Review

The Biology of Australian Weeds 41. *Pittosporum undulatum* Vent.

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Name

Pittosporum undulatum Vent. (Pittosporaceae), sweet pittosporum.

The Greek derivation of *Pittosporum* is *pittos* (pitch or resin) and *sporum* (seeds) in reference to the sticky, resinous mucilage that encases seeds in all species of this genus (Walsh and Albrecht 1996, Cayzer *et al*. 2000). Undulatum is from the Latin *undulatus* meaning wavy, relating to the species' distinctive undulating leaf margin. The species is known by many common names although sweet pittosporum is most typically applied in Australia (Mullett 1999a). Other, mostly outdated, names reflect the species' geographic origins and its ornamental and utilitarian attributes. These include native daphne, native laurel, Victorian laurel, New South Wales box tree, wave-leaved pittosporum, mock orange, cheesewood and engravers wood (Maiden 1889, 1920, Cooper 1956, Hayes 1964, Cronk and Fuller 1995). Maiden (1889, 1920) recorded that the Aboriginal people of southern New South Wales referred to *P. undulatum* as 'wallundundeyren', and that the Karnathun people of the Lake Tyers district in Gippsland, Victoria, knew the species as 'bart bart' or 'bart barb'.

Description

Pittosporum undulatum is a tall shrub or small tree with a densely-foliaged rounded canopy that reaches an average height of 8–15 m across the range of habitats occupied in Australia (Figure 1). This species displays considerable variation in habit in different habitat types. In sheltered warm temperate rainforest environments in Victoria and New South Wales, for example, *P. undulatum* individuals reach heights in excess of 30 m and have large, spreading canopies (Wakefield 1946, Cooper 1956). In harsher coastal environments, *P. undulatum* often displays a stunted and sheared habit. Individuals invading dry sclerophyll forest rarely exceed heights of 15 m and their canopies are comparatively compact and dense (Mullett 1999a).

Adult leaves are generally arranged in whorls or semi-whorls, which tend to be clustered at the end of branchlets (Figure 2). Adult leaves are entire and ovate to oblanceolate in shape, 6–17 cm long and 2–5 cm wide (Walsh and Albrecht 1996). The adaxial leaf surface is glossy dark green in contrast to pale green underneath. Reticulate venation is distinct on both glabrous surfaces and leaf margins are characteristically undulate.

Flowers are arranged in terminal umbel-like cymes (Walsh and Albrecht 1996). Average petal dimensions are length 13.7 mm and width 3.8 mm (Cooper 1956) although female flowers tend to be shorter and wider than male flowers (Cayzer *et al*. 2000). The five petals are apically recurved to reveal five stamens in male flowers and five staminodes resembling rudimentary scales in female flowers (Walsh and Albrecht 1996). The creamy-white flowers are fragrant and although this species is functionally dioecious, seed-producing flowers are occasionally observed on otherwise male-flowering trees (Steel 1911, Mullett 1996, 1999a, Cayzer *et al.* 2000). The green fruits become orange on maturity and are 13–16 mm long and 11–14 mm wide (Mullett 1999a). Fruits are bivalve or rarely trivalve and split on maturity to reveal an average of 20 to 30 orangey-red seeds. The seeds are presented in a sticky, coherent aggregate, which may attract potential dispersal agents (Figure 3). See Cayzer *et al*. (2000) for a more comprehensive botanical description of *P. undulatum* and its phylogenetic relationships.

History

Ornamental plantings

Early Australian botanists were most enthusiastic about the species' ornamental attributes (Figure 4). Both Mueller (1876) and Maiden (1889) drew attention to the species' attractive, fragrant, creamy-white flowers and recommended cultivation of *P. undulatum* for ornamental, amenity and hedge plantings. The species was known as native daphne and native laurel around this time, the Eurocentric association of which may have further contributed to the species' early popularity. As early as 1920, Maiden remarked that *P. undulatum* had been 'abundantly cultivated' and by the 1950s, it was regarded as one of the most common of the street trees in Melbourne and Sydney (Cooper 1956). Gardening enthusiasts also promoted cultivation of *P. undulatum* for its hardiness and adaptability to a range of soil types and climatic conditions (Hayes 1964, Miller 1964, Oakman 1964). Miller (1964, p. 35) for example, described *P. undulatum* to readers of *Australian Plants* as 'an ideal tree for specimen, windbreak and avenue planting'.

Despite growing acknowledgment and acceptance of the species' weedy status, it remains a popular ornamental specimen. As recently as 1993, for example, the gardening columnist of the *Frankston Standard*, a regional weekly newspaper in Victoria, suggested that bird-dispersed *P. undulatum* seedlings could be 'potted up and given to a friend' (Love 1993, p. 59).

Figure 1. Mature *Pittosporum undulatum* are typically 8–15 m in height with a dense rounded canopy.

Figure 2. ***Pittosporum undulatum*** **leaves are generally arranged in whorls that tend to be clustered at the end of branchlets. (a) Flowering twig, (b) Fruiting twig (adapted from a lithograph by E.A. King in Mueller 1920).**

Figure 3. ***Pittosporum undulatum*** **fruits are orange and split on maturity to reveal 20–30 seeds presented in a sticky-coherent aggregate, which is attractive to a range of frugivorous dispersal agents.**

This article was published after *P. undulatum* had been identified as a serious environmental weed in the Frankston region (City of Frankston, Shire of Hastings and Shire of Mornington *c*.1992).

