Review

The biology of Australian weeds
54. *Parkinsonia aculeata* L.

Rieks Dekker van Klinken[AD], **Shane D. Campbell**[BD], **Tim A. Heard**[AD], **John McKenzie**[B] and **Nathan March**[C]

[A] CSIRO Entomology, Long Pocket Laboratory, 120 Meiers Road, Indooroopilly, Queensland 4058, Australia.

[B] Queensland Department of Primary Industries and Fisheries, Tropical Weeds Research Centre, PO Box 187, Charters Towers, Queensland 4820, Australia.

[C] Queensland Department of Primary Industries and Fisheries, PO Box 53, Cloncurry, Queensland 4824, Australia.

[D] CRC for Australian Weed Management.

Name

Botanical name

The genus *Parkinsonia* (Caesalpinioideae) is named after John Parkinson, a seventeenth century English apothecary and botanist. The species name *aculeata* is derived from the Latin word meaning 'prickly' (Wilson and Miller 1987, Stewart *et al.* 1992). The plant was first described in Charles Plumier's Nova Plantarum Americanum Genera (1703) from plants growing in the West Indies (Hawkins 2001).

Relationships between caesalpinioid genera are still under dispute, but genera that are closely related to *Parkinsonia* include *Delonix*, *Peltophorum* and *Lemuropisum* (Doyle *et al.* 2000, Herendeen *et al.* 2003, Haston *et al.* 2005, Hawkins *et al.* 2007).

The genus *Parkinsonia* is considered to be congeneric with the paraphyletic Central American genus, *Cercidium* (Hawkins *et al.* 2007). All species are small trees and spreading shrubs that are found mainly in subtropical and tropical arid habitats (Polhill and Vidal 1981, Hawkins 1996, 1997, Hawkins and Harris 1998, Hawkins *et al.* 1999, Haston *et al.* 2005). Most species are American, distributed from the southern USA to Argentina (*P. aculeata*, *P. florida* (Benth. ex A.Gray) S.Watson, *P. microphylla* Torr., *P. peruviana* C.E.Hughes, Daza & Hawkins, *P. praecox* (Ruiz Lopez & Pavon) Hawkins, *P. texana* (A.Gray) S.Watson and *C. andicola* Griseb). In addition, there are three species in east Africa (*P. scioana* (Chiovenda) Brenan, *P. raimondoi* Brenan and *P. anacantha* Brenan), one in southern Africa (*P. africana* Sond.) and two undescribed species from the Horn of Africa (Polhill and Vidal 1981).

Common name

The plant is usually referred to as parkinsonia in Australia and Mexican palo verde and retama in the American literature. However, overseas it has many local names, including Jerusalem thorn, blue palo verde, horse bean tree, sessaban and Barbados flower fence (Hawkins 2001).

Taxonomy

Parkinsonia aculeata is easily delimited morphologically from all other *Parkinsonia* species (Hawkins 2001); however, considerable intra-specific genetic variation occurs across its distribution. Several genetically distinct populations have been identified across the Americas (Hawkins *et al.* 2007): (1) northern and western Mexico, south-western USA and Cuba; (2) eastern and southern Mexico and south-eastern USA; (3) Venezuela; (4) Central America; and (5) Argentina. The Argentine lineage (5) is estimated to have diverged from other lineages (1–4) about 9.1 million years ago, and the northern Mexico lineage (1) from the Mesoamerican-Venezuelan lineages (2–4) about 5.2 million years ago (both pre-dating formation of the Isthmus of Panama). Additional divergent populations may exist in South America, but these have not been sampled genetically.

Intra-specific morphological variation in *P. aculeata* has not been studied systematically, including in relation to genotypes. However, seeds have been reported to be twice as heavy in Arizona (mean *ca.* 161, range: 115–189 mg 'wet weight' of seeds collected from pods on trees and stored) as in Australia (mean *ca.* 85, range: 56–103 mg) (Woods 1988). Also, *P. aculeata* in Argentina has been reported anecdotally to be morphologically different from Australian plants, having brown, cylindrical pods (H. Cordo personal communication 2006) and distinctive plant architecture (M. Julien personal communication 2006).

Description

The following description is based on our own observations and those of others (Dimmit 1987, Stewart *et al.* 1992, Vitelli 1995, Ross 1998, Hawkins 2001, Parsons and Cuthbertson 2001).

In Australia *P. aculeata* is an unmistakeable plant with smooth, green bark and very distinctive pendulous leaves with minute, easily-shed pinnules (Figure 1). Plants typically grow to 5 to 7 m high and wide, although they can grow to 20 m high, with trunks to 40 cm in diameter at breast height at maturity (MacDicken and Brewbaker 1984). Plants can be either single-stemmed or multi-stemmed, with steeply ascending branches. Roots typically have a shallow main axis and numerous surface laterals. Leaves are shortly stalked, bipinnate, each with 1–4 pairs of pinnae. The pinnular rachi are very thin, green, flattened and ridged, and are 20 to 40 cm long with numerous minute (4–10 mm long) pinnules (secondary leaflets) on each edge (Figure 2a). Stiff, needle-sharp spines (modified leaf rachises) 5–15 mm long are formed at the base of each leaf (Figure 2a). The spines persist on the older branches and stems.

Flowers are bright yellow, fragrant, 2 cm in diameter with five-petalled corollas (Figure 2b). They are bilaterally symmetrical, with four petals 6–15 mm long becoming reflexed, and one erect petal which is either completely orange or has orange spots. Each flower is on a slender stalk and flowers are borne in groups of 8 to 12 in loose racemes (Figure 2b) arising from the leaf axils.

Figure 1. An adult *Parkinsonia aculeata* plant.

Pods, each containing 1–11 (typically 1–3) seeds, are 3 to 13 cm long, about 7 mm wide, flattened, constricted between the widely-spaced seeds, tapered at both ends and straw coloured when ripe (Figure 2c). Seeds are oblong, 8–12 mm long and 4–7 mm wide. The testa is green and soft when immature, becoming mottled brown and very hard when mature. The cotyledons are light yellow in the mature seed and the endosperm is tough, plastic and translucent, becoming brittle on maturity (Woods 1988). The embryo accounts for about 27–34% of total seed weight, the endosperm 25–33%, and the seed coat 40% (Woods 1988).

Parkinsonia aculeata has a mitotic chromosome number of 2*n* = 28 (Hawkins *et al*. 1999).

Distinguishing Parkinsonia aculeata from other taxa

In Australia *P. aculeata* can be confused with prickly acacia (*Acacia nilotica* (L.) Del.), mimosa bush (*A. farnesiana* (L.) Willd.) and mesquite (*Prosopis* species), 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'. *P. aculeata* can be most readily distinguished by its characteristic leaf structure, photosynthetic bark and large flowers that have open petals, as opposed to the other prickle bushes that have flowers with minute petals and form tight clusters (pompoms or lambs tails).

History

Parkinsonia aculeata was being cultivated in greenhouses in England by 1739. At that time it was very common in the Spanish West Indies and had been introduced into the English settlements in North America, for the 'beauty and sweetness of its flowers', and was predicted to 'soon become common in all host countries' (Miller 1739). Since then it has been introduced actively around the world, often first being introduced as an ornamental tree in towns and botanic gardens (Hughes 1989), but also for use as a hedging plant and for shade, windbreak, soil nitrogen fixation and rehabilitation purposes. These introductions have generally been casual, unsystematic and from unknown sources (Hughes 1989). Some details of its introduction through the British Empire, and later the British Commonwealth, have been reported by Streets (1962) and Troup and Joshi (1983), and more generally in Hawkins 2001. The Kew Herbarium holds specimens collected prior to 1850 from Iran (formerly Persia), Senegal, India, Pakistan and the Mascarenes (Mauritius, Réunion and Rodrigues) (Hawkins 2001).

Knowledge of its introduction and spread in Australia is based largely on anecdote. Its planting in Australia, as an evergreen hedge, was being advocated as early as 1876 (von Mueller 1876). The first Australian record we could find was of a planting in the Botanic Gardens in Sydney prior to 1901. However, its invasiveness in Central Queensland by the early 1900s (Bailey 1906) suggests that it was introduced soon after this area was widely settled in the 1860s. Genetic evidence suggests Australian populations may have

Figure 2. *Parkinsonia aculeata* plant parts: (a) leaf (long strap-like rachi with small pinnules along their edges) and thorns, (b) flowers and (c) pods.

originated from Venezuela and/or other closely-related Mesoamerican populations that were not included in the sampling (Hawkins *et al*. 2007). Also, populations sampled from Australia and Kenya may have originated from a single translocation event (Hawkins *et al*. 2007).

Anecdotal evidence suggests that, once in Australia, *P. aculeata* was quickly spread as an ornamental or shade tree for planting around homesteads, bores and dams (Anon. 1978, Miller and Pickering 1980, Woods 1986, Wilson and Miller 1987). For example, a mature *P. aculeata* plant was growing in front of the Borroloola Police Station prior to 1930, and is thought to have been the source of seeds for plantings at the homestead on nearby Mallapunyah Station where it subsequently became invasive over much of the 434 900 ha pastoral lease (Deveze 2004). *P. aculeata* was planted at Government Bore on Muckaty Station (Barkly Tablelands, Queensland) around the late 1930s for shade, and was commonly planted for shade throughout the Victoria River District in the 1960s (Larry Johns personal communication 2003).

By 1906 it was already considered a weed in parts of Queensland, especially along the Fitzroy River (Bailey 1906). By 1972 it had taken a firm hold in the Victoria River, Darwin and Gulf Districts and was reported to be undergoing a 'population explosion' despite having been in the Northern Territory for 'years' (Anon. 1972). By 1988 it was considered weedy in the Northern Territory (with major infestations reported from the Victoria River district and on black clay soil on the Barkly Tablelands), Queensland (flat downs country near Richmond and land adjacent to the Burdekin, Isaacs and Fitzroy Rivers) and Western Australia (along rivers in the Pilbara and Kimberley regions, with important infestations along the Ord, Fitzroy and De Grey Rivers) (Woods 1988). It was identified as one of Australia's 20 Weeds of National Significance in 1999 following a national prioritization process (Thorpe and Lynch 2000).

Distribution

Native

Parkinsonia aculeata is native to the Americas, where it is widely distributed in hot and dry regions (Figure 3); however, historically there has been considerable dispute as to its native range (Hawkins *et al*. 2007). This has probably been due to *P. aculeata* having been transported intentionally in the Americas for many centuries, and in much of its range only being recorded from highly disturbed habitats (such as roadsides, urban and wasteland sites), often in association with intentional plantings as ornamentals (Hughes 1989). Recent genetic work has shown that its native distribution includes parts of North, Central and South America (Hawkins *et al*. 2007) (Figure 3).

In the United States its distribution includes the South Texas Plains and Coastal Prairies in Texas (Everitt 1983), the Sonoran Desert (Carter 1974), and the warmer parts of the Mojave Desert (Dimmit 1987). Native populations in Central America appear to be quite restricted and disjunct, occurring as a series of isolated dense stands on deep black vertisols in southern Mexico, Guatemala, Nicaragua and Costa Rica (Hughes and Styles 1984, Hughes 1989) (Figure 3). These stands typically grow on saline, high-pH, seasonally waterlogged sites that were formerly lake-beds, or are seasonally flooded coastal estuaries and lagoons. It does not occur in adjacent dry forest or semi-arid thorn scrubs. In Brazil it occurs in semi-arid regions of the Sertao (Caatinga vegetation) which occupies most of the Brazilian northeast (Barbosa and Prado 1991).

Introduced – worldwide

Parkinsonia aculeata has a pan-tropical distribution following introduction as an ornamental, hedging, fodder and shade tree (Stewart *et al.* 1992, Woods 1992, Hawkins and Harris 1998, Wagner *et al.* 1999, PIER 2000, Hawkins 2001, R.D. van Klinken unpublished) (Figure 4). It frequently naturalizes; however, other than in Australia, records of it becoming a troublesome weed are relatively rare. In New Caledonia it has been reported as 'commonly occurring as populations which significantly affect yield or profitability, and its removal would have useful benefits' (Swarbrick 1997). An extensive naturalized population occurs near Nakuru in Kenya (Hawkins 2001).

Introduced – Australia

The distribution of *P. aculeata* has been mapped nationally in a 50 × 50 km grid, mainly through existing distributional records held by state departments and through expert knowledge (Figure 5). When considered at that grid scale, *P. aculeata* is now estimated to be present on over 3.3 million ha of Australia, although densities are very low throughout most grid cells.

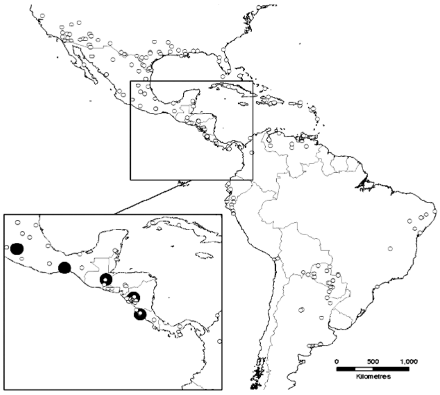

Figure 3. Distribution of *Parkinsonia aculeata* in the Americas (○) including dense stands in Central America (●).

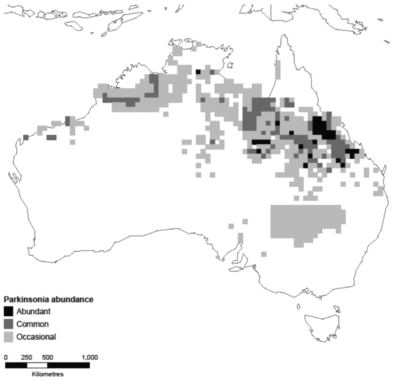

Figure 5. Current distribution and abundance of *Parkinsonia aculeata* in Australia. Source: Queensland Department of Primary Industries.

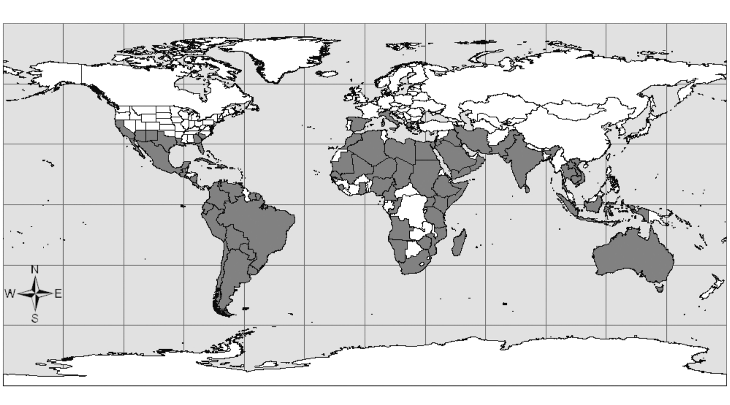

Figure 4. Countries or states (in USA) (shaded) where *Parkinsonia aculeata* has been recorded (see text).

