soil moisture beyond the zone effectively utilized by grasses.

Horses and sheep also contribute to dispersing mesquite, and can be managed in a similar way to cattle to reduce seed spread. The movement of native and feral animals is more difficult to manage, although the use of emu-proof fencing is being considered to restrict seed dispersal from Mardie Station (Western Australia). The reduction of feral pig numbers could potentially also reduce seed movement.

Commercial exploitation

The management of mesquite through stand management techniques is promoted elsewhere in the world as a means of commercially exploiting the plant whilst curtailing its weedy aspects (Felker and Patch 1996). Commercialization was suggested as a means for controlling mesquite in Australia by Dodd and Madin (1986). Since then a small company has been established (in 1990) to harvest mesquite products including honey, pods (for flour), mulch (for landscaping) and wood chips (for flavouring barbequed meat) from Mardie Station (R. Ward personal communication 1999), where exploitation is considered compatible with its current 'prevention of spread' status. The impact of this commercial harvesting on the Mardie infestation is likely to be insignificant. The production of wood chips from mesquite has also been considered by private interests in north Queensland, but utilization is not considered compatible with long term eradication programs and the release of biological control agents (Csurhes 1996).

Natural enemies

Native Australian insects. Native phytophages and pathogens have had a significant impact on mesquite within other parts of its introduced range (Tewari *et al.* 1998) and include *Oxyrachis tarandus* Fabricius (Hemiptera: Membracidae) which has been reported to kill entire trees, *Taragama siva* Lefevre (Lepidoptera: Lasiocampidae) which has completely defoliated plants, and *Poekilocerus pictus* Fabricius (Orthoptera: Aerididae) which can completely skeletonize plants (Yousuf and Gaur 1998). No specific surveys have been made of the mesquite fauna in Australia, although anecdotal evidence suggests several insects could have some impact. Among the most damaging are an unidentified cerambycid borer which kills *P. pallida* seedlings in north Queensland (S.D. Campbell unpublished 2000), stem-boring moths which kill juvenile potted plants, the seed-feeding bruchid *Caryedon serratus* Olivier (Panetta and Carstairs 1989, G. Donnelly personal communication 1999), and the crusader bug (Coreidae: *Mictis profana* (F.)) which attacks immature foliage and reproductives (R.D. van Klinken, unpublished 2000). The crusader bug also attacks a wide range of other plant species, and probably reduces growth rate and seed production on *Mimosa pigra* L. in the Northern Territory (Flanagan 1994).

Classical biological control. Over 945 phytophagous insect species, which attack all parts of the plant, have been recorded from *Prosopis* within its native range (Swenson 1969, Ward *et al.* 1977, Cordo and DeLoach 1987, Silva 1988). The feasibility of importing potential biocontrol agents to control *Prosopis* was first explored for native-range infestations in North America (DeLoach 1985). No releases resulted, although the South American mesquite fauna was surveyed (Cordo and DeLoach 1987), and several of the most damaging insects in North America were studied (Cuda and DeLoach 1998).

A biocontrol program was initiated in 1985 against mesquite in South Africa, where it was becoming an aggressive weed despite being considered beneficial by some parts of the community (Zimmermann 1991, Moran *et al.* 1993). Seed-feeding insects were therefore chosen as potential biological control agents with the intention of reducing the invasiveness of mesquite while preserving its beneficial attributes. Three species of seed feeders were released and have become established: *Algarobius prosopis* (Le Conte) (in 1987), *A. bottimeri* Kingsolver (in 1990) and *Neltumius arizonensis* (Schaeffer) (in 1993) (Coetzer and Hoffmann 1997). The Queensland Department of Natural Resources (QDNR) has since introduced *A. prosopis* (in 1996) and *A. bottimeri* (in 1997) into Australia after additional quarantine testing (Donnelly *et al.* 1997). Both species have subsequently become established in Queensland and Western Australia (G. Donnelly personal communication 1999). However, their impact is likely to be limited by vertebrate herbivores which consume most pods before the bruchids have the opportunity to damage the seeds (Moran *et al.* 1993, Coetzer and Hoffmann 1997). A third insect species, the psyllid *Heteropsylla texana* Crawford, was also tested in quarantine by QDNR in 1992 but was not considered specific enough to release (Donnelly 1995).

A biocontrol program against mesquite in Australia was initiated by CSIRO Entomology in 1994. Insect species which targeted vegetative foliage and reproductives (buds, flowers and pods) prior to their consumption by vertebrate herbivores, and which appeared to be impacting on mesquite in their native range, were selected for host-specificity studies. Four potential agents were studied: a coreid bug (*Mozena obtusa* Uhler) which feeds on immature reproductives and vegetative foliage (van Klinken 1999); a stem-girdling cerambycid (*Oncideres rhodosticta* Bates); a sap-sucking psyllid (*Prosopidopsylla flava* Burckhardt) which causes dieback (van Klinken 2000); and a leaf-tying gelechiid moth (*Evippe* sp. #1) which is a defoliator (van Klinken and Heard 2000). Only the latter two species from Argentina were specific to mesquite and releases of each have been made in Western Australia, New South Wales, Queensland and the Northern Territory since 1998. Both new agents appear to do equally well on all Australian mesquite taxa, and have the potential to curb the invasiveness of mesquite by increasing mortality rates of seedlings and juveniles, slowing development from germination to maturity, and decreasing pod production and longevity of mature plants. *Evippe* sp. #1 is established in most infestations. Highest densities have been observed at Mardie Station (Western Australia), where it is causing heavy (50–100%), prolonged leaf death and defoliation throughout most of the 150 000 ha infestation (Figure 13) (R.D. van Klinken, unpublished 2000). Establishment of the psyllid is yet to be confirmed. Many other potential agents are available in the native range.

Integrated management techniques

All of the individual control methods have limitations. For example, mechanical and chemical treatments are generally costly and need to be repeated over a long term, while the use of fire in many areas is limited by a lack of fuel and / or the cost in lost fodder. The available biological control agents are unlikely to kill healthy, mature trees and have to be effective across a wide range of climatic conditions. Eradication of many infestations is therefore unlikely.

To minimize the impact of *Prosopis*, a combination of control options can be integrated into the grazing management system. These include biological control agents, chemical control of isolated infestations, mechanical removal of dense infestations, strategic use of fire (including the use of techniques to maximize fuel loads), and minimizing seed dispersal by managing movement by stock and other potential vectors. Further work is still required to determine how these control options can be optimally integrated for the different *Prosopis* taxa and conditions in Australia. To prevent invasion entirely, regular property inspection and 'spot spraying' of young mesquite plants are required.

Figure 13. Almost total leaf-attack from the defoliating moth, *Evippe* sp. #1, at Mardie Station (Western Australia).

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