Factors contributing to the spread of P. undulatum

A suite of opportunistic frugivores exploit the species' abundant winter fruit crops and facilitate the dispersal of *P. undulatum* from ornamental plantings into nearby vegetation remnants (Gleadow 1982, Mullett 1996, 1999a,b). Invasion has been particularly severe in the drier forest types where changes to natural fire regimes and other disturbance factors have reduced the resilience of native vegetation to invasion by this fire-sensitive species (Mullett and Simmons 1995, Mullett 1999a). Changes in natural fire regimes are recognized as a key factor in the increased distribution and abundance of *P. undulatum* in natural and invaded habitats throughout south-eastern Australia (Gleadow and Ashton 1981, Adamson and Fox 1982, Buchanan 1991, Mullett and Simmons 1995, Mullett 1996, 1999a,b, 2001, Rose 1997a,b, Rose and Fairweather 1997). The species' inherent adaptability has further facilitated its invasion success in a diverse range of habitat types and climate regions (Mullett 1999a, 2001).

Distribution

Australia – natural range

The natural (pre-European settlement) range of *P. undulatum* is believed to extend seawards of the Great Dividing Range in south-eastern Australia from east of Westernport Bay in Victoria to Brisbane, Queensland (Gleadow and Ashton 1981) (Figure 5). The species occurs as a natural component of many habitat types throughout this extensive geographic range but is mainly associated with wet forest (Gleadow and Ashton 1981), rainforest ecotone (Barrett and Ash 1992) and rainforest communities (Beadle *et al*. 1972, Melick and Ashton 1991, Peel 1999).

It is generally accepted that the natural distribution of *P. undulatum* is confined to the seaward slopes of the Great Dividing Range in south-eastern Australia and that the natural occurrence of *P. undulatum* on the inland slopes would be restricted to a limited number of suitable locations (Mullett 1999a). Cooper (1956) suggested that the natural distribution of *P. undulatum* extended to the MacPherson Ranges, in southern Queensland although Narayan (1993) reported that the natural northern limit of *P. undulatum* could occur as far north as Bundaberg, Queensland. Additionally, an interesting natural outlying population of *P. undulatum* occurs at Carnarvon Gorge, some 720 km north west of Brisbane (Queensland Herbarium 1994).

The natural south-western extent of *P. undulatum* is also unclear. The approximate natural south-western distribution of *P. undulatum* has been variously described as: the Victorian Alps (Cooper 1956), Gippsland (Maiden 1920), the Mitchell River region (Floyd 1989), the Strzelecki Ranges (Gullan *et al.* 1981) and Westernport Bay (Bentham 1863). The species was listed in Victorian nursery catalogues from 1855 (Brookes and Barley 1992), which reduces the reliability of Bentham's 1863 account as an early indicator of this species' natural range.

Debates about the exact pre-European range of *P. undulatum* are now largely academic, given documented evidence of this species' invasion impacts in habitats subject to altered disturbance regimes (Mullett and Simmons 1995, Mullett 1996, 1999a,b, 2001). While the species' pre-European distribution is interesting in an evolutionary and ecological sense, it alone should not form the basis of any current day management prescriptions.

Invaded habitats in the species' natural range

Some populations of *P. undulatum* occurring within the species' natural geographic range are expanding in both distribution and local abundance, in response to altered ecological conditions (Adamson and Buchanan 1974, Adamson and Fox a

b

c

Figure 4. ***Pittosporum undulatum*** **has been widely cultivated for its ornamental attributes including: (a) distinctive undulating foliage, (b) fragrant creamy-white flowers, and (c) bright orange fruits.**

1982, Buchanan 1991, Rose 1997a,b, Rose and Fairweather 1997, Mullett 1999a,b, 2001). The species is a natural component of the wetter Gippsland forest types, for example, but many of these forests now support weedy populations of *P. undulatum* (Griffiths 1988, Ashwell 1991, Howell 1992). This trend is apparent in many coastal or near coastal communities in eastern Victoria and south-eastern New South Wales (Mullett 1999a,b, 2001). Some populations of *P. undulatum* occurring on Sydney sandstone are also considered to be actively expanding (Adamson and Buchanan 1974, Adamson and Fox 1982, Buchanan 1991, Rose 1997a,b, Rose and Fairweather 1997). Increasing local densities and movement from sheltered gully environments into adjacent vegetation communities on drier slopes is a common feature of this species' range expansion in natural habitats. This local population expansion usually occurs in response to altered fire regimes and increased dispersal opportunities (Adamson and Fox 1982, Mullett 1999a,b, 2001).

Australia – invaded range

Since the 19th century, *P. undulatum* has colonized a range of previously unexploited habitats in Victoria (Gleadow and Ashton 1981, Carr *et al*. 1992, Mullett 1993, 1999a, Mullett and Simmons 1995). Remnants of the drier forest and woodland vegetation types of the greater Melbourne region and the Mornington Peninsula have been especially affected (Gleadow and Ashton 1981, Mullett 1993, 1999a, Mullett and Simmons 1995). The species has also invaded wet forest communities along the Otway coast of south-western Victoria (Platt 1990) and the Dandenong Ranges east of Melbourne (Freshwater 1989). Heathlands and heathy woodlands, coastal vegetation, grasslands and grassy woodlands and substantial tracts of riparian vegetation have also been invaded by *P. undulatum* in Victoria (Carr *et al*. 1992). It is now found in most of the broad vegetation types occurring seawards of the Great Dividing Range in Victoria and is present as an occasional planting in town gardens north of the Great Dividing Range in Victoria, where the drier climatic conditions limit its spread into remnant vegetation (Mullett 1999a). *Pittosporum undulatum* is invasive in the Adelaide Hills and on the Fleurieu Peninsula, South Australia (Rhodes 1999, 2000) and is actively expanding its distribution and abundance in south-western Western Australia (Keighery 1999) and Tasmania (Carr 1993). The species is also well established on King (Gleadow and Ashton 1981), Norfolk (Gilmour and Helman 1989) and Lord Howe Islands (Pickard 1984).