Most infestations occur across semi-arid and semi-humid Australia, especially in central and north Queensland, the Barkly Region and the Victoria River District of the Northern Territory, and the Kimberley and Pilbara Regions of Western Australia. Although it is widespread in these regions, dense patches are associated primarily with flood-outs, water infrastructure (such as 'turkey nests'), watercourses and the edges of seasonally-flooded fresh-water wetlands. Elsewhere in Australia records are mostly of isolated plants, or relatively restricted, scattered infestations.

In Queensland extensive infestations occur primarily in riparian, flood-out and seasonally flooded habitats in Central Queensland (e.g. the Fitzroy River catchment), upper Lake Eyre Basin and in the Gulf of Carpentaria, with some infestations up to several kilometres across. Major aerial surveys have been undertaken of the Cooper Creek and Georgina – Diamantina catchments by Desert Channels Queensland since 2004. Analysis of these survey data indicates the total area of infestation across the region to be 600 000 ha (Brett Carlsson personal communication 2008). The bulk of these infestations are of low density and follow more or less linear bands associated with watercourses. While few populations are greater than 200 m diameter, some follow rivers semi-continuously for up to 80 km. A similar pattern is seen on the Cape River catchment in central-north Queensland (Lawes *et al.* 2003). With few exceptions, *P. aculeata* populations on Cape York Peninsula and southern Queensland are very sparse.

In the Northern Territory *P. aculeata* extends from the sandy plains of the Tanami to the wetlands of the wet-dry tropics; however, it is sufficiently dense to be considered a problem only in parts of the Gulf District, Barkly Tablelands and Victoria River District (Flanagan *et al.* 1996). Infestations reach their greatest extent in seasonally-flooded black soil plains on the Barkly Tablelands, where monocultures can reach several kilometres in length. In the Gulf district populations are mostly scattered, although *P. aculeata* continues to spread along rivers such as the MacArthur, Robinson and Calvert. In the Katherine River Region and the Victoria River District it is widely distributed, occurring in low densities along most major watercourses, although there are some high density patches such as on the Roper River. In central Australia (Lawes and Grice 2007) and the wet-dry tropics of the Northern Territory (the 'Top End') *P. aculeata* is widely distributed but sparse, with thickets rarely exceeding more than a dozen trees. Populations in central Australia are mostly within 30 m of watercourses.

Parkinsonia aculeata has been recorded from many of the river systems in the Kimberley and Pilbara regions of Western Australia, where scattered infestations occur along many hundreds of kilometres of water courses. In the Kimberley Region infestations are most extensive on the Fitzroy River. Around Kununurra it is primarily restricted to the banks of the Ord River, flood-outs and on the edges of wetlands. Most infestations are scattered, and dense thickets are generally isolated. In the Pilbara Region *P. aculeata* is almost entirely restricted to the riparian zone of the major rivers (all ephemeral), including along the Fortescue, Maitland, Harding, De Grey and Robe Rivers, and in the Millstream National Park. Dense stands occur on the Fortescue and De Grey Rivers. South of the Pilbara Region *P. aculeata* occurs as small isolated populations or as individual plants in the Upper Gascoyne and Murchison Districts. A single *P. aculeata* plant (about 1 m tall) has been found naturalized in the Southwest Agricultural area (J. Peirce personal communication 2001).

Naturalized populations of *P. aculeata* have been recorded from four sites in New South Wales: two clumps of individual plants near Broken Hill, a 250 ha patch along 20 km of the Narran River and 'about a dozen' plants at an abandoned homestead in Bourke Shire (March 2004, in Deveze 2004). The Narran River population is thought to have originated from Yerambah, a now-abandoned homestead upstream of the current infestation. In addition, there have been reported cases of single trees from council areas close to the Queensland border and from the Royal Botanical Gardens in Sydney (P. Gray personal communication 2000).

Records from South Australia are restricted to isolated plants in the vicinity of Port Augusta, Woomera and Copley townships. All occurrences are associated with historical plantings although plants have naturalized at each site (N. March personal communication 2008).

Potential distribution in Australia

Much of northern and eastern Australia is probably climatically suitable for *P. aculeata*, provided adequate soil moisture is available, with conditions being optimal in central Queensland (Figure 6a). On the broad scale *P. aculeata* has probably naturalized in the majority of suitable catchments (Figure 5). Within catchments *P. aculeata* is generally very sparsely and/or locally distributed, but there is little doubt that *P. aculeata* will continue to spread through the wetter habitats within its current range. Special efforts are currently underway to prevent its spread into Cape York Peninsula, the Lake Eyre and Murray Darling basins in Queensland and the blue-bush (*Maireana* spp.) swamps in the Barkly Tablelands (Deveze 2004).

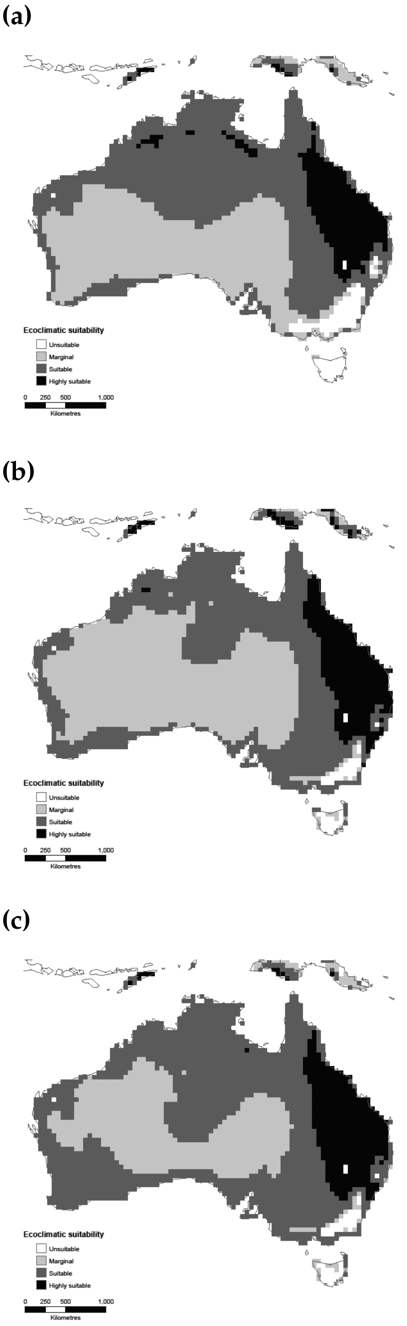

Figure 6. Potential Australian distribution of *Parkinsonia aculeata* with existing climate (a), and following a 2°C increase in temperature and 10% reduction in rainfall (b), and 10% increase in rainfall (c). Modelling was conducted in CLIMEX (Lawson *et al.* 2008, R.D. van Klinken *et al.* in prep.).

Climate change is expected to result in a southward extension of highly suitable areas in eastern Australia as a result of reduced cold stress (van Klinken *et al.* unpublished) (Figure 6). Also, in south-west Australia it is expected that there will be improved growing conditions and reduced cold-wet stress. Reduced rainfall is expected to result in the northern (tropical) interior becoming less suitable (Figure 6b), while increased rainfall is expected to increase the suitability of much of Australia (Figure 6c).

Landscape-scale modelling has been conducted to predict habitat suitability and susceptibility in the Desert Channels Region in south-western Queensland (R.D. van Klinken *et al.* unpublished data), where *P. aculeata* is predicted to remain restricted to the most mesic parts of the landscape.

Habitat

Parkinsonia aculeata has an outstanding ability to survive and grow under a wide range of environmental conditions (Hughes 1989). This includes arid regions to wet-dry tropical regions, with annual rainfall typically ranging between 250 and 1400 mm.

It can survive on a wide range of soil types, including deep sand, shallow and skeletal soils, rocky gullies and heavy, black cracking clay soils, where few other woody plants can survive (MacBride 1943, Stewart *et al*. 1992, Hawkins 2001). It grows well on moderately to extremely saline soils (Hughes 1989, Stewart *et al*. 1992, Hawkins 2001), occurring on salt-affected sandy rises along the Gulf of Carpentaria coastline in both the Burketown (Queensland) and Borroloola (Northern Territory) areas, and in seasonally-flooded coastal estuaries in Central America (Hughes 1989) (Figure 7a). It is also very tolerant to extremes in pH (3–11) (Stewart *et al*. 1992, Hawkins 2001, Parsons and Cuthbertson 2001). In coastal Peru it grows in arid habitats of extremely low rainfall in which few other species will grow (Figure 7b).

Parkinsonia aculeata plants can continue to grow with their root-systems inundated by water, and can survive more than nine months with the lower portion of their trunks under water (van Klinken 2005). Prolonged, repeated inundation will, however, result in stress and death. It is mildly frost tolerant, although dieback occurs after intense or extended frosts (Hocking 1993, in Hawkins 2001); for example, a cold frost period of about −6°C resulted in top-kill or death of most *P. aculeata* plants at study sites in central Australia (R.D. van Klinken unpublished data). *P. aculeata* is not limited by high temperatures in Australia.

Thicket formation rarely occurs away from the most mesic parts of the landscape, being most common along rivers, adjacent to water-storages, and in seasonally flooded habitats such as river levees, depressions that receive run-on or floodwater, the margins of lagoons and periodically inundated black soil plains (Wiggins and Porter 1971, Scrifres 1980, Benson and Darrow 1981, Everitt 1983, Woods 1988, Barbosa and Prado 1991, Deveze 2004). Thickets can also form in upland habitats that are never inundated, especially in semi-arid and semi-humid regions (Everitt 1983, van Klinken 2005, unpublished data). However, the occurrence of *P. aculeata* in upland habitats may, in part, be seed-limited as a result of poor seed dispersal in the absence of flooding (see later). Thicket formation is generally restricted to areas that are heavily grazed by livestock or feral animals, provided the herbivores (e.g. macropods, goats or sheep) do not also browse *P. aculeata* plants.

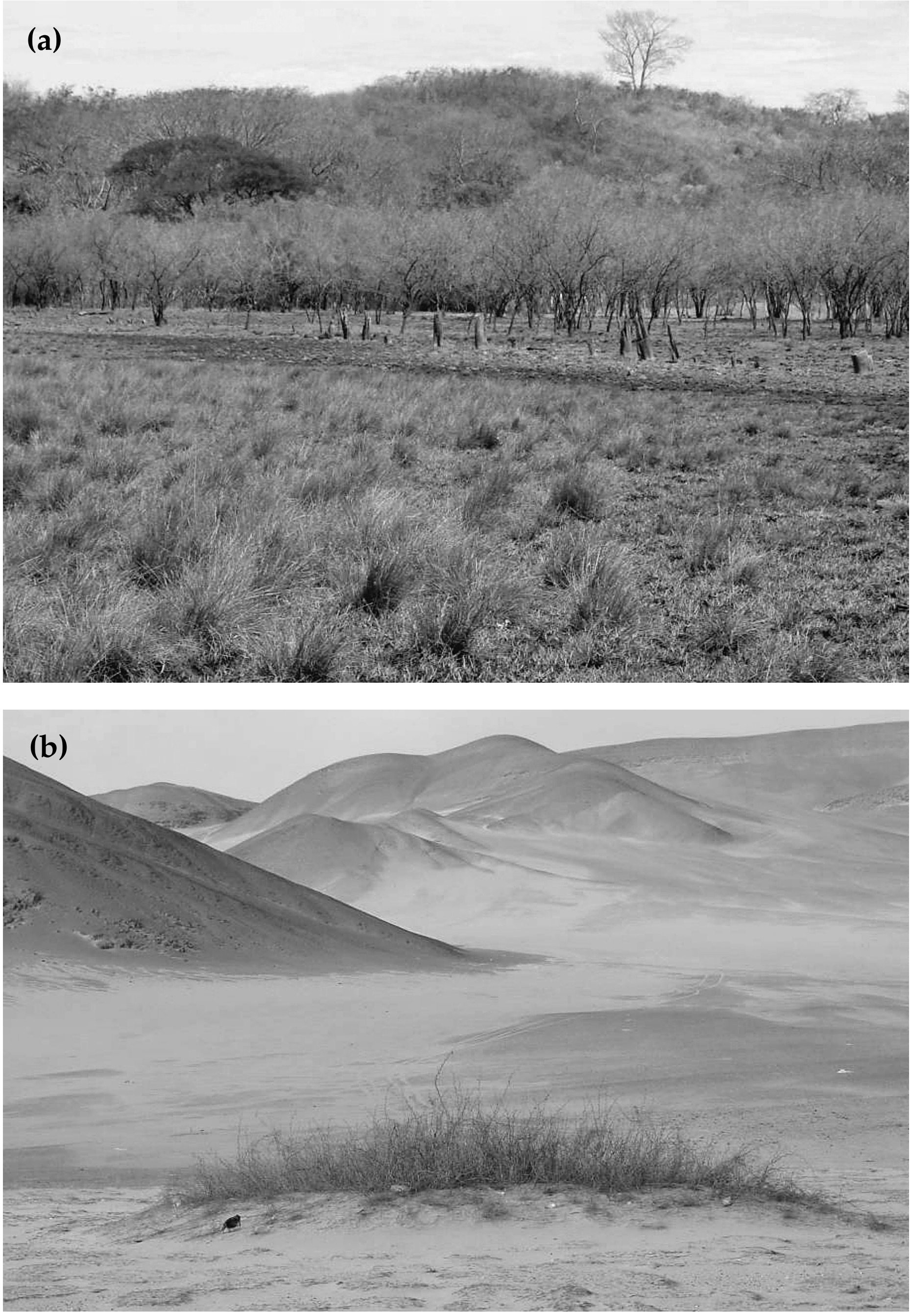

Figure 7. Native *Parkinsonia aculeata* populations in contrasting habitats: (a) dense population on black clay soil in an estuary (salt marsh) near Palo Verde National Park, Costa Rica and (b) a prostrate adult growing in the coastal desert of Peru.

Growth and development

Information on growth and development, reproduction and population characteristics has largely been obtained through research conducted in Australia between 1999 and 2007. Much of this work is yet to be published.

Morphology

Adult trees are typically shallow-rooted with numerous surface laterals (Parsons and Cuthbertson 2001). Trees can reshoot laterally from the main trunk down to about 20 cm below the soil surface following damage, such as after fire, frost, prolonged flooding, termite-feeding or mechanical disturbance. This can result in 20 or more branches arising from the root crown. Reshooting also occurs (typically along the whole main stem) if the tree has been pushed over by floods. Above-ground biomass of juveniles and adults can be estimated using plant height, canopy diameter or stem cross-sectional area, although stem area is the most robust predictor (Grice *et al*. 2002). The relationships between size and biomass are linear when plotted on log-log scales. Plant size is not, however, likely to be a good predictor of plant age (Grice *et al*. 2004, R.D. van Klinken unpublished data).

Perennation

No direct measurements of age have been recorded, although *P. aculeata* can be reasonably long-lived in the absence of stresses (probably >30 years). Nevertheless, field demographic and growth data collected throughout Australia (2000–2006, R.D. van Klinken unpublished data) and anecdotal observations from landholders and others suggest that plants rarely live for longer than 20 years in Australia.

Physiology

Parkinsonia aculeata is noted for its drought and salt tolerance and shows a number of physiological adaptations to deal with low water uptake, including greatly reduced leaf area and green photosynthetic bark (Stewart *et al*. 1992). Xerophytic modifications of the leaf include heavy cutinization of the persistent epidermis, sunken stomata, a hypodermal layer of water-containing cells and a photosynthetic cortex. Even though mature xeromorphic leaves may attain osmotic values of 26.5 atmospheres, they are shed in times of drought (Woods 1988). At first the pinnules are shed, with the leaf pinnae remaining to function as photosynthetic organs (Robertson and Lee 1976); however, under stress, the pinnae are also dropped and photosynthesis is restricted to the green stems (Wood 1988).

Bark photosynthesis has been described for the closely related *P. florida*, which is drought-deciduous and, like *P. aculeata*, has a large number of thin chlorophyllous branches (Adams and Strain 1969). Products of photosynthesis of the stem cortex are similar to those of leaf photosynthesis. Leafless trees under drought stress had considerable photosynthetic activity, at least during the non-growing period, with photosynthesis at 86% of that on foliated (unstressed) trees growing in a similar area in mid-winter. *P. aculeata* is a light-demanding plant, its growth being somewhat retarded in the shade (Hawkins 2001).

Seedlings of P. *aculeata* are remarkably tolerant of drought and soil variation. In a glasshouse experiment *P. aculeata* seedlings survived drought treatments (no drought, 30% and 10% above wilting point and no water) imposed from 4–18 weeks of age in sand, loam and clay soils (Lawes 2004). Above ground biomass increased in all soil types, and growth was fastest in clay, relatively rapid in loam, but restricted in the sandy soils.

Phenology

Leaf production occurs throughout the year, provided conditions remain warm and trees remain healthy; however, a major flush of leaf production generally occurs as day length begins increasing, provided conditions are warm. Pinnules appear to be relatively short-lived, surviving a few months. Facultative defoliation of rachises occurs in cooler regions such as central Queensland or central Australia. Leaf loss also occurs in response to other stresses, such as prolonged inundation, drought, or insect attack.

Peak flower production generally coincides with the major flush of foliage growth. Flowers are also produced throughout the remainder of the year in all but the cooler regions, but these are responsible for only a small proportion of total annual pod production. Soil moisture availability does not appear to affect flowering phenology as flowering is initiated during the dry season, and occurs simultaneously in adjacent wetland and uplands sites in Australia (van Klinken 2005). Peak flowering in Central America is from February to March, but is somewhat later in Mexico, the southern USA and India (April and May) (Hawkins 2001). Peak flowering in Tucson, Arizona, occurred over a 3–4 week period between April and June, with flowering continuing until September (Dimmit 1987). In Australia peak flowering occurs in August-September in hotter regions (e.g. the wet-dry tropics), but is delayed by a few months where winters are cool (e.g. the arid interior) (van Klinken and Flack 2008).

Most pods drop off the tree within six weeks of reaching maturity, although a small proportion of pods can remain on the tree for up to a year (van Klinken and Flack 2008). Pod fall can be slightly delayed for seasonally flooded trees due to both delayed maturation and delayed abscission (van Klinken 2005). Pods are indehiscent and must decay or be physically damaged to release the seed. Under warm wet conditions seed release can take a few months, but a small proportion of pods can remain intact for over a year in arid environments.

Mycorrhizae and nodules

Parkinsonia aculeata is now considered not to fix nitrogen (Sprent and Sutherland 1990, Stewart *et al*. 1992), although earlier it was reported to do so (Hughes 1986).

Reproduction

Floral biology

Flowers of *P. aculeata* are bee pollinated (Eisikowitch and Masad 1982, Lewis *et al*. 2000). Generalist bees such as species in the genera *Canephorula*, *Centris*, *Colletes* (references in Lewis *et al*. 2000) are recorded as flower visitors in the native range and large carpenter bees (*Xylocopa* sp.) have been observed on *P. aculeata* flowers in Australia and Costa Rica (T.A. Heard unpublished data). The UV-absorbent flag petal of *P. aculeata* has been shown to be an important recognition and orientation cue for visiting bees (Jones and Buchmann 1974).

Inflorescence maturity is acropetal, with pods that form at the base of the infructescence maturing first (Wyatt 1981). In Costa Rica there were on average 9.06 ovules per pod (range: 7–11) and 1.7 seeds per pod (range: 1–9) (Wyatt 1981). In Australia *P. aculeata* pods average 1.6 mature seeds per pod (range: 1–7) with little or no regional variation (van Klinken and Flack 2008). Pod maturation occurs within approximately three months of bud formation (van Klinken 2005).

Seed production

Parkinsonia aculeata starts to produce seeds in its second or third summer under the best possible conditions, but may take longer (Vitelli 1995, R.D. van Klinken unpublished data). Seed production typically begins when plants are about 1.5 m tall, increasing greatly with plant size at any one site and year (J. Pichancourt and R.D. van Klinken unpublished data). Large trees can produce at least 2500 seeds m^{-2} of projected canopy cover (van Klinken and Flack 2008, R.D. van Klinken unpublished data). Seed production varies considerably between years, sites and tree densities (dense cohorts of tall narrow adults produce few seeds per unit area), and trees may not flower at all during severe drought (Deveze 2004, p. 48). Variation in pod production is generally strongly positively correlated with foliage cover and, therefore, tree health. However, very stressed, almost leafless trees often produce a final crop of pods before death.

Seed dispersal

Pods fall close to the parent plant. Pods can float for up to 14 days (Stewart *et al*. 1992, Hawkins *et al*. 1999, although no data were provided), and the main natural dispersal mechanism for pods appears to be water. Long distance flotation may have aided its spread in certain areas, and *P. aculeata* is thought to have established on Galapagos Islands (Porter 1983, in Wilson and Miller 1987) by this means. Also, isolated populations found on sandy frontal dunes on the Gulf of Carpentaria in both Queensland and the Northern Territory are thought to have arisen from pods that reached there through westward tidal movements along the Northern Territory coastline from Queensland. Within catchments the importance of water dispersal is evidenced by the way infestations typically follow drainage lines, and the frequent emergence of seedlings along flood lines and among flood debris. Even in uplands habitats, water runoff can be sufficient to spread pods (and seeds) short distances from beneath the canopy of parent trees, aiding thicket formation.

Although herbivores have been implicated in the dispersal of seeds through their dung, we have found little evidence to support this claim. Pods have limited nutritional value and therefore are not adapted to dispersal by vertebrate herbivores, unlike mesquite and prickly acacia (van Klinken and Campbell 2001). In a feeding trial pigs did not eat *P. aculeata* pods unless they were coated in molasses (B. Lynes unpublished data, in Deveze 2004) and seeds and seedlings are rarely, if ever, reported from the dung of livestock. Nonetheless, incidental consumption of mature pods by livestock is possible. If pods were to be consumed a significant proportion of seeds would probably remain viable; for example, in the pig-feeding trial, 50% of seeds that passed through the digestive tract were viable, after taking 3–8 days to pass (B. Lynes unpublished data, in Deveze 2004).

Birds have also been implicated in dispersal (Lukitsch and Wilson 1999). However, seed drop data collected from litter traps placed under adult trees suggests that birds strip the seeds from almost, or newly, matured pods, subsequently discarding the seed coat (R.D. van Klinken unpublished data). No viable seeds would therefore be ingested for subsequent dispersal.

Parkinsonia aculeata does, however, have a surprisingly widespread distribution in Australia, which can not be explained solely by intentional plantings and dispersed by water. For example, infestations often occur scattered across upland habitats where no plantings have occurred. The most likely explanation is that seeds are dispersed in mud sticking to animals and machinery. The use of *P. aculeata* trees by livestock and other animals for shade, and the typically high seed densities under parent trees, support this hypothesis. Similarly, scotch broom (*Cytisus scoparius* (L.) Link) seeds, which are similar to *P. aculeata*, have been shown to be dispersed in mud on pig's feet (G. Watson personal communication 2005).

At a wider scale, historical, intentional dispersal of seed by humans is likely to be the most important means of long-distance dispersal across Australia and between countries. However, some outlying infestations, such as a single isolated plant found recently on the roadside in south-western Australia, cannot be explained in this way. The importance of transported livestock (and vehicles/stock carriers) in dispersing seeds (most probably in mud) still needs to be resolved.

Physiology of seeds, germination and seed banks

Dormancy and imbibition *Parkinsonia aculeata* has a relatively simple dormancy mechanism (van Klinken and Flack 2005, van Klinken *et al.* 2006, van Klinken, Lukitsch and Cook 2008). The seed coat confers hard-seeded (physical) dormancy through tightly packed palisade cells that are impregnated with water-repellent substances, while the embryo remains fully developed and non-dormant (Baskin and Baskin 1998). No physiological seed dormancy mechanisms have been observed (Everitt 1983, Alvarez Rangel 1984a, van Klinken and Flack 2005). Once the seed is released from dormancy, imbibition (where seeds swell to approximately twice their original size) will occur provided there is sufficient moisture (van Klinken and Flack 2005). Light is not required for germination (Everitt 1983, van Klinken unpublished data), but seeds will not germinate unless exposed to air. There is no evidence of secondary dormancy in the event that germination conditions are not met. Timing of dormancy release is, therefore, critical to ensure that germinating seeds have the greatest probability of survival.

Most fresh, field-collected seeds are typically viable (about 100%), and most are dormant (>80% when inundated at 20°C) (Chatterji and Mohnot 1964, Everitt 1983, Mohnot and Chatterji 1965, van Klinken and Flack 2005, van Klinken, Lukitsch and Cook 2008). *P. aculeata* seeds can be released from dormancy by a wide range of mechanisms, including intense dry heat (Scott 2006), physical damage to the seed coat, and artificial methods such as boiling and acid scarification (Mohnot and Chatterji 1965, Egley 1989, Teketay 1996). Under field conditions, wet heat (exposure to wet, warm to hot conditions) has been shown to be the primary mechanism (van Klinken *et al.* 2006, van Klinken, Lukitsch and Flack 2008). Most dormancy release, and subsequent imbibition, occurs within one day of inundation. Very few additional seeds will imbibe after four days of inundation at a particular temperature (Figure 8a). There is also a strong, positive, relationship between temperature and dormancy release when seeds are inundated (Figure 8a). This relationship can be described by a log-linear function above a threshold temperature of approximately 33°C and a quadratic function below that threshold (van Klinken and Flack 2005). Dormancy release is most sensitive to temperatures between approximately 25 and 35°C, which are also the temperatures at which seeds are likely to be exposed to wet conditions in summer rainfall regions, and the temperatures at which seed germination is greatest (see later).

Seeds from different Australian populations were tested, and the relationship between wet heat and dormancy release differed by up to a 6.6°C phase shift in the Y-intercept (Figure 8b). This is likely to significantly affect the seed bank dynamics of different seed populations (van Klinken and Flack 2005). The cause (and significance) of this phase shift is unknown, but it may be related to seed moisture content.

Intense dry heat from fires will have an important impact on seed dormancy (Scott 2006). It is likely that sufficient dry heat (e.g. 125°C for 8 minutes) will kill seeds while exposure to more intense heat for brief periods (e.g. 300°C for 1 minute) will release seeds from dormancy by altering seed coat properties. Fire, depending on its intensity, is therefore likely to kill surface seeds, releasing from dormancy some seeds that are close to the surface (<2 cm in depth), and not affecting seeds that are deeply buried.

Germination The relationship between germination and temperature has been described by van Klinken and Flack (2005) for imbibed seeds under saturated conditions. Non-dormant *P. aculeata* seeds germinated between 15 and 40°C. Germination was limited by cold stress at 20°C and below and heat stress above 35°C, resulting in increased seed death and decreased germination rates. Optimal conditions for germination were between approximately 25 and 35°C, with approximately 85% of non-dormant seeds successfully completing germination (defined as the radicle being as long as the seed) in a median time of 2.1–2.9 days, depending on temperature. These results generally agree with those from other germination trials (Chatterji and Mohnot 1964, Alvarez Rangel 1984b, Teketay 1996, Cochard 1999).

Seeds can germinate at any time of the year in Australia provided sufficient moisture availability and suitable temperatures; however, most germinate in the summer during periods that are sufficiently hot and wet to result in dormancy release and subsequent germination. In inundated habitats germination occurs either in the early wet season (when most or all seedlings are likely to subsequently drown) or as waters recedes.

Seed bank longevity Seeds will remain viable and dormant indefinitely if stored in cool, dry conditions (van Klinken, Lukitsch and Cook 2008, R.D. van Klinken unpublished data). In contrast, most seeds in the seed bank will lose dormancy and either germinate or die within one year under field conditions, although rates and

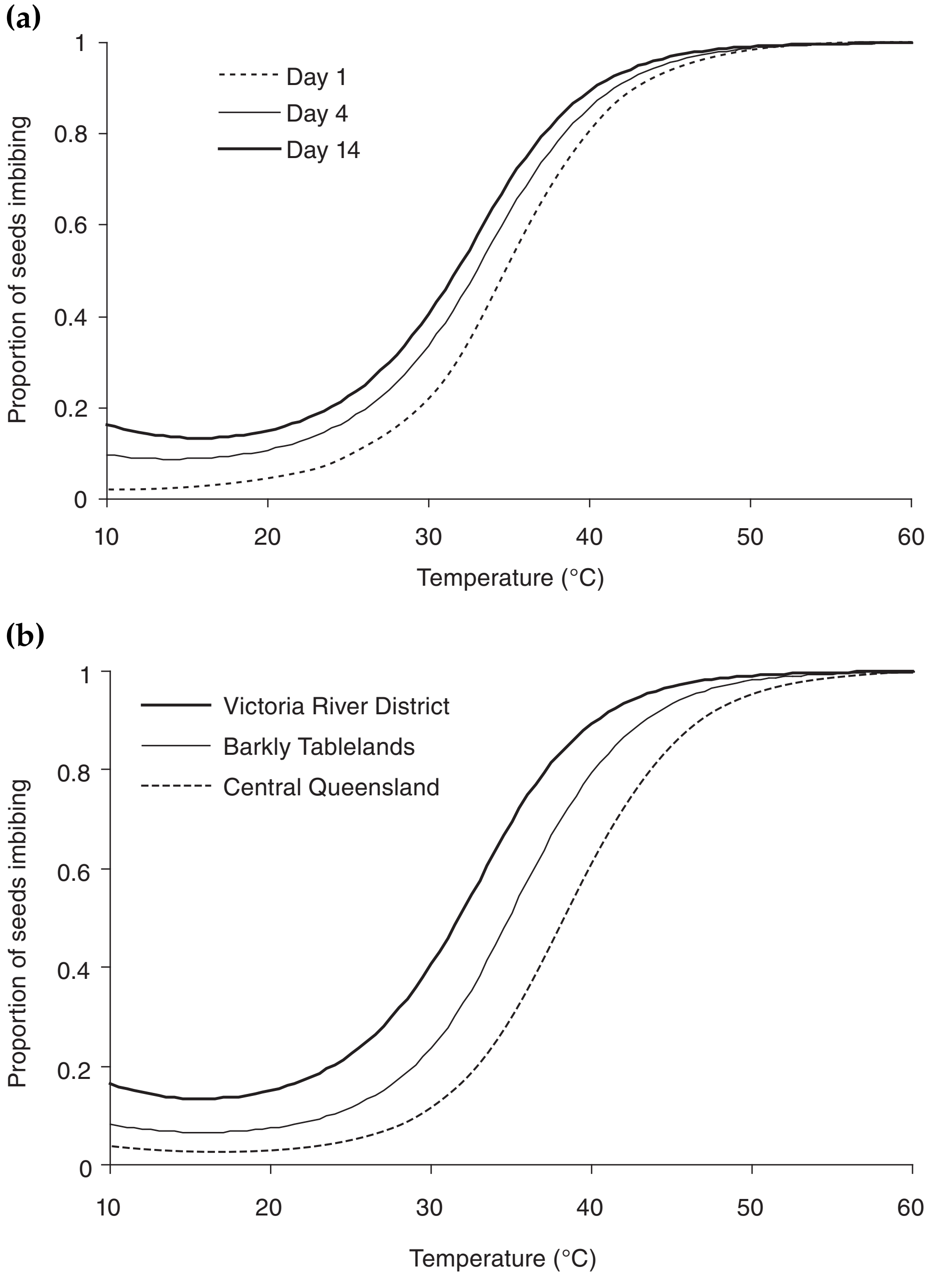

Figure 8. The relationship between water temperature and the proportion of seeds that are released from dormancy and subsequently imbibe: (a) with increasing inundation time and (b) for three Australian seed populations after four days of inundation (after van Klinken and Flack 2005).

timing of dormancy release will depend on the microclimate the seed is exposed to, specifically wet heat (van Klinken *et al*. 2006, van Klinken, Lukitsch and Cook 2008). There may also be population-level differences in the responsiveness of seeds to wet heat (Figure 8b).