World

Early enthusiasm for the species' ornamental and utilitarian attributes moved *P. undulatum* beyond Australian borders and into an array of locations throughout the temperate, sub-tropical and tropical zones (Figure 6). Remarkably, the earliest record of this species in cultivation outside Australia was 1789, when it was first planted in Britain (Cooper 1956, Elliot and Jones 1980). Cooper (1956) cites use of *P. undulatum* as an ornamental, hedge and shelter plant in the following locations: the Azores, Bermuda, Bolivia, the Canary

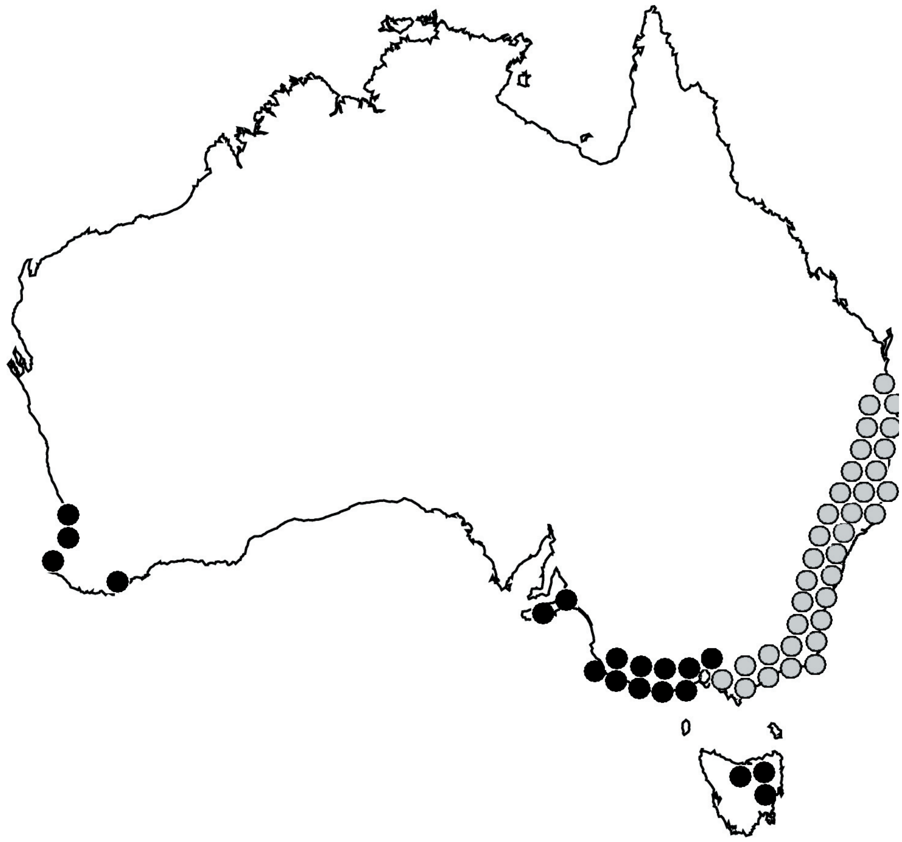

Figure 5. Distribution of *Pittosporum undulatum* in Australia. Shaded circles indicate the species' broad natural distribution along the eastern seaboard of south east Australia. Invasive populations occur within this natural range and are especially associated with settled areas along the coast. Dark circles indicate the distribution of *P. undulatum* populations outside the species' natural range in southern Australia.

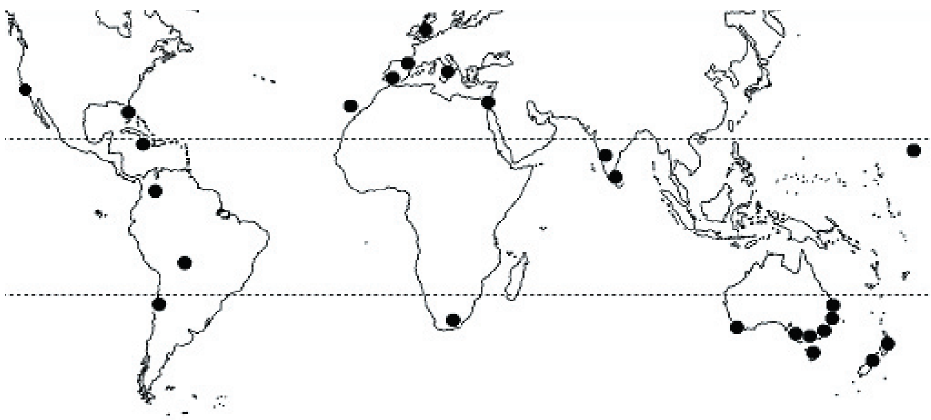

Figure 6. Current global distribution of *Pittosporum undulatum*.