A seed burial trial conducted over a 14 week period during the 2002–3 wet season in Darwin (wet-dry tropics) (van Klinken *et al*. 2006) compared a wide range of habitats (from open to dense grass cover and forest cover) and soil depths (from 0 to 20 cm) (Figure 9a). Micro-climate, through its effect on wet heat, explained the up to 16 fold difference in dormancy levels between treatments (Figure 9a). Over 80% of seeds were still dormant at 3 and 20 cm depth under dense grass and under canopy cover. In contrast, in the open treatment (no grass or canopy cover) less than 10% of seeds were still dormant after 14 weeks at 0 cm (when covered by a thin film of soil) and at 3 cm depth.

A national seed burial trial was conducted between 2001 and 2005 to determine seed bank longevity in different climate zones (wet-dry tropics to arid), habitats (soil types and inundation levels) and burial depths (van Klinken, Lukitsch and Cook 2008) (Figure 9b). Dormancy release was quickest for seeds buried during the wet season at upland sites in the Victoria River District, with only 3% of seeds remaining ungerminated after 35 days. The longest-lived seeds were those in wetlands (9% of seeds still dormant after almost four years) and those lying fully-exposed on the soil surface (57% of seeds after two years).

The combined results from this research demonstrate that the sensitivity of the seed coat to wet heat provides a mechanism to ensure that dormancy release will occur rapidly when conditions are optimal for seed germination and subsequent recruitment (i.e. warm to hot, wet conditions, when seeds are not inundated, when seeds are buried up to about 3 cm in the soil, and when there is little or no competition from the herbaceous or canopy layer). Conversely, seeds will be longest-lived where conditions are most buffered from high temperatures (e.g. under parent trees) or are relatively dry (e.g. on the soil surface). These environmental seed 'refuges' can become a source of future recruitment if conditions change, for example following the death of canopy trees or removal of the herbaceous layer.

Seedling establishment

Parkinsonia aculeata seedlings emerge as a single thorny stem. Seedlings can grow very rapidly, reaching an average height of 1.3 m in 18 months in an area of Pakistan with a mean summer temp of 32.5°C and an average rainfall of 180–200 mm (Sheikh *et al*. 1985), or 2 m or more per year 'in youth' with ample water (Dimmit 1987); however, such growth rates are rarely observed in Australia (R.D. van Klinken unpublished data).

Recruitment rates for *P. aculeata* are typically very low. Estimates based on seed rain, seed banks and annual demography surveys conducted at populations across Australia (2000–2007) average 0.1% (J. Pichancourt and R.D. van Klinken unpublished data). This includes some populations that had few or no recruits over a period of several years, despite substantial seed inputs. Factors resulting in high seedling mortality include desiccation through lack of follow up rains, inundation, cold frosts, fire, competition and failure of the shoot to reach the soil surface (e.g. through deep burial) (R.D. van Klinken unpublished data) and possibly pathogens (Toh *et al*. 2008).

Competition with grass results in delicate thin-stemmed, slow growing *P. aculeata* seedlings with reduced stress tolerance (J.R. McKenzie unpublished data). There is indirect evidence that agile wallabies (*Macropus agilis* (Gould)) selectively browse *P. aculeata* from soon after emergence until plants are too tall to reach (about 2 m). This is likely to be a primary reason for the lack of recruitment at one heavily-browsed research site in the Victoria River District

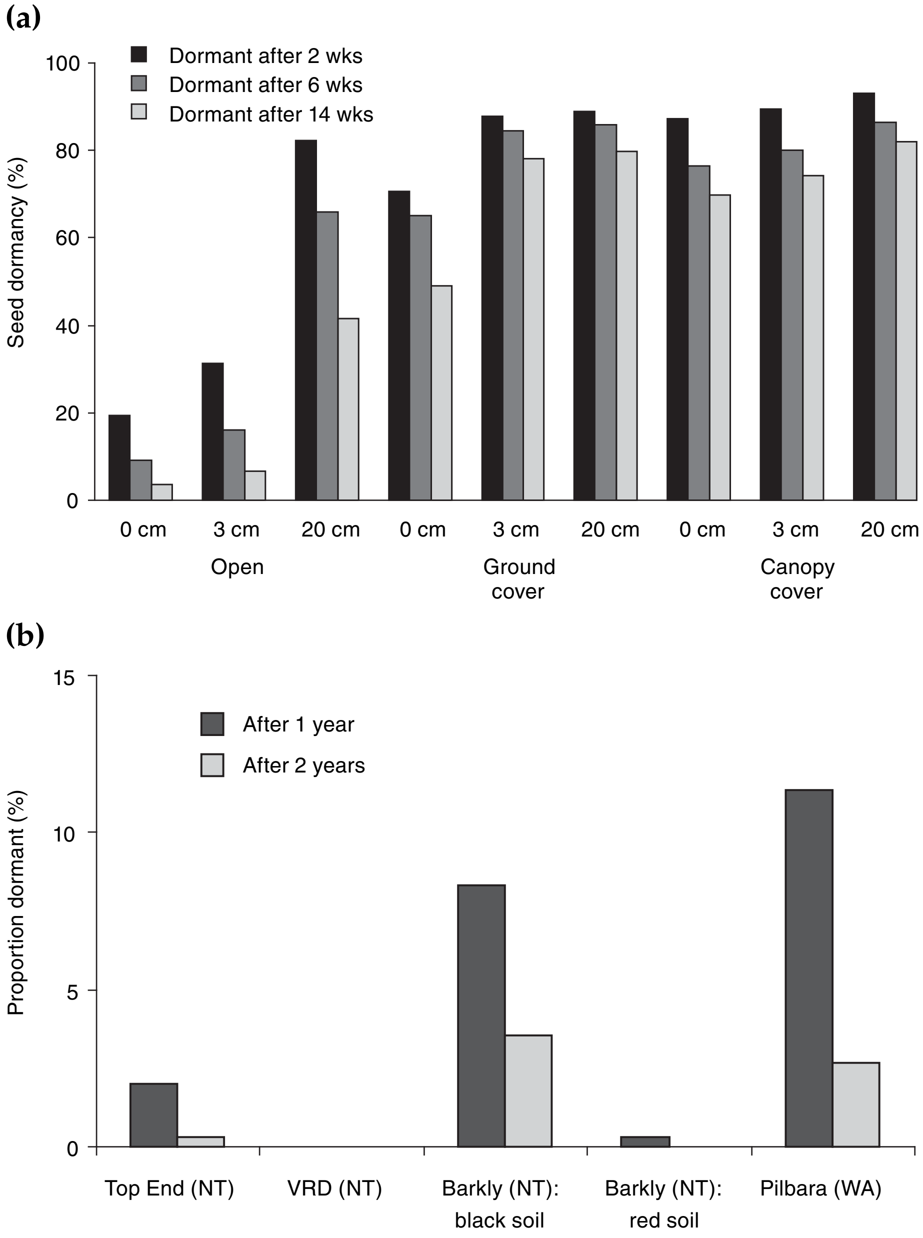

Figure 9. Seed bank longevity in upland habitats a) in a range of habitats and soil depths in the wet-dry tropics (near Darwin) (after van Klinken *et al.* 2006) and b) in different climatic regions and soil types when buried at 2 cm (after van Klinken, Lukitsch and Cook 2008).

that was fenced to exclude cattle (R.D. van Klinken unpublished data). Similar observations have been made for goats (East Timor, R.D. van Klinken unpublished observation) and camels (Queensland, Deveze 2004, p. 36). Cattle also may impact on recruitment when alternative food sources are limited. In central Queensland cattle have been observed to browse seedlings and juveniles during drought or late in the dry season, often killing the plants (Deveze 2004). In contrast, seedlings in the Barkly Tablelands showed little or no signs of being grazed, even when growing in holding yards (R.D. van Klinken unpublished data). Unidentified locusts have been observed to strip bark from seedlings, sometimes causing death.

Parkinsonia aculeata seedlings of all ages can survive considerable damage. If stripped of leaves they resprout from the leaf axils; if cut off above the cotyledonary node they resprout at this node (usually two shoots, one being dominant) (Woods 1988). Seedlings can even survive being cut off below the cotyledonary node, although survival is lower and final dry weight and length are significantly less than when seedlings are cut off above the cotyledons (Woods 1988). Most seedlings do, in fact, suffer tip damage, as is evidenced by high rates of multi-stemming among seedlings less than one year old (R.D. van Klinken unpublished data). This slows growth rates, and must affect the competitiveness of seedlings.

High recruitment events can occur, but these are generally rare and give rise to small dense patches (10s of square metres). They generally occur where seed banks are high, moisture conditions are ideal, and when there is limited herbaceous cover through the wet season. Large scale recruitment has been observed in extensive areas following flooding, such as on floodplains, where in some instances *P. aculeata* was not previously present and seeds had been transported and deposited from infestations located higher in the catchment.

Vegetative reproduction

Parkinsonia aculeata does not reproduce vegetatively; however, it can reshoot from basal buds located up to 20 cm below ground level following damage to the main stem. *P. aculeata* can also be propagated by root or shoot cuttings (Singh 1989, in Hawkins 2001).

Hybrids

Parkinsonia aculeata is the only *Parkinsonia* species known to have naturalized in Australia, and no hybrids have been recorded there; however, *P. aculeata* hybridizes readily with other *Parkinsonia* species in the Americas, including *P. microphylla* and *P. praecox* (Hawkins *et al.* 1999). *P. aculeata* × *P. microphylla* hybrids are fairly common wherever the two co-occur on the outskirts of Tucson and other desert cities (Dimmit 1987). These hybrids grow nearly as fast as *P. aculeata*, are fertile, and have extremely variable progeny (Dimmit 1987). *P. aculeata* × *P. praecox* hybrids are common within the area of sympatry of *P. aculeata*, and the geographically more narrowly distributed *P. praecox* (Hawkins 1997, Hawkins *et al.* 1999). The hybrid is fertile, and is probably the result of the increasing range of *P. aculeata* (Hawkins 1997). This hybrid has been formally named *Parkinsonia* × *carterae*. *P. aculeata* × *P. praecox* is sometimes favoured over either parent species as a fodder, shade and ornamental tree, and is thornless, unlike either parent tree (Hawkins 1997). The ornamental trade has intentionally created hybrids, including 'Desert Museum' which is probably a (*P. aculeata* × *C. microphylla*) × *C. florida* hybrid (Dimmit 1987).

Population

In Australia *P. aculeata* can form near-impenetrable thickets and thorn forests (Figure 10a,b); however, with relatively few exceptions (e.g. within ephemeral wetlands of the Queensland Gulf), high density patches are fairly small and localized within the landscape. More often, *P. aculeata* exists as sparse populations of mainly mature plants (Figure 10c). Dispersal, seed bank dynamics, recruitment success and adult longevity are all likely to be important in determining where and when thicket formation occurs, and for how long such thickets persist. Landscape models are currently being developed using Bayesian Belief Networks to predict in which parts of the landscape *P. aculeata* has the potential to develop dense stands (van Klinken, Seabrook *et al.* 2008).

Seed dispersal is critical in determining the way *P. aculeata* populations are distributed and structured across the landscape. Where the landscape is not inundated by water the seed bank is largely restricted to under, or just adjacent to, parent trees. This provides an opportunity for slow thicket formation, especially following the death of parent trees. The presence of isolated trees across upland habitats almost certainly reflects low rates of long distance dispersal, such as in mud carried from under parent trees on the hooves of animals.

In contrast, flooding results in the redistribution of seeds from under parent trees, provided it occurs at or soon after pod fall. Redistribution can occur in a number of ways depending on hydrology and other factors. For example, seeds can often be distributed across a flood plain, resulting in recruitment of relatively evenly-spaced new plants. Alternatively, seeds may be concentrated by eddies or micro-topography into restricted parts of the landscape (Hawkins *et al.* 1999), resulting in the formation of discrete thickets. Finally, seeds can be washed down watercourses, resulting in the isolated recruitment of new plants. The latter is common where flood waters flow quickly, such as within the banks of major rivers.

Patches of *P. aculeata*, whether seedlings or adults, frequently appear to consist primarily of plants of a similar age. This is likely to be the consequence of both large seed banks (such as under parent trees) and the infrequency of favourable recruitment conditions. Suitable micro-sites can often be provided through the death of parent trees or receding flood waters.

Parkinsonia aculeata populations can be very dynamic. For example, anecdotal evidence suggests that thicket formation and decline is cyclical in parts of central Queensland. A site in Nicaragua was observed to decline between 1999 and 2004 when all trees were old, many were dead or dying and no young trees were present (T.A. Heard unpublished data). Similarly, of over 23 demographic sites set up in healthy *P. aculeata* populations across Australia in 1999–2001, most had declined in adult density over the following 4–5 years (J. Pichancourt and R.D. van Klinken unpublished data). This was a consequence of both high mortality of existing plants and low (or zero) recruitment rates, despite high seed inputs. Mortality factors for adults and juveniles included dieback (Barkly Tableland), fire (Kimberley), termites (Kimberley, Top End), wet stress (Victoria River District wetland sites), and severe frost (central Australia), as well as unexplained causes (most sites). Accumulating evidence suggests that *P. aculeata* dieback, caused by one or more soil-borne pathogens (Diplock *et al.* 2006, 2008) may be an important driver of the often dynamic nature of *P. aculeata* patches in Australia. A possible mechanism is that the dieback pathogens build up within new *P. aculeata* populations until they reach a concentration where they are lethal to existing plants and to new recruits.