Islands, Ceylon (Sri Lanka), China, Chile, Colombia, England, France, Hawaii, India, Israel, Italy, Jamaica, New Zealand and the United States (Florida and California). As with its success in previously unexploited Australian environments, *P. undulatum* has thrived in many of these areas. It is regarded as a serious invader of native vegetation in many localities, especially Jamaica (Goodland and Healey 1996, 1997a,b), South Africa (Richardson and Brink 1985, Geldenhuys *et al*. 1986, Kruger *et al*. 1986), the Azores (Ramos 1995, 1996, Robertson 1997) and Hawaii (Haslewood and Motter 1984, Cronk and Fuller 1995).

Habitat

Climatic requirements

Pittosporum undulatum occurs in a range of habitat types and climatic regions throughout its extensive geographic distribution. The species occupies habitats in winter, spring and summer rainfall areas of south-eastern Australia where average annual rainfall varies from, for example, 1867 mm (Alstonville, New South Wales) to 723 mm (Belair, South Australia). While *P. undulatum* occurs in habitats subject to considerable variation in climatic conditions, its invasion has been most successful in dry forest habitats in the winter-spring rainfall zone seawards of the Great Dividing Range in Victoria. Typically, these Victorian habitats experience annual average rainfalls around 800–1100 mm, moderately hot summers, cool to cold winters and mild autumn and spring seasons.

The successful invasion of a diverse range of vegetation complexes on other continents and islands throughout the temperate, sub-tropical and tropical zones (Cooper 1956) is further evidence of the species' broad ecological amplitude. In the Blue Mountains Region of Jamaica for example, *P. undulatum* is highly invasive in sub-tropical montane rainforests where the average annual rainfall is 2690 mm (Cronk and Fuller 1995). The species' preadaption to a range of climatic conditions will likely facilitate its further spread across a range of habitat types and climate regions (Mullett 1999a).

Substratum

Pittosporum undulatum seedlings develop either taproots or diffuse root structures in response to particular edaphic conditions, thereby enabling establishment and persistence on a range of soil types (Gleadow 1982). Tolerance of a broad range of edaphic conditions, such as variation in soil type, depth, nutrient availability and water holding capacity, is indicated by the diverse range of habitat types occupied by *P. undulatum* (Mullett 1999a).

Plant associations

Pittosporum undulatum occurs in a diverse range of vegetation types including grasslands, heathlands, woodlands, dry, damp and wet sclerophyll forests and rainforests across its natural and invaded range in south-eastern Australia (Mullett 1999a). The species is a natural component of the wet sclerophyll forests dominated by *Eucalyptus cypellocarpa* L.A.S. Johnson (mountain grey gum), *E. radiata* Sieber. ex DC. (narrow-leaved peppermint), *E. viminalis* Labill. (manna gum), *E. muelleriana* A. W. Howitt (yellow stringybark), *E. globulus* ssp. *maidenii* (F. Muell.) J.B. Kirkp. (Maiden's gum) and *E. elata* Dehnh. (river peppermint), which extend from Gippsland into southern New South Wales (Gleadow and Ashton 1981). The species also occurs in warm temperate rainforests in this region, where it is often associated with other bird-dispersed species, including *Acmena smithii* (Poir.) Merr. and L.M. Perry (lilly pilly), *Rapanea howittiana* F. Muell. ex Mez (muttonwood) and *Elaeocarpus reticulatus* Sm. (blue olive-berry) (Melick and Ashton 1991, Peel 1999). It is also a common component of dry rainforest vegetation and it is often the dominant canopy species of this community in Victoria (Peel 1999).

In New South Wales, the species occurs naturally in wet sclerophyll forests and dry rainforest (scrub) communities and extends into sheltered areas in dry forests and woodlands (Makinson 1992). It is widespread along the coast and associated vegetation communities in New South Wales. Within these broad vegetation types, *P. undulatum* is associated with floristic assemblages characterized by *Eucalyptus pilularis* Sm. (blackbutt), *E. botryoides* Sm. (southern mahogany), *E. saligna* Sm. (Sydney blue gum) and *Corymbia maculata* (Hook.) K.D. Hill and L.A.S. Johnson (spotted gum).

In invaded forests west of the species' natural range in Victoria, *P. undulatum* is now a dominant component of the dry sclerophyll forests characterized by *Eucalyptus obliqua* L'Her. (messmate), *E. macrorhyncha* F. Muell. ex Benth. (red stringybark), *E. goniocalyx* F. Muell. ex Miq. (long-leaved box), *E. cephalocarpa* Blakely (silver-leaved stringybark) and *E. melliodora* A.Cunn. (yellow box) (Gleadow and Ashton 1981, Mullett and Simmons 1995). It has also invaded the wet *E. globulus* ssp. *globulus* Labill. (southern blue gum) forests along the Otway coast of south west Victoria (Platt 1990) and wet *E. regnans* F. Muell. (mountain ash) forests east of Melbourne (Freshwater 1989), especially those associated with human settlements. In South Australia, *P. undulatum* has invaded grassy woodland and dry forest vegetation on the Fleurieu Peninsula characterized by *E. microcarpa* Maiden (grey box), *E. camaldulensis* Dehnh. (river red gum), *E. leucoxylon* F. Muell. (yellow gum) and *E. obliqua* (Rhodes 1999, 2000).

Pittosporum undulatum invades a similarly diverse range of habitats on other continents and islands. It invades disturbed and undisturbed montane rainforest habitats in the Blue Mountains region of Jamaica, seriously threatening conservation and commercial values in that region (Goodland and Healey 1996, 1997a). In South Africa, populations of *P. undulatum* are now invading riparian forest and scrub communities in the western Cape region (Richardson and Brink 1985, Geldenhuys *et al*. 1986, Kruger *et al.* 1986). In the Azores, *P. undulatum* or 'Incenso' as it is known locally, is a serious invader of endemic lowland forest environments and, with other invasive plants, contributes to the homogenization of native vegetation communities (Ramos 1995, 1996, Robertson 1997). The species is naturalized in wet forest communities on several Hawaiian islands and has the potential to become a serious environmental weed in that region (Haslewood and Motter 1984, Cronk and Fuller 1995).

Growth and development

Morphology

It is assumed that environmental factors are critical to the morphological expression of *P. undulatum,* given that most of the genetic variation in this species is contained within populations and no geographic patterns of genetic differentiation are evident (Orso 1994). The degree of morphological variability displayed by *P. undulatum* in response to the range of environmental conditions experienced across its current range, is indicative of high phenotypic plasticity. This plastic, variable morphology was demonstrated in leaf characters sampled across natural and invasive south east Australian populations in which attributes such as mean leaf length, for example, varied from 99 to 148 cm (Mullett 1999a). Considerable phenotypic plasticity compensates for low genetic variation in *P. undulatum* (Orso 1994) and is regarded as an important factor in this species' continued invasion success across a range of habitat types and climate regions (Mullett 1996, 1999a,b, 2001).

Perennation

Pittosporum undulatum is a highly adaptable, long-lived evergreen perennial. It is preadapted to a range of environmental conditions and responds with vigorous coppicing to non-fatal physical damage from fire, drought, browsing and mechanical control.

Physiology

Pittosporum undulatum seedlings display high drought tolerance when grown in dense shade and under moderate temperatures (Gleadow and Rowan 1982). Drought-stressed seedlings have lower growth rates and net assimilation rates than well-watered plants, although severely wilted leaves can recover their turgidity with alleviation of water stress (Gleadow and Rowan 1982). With regard to light, *P. undulatum* reaches a growth compensation point at 1.6% full sunlight (Gleadow *et al*. 1983). While the species can tolerate deep shade, growth rates are greater under higher photon flux densities and in the absence of drought stress (Gleadow and Rowan 1982, Gleadow *et al*. 1983). This species displays characteristics typical of both sun- and shade-tolerant plants (Gleadow *et al*. 1983), providing it with an adaptive advantage and contributing to its invasion success in a range of habitats.

Phenology

Flowering occurs in spring and seed development commences immediately after pollination. Development continues over the summer and autumn months and fruits reach maturity in late autumn to early winter, when the orange capsules split to reveal numerous bright orange to red seeds encased in a sticky mucilage (Mullett 1996, 1999a). Most germination occurs in autumn, although some germination may occur in spring if conditions are favourable (Gleadow 1982).

Bud burst can occur up to five times in the seedling's first year, enabling rapid growth and competitive utilization of resources (Gleadow 1982). In adult plants, leaf buds containing five to ten leaves develop during autumn and winter and burst in late winter to early spring (Gleadow and Ashton 1981). Some individuals undergo a second growth flush in summer.

Reproduction

Floral biology

Introduced honeybees (*Apis mellifera* L.) are an important diurnal pollination agent of *P. undulatum*, especially in disturbed habitats (Mullett 1999a). Native pollinators remain elusive but are likely to include generalist diurnal and nocturnal invertebrates (Hamilton 1902).

Individuals reach reproductive maturity at four to five years (Gleadow 1982) and the species is functionally dioecious. The incidence of seed-producing flowers on otherwise male flowering trees is low, but appears to be higher in invasive populations and ornamental plantings than in natural populations (Mullett 1996, 1999a). Variable dioecism is evident in other *Pittosporum* species (Hamilton 1902, Cooper 1956, Godley 1979, Clarkson and Clarkson 1994, Cayzer *et al.* 2000), but some Australian *Pittosporum* species have differentiated into a unisexual or bisexual state (Walsh and Albrecht 1996).

Seed dispersal

The abundant *P. undulatum* fruit crop is exploited by a range of opportunistic frugivores, although pied currawongs (*Strepera graculina* Shaw) and European blackbirds (*Turdus merula* L.) are considered to be the main dispersal agents of *P. undulatum* in south-eastern Australia (Mullett 1996, 1999a, 2001). Pied currawongs have a greater potential to disperse *P. undulatum* seed over longer distances and are probably the most important dispersal vector of *P. undulatum* throughout south-eastern Victoria, southern New South Wales and the Sydney Region (Mullett 1999a). The more sedentary blackbirds contribute to increasing local densities of *P. undulatum*, especially in settled areas including Melbourne, in southern Victoria. Other frugivorous birds recorded feeding on *P. undulatum* are characteristically generalist or opportunistic species (Mullett 1999a,b) and include satin bowerbirds (*Ptilonrhynchus violaceus* Vieillot), silvereyes (*Zosterops lateralis* Latham), red-whiskered bulbils (*Pycnonotus jocosus* L.) and superb fruit-doves (*Ptilinopus superbus* Temminck) (Gannon 1935, Cooper 1959, Rose 1973, Forde 1986, Barker and Vestjens 1989, 1990, Mullett 1999a).