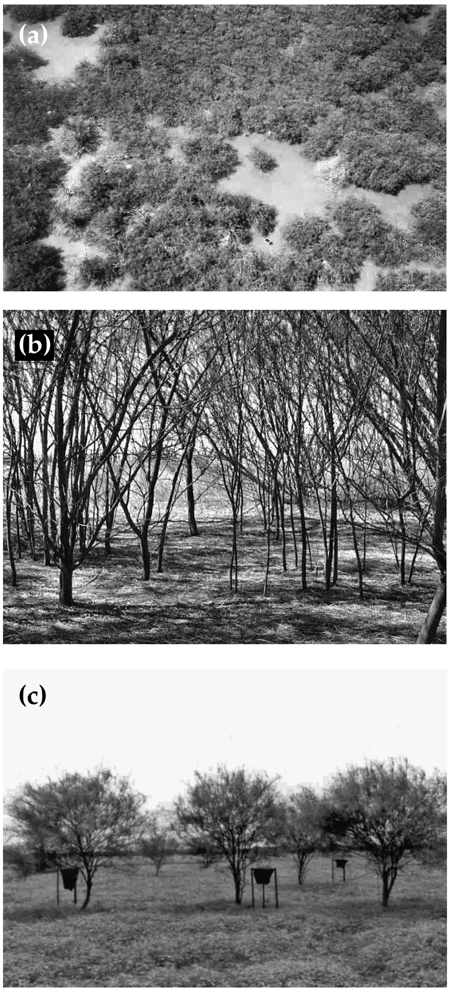

Figure 10. Invasive *Parkinsonia aculeata* populations: (a) aerial view of a dense infestation in an ephemeral wetland in the southern Gulf of Carpentaria region (Queensland), (b) understorey of a dense infestation in the Kimberley (Western Australia), and (c) a sparse population of adults in the Top End (Northern Territory).

Importance

Parkinsonia aculeata is an example of a plant that is both weedy and beneficial; however, in Australia its negative aspects far outweigh any actual or potential benefits.

Detrimental

Most of the detrimental effects of *P. aculeata* stem from its propensity to form dense, thorny, impenetrable thickets along drainage lines, depressions, ephemeral wetlands and, to a lesser extent, uplands across a large part of Australia (Figure 5). These are of both environmental and economic significance.

The greatest environmental impact is probably through the exclusion of the herbaceous layer (van Klinken 2006). *P. aculeata* trees are relatively shallow-rooted, but they may shorten the duration that ephemeral water bodies hold water. Dense patches are rarely greater than 1 ha so impacts on biodiversity are likely to be localized and limited to the infestation site (van Klinken 2006). At greatest risk are climatically suitable mesic habitats in arid and semi-arid regions, such as wetlands on the Barkly Tablelands (Northern Territory), wetlands and gorges in the Pilbara Region (Western Australia) (van Klinken 2006) and waterbird habitats of national significance across its potential distribution (Humphries *et al.* 1991). *P. aculeata* has become a problem in the wetlands of Palo Verde National Park in Costa Rica where it is native, with parts of the Palo Verde Lagoon becoming extensively invaded since the early 1980s (Trama 2004).

In production systems *P. aculeata* can also replace pasture, but existing infestations probably do not occur at a sufficient scale to cause significant and widespread reductions in carrying capacities (van Klinken 2006). Thicket formation does, however, interfere with stock management, impedes stock access to water, makes the maintenance of water points difficult and provides refuge for feral pigs (Deveze 2004). Both the formation and control of thickets may also exacerbate erosion problems (Wilson and Miller 1987). Thorns may injure hooves of animals and affect leisure and recreational activities, while its flowers are known to cause hay fever (Wilson and Miller 1987, Deveze 2004). In northern Mexico infestations choke irrigation channels (Hawkins 2001).

Actual and potential costs to Australia

Although *P. aculeata* is already widespread in Australia, existing infestations are not yet of sufficient scale to cause substantial production losses at the property scale or to cause catchment or regional scale environmental impacts. Most of the direct costs are related to increased property management costs, especially in relation to mustering, accessing water points and maintaining vehicle tyres, and on-ground control work to prevent *P. aculeata* from becoming a more serious problem. Costs to Australia will increase dramatically if *P. aculeata* continues to spread and thicket formation continues. However, actual and potential impacts have not been quantified.

Beneficial

Parkinsonia aculeata is widely used as an ornamental in dry areas throughout the Americas because of its spectacular bright yellow flowers; however, it is not generally considered to produce particularly valuable or high quality products (Hawkins 2001). Uses include hedges, windbreaks, shade, fuel (firewood and charcoal), paper-making and low quality fodder (Anon 1972, Allen and Allen 1981, MacDicken and Brewbaker 1984, Hughes 1989, Barbosa and Prado 1991, Stewart *et al*. 1992, Hawkins 2001). Although wood can be used for carpentry (Barbosa and Prado 1991), it is brittle and of dubious durability (Stewart *et al*. 1992). *P. aculeata* has been used in folk medicine (Barbosa and Prado 1991). Leaves, when made into an infusion, are considered in some areas to have medicinal and antiseptic properties and the infusion has been used to treat fevers, epilepsy and vomiting (Stewart *et al*. 1992, Hawkins 2001). Raw seeds have been used as a food source by humans in Mexico, children have been reported to eat flowers and seeds in West Africa, and seeds have been investigated as a minor food source in India (Hawkins 2001).

The fodder value of *P. aculeata* pods and foliage varies, and reports range from it being rarely eaten by livestock or wildlife (Everitt 1983) to being a potentially important fodder tree (MacDicken and Brewbacker 1984, Stewart *et al*. 1992, Hawkins 2001). It appears to be consumed by cattle only in times of shortage (Stewart *et al*. 1992), such as late in the dry season (Anon. 1972, Deveze 2004, p. 35, 45); however, it is browsed by sheep, goats and camels and, in some parts of the world, branches are lopped during dry periods to feed sheep and goats (Hawkins 2001).

Parkinsonia aculeata has been introduced pantropically, primarily as an ornamental, hedging and fodder tree (Stewart *et al*. 1992, Woods 1988, Hawkins 2001). In addition, its tolerance to drought, waterlogging and saline conditions has meant that it has often been promoted for rehabilitation and as a multi-purpose tree, particularly in harsh, degraded or marginal land (Hughes 1986, Hawkins 2001). It has been used for reforestation programs in several countries, including India, Sudan and Cape Verde (Le Heoerou 1984, Hughes 1989) and continues to attract attention as a candidate for the reforestation of degraded environments (Madany 1991, Rajaram and Janardhanan 1991, Stewart *et al*. 1992). However, its usefulness can be limited by its weedy tendencies (Hughes 1989).

In Australia *P. aculeata* appears to have been planted mainly as an ornamental and shade tree. Its potential for use in rehabilitation of Australia's arid regions has been discussed (Ratcliffe 1936, in Cook and Dias 2006), but we are not aware of it ever being used for that purpose.

Legislation

Parkinsonia aculeata has been declared in all states and territories. In Queensland it is classified as a Class 2 declared pest (landholders must take reasonable steps to keep land free of the weed; it is also prohibited to introduce, feed, keep, release, take for commercial use, supply or transport). In the Northern Territory the species is classified as Category B (growth and spread to be controlled). In Western Australia it is declared as P1 (prevention of trade, sale or movement), P2 (eradicate) or P4 (contain) according to districts. In New South Wales it is declared in Category W1 (presence must be notified to the local control authority and the weed must be fully and continuously suppressed and destroyed). In South Australia *P. aculeata* is notifiable throughout the state, and plants must be destroyed. It is not naturalized in Victoria, the ACT or Tasmania, where it is declared as a restricted or prohibited plant.

Weed management

History

Parkinsonia aculeata was already recognized as a threat in Australia at the start of the twentieth century (Bailey 1906). Control work was commenced at least by 1940 in the Fitzroy Shire (Queensland) (N. Mills unpublished report March 2000). Research into *P. aculeata* control began as early as the 1950s, and the first recommendation was 2,4,5-T in diesel (NWS 2000). This was the standard method of control in all areas of infestation on properties and government reserves until the chemical stopped being used in the early 1990s. In addition to this, some landholders utilized fire and mechanical control. A biological control program, jointly funded by Queensland, the Northern Territory and Western Australia, commenced in the 1980s (Woods 1986). Research on chemical control methods also recommenced in the early 1980s as the weed problem became more serious. Major on-ground control work also commenced around that time and has continued through to today. For example, in Queensland $A233 706 was spent on eight Strategic Weed Eradication and Education Program projects in five shires between 1995 and 1998 (NWS 2000).

In 1999 *P. aculeata* was recognized as one of the 20 Weeds of National Significance, i.e. as one of the worst weeds in Australia (Thorpe and Lynch 2000). As a consequence, in 2000 a National Strategic Plan was developed which aimed to deliver four key outcomes: (i) *P. aculeata* management is coordinated and maintained at a national level; (ii) Zone A infestations (containment zones) are reduced; (iii) Zone B infestations (active control zone) are minimized; and (iv) Zone C (eradication zone) infestations are eradicated and *P. aculeata* is prevented from spreading (NWS 2000). Considerable federal funding was made available to help address the on-ground management, research and extension priorities identified in this strategy. For example, approximately $A2 million of federal funding was directed towards management of *P. aculeata* between 2001 and 2005. This was matched by at least the same amount of cash or in-kind contributions from other stakeholders (Martin and van Klinken 2006). This funding provided a catalyst for major on-ground control programs in Queensland, the Northern Territory and western NSW. In the Desert Channels Region (in Queensland) alone, approximately 300 000 ha of *P. aculeata* infestations as well as occurrences along 500 km of drainage lines were treated in 2002–2003.

A range of control techniques are now available to manage *P. aculeata*, including the use of herbicides, machinery, fire and grazing (Vitelli 1995, Deveze 2004). Choice of the best or most appropriate method depends on a number of factors, including seasonal conditions, the type of country infested, extent of the infestation, identified environmental or economic risks and the resources available (Deveze 2004). Irrespective of what control method is used, high densities of new recruits can appear following initial control, and it will be necessary to undertake several follow-up treatments.

Herbicides

Presently, there are a limited number of herbicides available for the control of *P. aculeata* in Australia (Table 1) (Vitelli 1995, Deveze 2004); however, those that are registered are highly effective when applied at the recommended life stages and under favourable climatic conditions (Deveze 2004, McKenzie *et al*. 2004). Selection of the most appropriate method of application is very important, with options available including basal bark and cut stump spraying, and ground and aerial applications of both foliar and soil applied herbicides (Table 1) (Vitelli 1995, Deveze 2004).

Basal bark spraying and cut stump applications are best suited for treating scattered to light infestations. Because of the high labour input required with these techniques, treatment of denser infestations becomes less economical. For example, in a large integrated trial undertaken on *P. aculeata*, basal bark spraying of a dense infestation (average density of 2200 plants ha^{-1}) cost $A420 ha^{-1} (McKenzie *et al*. 2004). Best results for basal bark treatment are achieved when the plants are growing actively, whereas cut stump treatment is effective throughout the year (Deveze 2004).

Foliar spraying of the foliage and green stems of *P. aculeata* is a highly effective control method for treatment of actively growing seedlings and young plants up

Table 1. Registered herbicides for *Parkinsonia aculeata* control in Australia[A] (adapted from Deveze 2004 and Infopest July 2008, Biosecurity Queensland, Department of Primary Industries and Fisheries, Brisbane).

Active chemical constituents	Application method	States/Territories where registered	Rate
Tebuthiuron (200 g kg^{-1})	Aerial	Qld and NT	10–15 kg ha^{-1}
	Soil	Qld, NT and WA	10–15 kg ha^{-1} (1–1.5 g m^{-2})
Triclopyr (300 g L^{-1}) + picloram (100 g L^{-1})	Aerial (helicopter only)	Qld and NT	3 L ha^{-1}
	Foliar (overall spray)	Qld, NT and WA	350 mL 100 L^{-1} water
Triclopyr (300 g L^{-1}) + picloram (100 g L^{-1}) + aminopyralid (8 g L^{-1})	Aerial (helicopter only)	Qld, NT and WA	3 L ha^{-1}
	Foliar (overall spray)	Qld, NT and WA	350 mL 100 L^{-1} water
Triclopyr (240 g L^{-1}) + picloram (120 g L^{-1})	Basal bark and cut stump	All states/territories	1 L 60 L^{-1} diesel
Hexazinone (250 g L^{-1})	Soil – spot spray (individual tree)	Qld, NSW, WA and ACT[B]	4 mL per spot, 1 spot for each bush or tree
	Soil – spot spray (grid pattern)	Qld, NSW, WA and ACT[B]	1 mL per spot to 1m tall, 4 mL per spot to 5 m tall

[A] Refer to individual product labels for details on the situations in which the products can be sprayed and the best times to spray.

[B] Velpar® L is not registered for use in the ACT.

to a height of 1.5–2 m (Deveze 2004). As for basal bark and cut stump applications, foliar spraying becomes expensive as the density of *P. aculeata* increases. For dense infestations, aerial application of foliar herbicides can be undertaken, but efficacy may vary depending on the density and size of the plants. McKenzie *et al.* (2004) reported only 66% mortality of a dense infestation following aerial spraying and concluded that this may have been because there were many plants larger than 2 m in height located within the field site. In a trial undertaken to quantify the efficacy of aerial spraying, it was concluded that there was a direct inverse relationship between plant size and mortality (J.S. Vitelli unpublished 2006).

The use of residual herbicides is favoured by many land managers who prefer not to revisit treated areas and continually treat new recruits (Landsberg *et al.* 2006). Such herbicides can be applied through ground based applications, or aerially. For the two registered products, hexazinone and tebuthiuron, McKenzie *et al.* (2004) achieved 97% and 81% mortality respectively, in a dense infestation after one season. After two wet seasons mortality further increased to 99% and 95% respectively. Hexazinone was applied individually to each plant for medium to scattered infestations and as a meter-by-meter grid format for dense overlapping canopy infestations, whereas tebuthiuron was broadcast from an aeroplane. The cost associated with the broadscale application of tebuthiuron averaged \$A180 ha^{-1}, slightly more than that for aerially applying a liquid herbicide (\$A154 ha^{-1}) (McKenzie *et al.* 2004). The ground application of hexazinone proved much more expensive (\$A270 ha^{-1}) and is more appropriate for scattered to light infestations.