Accounts of mammal species dispersing *P. undulatum* seed also implicate generalist, opportunistic introduced and native species, including the black rat (*Rattus rattus* L.), red fox (*Vulpes vulpes* L.) and common brushtail possum (*Trichosurus vulpecula* Kerr) (Mullett 1999a). It is possible that other mammals will adapt over time to the abundant food resource provided by the *P. undulatum* winter fruit crop, especially as the abundance of traditional food resources contracts in invaded and otherwise modified environments.

Germination

Germinability is high in seeds collected from natural and invaded habitats and in seeds voided by the principal dispersal agents of this species in south-eastern Australia (Mullett 1999a). Optimum germination occurs between 18–21° C under laboratory conditions (Gleadow 1982) and in the field, most *P. undulatum* germination occurs in autumn. Seeds extracted from pied currawong pellets and blackbird scats achieved 92 and 96% germination respectively and were not significantly different in germinability from control seed (97%) (Mullett 1999a). Fresh seeds collected from pre- and post-dehiscent *P. undulatum* fruits across the natural and invaded range of this species also achieved high germination success (Mullett 1999a). No significant differences were evident between the germinability of seeds collected from pre- and post-dehiscent *P. undulatum* fruits, indicating that effective seed dispersal can theoretically occur when seed dispersal agents such as pied currawongs feed on immediately pre-dehiscent fruits (Mullett 1999a).

Seeds not removed by frugivores persist as a terminal structure for many months before falling beneath the parent plant. Litter-fall peaks in spring, approximately two months after seed set, offering seed dispersed by frugivorous or autochorous modes some protection from desiccation over the summer months (Gleadow 1982). Late autumn is recognized as the main germination period in this species (Gleadow 1982). Some *P. undulatum* seeds germinate in spring following the winter fruiting period, but high temperatures and low relative humidities prevent summer germination in most years (Gleadow 1982). Seedlings are reasonably drought tolerant, especially under shaded conditions (Gleadow and Rowan 1982).

Hybrids

Pittosporum undulatum ssp. *emmettii* has been reported as a rare endemic of Tasmania (Stones and Curtis 1978), although this species is likely to be synonymous with the *P. undulatum* × *P. bicolor* Hook. (banyalla) hybrid found at a limited number of sites throughout southern Victoria (Cayzer *et al*. 2000). The *P. undulatum* ssp. *emmettii* type specimen was collected in the Arthur River region of Tasmania in 1874 and was initially considered to be *P. undulatum* (Rodway 1903). *Pittosporum undulatum* is not considered indigenous to Tasmania (Carr 1993) but it is possible that the species was introduced as an ornamental planting when tin mining settlements were established in the region in the 1870s (Blainey 1967).

Isolated occurrences of this putative hybrid have been recorded within the natural and invaded range of *P. undulatum* in Victoria (Robin and Carr 1986, Floyd 1989, Ashwell 1991, Carr 1993) and New South Wales (Makinson 1992). Individuals display characters intermediate between *P. undulatum* and *P. bicolor*, although morphological attributes are quite variable within and between individuals. In a recent revision of *Pittosporum,* Cayzer *et al.* (2000) suggested that the hybrid was described as a sub-species in error. Hybridization between *P. undulatum* and *P. revolutum* Dryand. (rough-fruit pittosporum) (Cooper 1956) and *P. undulatum* and the New Zealand ornamental, *P. tenuifolium* Sol. ex Gaertn. (James Stirling pittosporum) have also been reported (Carr 1993).

Population dynamics

The establishment of *P. undulatum* individuals from successive generations is generally restricted to the base of eucalypts or other mature trees or shrubs (Figure 7), as these offer perching sites for frugivorous dispersers that preferentially defecate or regurgitate undigested seeds whilst perching (Mullett 1999a). This initiates the contagious distribution pattern typical of invading populations of *P. undulatum*. Thereafter, the pattern of seedling establishment and subsequent clump development is primarily influenced by the characteristics of the dispersal site.

Gleadow (1982) suggests that the *P. undulatum* clumping pattern is influenced by seedling response to microclimatic conditions. Seedling survival is higher under shaded conditions (Gleadow and Rowan 1982) although shading and other competitive effects appear to reach a critical point within *P. undulatum* clumps, where the micro-environment is hostile even to conspecific seedlings (Mullett 1999a). Seedling establishment and juvenile survival are more likely to occur beneath the moderate canopy cover of eucalypts and other trees and shrubs, compared to the dense canopy cover of adult conspecifics (Mullett 1999a). Opportunistic frugivores, such as pied currawongs and European blackbirds, play a crucial role in transporting *P. undulatum* seed away from the inhibiting environment of the parent plant, where survival and persistence is less likely (Mullett 1999a). The satellite populations that establish via this dispersal mechanism increase the species' potential for expansion in local distribution and abundance.

Significant differences are evident in *P. undulatum* population densities between natural and invaded habitats (Mullett 1999a). Densities are on average 2.7 times higher in invading populations, compared to natural populations sampled (Mullett 1999a). Population profiles are also skewed towards the early developmental stages in invasive populations compared to natural

Figure 7. 'Clumps' of *Pittosporum undulatum* initially radiate out from the base of eucalypts and other trees and shrubs. These trees and shrubs provide perches for frugivorous dispersal agents that eliminate seed while perching.

populations. In a recently invaded dry forest remnant near Portland, Victoria, for example, juveniles and seedlings accounted for 80% of the *P. undulatum* population sampled (Mullett 1999a).

Importance

Detrimental

Pittosporum undulatum is recognized as one of Victoria's most serious environmental weed species (Carr *et al*. 1992, Mullett and Simmons 1995) and is arguably the most successful native weed in south-eastern Australia (Mullett 2001). The species exerts a considerable influence on the composition, structure and function of natural and invaded plant communities (Mullett and Simmons 1995, Mullett 1999a,b, 2001). Declines in the richness and cover-abundance of native plant species are the principal impacts of *P. undulatum* invasion and these effects are consistently recorded at invaded sites (Mullett 1993, 1999a, 2001, Mullett and Simmons 1995).

Changes in the composition of invaded communities are a further consequence of *P. undulatum* invasion. Studies conducted in Victoria and New South Wales indicate that dry sclerophyllous species appear to be most affected (Mullett and Simmons 1995, Rose 1997a,b, Rose and Fairweather 1997, Mullett 1999a). Different impacts are also exerted on various lifeform guilds. The richness and cover-abundance of species comprising the lower strata guilds: the herbs, grasses, twiners/trailers and low shrubs, were especially affected at invaded sites (Mullett 1999a). Tall shrub and tree species were comparatively less affected by *P. undulatum* invasion, although the true impact on these guilds may unfold over time with lack of regeneration opportunities and continued competition pressures. Faunal populations are also likely to be affected by the invasion-driven simplification of habitat resources, especially at the ground layer (Brown *et al*. 1991, Mullett 1999a, 2001).

High *P. undulatum* cover-abundance disrupts a range of ecosystem-level properties and functions, including ultimately, the rate and direction of community succession (Mullett 1999a). Shade cast by the dense *P. undulatum* canopy substantially alters light regimes, contributing to changes in microclimatic conditions (Mullett and Simmons 1995). The microclimate beneath the *P. undulatum* clump canopy is further modified by *P. undulatum* litter fall, which differs in seasonality, abundance and nutrient composition from that of other dominant species in invaded communities (Gleadow and Ashton 1981). These changes contribute to the further alteration of fire regimes at invaded sites, which may ultimately favour *P. undulatum* and other fire-sensitive species adapted to shaded, mesic environments, over the preceding suite of species adapted to drier conditions and more frequent fires. The pre-adaptation and adaptability of *P. undulatum* to a range of environmental conditions and its ability to tolerate shading (Gleadow *et al.* 1983), drought stress (Gleadow and Rowan 1982) and other perturbations, increases the likelihood that this species will maintain its dominance through successional phases (Mullett 1999a). *Pittosporum undulatum* invasion represents a serious, on-going threat to biodiversity conservation in south-eastern Australia (Mullett 1993, 1996, 1999a,b, 2001, Mullett and Simmons 1995, Rose 1997a,b, Rose and Fairweather 1997).

Beneficial

Pittosporum undulatum is the most widely planted of the *Pittosporum* species in Australia and throughout the world. Potential benefits derived from the species' ornamental, hedge and windbreak attributes are, however, offset in the many regions where the species has become invasive. It is also utilized in revegetation programs in south-eastern Victoria and New South Wales because of its adaptability and value as a pioneer species (Mullett 1999a,b). Use of this species for revegetation purposes is discouraged (Mullett 1999b, 2001) given documented evidence of the species' invasion impacts in habitats within both its natural and invaded range (Mullett 1993, 1999a, Mullett and Simmons 1995).

Early in the 20th century, the close-grained *P. undulatum* timber was used for varied specialist purposes including engraving, golf sticks and tool handles (Maiden 1920, Cooper 1956). Research on the composition of *P. undulatum* fruit was also conducted around this time (Maiden 1889, Threlfall 1895, Power and Tutin 1906). Bosisto 1862 (in Maiden 1920, p. 126) reported that essential oils distilled from *P. undulatum* flowers produced an 'exceedingly agreeable, jasmine-like odour' and Maiden (1889, p. 230) noted that the 'wound of a dog' healed with 'amazing quickness' after application of *P. undulatum* gum resin. These and other potential uses of *P. undulatum* have remained largely unexplored in Australia. In the Blue Mountains region of Jamaica, however, invading populations of *P. undulatum* are currently utilized as an important source of timber, firewood and charcoal (Goodland and Healey 1996).

Legislation

Potential legislative and policy conflicts may arise in New South Wales and Victoria due to the species' dual native and weedy status (Mullett 2001). In Victoria, for example, managers of areas reserved under the *National Parks Act 1975*, must 'preserve and protect indigenous flora' and 'eradicate and control exotic flora' (State of Victoria 1975). *P. undulatum* may fall into both categories, especially in reserves within the species' natural range where many indigenous populations are becoming invasive. Further, the invasion by *P. undulatum* into habitats outside its natural range in Victoria was listed in 1994, as a 'potentially threatening process' under schedule three of the Victorian *Flora and Fauna Guarantee Act 1988* (Scientific Advisory Committee 1994). An action statement has not yet been developed for this listing, despite the legislative requirement that this occurs as soon as possible after the listing process (State of Victoria 1990). The species has also been listed as a component of a rare plant community (dry rainforest (limestone) community) under schedule two of the same Act (Scientific Advisory Committee 1996).