Mechanical options

Parkinsonia aculeata can be killed using mechanical techniques, some of which become more economical as the density of infestations increases. Available options include grubbing, stick raking, cutter barring, blade ploughing and chain pulling (Deveze 2004). Costs of control have been estimated in recent trials (see below), although it should be noted that diesel prices have increased considerably since then.

As for many woody weeds, mechanical clearing of *P. aculeata* is most successful when the roots of plants are removed or sheared off below the bud zone (20–30 cm below ground) (Deveze 2004). McKenzie *et al.* (2004) found that blade ploughing was extremely effective for treating dense infestations, with greater than 90% mortality achieved, irrespective of whether a back mounted or front mounted blade plough was used. The front mounted machine was slightly cheaper at controlling *P. aculeata* (\$A126 ha^{-1}) on a per unit area basis compared with the back mounted option (\$A156 ha^{-1}), probably because of its greater manoeuvrability. Use of a bulldozer with a standard blade achieved only 43% mortality yet cost almost as much as blade ploughing. McKenzie *et al.* (2004) suggested that if bulldozers with standard blades are all that is available, careful manoeuvring of the blades at an angle may enable plants to be dug out with a large portion of root. This would, however, take longer, thereby increasing the cost of treatment. Use of tractors mounted with blades or small cutter bars could be a feasible option for treating scattered infestations of plants, as has been used for treatment of some prickly acacia infestations in western Queensland. In central Queensland a small Ellrott plough has been attached to a Bobcat and is proving very effective at treating isolated *P. aculeata* plants and other woody weeds.

The cheapest mechanical option to implement for dense infestations of woody weeds is chain pulling. However, *P. aculeata* appears to be quite tolerant of this technique, with results from one study finding that less than 30% mortality occurred even after infestations were chained successively in opposite directions (double pulled) (McKenzie *et al.* 2004). The main benefit of chain pulling is that plants may be prevented from seeding for a period of time, thereby reducing replenishment of the seed bank.

In many instances, broad scale mechanical control of woody weeds will cause considerable disturbance and potentially create an environment conducive to large scale seedling recruitment. In the absence of any follow up activities the problem can soon become worse than it initially was. Conversely, promoting a favourable environment for germination can help deplete the seed bank more quickly than normal and shorten the length of time during which follow up control may be needed (Campbell and Grice 2000).

There are some legislative restrictions that may influence whether mechanical techniques can be used in certain situations. For example, in Queensland, it is generally necessary to obtain a permit under the Vegetation Management Act 1999 to use machinery in riparian areas (Vitelli 2000, Vitelli and Pitt 2006).

Fire

Anecdotal evidence has provided mixed reports on the efficacy of fire as a control option for *P. aculeata*. They include suggestions of high mortality being achieved through cool low intensity burns to limited control after hot fires (Deveze and Kendrick 2004, in Deveze 2004, McKenzie *et al.* 2004, in Deveze 2004). Preliminary results from a trial undertaken to quantify the efficacy of different intensity fires (headfires *versus* backfires) imposed in various seasons, suggest that high kill rates can be achieved for all size classes of *P. aculeata*. Efficacy does, however, vary depending on the season and intensity of burning (Grice *et al.* 2004).

It is likely that a large portion of *P. aculeata* seeds located on or close to the soil surface will be killed by fires (Scott 2006). Buried seeds, however, will generally survive. The insulating ability of soil negates the high temperatures produced by fires, with only small increases being recorded 1 cm below ground during most grass fires (Bebawi and Campbell 2002, Campbell and Setter 2002). For surviving seeds, dry heat from burning can compromise the seed coat, releasing the seed from dormancy (Scott 2006). Removal of vegetation through fire can also result in seeds being exposed to wet, hot conditions (wet heat) following rainfall, which is the key dormancy release mechanism for this species (van Klinken 2005). The implication for management is that removal of herbaceous cover by burning is likely to expedite the run down of the seed bank by triggering dormancy release and subsequent germination. This is a desirable scenario, provided land managers are in a position to treat any seedling regrowth before it has the opportunity to reach reproductive maturity.

Although fire offers an effective tool, its use is frequently limited by lack of fuel load, social or cultural constraints, the safety risk of late dry season burns, the desire to conserve fodder, and concerns about non-target environmental effects, particularly in wetland and riparian habitats (Deveze 2004).

Flame throwers have been tested as an individual treatment for *P. aculeata* where chemical and mechanical controls are inappropriate or ineffective (Vitelli and Madigan 2004). Flaming for 10 seconds around the entire circumference of the base of individual plants (5 cm above ground level) at a maximum temperature of 820°C killed 83% of the treated plants at a cost of 7.5 cents per plant (Vitelli and Madigan 2004). This practice would be most appropriate for treating small and/or scattered infestations.

Grazing management systems

There is a paucity of information in the literature on the effects that grazing and browsing have on *P. aculeata* dispersal, recruitment or control. Several landholders suggest that cattle will browse *P. aculeata* foliage (Deveze 2004), but this happens generally only when available grass is limited or of low nutritive value, such as at the end of the dry season prior to first storms. Under these circumstances cattle can eat whole stems to 2 cm in diameter, sometimes killing the plants (Deveze 2004). Plant analysis studies have found that *P. aculeata* has low leaf fodder value due to its moderate to high total fibre content levels, a nitrogen content of 3.7%, and no condensed or hydrolyzable tannins, which usually indicate high digestibility (Hunter and Stewart 1993). Nonetheless, some animals, especially macropods, goats and camels, can preferentially browse *P. aculeata*, substantially reducing growth and survival of seedlings and juveniles.

Parkinsonia aculeata seedlings are relatively poor competitors, and heavy pasture cover is therefore likely to limit recruitment through competition for light and moisture. In fact, high densities of vigorous *P. aculeata* seedlings have only been noted where there is little herbaceous cover. It is not yet known how important grazing management is for reducing *P. aculeata* recruitment relative to other factors such as flooding (or the absence thereof). Also, it is possible that spelling pastures to promote competition may produce adverse results by allowing seedlings to grow freely in situations where cattle browse this weed. The effect of grazing on *P. aculeata* recruitment is likely to vary with habitats, for example, perennial *versus* annual grasses pastures, riparian areas that are dominated by approximately 2 m tall cane-grass (*Chionachne cyathopoda* (F.Muell.) Benth), and seasonal wetlands where annual grasses might begin growing before water recedes.

Recently, a small but increasing number of northern Australian landholders have been using camels for woody weed control (Deveze 2004). Preliminary studies undertaken to quantify their impacts found that camels selectively browsed fresh growth of *P. aculeata*, including flowers, young pods and leaves (McKenzie *et al.* 2006). Consequently, if paddocks are stocked at a sufficiently high density they can reduce the quantity of *P. aculeata* seeds produced to negligible levels. This in turn results in minimal replenishment of the seed bank and less seedling recruitment in future years.

If mature pods are present on plants, camels may consume them inadvertently or if there is no other preferred food available (McKenzie *et al.* 2006). Camel dung from within infested paddocks contained only small numbers of viable seeds (average of less than two seeds within 30 samples), with a maximum recording of 11 seeds (McKenzie *et al.* 2006). A complementary study suggested that approximately 15% of consumed seeds remain viable after ingestion by camels (J. McKenzie unpublished data). From these findings it was concluded that when camels are confined to an infested area, the threat of seed spread is inconsequential compared to the benefits of both fewer seeds being produced and a low seed viability of consumed seeds; however, in areas where camels are not confined, they may act as vectors for dispersal into clean areas (McKenzie *et al.* 2006). Whether repeated damage by camels could eventually cause mortality of adult *P. aculeata* plants has not been determined. The impacts of camels to off-target species should also be considered when contemplating their use as a tool for *P. aculeata* management, because under some grazing regimes camels have the potential to contribute to a decline in preferred forage species (Dorges and Heucke 2003).

The unexplained presence of *P. aculeata* in upland situations suggests livestock might play a role in seed dispersal, either through dung or in mud. Until the means of dispersal has been confirmed, it should be presumed that livestock can pose at least a small risk of seed dispersal, and livestock movement from infested to clean areas needs to be managed accordingly (see van Klinken and Campbell 2001).

Commercial exploitation

No *P. aculeata* products have been identified that can be exploited on a commercial scale in Australia.

Natural enemies

Native natural enemies in the introduced range There are relatively few native insect herbivores on *P. aculeata* in Australia. In the Northern Territory only 17 species of insects were found feeding on the weed, and none was common (C. Wilson personal communication 2008). The most damaging was the giant termite (Mastotermitidae: *Mastotermes darwiniensis* Froggatt) which is capable of killing mature plants, although plants may survive and send up fresh suckers (R.D. van Klinken personal observation). Other species were seven species of stem sucking bugs, two pod and seed feeders, two species of grasshoppers and a case moth caterpillar that chews leaves. The combined impact of all of these on the plant was considered to be negligible; however, there are reports of insects being locally abundant and damaging, including an unidentified coccid that reaches high densities causing the gnarling of growth tips (Victoria River District, R.D. van Klinken unpublished data) and stem borers (Halls Creek [Kimberley], N. Wilson personal communication 2001). These insects often appear to be most abundant on plants that are already stressed from other causes. The univoltine, pantropical, seed feeding moth, *Mesophleps palpigera* (Walsingham) (Gelechiidae) is widespread. It oviposits on tree pods just prior to seed maturation and has caused up to 33% seed mortality in some samples, although seed predation rates are generally no more than a few percent (van Klinken 2005, van Klinken and Flack 2008).

A natural dieback phenomenon has been widely observed across the Australian distribution of *P. aculeata* (excluding the Pilbara Region and Central Australia) for at least 50 years (Diplock *et al*. 2008). It causes widespread deaths of individuals and populations of plants. In some regions it has been identified anecdotally as the factor preventing *P. aculeata* from becoming an important problem. Research to identify the causal agent is continuing, but likely causative agents include *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl., *Fusicoccum dimidiatum* (Penz.) D.F.Farr and *Fusarium* sp., all of which are generalist root-borne pathogens (Diplock *et al*. 2006, 2008). Pathogens also cause death of newly germinating seedlings in laboratory tests, although it is not yet known what impacts they might have under natural conditions. In a laboratory study, the pathogenicity of 84 pathogen isolates extracted from *P. aculeata* plants sampled across Australia was tested against germinating *P. aculeata* seedlings (Toh *et al*. 2008). Pathogenicity varied greatly, but five isolates from the Northern Territory, Western Australia and Queensland (*Lasiodiplodia* spp., *Fusicoccum* sp. and an unidentified isolate) caused almost 100% seedling mortality. Despite extensive sampling for internal pathogens on *P. aculeata* in its native range no symptoms have been found. A total of 76 sites have been sampled, with 50 stems cut and inspected for vascular staining or other signs of pathogens at each site. The sites are distributed in Mexico, Costa Rica, Venezuela, Guatemala, Brazil, Peru, Puerto Rico, Paraguay and Dominican Republic.

In a survey of the natural enemies of *P. aculeata* in Kenya, only nine species of insects were found and all were indigenous polyphagous species (Robertson 1988). Natural enemies have also been reported on *P. aculeata* in India, including the seed-feeding moth *Enarmonia malesana* (Meyrick), and the sap-sucking mealy-bugs *Icerya aegyptiaca* (Douglas) and *Pseudoaonidia* sp. (Troup and Joshi 1983).

Classical biological control Investigations into the potential biological control of *P. aculeata* began in 1983 with a joint project between state government agricultural agencies in Queensland, Western Australia and the Northern Territory (Woods 1986). The Australian Weed Committee approved *P. aculeata* as a target for biological control in Australia in 1983 (Donnelly 2000).

Surveys were conducted from April 1983 until January 1987 from bases in Texas and Arizona (USA) and Guerrero (Mexico) (Woods 1986, 1988, 1992). These surveys were conducted in the states of Texas, Arizona (USA), Tamaulipus, Nuevo Leon, Sonora, Sinaloa, Baja California, Michoacan, Guerrero, Oaxaca, San Luis Potosi, Hidalgo (Mexico) and Guanacaste (Costa Rica). An emphasis was placed on collecting in the Sonoran desert because it was thought to be the centre of origin of the genus and other areas had not yielded many insects (Woods 1988). North America (USA and northern Mexico) was surveyed thoroughly, but only limited surveying was conducted in Central America (including southern Mexico and Costa Rica).

Two mite species and 142 insect species were collected from *P. aculeata* during the surveys (54 from Arizona, 38 from Texas, 69 from Mexico and 16 from Costa Rica). Species diversity at least partly reflected sampling effort. Most insects were polyphagous, with many utilizing the genera *Prosopis*, *Acacia* and other species of *Parkinsonia*. In comparison with other plant species, a large number (44) of phytophages were polyphagous 'Homoptera'. On the basis of field host records only eight species (6%) were considered to be sufficiently host-specific to be considered for biological control in Australia (Woods 1988). Only the polyphagous bruchids, *Stator limbatus* (Horn) and *Mimosestes amicus* (Horn), were widespread in North and Central America. A few other insects were widely distributed in Arizona, Texas and Mexico.

Twelve insect species (eight from the Sonoran Desert Region, and the rest from southern USA and Mexico) were identified as potential biological control agents because of the damage they caused (Woods 1988). Several of these were excluded on the basis of their broad host range. The two with greatest potential, *Rhinacloa callicrates* Herring (a sap-sucking mirid) and *Mimosestes ulkei* (Horn) (a seed-feeding bruchid) were released in Queensland in 1993 (Julien and Griffiths 1998) and the Northern Territory in 1989 (Donnelly 2000) and 1994 (Flanagan *et al*. 1996) respectively. A third insect from Argentina, the seed-feeding bruchid, *Penthobruchus germaini* Pic., was identified from the literature as a potential agent and was released in Australia from 1995 (Briano *et al*. 2002, van Klinken 2005, van Klinken and Flack 2008). Several other insects with high potential may deserve re-evaluation, especially the tortricid, *Ofatulena luminosa* Heinrich, which attacks tips and green seeds. It was originally excluded because it is difficult to rear and test for host specificity, but new techniques may be applied to assess this insect. Also, the bruchid, *Mimosestes amicus* Horn deserves reappraisal. The host range of this species appears to be too wide, but research on the occurrence of races or cryptic species with limited host ranges may be useful.

Rhinacloa callicrates has been released across northern Australia in large numbers (500 000 in Queensland alone). Although it reaches very high, damaging densities in its native range, and has established in central Queensland, it has never been observed to reach damaging densities there (Donnelly 2000). Failure to establish in the Kimberley could be because temperatures and relative humidity are too high (G. Donnelly personal communication 1999), although this has not been tested.

The two seed-feeders were released between 1995 and 1999 on *P. aculeata* throughout much of its range in Australia (Donnelly 1998, Lockett *et al*. 1999, Lukitsch and Wilson 1999), including the Kimberley (Western Australia). *Mimosestes ulkei* oviposits on nearly mature pods either on the tree or on the ground (Woods 1985). It appears to have established at relatively few sites and, where measured, the seed mortality rates have been low (maximum of 5.3% of seeds in the Northern Territory) (Donnelly 1998, Lockett *et al*. 1999) (see also Woods 1988). It has not been reported in the past several years. In contrast, *Penthobruchus germaini* established easily, and dispersed readily; including to Alcoota station in the Alice Springs Region several hundred kilometres from the closest known release site (van Klinken and Flack 2008). *P. germaini* passes through several generations a year, and oviposits primarily on pods on the tree (Briano *et al*. 2002, van Klinken 2005, van Klinken and Flack 2008) (Figure 11). There was an initial anecdotal report of seed mortalities exceeding 99% of available seeds in central Queensland (Donnelly 1998). However, seed consumption rates were relatively low during national surveys conducted between 2000 and 2004 (van Klinken 2005, van Klinken and Flack 2008), and the agent is therefore unlikely to be causing any population-level impacts. Studies showed that beetle populations were unable to track sudden seasonal fluctuations in pod supply, resulting in a lag-phase between seed availability and beetle numbers. Also, high egg parasitism (10–70%) by a trichogrammatid wasp (*Uscana* sp.) is likely to be a key regulating factor through its effect on egg survival, and indirectly on adult densities. Even without egg parasitism, the unexplained failure of

6–44% of unparasitized eggs to hatch, high unexplained larval mortality within seeds (62%) and slightly aggregated (negative binomial) oviposition, means that average egg densities would need to be over 8.5 eggs per seed to achieve 80% seed mortality (van Klinken and Flack 2008).

Existing agents therefore do not appear to be having a significant impact, and new potential agents are unlikely to be found in the United States or northern Mexico. However, Central and South America have not been surveyed properly. Native-range surveying was reinitiated by CSIRO Entomology in 1999 in Mexico, Guatemala, Nicaragua, Costa Rica and Venezuela, where a total of 101 sites were visited at least once between 1999 and 2005 (Heard 2006).

The discovery that the current broad distribution and deep genetic structuring of *P. aculeata* reflects very old dispersal events (Hawkins *et al*. 2007) stimulated interest in survey work in South America. Hawkins *et al*. (2007) focussed on North America, but the Venezuelan samples and the one Argentina sample differed strongly (although populations from Peru, Bolivia, Paraguay and Ecuador were not included in the study). This genetic information, in combination with observations made during recent field trips in Brazil, Ecuador and Peru, indicates that *P. aculeata* is native to these areas and arrived there millions of years ago, and that these populations may harbour unique and specific co-evolved natural enemies. By early 2008, approximately 340 species had been recorded from a total of 190 sites in eight countries, including Ecuador, Brazil and Peru, which had not been searched before. Only a subset of these is likely to be herbivorous on *P. aculeata* (Figure 12). Disappointingly, few appear to be damaging, wide ranging and common, attributes desired in biocontrol agents (T.A. Heard unpublished data).

Several insect species, however, show potential as biocontrol agents. The tortricid (Cochylinae) moth, *Rudenia* near *leguminana* Busck, is one of the most common and consistently-found herbivores in the native range. The larva lives in a hole that it bores in the stem tip, eventually killing it. This species appears to be wide ranging geographically and has a wide host range that includes *Acacia*; however, molecular sequencing of the CO2 mitochondrial gene indicates strong genetic differentiation of the populations from different provenances. Furthermore, preliminary host testing of a provenance from Mexico indicates specificity to *P. aculeata*. Hence, there is a possibility of the existence of races or cryptic species with limited host ranges. Rearing is not difficult and the feeding damage to leaves and boring damage to tips are impressive.

In addition to the insects, a fungal pathogen, *Septoria* sp., is considered a promising potential biocontrol agent for *P. aculeata*. In Nicaragua it has been observed to cause rachis and branch cankering leading to significant damage and die-back (H. Evans personal communication 2007).

Some native-range surveys have also been conducted in Argentina and Paraguay by the USDA (H. Cordo personal communication 2007). Potential agents were identified, including a geometrid moth (Briano *et al.* 2002). Stem-boring cerambycid beetles have also been surveyed near Buenos Aires, Argentina (di Iorio 1993).

Acknowledgments

We thank Rob Parr, Noel Wilson (Agriculture Western Australia), Alan Thompson (CALM WA), Jim Begley, Grant Flanagan, John Gavin, Bert Lukitsch, John McMahon, John Peart, Steve Wingrave (NT Weeds Branch), Ben Lawson (University of Queensland), Tony Grice and Roger Lawes (CSIRO) for their unpublished data and observations, the many participants of parkinsonia research workshop series (2000–2006) for their contributions towards improving our understanding of parkinsonia, Lauren Quinn for assistance with the maps, Tony Grice for comments on a draft manuscript and the Australian Federal Government for funding assistance (Department of Agriculture, Forestry and Fisheries).

References

Adams, M.S. and Strain, B.R. (1969). Seasonal photosynthetic rate in stems of *Cercidium floridum*. *Photosynthetica* 3, 55-62.

Allen, O.N. and Allen, E.K. (1981). The Leguminosae. *In* 'A source book of characteristics, uses and nodulation'. (University of Wisconsin Press, Madison, Wisconsin, USA).

Anon. (1972). Parkinsonia, a weed to watch. *Turnoff* 4, 18-9.

Anon. (1978). Parkinsonia. WADA Agriculture Protection Board Advisory Leaflet, 37 pp.

Alvarez Rangel, R.A. (1984a). Caracterizacion de los mecanismos de control de la latencia y germinacion de las semillas de *Parkinsonia aculeata* L.1. Respuestas de las semillas a los tratamientos para romper la latencia y sus implicaciones ecologicas. *Revista de la Facultad de Agronomia (Maracay, Unversidad Central de Venezuela)* 8, 5-30.

Alvarez Rangel, R.A. (1984b). Caracterizacion de los mecanismos de control de la latencia y germinacion de las semillas de *Parkinsonia aculeata*. II. Respuestas de las semillas a algunos factores ambientales y sus implicaciones ecologicas. *Revista de la Facultad de Agronomia (Maracay, Unversidad Central de Venezuela)* 8, 31-45.

Bailey, F.M. (1906). 'Weeds and suspected poison plants of Queensland'. (H. Pole and Co., Brisbane).

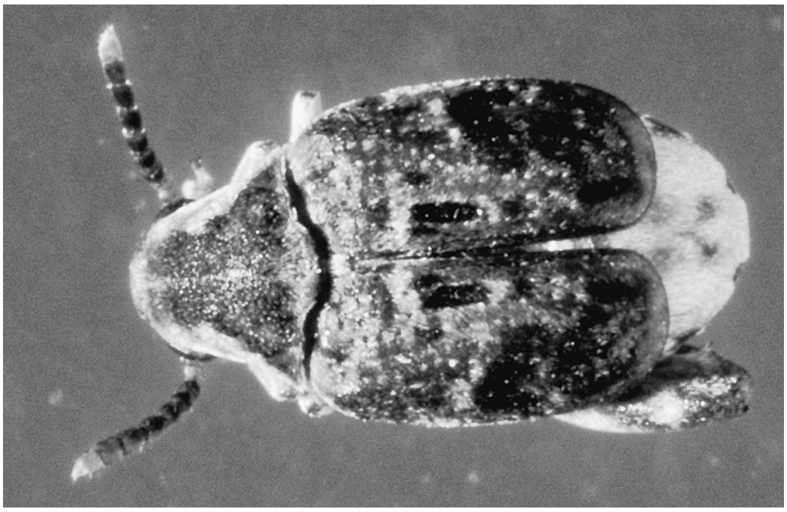

Figure 11. An adult *Penthobruchus germaini*. Image provided by Biosecurity Queensland.

Figure 12. Larvae and leaf feeding damage on a *P. aculeata* growing tip caused by an unidentified geometrid moth in Guatemala.

Barbosa, D.C.A. and Prado, M.G. (1991). Quantitative analysis of the growth of *Parkinsonia aculeata* L. in a greenhouse. *Phyton* 52, 17-26.

Baskin C.C. and Baskin J.M. (1998). 'Seeds: ecology, biogeography and evolution of dormancy and germination'. (Academic Press, New York).

Bebawi, F.F. and Campbell, S.D. (2002). Effects of fire on germination and viability of bellyache bush (*Jatropha gossypifolia*) seeds. *Australian Journal of Experimental Agriculture* 42, 1063-9.

Benson, L. and Darrow, R.A. (1981). 'Trees and shrubs of the south western desert'. (University of Arizona Press, Tucson).

Briano, J.A., Cordo, H.A. and DeLoach, C.J. (2002). Biology and field observations of *Penthobruchus germaini* (Coleoptera: Bruchidae), a biological control agent for *Parkinsonia aculeata* (Leguminosae: Caesalpinioideae). *Biological Control* 24, 292-9.

Campbell, S.D. and Grice, A.C. (2000). Weed biology: a foundation for weed management. *Tropical Grasslands Journal* 34, 271-9.

Campbell, S.D. and Setter, C.L. (2002). Mortality of *Prosopis pallida* (mesquite) following burning. *Australian Journal of Experimental Agriculture* 42, 581-6.

Carter, A.N. (1974). The genus *Cercidium* (Leguminosae, Caesalpinioideae) in the Sonoran Desert of Mexico. *Proceedings of the California Academy of Sciences, Fourth Series* 40, 17-57.

Chatterji, U.N. and Mohnot, K. (1964). Ecophysiological studies on the germination of seeds of certain arid zone plants: Part 1 – Germination experiments with the seeds of *Parkinsonia aculeata*. Proceeding on Problems of Indian Arid Zone pp. 135-9. (Ministry of Education, Government of India, New Delhi).

Cochard, R. (1999). A seed ecology study of *Parkinsonia aculeata* L. Honours thesis, School of Tropical Environment Studies and Geography, James Cook University of North Queensland.

Cook, G.D. and Dias, L. (2006). It was no accident: deliberate plant introductions by Australian government agencies during the 20th century. *Australian Journal of Botany* 54, 601-25

Deveze, M. (ed). (2004). 'Parkinsonia national case study manual'. (QNRME, Brisbane).

di Iorio, O.R. (1993). Cerambycidae (Coleoptera) y otros insectos asociados a *Parkinsonia aculeata* (Leguminosae) en Argentina. (Cerambycidae (Coleoptera) and other insects associated with *Parkinsonia aculeata* (Leguminosae) in Argentina). *Revista de Biologia Tropical* 41, 463-70.

Dimmit, M.A. (1987). The hybrid Palo Verde 'Desert Museum': a new superior tree for desert landscapes. *Desert Plants* 8, 99-103.

Diplock, N., Galea, V. and van Klinken, R.D. (2008). Movement of dieback front through a stand of parkinsonia – a time series study. Proceedings of the 16th Australian Weeds Conference, eds R.D. van Klinken, V.A. Osten, F.D. Panetta and J.C. Scanlan, p. 186. (Queensland Weeds Society, Brisbane).

Diplock, N., Galea, V., van Klinken, R.D. and Wearing, A. (2006). A preliminary investigation of dieback on *Parkinsonia aculeata*. Proceedings of the 15th Australian Weeds Conference, eds C. Preston, J.H. Watts and N.D. Crossman, pp. 585-7. (Weed Management Society of South Australia, Adelaide).

Donnelly, G.P. (1998). Levels of attack and destruction of *Parkinsonia aculeata* seeds by bruchid biological control agents. Proceedings of the Sixth Australasian Applied Entomological Research Conference Volume 2, eds M.P. Zalucki, R.A.I. Drew and G.G. White, p. 310. (University of Queensland Press, Brisbane)

Donnelly, G.P. (2000). Biology and host specificity of *Rhinocloa callicrates* Herring (Hemiptera: Miridae) and its introduction and establishment as a biological control agent of *Parkinsonia aculeata* L. (Caesalpiniaceae) in Australia. *Australian Journal of Entomology* 39, 89-94.

Dorges, B. and Heucke, J. (2003). Demonstration of ecologically sustainable management of camels on aboriginal and pastoral land. National Heritage Trust Final Report on project number: 200046. www.camelsaust.com.au/NHT report2003.doc.

Doyle, J.J., Chappill, J.A., Bailey, C.D. and Kajita, T. (2000). Towards a comprehensive phylogeny of legumes: analyses of rbcL sequences and a general data set. *In* 'Advances in legume systematics', Part 9, eds P.S. Herendeen and A. Bruneau. (Royal Botanic Gardens, Kew).

Egley, G.H. (1989). Water-impermeable seed coverings as barriers to germination. *In* 'Recent advances in the development and germination of seeds', ed. R.B. Taylorson, pp. 207-23. (Plenum Press, New York).

Eisikowitch, D. and Masad, Y. (1982). Preferences of honeybees for different ornamental nectar-yielding plants during the dearth period in Israel. *Bee World* 63, 77-82.

Everitt, J.H. (1983). Seed germination characteristics of two woody legumes (Retama and Twisted Acacia) from South Texas. *Journal of Range Management* 36, 411-4.

Flanagan, G.J., van Rangelrooy, D.S. and Kerin, S. (1996). Integrated management of *Parkinsonia aculeata* on the Roper River, Northern Territory, Australia. Proceedings of the IX International Symposium on Biological Control of Weeds, eds V.C. Moran and J.H. Hoffmann, pp. 441-3. (University of Cape Town, Cape Town).

Grice, A.C., Campbell, S.D., McKenzie, J.R., Whiteman, L.V. and Lukitsch, B.V. (2002). Size-biomass relationships for Australian populations of the invasive rangeland shrub *Parkinsonia aculeata* L. *Rangelands Journal* 24, 207-18.

Grice, A.C., Campbell, S.D., McKenzie, J.R., Whiteman, L.V., Pattison, M., Headricks, K. and Andrew, M.H. (2004). Problems of population structure exemplified by the invasive tropical shrub *Parkinsonia aculeata* L. in northern Australia. *Rangelands Journal* 26, 237-48.

Haston, E.M., Lewis, G.P. and Hawkins J.A. 2005. A phylogenetic reappraisal of the *Peltophorum* group (Caesalpinieae: Leguminosae) based on the chloroplast *trnL-F*, *rbcL* and *rps16* sequence data. *American Journal of Botany* 2, 1359-71.

Hawkins, J.A. (1996). Systematics of *Parkinsonia* L. and *Cercidium* Tul. (Leguminosae: Caesalpinioideae.). PhD thesis, Linacre College, Oxford.

Hawkins, J.A. (1997). Systematics of *Parkinsonia* and *Cercidium*. *Oxford Forestry Institute Research Highlights* 4, 1-2.

Hawkins, J.A. (2001). *Parkinsonia aculeata* (Mexican palo-verde). *In* 'Forestry compendium'. (CABI Publishing, Oxon, UK).

Hawkins, J.A., Boutaoui, N., Cheung, K.Y., van Klinken, R.D. and Hughes, C.E. (2007). Intercontinental dispersal prior to human translocations revealed in a cryptogenic invasive plant. *New Phytologist* 175, 575-87.

Hawkins, J.A. and Harris, S.A. (1998). RAPD characterisation of two neotropical hybrid legumes. *Plant Systematics and Evolution* 213, 43-55.