Weed management

A number of physical, chemical and ecological control options are available to manage invasive populations of *P. undulatum*. To date, however, control programs have had limited success due to an inadequate understanding of the species' biology, ecology and community interrelationships and, fundamentally, to insufficient resource allocation (Mullett 1999a). Whether control programs are devised and implemented by government agencies or community groups, it is vital that the relatively few opportunities available for *P. undulatum* control and management are maximized.

Management objectives need to be clearly established prior to the implementation of *P. undulatum* control programs. The species plays an important role in the community ecology of natural and invaded sites and managers need to anticipate the community response to reduced densities of *P. undulatum* and determine the appropriate control techniques to promote the desired species composition. This requires an adequate understanding of the composition, dynamics and regeneration characteristics of the invader and the invaded community (Randall 1997).

As for most environmental weed species, control of *P. undulatum* is likely to be most effective in the early invasion stages. Delaying control will reduce the potential for community restoration and increase the long-term demand for management resources. Specific, targeted weed management prescriptions are required to effectively manage invasive populations of this species across its natural and invaded range (Mullett 2001). Encouraging replacement of ornamental plantings of *P. undulatum* with suitable non-invasive indigenous species is fundamental to the long term management of this species. This measure may also have beneficial flow-on effects, including a reduction in weedy fleshy-fruit resources for adaptive frugivores such as pied currawongs and European blackbirds.

Herbicides

Targeted control programs for *P. undulatum* often utilize the cut and paint method whereby individual trees are felled and cut stumps are immediately treated with herbicides (usually glyphosate undiluted or 1:3). This method provides instantly gratifying results, but the consequent increase in light infiltration may create a substantial disturbance to local site conditions, which opportunistic weed species may exploit, particularly in the absence of follow-up monitoring and control. Felled individuals are generally left on-site, which raises further concerns about the potential influence of allelopathic properties present in decaying leaf matter, although studies conducted by Tunbridge *et al*. (2000) indicate that allelopathic effects are likely to be negligible.

A more appropriate control method for *P. undulatum* is the drill and fill technique whereby herbicides are injected into the trunk and the canopy contracts over time (Mullett 1996). In the wet forests east of Melbourne, glyphosate application to drilled holes of 8–15 mm diameter, about 50 mm deep and spaced 4–6 cm apart on the trunk about 20–50 cm above ground level and also below the main branches is very effective in killing mature *P. undulatum* plants (Gillespie 1991). Glyphosate is the most commonly used herbicide against *P. undulatum*, although good results with Tordon (picloram and 2,4-D) were reported in Jamaica (Goodland and Healey 1997a). Bush regenerators in South Australia, also recommend a mix of Triclopyr and diesel (1:30) for application to cut stumps (Robertson 1994).

Other treatments

Fire. In the appropriate context, prescribed burning may be the most cost-effective and ecologically sound method of controlling invasive populations of *P. undulatum*. Prescribed burning is often recommended as an effective means of controlling invasive populations of *P. undulatum,* as fires intense enough to kill the basal buds in the trunk are generally fatal (Gleadow and Ashton 1981, Narayan 1993). While this technique may be effective in reducing densities of *P. undulatum*, the intensities of prescribed and naturally occurring fires are controlled to the extent that this approach is rarely successful, particularly in an urban or urban-fringe context where most *P. undulatum* invasions occur. Further, it may be difficult to implement fires of an appropriate intensity in areas heavily invaded by *P. undulatum*, because of the dense shading and consequent changes in the composition and moisture content of fuels (Twentyman 1990). Mature *P. undulatum* plants can recover from low-intensity fires and benefits gained from prescribed burning may be lost in the absence of follow-up monitoring and management. For example, initial increases in species richness were recorded in the spring following a small (~3 ha) low-intensity autumn fire in a dry open woodland community dominated by *P. undulatum* on the Mornington Peninsula, Victoria (Narayan 1993), but coppicing of damaged plants and colonization by bird-dispersed seedlings were evident in ensuing years.

Prescribed burning will not be appropriate in all communities invaded by *P. undulatum* and this control technique should be used with caution, even in the drier forest types adapted to more frequent fires. Small populations of fire-responsive weeds such as *Chrysanthemoides monilifera* ssp. *monilifera* L. (boneseed) and *Genista monspessulana* (L.) L.A.S Johnson (broom), for example, may also be present in the local flora and could benefit from a burn implemented to reduce the density of *P. undulatum*. The importance of anticipating the response of both the target weed and the plant community to this and other control techniques can not be underestimated.

Further studies on *P. undulatum* and community response to fire may provide useful information for future application of this management technique, but the utility of this approach will be largely determined by external influences such as community attitudes and perceptions of risk (Twentyman 1990).

Natural enemies

Biological control of invading populations of *P. undulatum* may be appropriate in areas outside Australia and an annotated list of potential agents is included in Goodland and Healey (1997a). None of these agents directly impacts upon reproductive structures, although further investigation throughout the natural range of this species may reveal other potential agents. Natural populations of *P. undulatum* are prone to various types of leaf blight and attack by a range of invertebrates. Biological control is not a feasible option for reducing densities of invasive populations of *P. undulatum* in south-eastern Australia, given the inherent risk of damage to natural populations in this region, but may be an appropriate approach in invaded habitats in south-western Western Australia.

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