Hawkins, J.A., White, L., Hughes, C.E., Contreras-Jiménez, J.L. and Mercado, P. (1999). Investigation and documentation of hybridisation between *Parkinsonia aculeata* and *Cercidium praecox* (Leguminosae: Caesalpinioideae). *Plant Systematics and Evolution* 216, 49-68.

Heard, T.A. (2006). *Parkinsonia aculeata*: surveys for natural enemies, native range ecological studies and prospects for biological control. Proceedings of the 15th Australian Weeds Conference, eds C. Preston, J.H. Watts and N.D. Crossman, pp. 581-4. (Weed Management Society of South Australia, Adelaide).

Herendeen, P.S., Bruneau, A. and Lewis, G.P. (2003). Phylogenetic relationships in the caesalpinioid legumes: a preliminary analysis based on morphological and molecular data. *In* 'Advances in legume systematics, Part 10', eds B.B. Klitgaard and A. Bruneau, pp. 37-62. (Royal Botanic Gardens, Kew).

Hughes, C.E. (1986). Progress in collection and evaluation of NFT germplasm from

Central America. *Nitrogen Fixing Tree Research Reports* 4, 49-51.

Hughes, C.E. (1989). Intensive study of multipurpose tree genetic resources. Unpublished report, Oxford Forestry Institute, UK.

Hughes, C.E. and Styles, B.T. (1984). Exploration and seed collection of multiple-purpose dry zone trees in central America. *The International Tree Crops Journal* 3, 1-31.

Humphries, S.E., Groves, R.H. and Mitchell, D.S. (1991). Plant invasions of Australian ecosystems: a status review and management directions. *In* 'Kowari 2'. (Australian National Parks and Wildlife Service, Canberra).

Hunter, I.R. and Stewart, J.L. (1993). Foliar nutrient and nutritive content of Central American multipurpose tree species growing at Comayagua, Honduras. *Commonwealth Forestry Review* 72, 193-7.

Jones, C.E.Jr. and Buchmann, S.L. (1974). Ultraviolet floral patterns as functional orientation cues in hymenopterous pollination systems. *Animal Behaviour* 22, 481-5.

Julien, J.H. and Griffiths, M.W. (1998). 'Biological control of weeds: a world catalogue of agents and their target weeds', 4th edition. (CABI Publishing, Wallingford).

Landsberg, R., Vitelli, M., Shepherd, B., Jayo, R. and Whalan, R. (2006). A catchment approach to parkinsonia control – can it be done? Proceedings of the 15th Australian Weeds Conference, eds C. Preston, J.H. Watts and N.D. Crossman, p. 481-3. (Weed Management Society of South Australia, Adelaide).

Lawes, R.A. (2004). Temporal fluctuations of *Parkinsonia aculeata* L. seedling germination and growth in three Australian rangelands habitats. Proceedings of the 14th Australian Weeds Conference, eds B.M. Sindel and S.B. Johnson, pp. 164-7. (Weeds Society of New South Wales, Sydney).

Lawes, R.A. and Grice, A.C. (2007). Controlling infestations of *Parkinsonia aculeata* in a riparian zone at the landscape scale. *Austral Ecology* 32, 287-93.

Lawes, R.A., Whiteman, L.V. and Grice, A.C. (2003). Mapping the distribution of *Parkinsonia aculeata* in the Cape River catchment in northern Queensland, Australia. *Plant Protection Quarterly* 18, 152-6.

Lawson, B.E., van Klinken, R.D., Day, M.D., Heard, T.A. and Zalucki, M.P. (2008). Improving the agent selection, release and evaluation process: the role of bioclimatic modelling. Proceedings of the 16th Australian Weeds Conference, eds R.D. van Klinken, V.A. Osten, F.D. Panetta and J.C. Scanlan, pp. 510-2. (Queensland Weeds Society, Brisbane).

Le Houerou, H.N. (1984). Forage and fuel plants of N. Africa, near and middle East. *In* 'Plants for arid lands', ed. G.E. Wickens, pp. 117-39. (George Allen and Unwin, London).

Lewis, G.P., Simpson, B.B. and Neff, J.L. (2000). Progress in understanding the reproductive biology of the Caesalpinioideae (Leguminosae). *In* 'Advances in legume systematics, part 9', eds P.S. Herendeen and A. Bruneau, pp. 65-78. (Royal Botanic Gardens, Kew).

Lockett, C., Gray, E. and Donnelly, G. (1999). The prevalence of seed damage by the introduced bruchid, *Penthobruchus germaini* (Coleoptera: Bruchidae), a biological control agent for parkinsonia (*Parkinsonia aculeata*), in far north and central Queensland. Proceedings of the 12th Australian Weeds Conference, eds A.C. Bishop, M. Boersma and C.D. Barnes, pp. 431-5. (Tasmanian Weeds Society, Hobart).

Lukitsch, B. and Wilson, A. (1999). Distribution and impact of the mature seed feeding bruchid, *Penthobruchus germaini* on *Parkinsonia aculeata* in northern Australia. Proceedings of the 12th Australian Weeds Conference, eds A.C. Bishop, M. Boersma and C.D. Barnes, pp. 436-40. (Tasmanian Weeds Society, Hobart).

MacBride, J.F. (1943). 'Flora of Peru. *Fieldiana* 13 (3)'. (Field Museum of Natural History, Chicago).

MacDicken, K.G. and Brewbaker, J.L. (1984). Descriptive summaries of economically important nitrogen fixing trees. *Nitrogen Fixing Tree Research Reports* 2, 46-54.

McKenzie, J.R., Pattison, M.J., Campbell, S.D. and Vitelli, J.S. (2006). The effect camels have on ability of parkinsonia (*Parkinsonia aculeata* L.) to set seed. Proceedings of the 15th Australian Weeds Conference, eds C. Preston, J.H. Watts and N.D. Crossman, pp. 886-9. (Weed Management Society of South Australia, Adelaide).

McKenzie, J.R., Pattison, M.J., Steele, K.E., Campbell, S.D. and Vitelli, J.S. (2004). Controlling dense infestations of parkinsonia (*Parkinsonia aculeata* L.). Proceedings of the 14th Australian Weeds Conference, eds B.M. Sindel and S.B. Johnson, pp. 173-6. (Weed Society of New South Wales, Sydney).

Madany, M.H. (1991). Living fences: Somali farmers adopt an agroforestry technology. *Agroforestry Today* 3, 4-7.

Martin, T. and van Klinken, R.D. (2006). Value for money?: investment in weed management in Australian rangelands. *Rangeland Journal* 28, 63-75.

Miller, I.L. and Pickering, S.E. (1980). Parkinsonia, a noxious weed. Agnote. (Northern Territory Department of Primary Production, Darwin).

Miller, P. (1739). 'The gardeners dictionary', 3rd edition. (London).

Mohnot, K. and Chatterji, U.N. (1965). Chemico-physiological studies on the imbibition and germination of seeds of *Parkinsonia aculeata* Linn. *Oesterreichische Botanische Zeitschrift* 112, 576-85.

NWS (2000). National parkinsonia weed management strategy. (Queensland Department of Natural Resources, Coorparoo).

Parsons, W.T. and Cuthbertson, E.G. (2001). 'Noxious weeds of Australia, second edition'. (CSIRO Publishing, Melbourne).

PIER (Pacific Islands Ecosystems at Risk) (2000). Invasive plant species: *Parkinsonia aculeata*. www.hear.org/pier. Accessed March 2008.

Plumier, L. (1703). 'Nova plantarum Americanum genera'. (Regis and Regiae Scientiarum Academiae Typographum, Paris).

Polhill, R.M. and Vidal, J.E. (1981). Caesalpineae. *In* 'Advances in legume systematics', Volume 1, ed. R.M. Polhill, P.H. Raven, pp. 81-95. (Royal Botanic Gardens, Kew).

Rajaram, N. and Janardhanan, K. (1991). Studies on the underexploited tree pulses, *Acacia catechu* Willd., *Parkinsonia aculeata* L. and *Prosopis chilensis* (Molina) Stunz: chemical composition and antinutrutional factors. *Food Chemistry* 43, 265-73.

Robertson, I.A.D. (1988). 'A survey of the natural enemies of *Parkinsonia aculeata* in Kenya', 4 pp. Unpublished report of CABI Kenya Station.(CABI, Nairobi).

Robertson, K.R. and Lee, T. (1976). The genera of Caesalpiniodeae in the southwestern United States. *Journal of the Arnold Arboretum* 57, 1-54.

Ross, R.H. (1998). Caesalpiniaceae: *Parkinsonia. Flora of Australia* 12, 69-70.

Scott, K.A. (2006). Seed coat morphology of *Parkinsonia aculeata* L. and pattern of heat-induced fractures. Proceedings of the 15th Australian Weeds Conference, eds C. Preston, J.H. Watts and N.D. Crossman, pp. 268-9. (Weed Management Society of South Australia, Adelaide).

Scrifres, C.J. (1980). 'Brush management. principles and practices for Texas and the southwest'. (Texas A&M Press, College Station).

Sheikh, M.I., Shah, B.H. and Aleem, A. (1985). Effect of rainwater harvesting methods on the establishment of tree species. *Forest Ecology and Management* 8, 257-64.

Sprent, J.I. and Sutherland, J.M. (1990). Nitrogen fixing woody legumes. *Nitrogen Fixing Tree Research Reports* 8, 17-23.

Stewart, J.L., Dunsdon, A.J., Hellin, J.J. and Hughes, C.E. (1992). Wood biomass estimation of Central American dry zone trees. Oxford Forestry Institute Tropical Forestry Papers 26, Oxford.

Streets, R.J. (1962). 'Exotic forest trees in the British Commonwealth'. (Clarendon Press, Oxford).

Swarbrick, J.T. (1997). Weeds of the Pacific Islands. Technical paper No. 209. South Pacific Commission, Noumea, New Caledonia. 124 pp.

Teketay, D. (1996). Germination ecology of twelve indigenous and eight exotic multipurpose leguminous species from Ethiopia. *Forest Ecology and Management* 80, 209-23.

Thorpe, J.R. and Lynch, R. (2000). 'The determination of Weeds of National Significance'. (National Weeds Strategy Executive Committee, Launceston).

Toh, R., Galea, V., Diplock, N. and van Klinken, R.D. (2008). Evaluation of fungal isolates for potential use as mycoherbicides for seedbank reduction of *Parkinsonia aculeata*. Proceedings of the 16th Australian Weeds Conference, eds R.D. van Klinken, V.A. Osten, F.D. Panetta and J.C. Scanlan, pp. 284-6. (Queensland Weeds Society, Brisbane).

Trama, F. (2004). Restauración de humedal Palo Verde para aves. *Revista ambientico*, no. 129. Online resource: www.ambientico.una.ac.cr/129/index.htm. Accessed March 2008.

Troup, R.S. and Joshi, H.B. (1983). The silviculture of Indian trees. Vol IC. Leguminoseae. (Controller of Publications, Delhi).

van Klinken, R.D. (2005). Total annual seed loss on a perennial legume through predation by insects: the importance of within-season seed and seed-feeder dynamics. *Austral Ecology* 30, 414-25.

van Klinken, R.D. (2006). Parkinsonia biocontrol: what are we trying to achieve? *Australian Journal of Entomology* 45, 268-71.

van Klinken, R.D. and Campbell, S. (2001). Biology of Australian weeds. 37. *Prosopis* L. species. *Plant Protection Quarterly* 16, 2-20.

van Klinken, R.D. and Flack. L. (2005). The relationship between wet heat and hard-seeded dormancy and germination. *Weed Science* 53, 663-9.

van Klinken, R.D. and Flack, L. (2008). What limits predation rates by a specialist seed feeder? *Journal of Applied Ecology* 45, 1600-11.

van Klinken, R.D., Flack, L. and Pettit, W. (2006). Wet-season dormancy release in seed banks of a tropical leguminous shrub is determined by wet heat. *Annals of Botany* 98, 875-83.

van Klinken, R.D., Lukitsch, B. and Cook, C. (2008). Interaction between seed dormancy-release mechanism, environment and seed bank strategy for a widely distributed perennial legume (*Parkinsonia aculeata*, Caesalpinaceae). *Annals of Botany*. 102, 255-64.

van Klinken, R.D., Seabrook, L., Smith, C., Ryan, J. and McAlpine, C. (2008). Using spatial models and a Bayesian belief network to predict risk of parkinsonia invasion at a landscape scale in northern Australia. Proceedings of the 16th Australian Weeds Conference, eds R.D. van Klinken, V.A. Osten, F.D. Panetta and J.C. Scanlan, p. 194. (Queensland Weeds Society, Brisbane).

Vitelli, J.S. (1995). Parkinsonia. *In* 'Exotic weeds and their control in north west Queensland', ed. N. March, p. 34-5 (Department of Lands, Brisbane).

Vitelli, J.S. (2000). Options for effective weed management. *Tropical Grasslands* 34, 280-94.

Vitelli, J.S. and Madigan, B.A. (2004). Evaluation of a hand-held burner for the control of woody weeds by flaming. *Australian Journal of Experimental Agriculture* 44, 75-81.

Vitelli, J.S. and Pitt, J.L. (2006). Assessment of current weed control methods relevant to the management of the biodiversity of Australian Rangelands. *The Rangeland Journal* 28, 37-46.

von Mueller, F. (1876). 'Select plants readily eligible for industrial culture or naturalisation in Victoria, with indications of their native countries and some of their uses'. (M'Carron, Bird and Co., Melbourne).

Wagner, W.L., Herbst, D.R. and S.H. Sohmer (1999). 'Manual of the flowering plants of Hawai'i'. 2 volumes. Bishop Museum Special Publication 83. (University of Hawai'i and Bishop Museum Press, Honolulu)

Wiggins, I.L. and Porter, D.M. (1971). 'Flora of the Galapagos Islands'. (Stanford University Press, California).

Wilson, C.G. and Miller, I.L. (1987). Parkinsonia in the Northern Territory. Northern Territory Department of Primary Industry and Fisheries Technical Bulletin. No. 106.

Woods, W. (1985). Bruchid seed beetles for control of *Parkinsonia aculeata* in Australia. Proceedings of the VI International Symposium on Biological Control of Weeds, ed. E. Delfosse, pp. 855-62. (Agriculture Canada, Ottawa).

Woods, W. (1986). Biological control of parkinsonia. *Western Australian Journal of Agriculture* 27, 80-3.

Woods, W. (1988). The potential for biological control of *Parkinsonia aculeata* L.: phytophagous insects collected from the USA, Mexico and Costa Rica and the effect of insect damage on the growth and survival of the plant. M.Sc. thesis, University of Western Australia, Perth.

Woods, W. (1992). Phytophagous insects collected from *Parkinsonia aculeata* (Leguminoseae: Caesalpiniaceae) in the Sonoran Desert Region of the south western United States and Mexico. *Entomophaga* 37, 465-74.

Wyatt, R. (1981). Components of reproductive output in five tropical legumes. *Bulletin of the Torrey Botanical Club* 108, 67-75.